

Behavioral and Physiological Characteristics of the Antarctic Krill, *Euphausia superba*¹

LANGDON B. QUETIN AND ROBIN M. ROSS

Marine Science Institute, University of California at Santa Barbara,
Santa Barbara, California 93106

SYNOPSIS. The antarctic krill, *Euphausia superba*, is considered a success in the intensely seasonal environment of the Southern Ocean because of its abundance and central role as an important food item for many of the larger carnivores in the ecosystem. The behavioral and physiological characteristics that foster this success are: (1) the ability to find concentrations of food in several types of habitat and efficiently exploit whatever food is available; (2) the close correspondence of the life cycle with seasonal cycles of food availability; and (3) a combination of physiological mechanisms that enable krill to survive the long winter period of low food availability. We evaluated the relative importance of the following four major winter-over mechanisms that have been proposed for adult krill west of the Antarctic Peninsula. The three-fold reduction in metabolic rate is the most important winter-over mechanism for these adults, although lipid utilization and shrinkage also help satisfy energy requirements in the winter. Alternate food sources did not appear to contribute significantly as a winter energy source. However, the extent, predictability and complexity of the ice cover in a region during winter may have a great influence on the relative importance of these winter-over mechanisms for different populations. Ice cover in the waters west of the Antarctic Peninsula is unpredictable and smooth surfaced when it occurs, providing the krill with little refuge from predation. In multi-year pack ice of the Weddell Sea, however, ice cover is predictable and extensive, and there is a complex undersurface that provides hiding places. In this multi-year ice, adult krill have been observed under the ice feeding, whereas west of the Antarctic Peninsula most adult krill are in the water column in the winter and are not feeding. The balance between acquiring energy and avoiding predation may be different in these two regions in the winter because of differences in predictability and complexity of the ice cover.

INTRODUCTION

The habitat of the antarctic krill, *Euphausia superba*, is an environment dominated by extreme seasonal changes in day-length, food availability and ice cover. In areas where krill are most abundant, day-length ranges from constant light or near constant light in December to constant darkness or only a few hours of dusk in June. The amount of light reaching the surface governs both the maximum amount of energy available for photosynthesis and the ambient temperature of the air and water. As temperatures decrease in the winter, sea ice forms—covering more than 20 million km² of the sea surface at its maximum extent, five times the minimum in spring and summer (Garrison and Siniff, 1986). This annual advance and retreat of the ice-covered area affects total annual

primary production in several ways. First, the sea ice cover limits the availability of light to the phytoplankton in the water column, but it also provides a habitat in which organisms can live and grow, close to whatever incident light is available. Despite low light levels, significant net primary production occurs in both the sea ice and the water column in late winter (Kottmeier and Sullivan, 1987). Second, phytoplankton production in both the water column and the sea ice increases dramatically in the spring, as the melting ice creates vertical stability in the water column. Recent research has shown that as the ice edge retreats a series of blooms follows, continuing from September until December. The increase in standing stock from these ice edge blooms extends to about 250 km from the ice edge (Smith *et al.*, 1988). The production involved is substantial, and in some years can increase annual primary production estimates for the Southern Ocean by 60% (Smith and Nelson, 1986; Smith *et al.*, 1988). Open water phytoplankton blooms

¹ From the Symposium on Antarctic Marine Biology presented at the Annual Meeting of the American Society of Zoologists, 27-30 December 1988, at San Francisco, California.

peak from December through February (El-Sayed, 1985). Most investigators believe that primary production in the Southern Ocean is limited by wind-induced turbulence, not nutrients, and that productivity is higher in nearshore coastal regions and in regions of upwelling than in the open ocean (El-Sayed, 1985; Smith *et al.*, 1988). These pulses in primary production and their locations are predictable. Although primary production is not zero in the winter (Kottmeier and Sullivan, 1987), the intense seasonality in food availability means that growth, reproduction and feeding in herbivores also must be seasonal, and that organisms must be able to survive long periods when food is scarce or non-existent.

E. superba is a pelagic shrimp-like crustacean that grows to 50 to 60 mm in total length and can swim as well as small fish such as anchovy or sardines (Hamner *et al.*, 1983). For most of its life cycle the antarctic krill occurs in the upper 200 m of the water column in discrete schools or swarms, in densities up to 20,000 to 30,000 m⁻³. Schools vary in size from about 200 m in one horizontal dimension and several meters thick (Hamner, 1984) to the rare "super swarm" over 12 km long (Macaulay *et al.*, 1984).

Although krill are circumpolar in distribution, high concentrations of krill are found in only a few locations (Marr, 1962; Laws, 1985). Close to the antarctic continent and its associated shelf and slope, the winds come from the east, creating the counterclockwise East Wind Drift. The clockwise West Wind Drift forms a ring in the northern part of the Southern Ocean between the Antarctic Convergence and the East Wind Drift. Some krill are found in parts of the West Wind Drift, but most are concentrated within the area covered by the annual advance and retreat of sea ice, the East Wind Drift and its associated gyres and eddies. This distribution is suggestive of a close coupling between ice edge blooms and krill populations. It is important to recognize that krill are as much creatures of the ice edge and the semi-enclosed bays and straits where productivity is the greatest as they are of the open

ocean. The largest concentration of *E. superba* is found in waters to the north and east of the Antarctic Peninsula, continuing east into the Scotia Sea and the Weddell Sea gyre (Laws, 1985).

E. superba is a "success" from several different vantage points. First, this one species is the most important "macrozooplanktonic" herbivore in the Southern Ocean, unlike most other oceans where much of the primary production is grazed by copepods (Clarke, 1985). Although krill are capable of ingesting animal prey (Price *et al.*, 1988), in the summer freshly collected krill have dark green hepatopancreases, suggesting that the primary food source at this time is phytoplankton. The high biomass of krill is present year-round, and can be over 50% of the total zooplankton biomass in the epipelagic layer (Hopkins, 1985). Second, the result of this year-round dominance is that krill are the primary food source for a large number of species (Laws, 1985), and may deserve to be called a "keystone species" for the Southern Ocean ecosystem. In fact, in the Southern Ocean, most vertebrates directly depend on krill as a food source (Fig. 1).

Originally the Southern Ocean was characterized as a simple linear food chain: diatoms to krill to consumers. As we learned more about the interactions in this ecosystem, however, the simple food chain concept had to be replaced with a complex food web (Fig. 1). Although the base of the food web is still phytoplankton, both diatoms and nanoplankton must be included as primary producers. The food web includes herbivores both smaller and larger (salps) than krill (Lanckratz *et al.*, 1989), a substantial link to the benthos (Smith *et al.*, 1988), and a role for the microplankton (Hewes *et al.*, 1985). Krill are eaten by birds, including albatrosses, petrels and three species of penguins (Laws, 1985), by demersal fish (Nototheniiformes) (Kock, 1985) and pelagic fish (Williams, 1985), by four species of seals (Laws, 1985; Siniff and Stone, 1985), by squid (Nemoto *et al.*, 1985) and by baleen whales (Laws, 1985). Krill are from 33 to over 90% of the diet of these larger marine carnivores. Annual consumption of krill by these predators is esti-

a multi-species fishery (May *et al.*, 1979), *i.e.*, man is only one of many predators on krill. Such management schemes rely on models of the life cycle and biology of the species that may or may not be correct. For instance, in the late 1970s scientists estimated from analysis of length-frequency data that the lifespan of krill ranged from two to four years (reviews: Ettershank, 1984; Siegel, 1987). The combination of high biomass and a short lifespan suggested that annual production was high, and that populations of krill could sustain a large fishery. However, a management scheme based on this age estimate would have been a poor one. In the last decade, age determinations of krill with the fluorescent age pigment technique and with computer-aided analysis of length-frequency data all suggest that the adult life of krill lasts five or six years, so the total life span is close to eight years, over twice the earlier estimates (Ettershank, 1984; Siegel, 1987; Berman *et al.*, 1989). Estimates of total annual production of krill must be reduced accordingly (Ross and Quetin, 1988).

The abundance and central role of krill attest to its success in the Southern Ocean. We will describe the behavioral and physiological characteristics that allow *E. superba* to thrive with a food supply that is strongly seasonal and patchy geographically, and will discuss the possible role of ice in determining food availability and life history strategies. The characteristics of krill that underwrite its success can be grouped into three categories: (1) krill are able to find concentrations of food and efficiently exploit whatever food is available, wherever it is available; (2) the growth and reproductive cycles of krill are keyed to the seasonal cycles of food availability and food habitat; and (3) a combination of physiological mechanisms enables krill to survive the long winter period of low food availability.

FOOD SEARCHING AND GATHERING ABILITY

The food gathering ability depends on the complex morphology of the feeding basket and the variety of feeding behaviors

exhibited by *E. superba*. The feeding basket is formed when the six pairs of thoracic appendages and associated setae move apart during feeding. Water and food particles enter the food basket from the front and the food particles become trapped on the filter formed by the primary, secondary and tertiary setules (Hamner, 1988) (Fig. 2). The filter can trap small particles, with mean intersetal intervals for primary setae from 34.5 to 58.2 μm and for secondary setae from 6.5 to 9.3 μm in adult krill (McClatchie and Boyd, 1983). The water is forced out laterally through the filter, and the food particles are moved from the filter to the mouth with the comb setae and tips of the filter setae (Hamner, 1988). With this large feeding basket and fine mesh, krill are able to capture and retain a wide size range and type of free floating particles, from small phytoplankton cells to microplankton such as tintinnids. Krill also have a variety of feeding behaviors, ranging from compression filtration, the rhythmic expansion and compression of the feeding basket, to raptorial feeding (Price *et al.*, 1988), to using the thoracic appendages to scrape algae off the bottom of sea ice (Hamner *et al.*, 1983; Stretch *et al.*, 1988). Krill can and do eat both plant and animal matter, as is clear from the variety of feeding behaviors observed, and the presence in their stomachs of both tintinnid loricae and crustacean remains. Given the green color of the hepatopancreases of freshly collected krill in the summer, however, *E. superba* is primarily a herbivore when phytoplankton is abundant.

The necessary complements to this well-designed feeding basket and repertoire of behaviors are the swimming, schooling and chemosensory characteristics of krill (Hamner *et al.*, 1983) which enable krill to search for concentrations of phytoplankton. Adult krill are strong swimmers and have been observed moving distances of greater than 10 kilometers a day (Kanda *et al.*, 1982). They may follow the retreating ice edge and associated blooms and search out areas of high standing stock in the protected bays and straits, identifying areas of high phytoplankton concentration by chemical stimuli and remaining in these

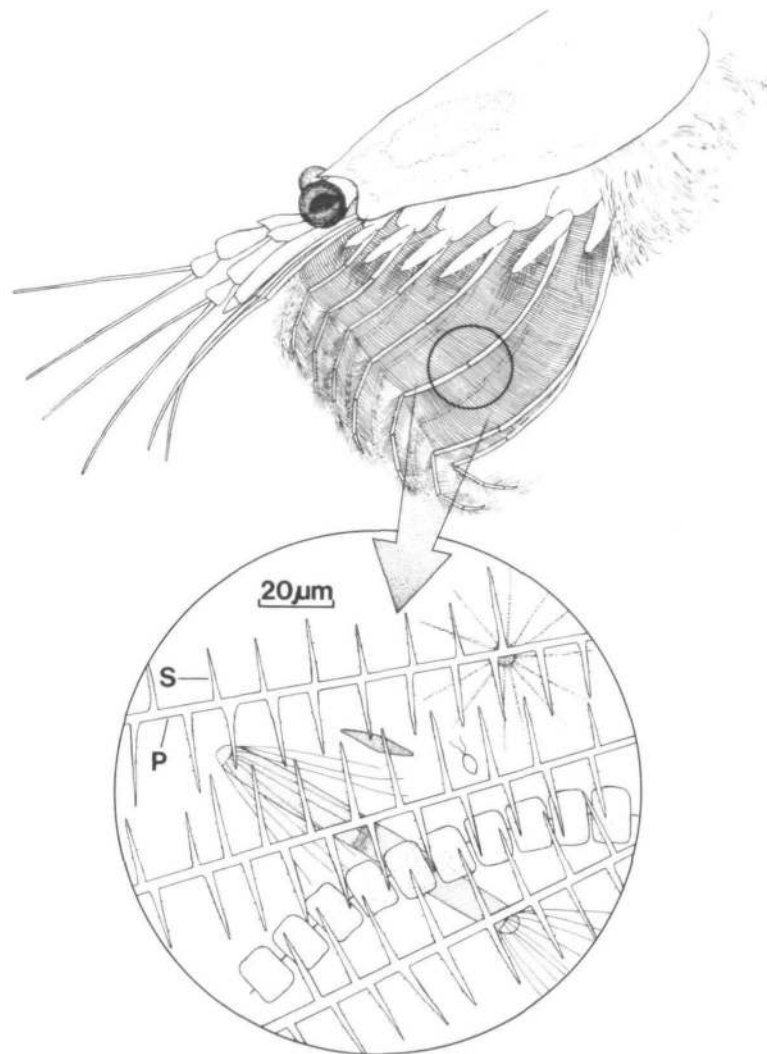


FIG. 2. The feeding basket of *Euphausia superba*, and the size of common food items in relation to the mesh of the filter. P = primary filter setae, S = secondary filter setae.

areas until the food supply is depleted (Antezana and Ray, 1983). Evidence does not support recent arguments by Smith *et al.* (1988) that krill are "planktonic" or weak swimmers unable to move with a retreating ice edge.

CYCLES OF GROWTH AND REPRODUCTION

Seasonal cycles of growth and reproduction in *E. superba* are marked and keyed to seasonal cycles of light and food in the environment (Fig. 3). Food concentrations are high in the water column during the tra-

ditional summer phytoplankton blooms, during the ice edge blooms in the spring and occasionally in the fall either as a fall bloom of ice algae on the underside of floes (Hoshiai, 1977) or when the phytoplankton are concentrated in the surface layer of frazil ice (Garrison *et al.*, 1986). Concentrations of ice algae can also be significant in the winter and are many times those in the water column (Kottmeier and Sullivan, 1987). The timing and vertical distributions of the embryos and different larval stages shown in Figure 3 are based on

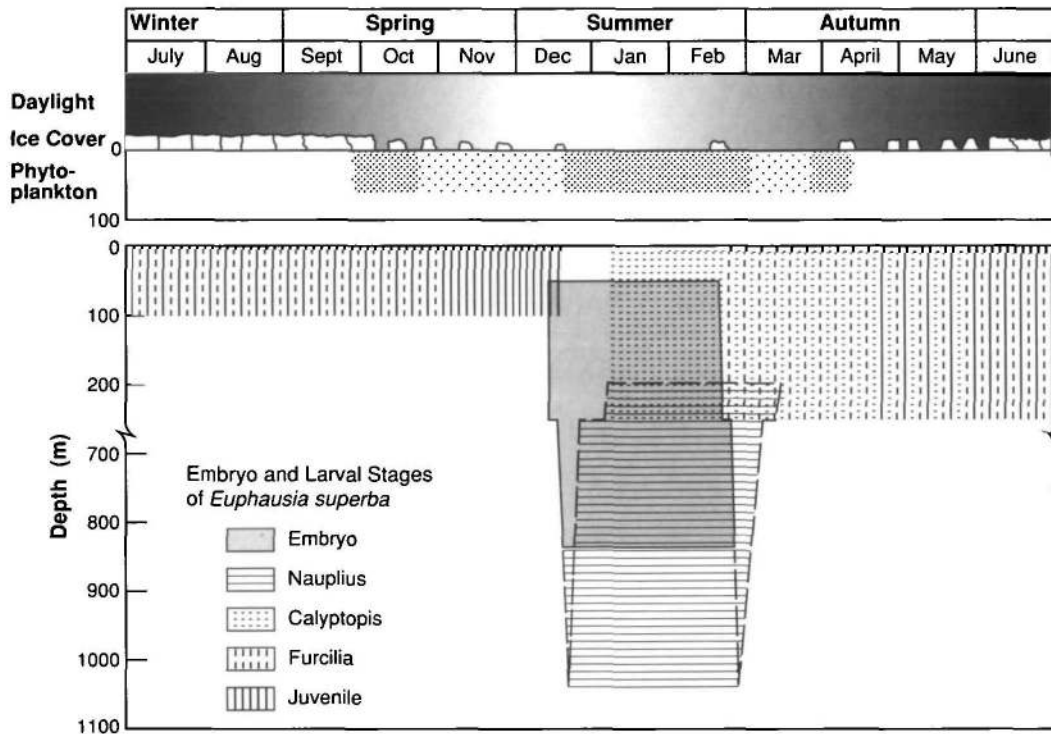


FIG. 3. Seasonal cycles of daylight, ice cover and phytoplankton concentration in the Southern Ocean, as correlated with the life cycle of *Euphausia superba*. Vertical distribution of embryos and larval stages is also indicated. Larvae are shallower in the spring than in summer and fall when they migrate diel between the surface layers and below 200 m (unpublished data).

previous work on the timing of the spawning season (Ross and Quetin, 1986), embryo and larval developmental times (Ross *et al.*, 1988), sinking rates of embryos (Quetin and Ross, 1984; Ross and Quetin, 1985) and the vertical distribution of larval stages (Nast, 1978; Hempel and Hempel, 1986; Quetin and Ross, unpublished data).

Production of embryos and larvae is timed so the first feeding stage appears in the surface layers at the same time as the summer phytoplankton bloom. However, the ovary begins to mature in September and October, and thousands of tiny eggs begin to develop before the open water blooms begin (Bargmann, 1945). Production of eggs requires energy and these ice-associated sources of primary production are an available source of food at a time when reproductive krill require large amounts of food and when open water concentrations of phytoplankton are low.

Although the degree of dependence of krill on ice edge blooms and late winter production of ice algae for food during the spring has not been quantified, adults have been found under the ice and feeding on ice algae in spring in the Weddell Sea (Marshall, 1988), off Enderby Land (O'Brien, 1987) and in the Bransfield Strait (unpublished data) in mid- to late spring.

The timing and intensity of spawning and subsequent larval hatching fluctuate both between years and locations. In waters west of the Antarctic Peninsula, spawning begins in early to mid-December and may last for 2.5 to 3 months (Ross and Quetin, 1986). Spawning begins later in the Prydz Bay region (January), but also lasts until mid-March (Hosie *et al.*, 1988). *E. superba* is a multiple-spawner and releases several batches of embryos during each spawning season (Ross and Quetin, 1983; Cuzin-Roudy, 1987). In productive regions, indi-

vidual females release a batch of about 2,000 embryos about every 10 days. Because the energy required for this level of reproduction is very high, such fecundities probably only occur in specific areas of the Southern Ocean where food availability is high during most of the summer. In areas of low productivity, the number of batches of eggs may be less or reproduction may not occur at all (Ross and Quetin, 1986). Distinct spawning grounds do exist (Marr, 1962), and they are generally located where seasonal phytoplankton blooms last the longest and reach the highest biomass.

After spawning, embryos sink rapidly out of the surface layers, and hatch at 850 to 1,000 m after 4.5 to 6 days, depending on the temperature structure of the water column (Quetin and Ross, 1984; Ross and Quetin, 1985) (Fig. 3). The newly hatched nauplii are weak swimmers and probably continue to sink for a day or so, then begin to ascend to the surface (Marschall and Hirche, 1984). The first three larval stages (nauplii) are found below 250 m, but the Calyptopis 1 larvae, the first stage with a mouth and feeding appendages, are usually found in the lighted surface layer with their food source—phytoplankton (Marschall, 1985). Krill have a long and complex larval sequence after the naupliar stages: three calyptopis stages and six furcilia stages before the metamorphosis into juvenile at four months if food is plentiful (Ikeda, 1985), or not until nine months (mid-November) under winter conditions of low food and temperatures (Ross *et al.*, 1987). The availability of food once the Calyptopis 1 larvae reach the surface is critical. The hatching larvae have enough energy stores to tolerate about 10 to 14 days of starvation after metamorphosis, but further starvation results in eventual death even if food becomes available later (Ross and Quetin, 1989). Since the exact timing and length of phytoplankton blooms in the Southern Ocean are not that predictable, not all calyptopis arriving at the surface may survive on the food available to them.

The ability to release many batches of embryos during the austral summer is of great survival value, giving the adults several chances to produce larvae that will

develop into the first feeding stage in an environment with sufficient food. This strategy of producing many small embryos without large reserves means that the larvae must feed themselves soon after hatching. Not only must the timing be such that the larvae can feed soon after reaching the surface, but food must also be available long enough for the larvae to survive the early critical stages and prepare for the long winter.

WINTER-OVER MECHANISMS

The third set of biological characteristics that allow *E. superba* to thrive in this intensely seasonal environment are the winter-over mechanisms. Four major hypotheses, shrinkage, lipid utilization, switching of food sources, and "hibernation," have been proposed to explain how krill survive the six-month winter period of low food, low light and often extensive ice cover. To test these hypotheses and to estimate their relative importance for populations of adult *E. superba* west of the Antarctic Peninsula we compared the physiological condition of krill in the field at different times of year (Table 1). In this paper we will present the preliminary results of these experiments, but leave a detailed description of the experiments and the complete seasonal trends for later publication. Although each experiment only addressed one of the hypotheses, we can use the results of all the experiments to evaluate the relative importance of each potential winter-over mechanism.

Shrinkage

Krill may use their own body lipids and proteins when starved and shrink in total length so they do not have to maintain the same body volume (Ikeda and Dixon, 1982). In the laboratory, adult krill have survived for over 211 days without food, proving that they can easily survive winter without eating. When starved for long periods individuals shrink 1 to 2% during each intermolt period of about a month. However, Stepnik (1982), in an analysis of length-frequencies of *E. superba* from Admiralty Bay, found that positive growth occurred in late winter and early spring, suggesting

TABLE 1. *Experiments and samples to test the four major winter-over mechanisms proposed.**

Mechanism	Test	Month/Year
Shrinkage	Compare the growth rates of krill in the field in late summer/early fall and winter	Mar/Apr 85 and Aug/Sept 85
Lipid utilization	Compare lipid content at the end of the summer and in late winter	Mar/Apr 84, 85 and Aug/Sept 85
Switch food source (Carnivory)	Compare rates of ingestion of phytoplankton and fecal pellet production, summer and winter	Feb/Mar 85 and Aug/Sept 85
"Hibernation"	Compare metabolic rates at ambient temperatures summer and winter	Jan and Jul 87

* All adult krill were collected from the waters west of the Antarctic Peninsula, in the Bransfield Strait and north of the South Shetland Islands.

that shrinkage may not occur in field populations.

We tested the shrinkage hypothesis by measuring linear growth increments of individuals maintained in groups of 100 at ambient temperatures during different times of the year, eliminating the assumption necessary in length-frequency analyses that the same population is sampled each month. In late summer and early fall, growth was positive (1.75 to 4.40% per intermolt period) (Fig. 4), and intermolt periods calculated for each group of krill were 2.5 to 4.5 weeks. Growth in the winter was negative (-0.16 to -2.03% per intermolt period) (Fig. 4), and intermolt periods were twice as long. Krill not only shrink in linear dimension during the winter, with a concomitant reduction in wet weight, they also lose volume, *i.e.*, get thinner. The relationship between total length and wet weight changes with season, indicating that krill of any one length lose weight during fall and winter (unpublished data). The wet weight of a krill 42 mm long decreases from 667 mg to 542 mg, a loss of 125 mg, during the six-month period between March and September. The protein and lipid in this wet weight fraction are additional sources of energy during the winter. We now have clear evidence that shrinkage in both total length and in proportional volume occurs in *E. superba* in the winter west of the Antarctic Peninsula.

Lipid utilization

Stored lipids may be used as an energy source during winter. Wax esters are thought to be long-term energy reserves

that are particularly useful during winter-over periods and long-term starvation of herbivores (Lee *et al.*, 1970; Sargent and Henderson, 1986). So the degree of dependence on phytoplankton food should dictate whether lipid reserves for winter are large or small and what form they take. The lack of wax esters in antarctic krill (Clarke, 1984) and the lack of unequivocal evidence for lipid storage in some other form suggested krill do not utilize lipids as an energy source during winter (Mauchline and Fisher, 1969; Clarke, 1984). However, previous samples of krill analyzed for lipid content did not cover the critical times of late summer, fall and winter.

We analyzed samples of male and female krill in late summer-early fall and in late winter for total lipid content, as percent of wet weight, with a charring method (Marsh and Weinstein, 1966). The average lipid content of the combined sexes was 7.48% in fall, dropping to 3.86% in late winter (Fig. 5). Late winter lipid content of adults was similar to that found in immatures in December (Clarke, 1984) and in adults in December (unpublished data). Loss of half the total lipid during fall and winter indicates that lipid reserves are used during the winter for energy.

Switch food sources

The possibility of switching to lipid-rich copepods (Boyd *et al.*, 1984) or detritus (Kawaguchi *et al.*, 1986b) as a food source in winter is often mentioned. But relying solely on animal matter for food in the winter is unlikely. Even in summer, normal densities of both copepods and protozoans

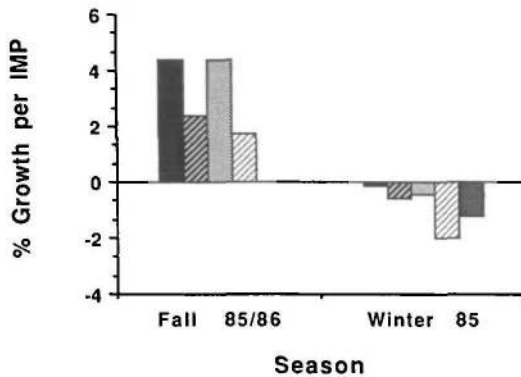


FIG. 4. Growth (% of length per intermolt period [IMP]) of adult *Euphausia superba* in fall and winter. Each bar is the mean growth of krill that molted during the experiment, 10 to 25 in each experiment.

in the upper 100 m are too low to meet minimum summer metabolic needs (Price *et al.*, 1988). In fall copepods migrate to deeper depths to spend the winter, reducing densities further. Detritus may add to the available food in some areas, but the small antarctic shelf could not generate enough detritus to feed the entire population of antarctic krill.

Two types of experiments were used to test whether *E. superba* switches from eating primarily phytoplankton to other food sources, such as lipid-rich copepods, in the winter. First, *in situ* rates of ingestion of phytoplankton were measured with a modification of the gut fluorescence technique of Dagg and Wyman (1983). The gut fluorescence method measures ingestion of plant material, but not total ingestion if krill utilize additional food sources such as copepods or detritus. However, fecal pellet production and total ingestion are correlated. If krill are ingesting significant amounts of animal or detrital material in the winter, then the seasonal trends in fecal pellet production and in phytoplankton ingestion will not be the same. Fecal pellet production was measured by quantitatively collecting all the fecal pellets produced by freshly collected krill in short experiments, and measuring organic carbon in the fecal pellets.

Ingestion rates decreased from $5 \mu\text{g chl a g wwt}^{-1} \text{ h}^{-1}$ in late February to near zero

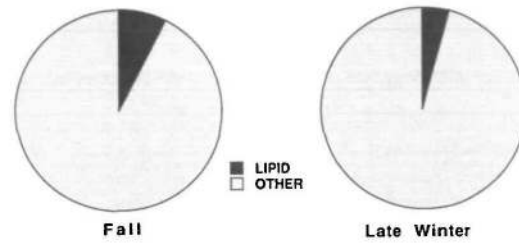


FIG. 5. Lipid as the proportion of wet weight of adult *Euphausia superba* in fall and winter. Lipid content shown is the average of krill collected from five schools in late winter and six schools in late March and April. Lipid content of males and females was determined separately and then averaged to get the average lipid content of the population.

in early fall (Quetin *et al.*, 1988), and remained very low throughout the winter (unpublished data). Winter rates of phytoplankton ingestion were less than 2% of summer rates. Fecal pellet production rates decreased from $186 \mu\text{g C d}^{-1}$ in late summer to less than 3% of the summer rates during late winter. Since both the rates of fecal pellet production and ingestion of phytoplankton in winter were less than 2 to 3% of summer rates, we believe that adult krill do not derive a large proportion of their energy from carnivory in winter.

"Hibernation"

The final hypothesis is that *E. superba* "hibernates" or enters a state of severely reduced metabolism and only swims enough to remain in the water column during winter. Some evidence suggests that metabolic rates of *E. superba* are twice as high in September as in August (Kawaguchi *et al.*, 1986a). Lower energy requirements would reduce the energy needed from other food sources.

To test whether the metabolic rate of *E. superba* is greatly reduced in winter months, we measured the oxygen consumption rate of a large size range of adult krill by incubating individuals in closed bottles at ambient temperature and then measuring oxygen concentration in the bottles with a micro-Winkler technique (Carritt and Carpenter, 1966). The experiments were conducted at 2°C in January and at -1.5°C in July (Fig. 6). The rates of oxygen con-

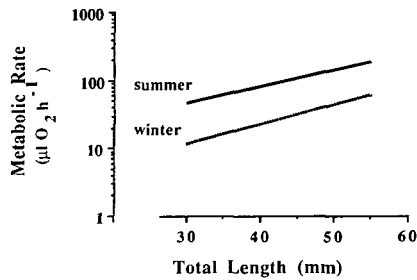


FIG. 6. Metabolic rate ($\mu\text{l O}_2 \text{ h}^{-1}$) of adult *Euphausia superba* in the summer (2°C) and winter (-1.5°C). Lines represent the relationship between total length and oxygen consumption rate: summer, $\log \text{VO}_2 \text{ (ml h}^{-1}\text{)} = 0.0241 \text{ TL (mm)} - 2.0551$, $r^2 = 0.70$; winter, $\log \text{VO}_2 \text{ (ml h}^{-1}\text{)} = 0.0285 \text{ TL (mm)} - 2.2258$, $r^2 = 0.67$.

sumption in winter were only 33% of those in summer, a significant reduction in energy requirements from summer to winter. This reduction can be partially attributed to the fact that krill are not feeding in the winter, as Ikeda and Dixon (1984) believe that the oxygen consumption rates of non-feeding krill are only 62.5% those of feeding krill. Yet about half the decrease in energy requirements from summer to winter is unexplained by the lack of feeding, and may be due to other behavioral changes such as a decrease in swimming activity or to physiological changes on a cellular level such as decreases in metabolic enzyme activity.

Relative importance of winter-over mechanisms

We used these data to evaluate the relative importance of the different hypothesized winter-over mechanisms for a 42-mm adult *E. superba*. A six-month period of low food availability, from the last of the late summer blooms to the beginning of the ice edge blooms and late winter/early spring production in the sea ice community, was used as the time span for all the calculations. Summer metabolic rates were used to predict the calories required from mid-March to mid-September. We calculated the calories saved by the reduction of the metabolic rate in the winter from the difference between summer and winter rates. We calculated the calories in the protein and lipid fraction of the wet weight loss that accompanied shrinkage (both the

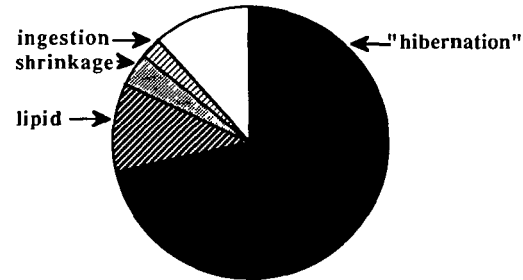


FIG. 7. Relative importance of the four major winter-over mechanisms proposed for *Euphausia superba* in the waters west of the Antarctic Peninsula. The entire circle represents the energy requirement for the six months of low food availability as predicted from the summer metabolic rates. The white segment is the portion of the energy requirement that remains unexplained.

decrease in total length as predicted from average negative growth rates in winter and the loss in volume) over the six-month winter period from the chemical composition (% protein, % lipid) of the animals, the relationships between total length and wet weight in March and September, and accepted conversion constants. Calories used from stored lipid reserves were estimated from the decrease in % lipid from March to September, the wet weights in March and September and accepted conversion constants. The contribution of ingestion during the winter was estimated from average fecal pellet production rates in terms of carbon and accepted conversion constants.

We presented each savings in energy or contribution to energy available to satisfy requirements as a percent of the total metabolic requirement for the six months as predicted by summer metabolic rates (Fig. 7). "Hibernation," or the lowered metabolic rate, was by far the most important mechanism for successfully surviving the winter. Over 71% of the anticipated energy requirements was saved by this lowering of metabolic rates. Direct lipid utilization provided almost 11% of the energy, and utilization of the protein and lipid in the body from shrinkage in both total length and in volume provided another 4% of the predicted energy requirement. Although ingestion was very low during winter, it

satisfied some of the energy requirements. With our preliminary evaluation of the four hypothesized winter-over mechanisms, the source of nearly 90% of the predicted energy requirements for an adult krill wintering-over west of the Antarctic Peninsula can be identified (Fig. 7).

However, this balance may be quite different in other regions of the Southern Ocean. For instance, in areas of lower productivity, lipid reserves may not be as high, so either additional shrinkage or weight loss may occur. The role of ice and ice algae in the availability of food during different times of year and in the known distribution patterns of *E. superba* has been discussed, but the predictability, extent and morphology of the ice cover during the winter may also play a role in determining the relative importance of the suggested winter-over mechanisms.

ROLE OF ICE AND ICE ALGAE

During fall, winter and spring the role of ice and ice algae in the life history and energetics of *E. superba* may be more important than during austral summer because of the simultaneous increase in the areal extent of sea ice and decrease in phytoplankton biomass in the water column. There are few observations and even fewer quantitative estimates of the importance of sea ice and ice algae to the winter-over existence of *E. superba* (Table 2). During AMERIEZ cruises in the northern Weddell Sea in fall and early spring Ainley *et al.* (1988), Daly and Macaulay (1988), and Lancraft *et al.* (1989) found krill larvae and juveniles associated with the ice edge and adults more common away from the ice edge in the water column or deeper in the pack ice in the Weddell Sea. Marschall (1988) recorded distributions of adult krill under the ice deep in the Weddell Sea with an ROV and trawl collections during spring and with surface observations from the ship during late winter in the same area. In the spring, adults were feeding on ice algae, and winter reports of krill with greenish-brown hepatopancreases from these areas imply adult krill were also feeding on ice algae during winter. Marschall (1988) also found adult krill more often associated with

the underside of ridged and over-raftered ice (multi-year ice) than with the smoother underside of annual or first-year ice.

West of the Antarctic Peninsula annual ice predominates and the ice habitat resembles the annual ice zone of the Weddell Sea (Quetin and Ross, personal observation). In these waters adults are in the water column beneath sea ice and are not closely associated with the under surface of the sea ice in mid-winter (Guzman, 1983; Quetin and Ross, unpublished observation). However, they do feed on ice algae in the early spring (Quetin and Ross, unpublished observation) as also reported by O'Brien (1987) in Enderby Land. These observations suggest that during winter adult krill in areas of annual or smooth ice are not directly underneath the ice and do not feed on ice algae, possibly because there is not enough ice structure to serve as a refuge from predation and/or enough ice algae to give them an energetic advantage if they do feed. Therefore the importance of ice algae in the winter energetics of adult krill is small in areas of annual ice. However, multi-year ice in the Weddell Sea may have higher algal concentrations than annual sea ice and the inherent structural complexity may enable adult krill to inhabit the underside of the sea ice and feed on ice algae without experiencing heavy predation pressure.

Larvae and juveniles, on the other hand, do feed on ice algae in areas of annual or smooth ice in both winter and spring. Guzman (1983), Kottmeier and Sullivan (1987) and Quetin and Ross (1988) have all seen larvae feeding on the underside of the sea ice from early to late winter west of the Antarctic Peninsula as have Daly and Macaulay (1988) and Marschall (1988) in the spring in the Weddell Sea. Most krill predators appear to prefer eating larger or adult krill, so the relatively small size of larvae compared to adults may give them a refuge from predation and allow them to occupy the smooth ice zones during winter without high predation pressure. The distribution of larvae during mid-winter suggests that larvae and adults do not winter-over in the same way. Possibly larvae have not had time to accumulate sufficient lipid

TABLE 2. Observations of the distribution and feeding behavior of adult and juvenile *Euphausia superba* in the Weddell Sea and the waters west of the Antarctic Peninsula.

Reference	Area/Time	Method	Adults	Juveniles
Weddell Sea				
Ainley <i>et al.</i> , 1988	nw Weddell spr 83, fall 86	seabird stomachs	under pack ice (100 km), in open water	at ice edge, under pack ice
Daly and Macaulay, 1988	w Weddell spr 83, fall 86	acoustic, nets, deck obs., divers	in open water	undersurface of floes, feeding
Marschall, 1988	e and s Weddell win and spr 86	ROV	under complex ice, feeding	under complex ice, feeding
West of Antarctic Peninsula				
Guzman, 1983	Bransfield Str	acoustic	in ice free zones, not feeding	under pack ice, feeding
Kottmeier and Sullivan, 1987	Bransfield Str	divers	—	under pack ice with ice algae
Quetin and Ross, 1988, unpubl. data	Bransfield Str, Palmer Basin	acoustic, divers	in water column, not feeding	under ice, feeding

stores during a short single summer so may be less resistant to starvation than adult krill. Their small size, continued development during winter, and postulated lack of lipid reserves all suggest that larvae may need to feed in winter. Thus, larvae will have a greater dependence on ice algae in the winter than do adults.

Our physiological measurements of the winter-over mechanisms of adult krill are consistent with field observations in winter (Table 2). Adults do not feed, have lowered metabolic rates, and negative or zero growth rates. Without physiological measurements it is impossible to evaluate the importance of ice algae to the annual energetics of krill inhabiting the underside of multi-year ice during winter. Conclusions about the importance of ice algae to the energetics of adult krill in winter in multi-year ice based on field observations to date would be premature, especially given quantitative physiological data for krill found in other areas. Further studies will be necessary to determine whether the refuge from predation afforded by the structure of multi-year ice enables adult krill to fulfill a significant portion of their annual energetic requirements by feeding on ice algae in winter. Recent evidence indicates that this is not the case in other areas.

Significant seasonal, geographical and interannual variations occur in the ice cover

of the Southern Ocean (Zwally *et al.*, 1983), and have been used to predict variations in primary production associated with receding marginal ice zones (Smith *et al.*, 1988). These interannual variations in ice cover and spring and summer marginal ice zone productivity may have important effects on the population dynamics, rates of reproduction, and recruitment of *E. superba*. Ice algae is probably an important food source for krill in spring before the summer phytoplankton blooms develop. In the spring larvae continue to develop and grow and the ovaries and testes of the adults start to mature in preparation for the reproductive season, thus increasing energetic requirements. West of the Antarctic Peninsula, where krill are concentrated and where most of our research occurs, interannual variability in ice extent can be significant even when interannual variability in ice extent in the Southern Ocean as a whole is low (Smith *et al.*, 1988). The winter of 1985 was particularly mild west of the Antarctic Peninsula, and even in August and September the Bransfield Strait was not frozen and the *R/V Polar Duke* did not encounter pack ice until well south of Anvers Island (Fig. 8a). The winter of 1987 was cold, with the pack ice extending over 150 km north of the South Shetland Islands as early as June (Fig. 8b). Interannual variability in the extent of the annual sea ice

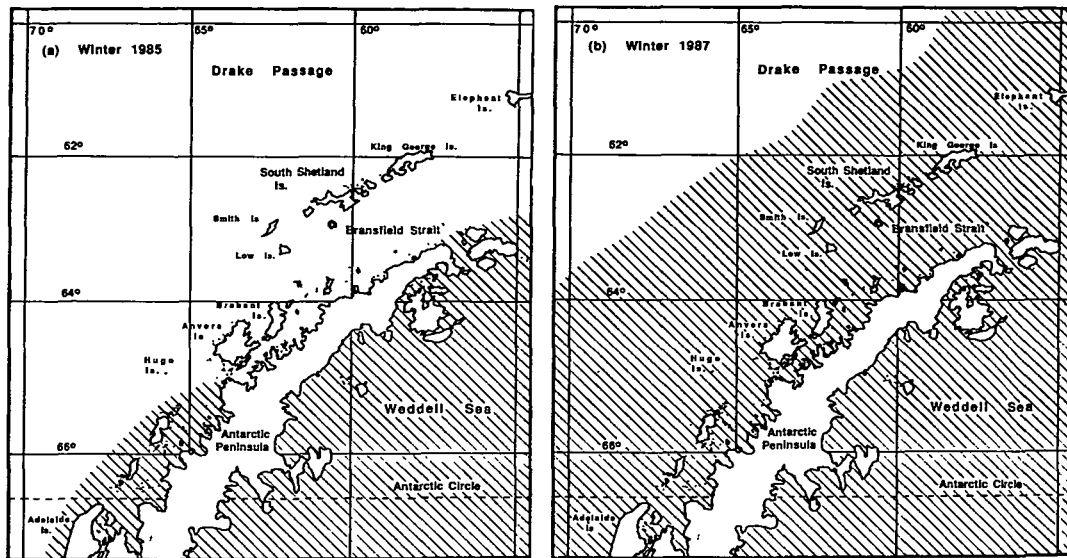


FIG. 8. The extent of ice cover in the waters west of the Antarctic Peninsula and the northwestern Weddell Sea during two winters in the 1980s: (a) August and September 1985; (b) June and July 1987.

and associated blooms may be an important factor in the ability of larvae to develop and in the distribution and reproductive success of adults, as seen in the Arctic where interannual differences in egg production rates of copepods appear to be a function of warm and cold years and the extent of the sea ice (Smith and Vidal, 1986).

CONCLUSIONS

The antarctic krill, *E. superba*, is very successful in this environment of extremes, successful because it is able to cope with a food supply that is both patchy and seasonal. The success of this species has its roots in a combination of biological and physiological factors, not the least of which is a suite of winter-over mechanisms that allow it to survive a long period of very low food availability.

ACKNOWLEDGMENTS

Discussions with many colleagues who work in the Antarctic have been useful as we explored the differences between regions of the Southern Ocean. We also thank the captains and crews of the research vessels *R/V Hero* (USAP 82 to 84) and *R/V Polar Duke* (USAP 85 to 89) who have been of invaluable help in our search for

antarctic krill. E. Kirsch, M. O. Amsler and a vast number of volunteers helped conduct experiments, take samples and analyze data from numerous cruises. Our research has been supported by the National Science Foundation, Division of Polar Programs, Grant No. DPP82-18356 to Quetin and Ross, and Grant No. DPP85-18872 to Ross and Quetin.

REFERENCES

- Ainley, D. G., W. R. Fraser, and K. L. Daly. 1988. Effects of pack ice on the composition of micro-nektonic communities in the Weddell Sea. In D. Sahrhage (ed.), *Antarctic ocean and resources variability*, pp. 140-146. Springer-Verlag, Berlin, Heidelberg.
- Antezana, R. and K. Ray. 1983. Aggregation of *Euphausia superba* as an adaptive group strategy to the Antarctic ecosystem. In S. B. Schnack (ed.), *On the biology of krill Euphausia superba*, pp. 199-215. Alfred-Wegener-Institute for Polar Research, Bremerhaven, FRG.
- Bargmann, H. E. 1945. The development and life-history of adolescent and adult krill, *Euphausia superba*. *Discovery Rep.* 23:103-176.
- Berman, M. S., A. L. McVey, and G. Ettershank. 1989. Age determination of antarctic krill using fluorescence and image analysis of size. *Polar Biol.* 9:267-271.
- Boyd, C. M., M. Heyraud, and C. N. Boyd. 1984. Feeding of the antarctic krill *Euphausia superba*. *J. Crust. Biol.* 4(Spec. No. 1):123-141.
- Carritt, D. E. and J. H. Carpenter. 1966. Comparison

- and evaluation of currently employed modifications of the Winkler methods for determining dissolved oxygen in sea water: A NASCO report. *J. Mar. Res.* 24:286–317.
- Clarke, A. 1984. Lipid content and composition of antarctic krill, *Euphausia superba* Dana. *J. Crust. Biol.* 4(Spec. No. 1):285–294.
- Clarke, A. 1985. Food webs and interactions: An overview of the Antarctic ecosystem. In W. N. Bonner and D. W. H. Walton (eds.), *Antarctica*, pp. 329–350. Pergamon Press, Oxford, New York, Toronto, Sydney, Paris, Frankfurt.
- Cuzin-Roudy, J. 1987. Gonad history of the antarctic krill *Euphausia superba* Dana during its breeding season. *Polar Biol.* 7:237–244.
- Dagg, M. J. and K. D. Wyman. 1983. Natural ingestion rates of the copepods *Neocalanus plumchrus* and *N. cristatus* calculated from gut contents. *Mar. Ecol. Prog. Ser.* 13:37–46.
- Daly, K. L. and M. C. Macaulay. 1988. Abundance and distribution of krill in the ice edge zone of the Weddell Sea, austral spring 1983. *Deep-Sea Res.* 35:21–41.
- El-Sayed, S. Z. 1985. Plankton of the Antarctic seas. In W. N. Bonner and D. W. H. Walton (eds.), *Antarctica*, pp. 135–153. Pergamon Press, Oxford, New York, Toronto, Sydney, Paris, Frankfurt.
- Ettershank, G. 1984. A new approach to the assessment of longevity in the antarctic krill *Euphausia superba*. *J. Crust. Biol.* 4(Spec. No. 1):295–305.
- Garrison, D. L., C. W. Sullivan, and S. F. Ackley. 1986. Sea ice microbial communities in Antarctica. *BioScience* 36:243–250.
- Garrison, D. L. and D. B. Siniff. 1986. An antarctic perspective. *BioScience* 36:238–242.
- Guzman, O. 1983. Distribution and abundance of antarctic krill (*Euphausia superba*) in the Bransfield Strait. In S. B. Schnack (ed.), *On the biology of krill Euphausia superba*, pp. 169–190. Alfred-Wegener-Institute for Polar Research, Bremerhaven, FRG.
- Hamner, W. M. 1984. Aspects of schooling in *Euphausia superba*. *J. Crust. Biol.* 4(Spec. No. 1):67–74.
- Hamner, W. M. 1988. Biomechanics of filter feeding in the antarctic krill *Euphausia superba*: Review of past work and new observations. *J. Crust. Biol.* 8:149–163.
- Hamner, W. M., P. P. Hamner, S. W. Strand, and R. W. Gilmer. 1983. Behavior of antarctic krill, *Euphausia superba*: Chemoreception, feeding, schooling, and molting. *Science* 220:433–435.
- Hempel, I. and G. Hempel. 1986. Field observations on the developmental ascent of larval *Euphausia superba* (Crustacea). *Polar Biol.* 6:121–126.
- Hewes, C. D., O. Holm-Hansen, and E. Sakshaug. 1985. Alternate carbon pathways at lower trophic levels in the Antarctic food web. In W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), *Antarctic nutrient cycles and food webs*, pp. 277–283. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.
- Hopkins, T. L. 1985. Food web of an antarctic mid-water ecosystem. *Mar. Biol.* 89:197–212.
- Hoshiai, T. 1977. Seasonal change of ice communities in the sea ice near Syowa Station, Antarctica. In M. J. Dunbar (ed.), *Polar oceans*, pp. 307–317. Arctic Inst. North America, Calgary, Canada.
- Hosie, G. W., T. Ikeda, and M. Stolp. 1988. Distribution, abundance and population structure of the antarctic krill (*Euphausia superba* Dana) in the Prydz Bay region, Antarctica. *Polar Biol.* 8:213–224.
- Ikeda, T. 1985. Life history of antarctic krill *Euphausia superba*: A new look from an experimental approach. *Bull. Mar. Sci.* 37:599–608.
- Ikeda, T. and P. Dixon. 1982. Body shrinkage as a possible over-wintering mechanism of the antarctic krill, *Euphausia superba* Dana. *J. Exp. Mar. Biol. Ecol.* 62:143–151.
- Ikeda, T. and P. Dixon. 1984. The influence of feeding on the metabolic activity of antarctic krill (*Euphausia superba* Dana). *Polar Biol.* 3:1–9.
- Kanda, K., K. Takagi, and Y. Seki. 1982. Movement of the larger swarms of antarctic krill *Euphausia superba* population off Enderby Land during 1976–1977 season. *J. Tokyo Univ. Fish.* 68:25–42.
- Kawaguchi, K., S. Ishikawa, and O. Matsuda. 1986a. The overwintering strategy of antarctic krill (*Euphausia superba* Dana) under the coastal fast ice off the Ongul Islands in Lutzow-Holm Bay, Antarctica. *Mem. Natl. Inst. Polar Res. (Spec. Issue)* 44:67–85.
- Kawaguchi, K., O. Matsuda, S. Ishikawa, and Y. Naito. 1986b. A light trap to collect krill and other micronektonic and planktonic animals under the Antarctic coastal fast ice. *Polar Biol.* 6:37–42.
- Kock, K.-H. 1985. Krill consumption by Antarctic notothenioid fish. In W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), *Antarctic nutrient cycles and food webs*, pp. 437–444. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.
- Kottmeier, S. T. and C. W. Sullivan. 1987. Late winter primary production and bacterial production in sea ice and seawater west of the Antarctic Peninsula. *Mar. Ecol. Prog. Ser.* 36:287–298.
- Lancraft, T. M., J. J. Torres, and T. L. Hopkins. 1989. Micronekton and macrozooplankton in the open waters near antarctic ice edge zones (AMERIEZ 1983 and 1986). *Polar Biol.* 9:225–233.
- Laws, R. M. 1985. The ecology of the Southern Ocean. *Am. Sci.* 73:26–40.
- Lee, R. F., J. C. Nevenzel, and G.-A. Paffenhofer. 1970. Wax esters in marine copepods. *Science* 167:1510–1511.
- Macaulay, M. C., T. S. English, and O. A. Mathisen. 1984. Acoustic characterization of swarms of antarctic krill (*Euphausia superba*) from Elephant Island and Bransfield Strait. *J. Crust. Biol.* 4(Spec. No. 1):16–44.
- Marr, J. W. S. 1962. The natural history of the antarctic krill (*Euphausia superba* Dana). *Discovery Rep.* 32:33–464.
- Marschall, H.-P. 1985. Structural and functional analyses of the feeding appendages of krill larvae. In W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), *Antarctic nutrient cycles and food webs*, pp.

- 346–354. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.
- Marschall, H.-P. 1988. The overwintering strategy of antarctic krill under the pack-ice of the Weddell Sea. *Polar Biol.* 9:129–135.
- Marschall, H.-P. and H.-J. Hirche. 1984. Development of eggs and nauplii of *Euphausia superba*. *Polar Biol.* 2:245–250.
- Marsh, J. B. and D. B. Weinstein. 1966. Simple charring method for determination of lipids. *J. Lipid Res.* 7:574–576.
- Mauchline, J. and L. R. Fisher. 1969. The biology of euphausiids. *Adv. Mar. Biol.* 7:1–454.
- May, R. M., J. R. Beddington, C. W. Clark, S. J. Holt, and R. M. Laws. 1979. Management of multispecies fisheries. *Science* 205:267–277.
- McClatchie, S. and C. M. Boyd. 1983. Morphological study of sieve efficiencies and mandibular surfaces in the antarctic krill, *Euphausia superba*. *Can. J. Fish. Aquat. Sci.* 40:955–967.
- Nast, F. 1978. The vertical distribution of larval and adult krill (*Euphausia superba* Dana) on a time station south of Elephant Island, South Shetlands. *Meeresforsch.* 27:103–118.
- Nemoto, T., M. Okiyama, and M. Takahashi. 1985. Aspects of the roles of squid in food chains of marine Antarctic ecosystems. In W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), *Antarctic nutrient cycles and food webs*, pp. 415–420. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.
- O'Brien, D. P. 1987. Direct observations of the behavior of *Euphausia superba* and *Euphausia crystallorophias* (Crustacea: Euphausiacea) under pack ice during the Antarctic spring of 1985. *J. Crust. Biol.* 7:437–448.
- Price, H. J., K. R. Boyd, and C. M. Boyd. 1988. Omnivorous feeding behavior of the antarctic krill *Euphausia superba*. *Mar. Biol.* 97:67–77.
- Quetin, L. B. and R. M. Ross. 1984. Depth distribution of developing *Euphausia superba* embryos, predicted from sinking rates. *Mar. Biol.* 79:47–53.
- Quetin, L. B. and R. M. Ross. 1988. Summary of WINCRUISE II to the Antarctic Peninsula during June and July 1987. *Ant. J., U.S.* 23:149–151.
- Quetin, L. B., R. M. Ross, and M. O. Amsler. 1988. Field ingestion rates of *Euphausia superba*. *EOS* 68:1785.
- Ross, R. M. and L. B. Quetin. 1983. Spawning frequency and fecundity of the antarctic krill *Euphausia superba*. *Mar. Biol.* 77:201–205.
- Ross, R. M. and L. B. Quetin. 1985. The effect of pressure on the sinking rates of the embryos of the antarctic krill *Euphausia superba*. *Deep-Sea Res.* 32:799–807.
- Ross, R. M. and L. B. Quetin. 1986. How productive are antarctic krill? *BioScience* 36:264–269.
- Ross, R. M. and L. B. Quetin. 1988. *Euphausia superba*: A critical review of estimates of annual production. *Comp. Biochem. Physiol.* 90B:499–505.
- Ross, R. M. and L. B. Quetin. 1989. Energetic cost to develop to the first feeding stage of *Euphausia superba* Dana, and the effect of delays in food availability. *J. Exp. Mar. Biol. Ecol.* 133:103–127.
- Ross, R. M., L. B. Quetin, M. O. Amsler, and M. C. Elias. 1987. Larval and adult antarctic krill, *Euphausia superba*, winter-over at Palmer Station. *Ant. J., U.S.* 22:205–206.
- Ross, R. M., L. B. Quetin, and E. Kirsch. 1988. Effect of temperature on developmental times and survival of early larval stages of *Euphausia superba* Dana. *J. Exp. Mar. Biol. Ecol.* 121:55–71.
- Sargent, J. R. and R. J. Henderson. 1986. Lipids. In E. D. S. Corner and O. Hara (eds.), *The biological chemistry of marine copepods*, pp. 59–108. Clarendon Press, Oxford.
- Siegel, V. 1987. Age and growth of antarctic Euphausiacea (Crustacea) under natural conditions. *Mar. Biol.* 96:483–495.
- Siniff, D. B. and S. Stone. 1985. The role of the leopard seal in the tropho-dynamics of the Antarctic marine ecosystem. In W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), *Antarctic nutrient cycles and food webs*, pp. 555–560. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.
- Smith, S. J. and J. Vidal. 1986. Variations in the distribution, abundance, and development of copepods in the southeastern Bering Sea in 1980 and 1981. *Cont. Shelf Res.* 5:215–239.
- Smith, W. O., Jr., N. K. Keene, and J. C. Comiso. 1988. Interannual variability in estimated primary productivity of the antarctic marginal ice zone. In D. Sahrhage (ed.), *Antarctic ocean and resources variability*, pp. 131–139. Springer-Verlag, Berlin, Heidelberg.
- Smith, W. O., Jr. and D. M. Nelson. 1986. Importance of ice edge phytoplankton production in the Southern Ocean. *BioScience* 36:251–257.
- Stepnik, R. 1982. All-year populational studies of Euphausiacea (Crustacea) in the Admiralty Bay (King George Island, South Shetland Islands, Antarctic). *Pol. Polar Res.* 3:49–68.
- Stretch, J. J., P. P. Hamner, W. M. Hamner, W. C. Michel, J. Cook, and C. W. Sullivan. 1988. Foraging behavior of antarctic krill *Euphausia superba* on sea ice microalgae. *Mar. Ecol. Prog. Ser.* 44:131–139.
- Williams, R. 1985. Trophic relationships between pelagic fish and euphausiids in Antarctic waters. In W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), *Antarctic nutrient cycles and food webs*, pp. 452–459. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.
- Zwally, H. J., C. L. Parkinson, and J. C. Comiso. 1983. Variability of antarctic sea ice and changes in carbon dioxide. *Science* 220:1005–1012.

