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Smithsonian at the Poles

Contributions to
International Polar Year Science

*Igor Krupnik, Michael A. Lang,
and Scott E. Miller
Editors*

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Life under Antarctic Pack Ice: A Krill Perspective

Langdon B. Quetin and Robin M. Ross

ABSTRACT. The life cycle of the Antarctic krill, *Euphausia superba*, intersects in space and time with the expansion and contraction of annual pack ice. Consequently, the circumpolar distribution of krill has often been defined as generally limited to an area bounded by the maximum extent of pack ice. Pack ice has both direct and indirect effects on the life cycle of krill. During the austral winter, larval krill are found in direct association with the underside of the ice and feed on the small plants and animals that constitute the sea ice microbial community, a food source relatively abundant in winter compared to food sources in the water column. Indirectly, melting pack ice in late winter or early spring stabilizes the water column and promotes growth of the preferred food of krill, which, in turn, likely provides the fuel for egg production during the summer months. Thus, the warming trend west of the Antarctic Peninsula with attendant changes in both the timing and duration of winter ice has implications for the population dynamics of krill. Given the complexity of the habitat–life cycle interaction, research on Antarctic krill involves diverse sampling tools that are dependent on the size and habitat of krill during a particular stage of their life cycle, and the nature of the study itself. In particular, and pertinent to the topic of diving in polar research, the research has been greatly enhanced by diving techniques developed to allow both observation and sampling of krill in their winter pack-ice habitat.

INTRODUCTION

One of the reasons that Antarctic krill, *Euphausia superba*, has been a focus of international research in the Antarctic since the Discovery days, before World War II, is that it is viewed as a key species in the Southern Ocean ecosystem. Various investigators have referred to Antarctic krill, *Euphausia superba*, as a keystone (Moline et al., 2004) or core or key (Quetin and Ross, 2003) or dominant (Ju and Harvey, 2004) species in the pelagic ecosystem of the Southern Ocean. The rationale for the use of these terms has been based on the facts that it is among the world's most abundant metazoan species (Nicol, 1994) and that it is important in the diets of many of the species of the upper trophic levels (Everson, 2000). However, given the suggestion that the term *keystone species* only refers to those species exercising an effect on ecosystem function disproportionate to abundance and thus is almost always a predator (Power et al., 1996), Antarctic krill may be more accurately defined as a *foundation species* in the

sense of Dayton (1972). A foundation species is one that controls community dynamics and modulates ecosystem processes such as energy flux, and whose loss would lead to system-wide changes in the structure and function of the ecosystem (Ellison et al., 2005). Understanding that Antarctic krill may be a foundation species in many regions of the pelagic Southern Ocean highlights the need to elucidate the factors affecting its population dynamics and its possible response to climate change. After introducing the concept of Antarctic krill as a foundation species, and the pack ice as a habitat, we focus on what has been learned about interactions between krill life history and the pack ice habitat, as well as the importance of viewing seasonal sea ice dynamics from a krill perspective.

FOUNDATION SPECIES

Distribution and Biomass

Several characteristics of the distribution and biomass of Antarctic krill suggest it is a foundation species. First, the distribution of Antarctic krill is circumpolar. However, abundance is patchy with highest abundances in the southeast Atlantic. Most krill are found within the area south of the northern extent of annual sea ice and within the boundaries of minimal and maximal sea ice, with the exception of krill around South Georgia (Marr, 1962; Laws, 1985; Siegel, 2005). This coherence led investigators to postulate a key role for seasonal pack ice in the life cycle and population dynamics of Antarctic krill.

Second, Antarctic krill often dominate the zooplankton biomass in the upper 200 m of the seasonal sea ice zone (Hopkins, 1985; Hopkins and Torres, 1988; Miller and Hampton, 1989; Ward et al., 2004; Siegel, 2005). Antarctic krill biomass was recently resurveyed in Area 48, the southwest Atlantic, during the CCAMLR 2000 Survey (Hewitt et al., 2004). From these results, acoustic estimates of the circumpolar krill biomass were estimated to be 60–155 million metric tones (Nicol et al., 2000), within the range estimated consumed by predators (Everson, 2000; Barrera-Oro, 2002). However, krill biomass in a region varies substantially—seasonally with shifts in population distribution, interannually due to variation in recruitment success during its lifespan, and within a season due to local oceanographic variables (Siegel, 2005; Ross et al., 2008).

Role in Ecosystem

Due in part to its high biomass and in part to the fact that there are no true prey substitutes in the seasonal sea-ice zone for upper-level predators, Antarctic krill dominate

energy flow to upper trophic levels (Barrera-Oro, 2002). In a review of the diets of Southern Ocean birds, Croxall (1984) identified both (1) species highly dependent on Antarctic krill, for example, the brushtail penguins up to 98%, and (2) species whose diet was only 16–40% krill, namely, flying seabirds such as albatrosses and petrels. All Antarctic seals depend somewhat on Antarctic krill, with the exception of the elephant seal (Laws, 1984). The crab-eater seal is a specialist on these euphausiids whereas the diet of leopard seals is only about 50% krill. Baleen whales (minke, blue, fin, sei, and humpback) feed predominantly on Antarctic krill. Lastly, both fish and squid (Everson 2000) are known predators of krill. In particular, the mesopelagic myctophid *Electrona antarctica* is an important predator of krill (Hopkins and Torres, 1988; Lancraft et al., 1989; 1991; Barrera-Oro, 2002).

One aspect of the Southern Ocean ecosystem that lends support to the characterization of Antarctic krill as a foundation species is that there is little functional redundancy in prey items for the upper-trophic-level predators in the food web. Another large and sometimes biomass-dominant grazer in the zooplankton is the salp, *Salpa thompsoni*. However, although some fish are known to ingest *S. thompsoni*, its high water content and the variation in biomass by orders of magnitude during the spring/summer season due to its characteristic alternation of generations renders it a less desirable food item. The pelagic fish fauna in the Southern Ocean, a logical alternate source of food, is relatively scarce and only a minor component of the epipelankton of the Antarctic Ocean (Morales-Nin et al., 1995; Hoddell et al., 2000), except in the high latitude regions of the cold continental shelf (high Antarctic) such as the Ross Sea or the southern Weddell Sea, the habitat of the nototheniid *Pleuragramma antarcticum*. In deeper pelagic waters, (>500 m) the mesopelagic myctophid *E. antarctica* is the dominant fish (Barrera-Oro, 2002), and is available as prey to diving birds and seals when it migrates into the upper 0–300 m during the night (Robison, 2003; Loots et al., 2007). However, in many regions of the Southern Ocean neither of these two species would be available in high enough biomass as an alternate prey if *Euphausia superba* disappeared.

Although Antarctic krill themselves are omnivorous and do ingest both plant and animal matter (Atkinson and Snýder, 1997; Schmidt et al., 2006), they are very important herbivorous grazers and their growth and reproduction rates appear to be tightly linked to phytoplankton concentrations, particularly diatoms (Ross et al., 2000; Schmidt et al., 2006; Atkinson et al., 2006). This short link between

primary producers and the upper trophic levels creates a very efficient transfer of energy to the top-level predators.

The role of Antarctic krill as one of the dominant macrozooplanktonic grazers, particularly of the larger phytoplankton, suggests that grazing by krill affects phytoplankton community composition and is a significant loss term in some years (Ross et al., 1998; Garibotti et al., 2003; Daniels et al., 2006). Daniels et al. (2006), in a network analysis of the pelagic food web on the shelf west of the Antarctic Peninsula, found that in years of high primary production and high krill abundance, more than 50% of the large phytoplankton cells were ingested by Antarctic krill. In addition, its production of large fast-sinking fecal pellets (Ross et al., 1985; Fowler and Small, 1972; Cadée et al., 1992; González, 1992; Turner, 2002) enhances its contribution to carbon sequestration (Smetacek et al., 2004).

PACK ICE HABITAT FROM KRILL PERSPECTIVE

Three types of pack ice can be delineated: seasonal, perennial, and marginal (Eicken, 1992). During the annual growth and melt cycle, the proportion of each type varies, which in turn means that the ecological habitats provided by each vary in space and time. Seasonal pack ice is a circumpolar environment that grows each fall and shrinks each spring, covering a vast area at its greatest extent. In the winter and spring, seasonal pack ice has phytoplankton/ice algal standing stocks that are one to three orders of magnitude higher than in the water column immediately below. This annual phenomenon thus provides a source of food for grazers (microheterotrophs, copepods, euphausiids) during times in the annual cycle when food resources in the water column are low. The process of formation of seasonal pack ice involves frazil ice formation scavenging particles from the water column, congelation into pancake ice, and aggregation into ice floes. Once the floes are 0.5 to 0.7 m thick, the annual ice only thickens by processes of deformation, particularly over-rafting. The seasonal pack ice, particularly the zone of highly over-rafted ice, is a favored habitat of Antarctic krill (*Euphausia superba*) in winter (Marschall, 1988; Smetacek et al., 1990; Quetin et al., 1996; Frazer et al. 1997; 2002). The perennial pack ice, in contrast, is a mixture of annual and primarily second year sea ice, and the water column below perennial pack ice tends to have even lower phytoplankton concentrations than below seasonal sea ice due to the increased light attenuation.

In the main body of this contribution, we will illustrate how putting one's self into the winter habitat as a diver, or taking on the krill perspective, has allowed unique in-

sight into the physiological and behavioral adaptations of Antarctic krill to winter conditions. In turn, this insight allows us to further our understanding of the impact of climate change. We will focus on the increased understanding over the last 25 years of interactions between the krill life cycle and seasonal sea ice dynamics as gained from both long-term research conducted in the summer months and from cruises conducted during winter months. Lastly, we will put these results into the context of climate warming and its effect on seasonal sea ice dynamics west of the Antarctic Peninsula.

BACKGROUND OBSERVATIONS

LIFE HISTORY OF ANTARCTIC KRILL

Characteristics of Life Cycle

Antarctic krill is a relatively large (maximum length about 60 mm) and long-lived crustacean that occurs in schools, leading Hamner et al. (1983) to suggest that it has attributes more like small fish such as an anchovy or sardine than like a zooplankton. The life cycle of this euphausiid is complex, with 11 larval stages over the first 9 to 10 months, at least 1 year as a juvenile/subadult, and then 3 to 4 years as an adult. First reproduction can be as early as the third summer (Age Class 2+), but may be delayed if food resources are inadequate (Ross and Quetin, 2000). Ovarian development begins in the spring, fueled by food ingested during that time and not by stored reserves (Hagen et al., 2001). The embryos sink rapidly and hatch in deep water and the nauplii swim toward the surface (Marr, 1962; Quetin and Ross, 1984; Hofmann et al., 1992). The krill in their first feeding stage (Calyptopis 1) reach the surface approximately three weeks after hatching, and must find sufficient food for continued development within a few weeks or else they die (Ross and Quetin, 1989). The larvae spend their first winter in the late furcilia stages; they begin to metamorphose into juveniles and then subadults at the end of winter and throughout the spring.

Critical Periods

Three facets of the influence of seasonal pack ice on the population dynamics of Antarctic krill have emerged from the research of multiple investigators. Here we briefly describe how two of the three critical periods interact with the seasonal cycles within the pack ice habitat (Figure 1).

First, in the austral spring as the ovary begins to develop, investigators postulate that the female must store

lipid in the “fat body” from ongoing ingestion to reach a threshold or ovarian development cannot continue (Cuzin-Roudy, 1993; Cuzin-Roudy and Labat, 1992; Ross and Quetin, 2000; Quetin and Ross, 2001), as shown for another species of euphausiid (Cuzin-Roudy, 2000). Thus, an individual female will only reproduce during a summer following a spring with adequate food sources. Each austral spring, the retreat and melting of the seasonal pack ice sets up the conditions for marginal ice-edge blooms, providing an important and timely food resource for female krill for ovarian development and eventual spawning.

Second, the larva needs to feed within 10–14 days of the time of metamorphosis into the first feeding stage or it passes the point-of-no-return and will not survive even if food becomes available later (Ross and Quetin, 1989).

For this critical period, the effect of seasonal sea ice is indirect, through the impact of the seasonal sea ice cycle on annual primary production and the timing of blooms (Vernet et al., 2008).

Lastly, although adult krill tolerate prolonged starvation and could survive a winter without food (Ikeda and Dixon, 1982), larval krill have a much lower starvation tolerance (for furcilia 6, about 6 wks) (Ross and Quetin, 1991; Quetin et al., 1996; Meyer and Oettl, 2005). Sea-ice microbial communities (SIMCOs) provide larval krill an alternate food source in the winter when food in the water column is at an annual low. In winter, larval krill from the under-ice habitat are in better condition than those from open water, as measured by condition factor, lipid content and in situ growth rates (Ross and Quetin, 1991), supporting this concept.

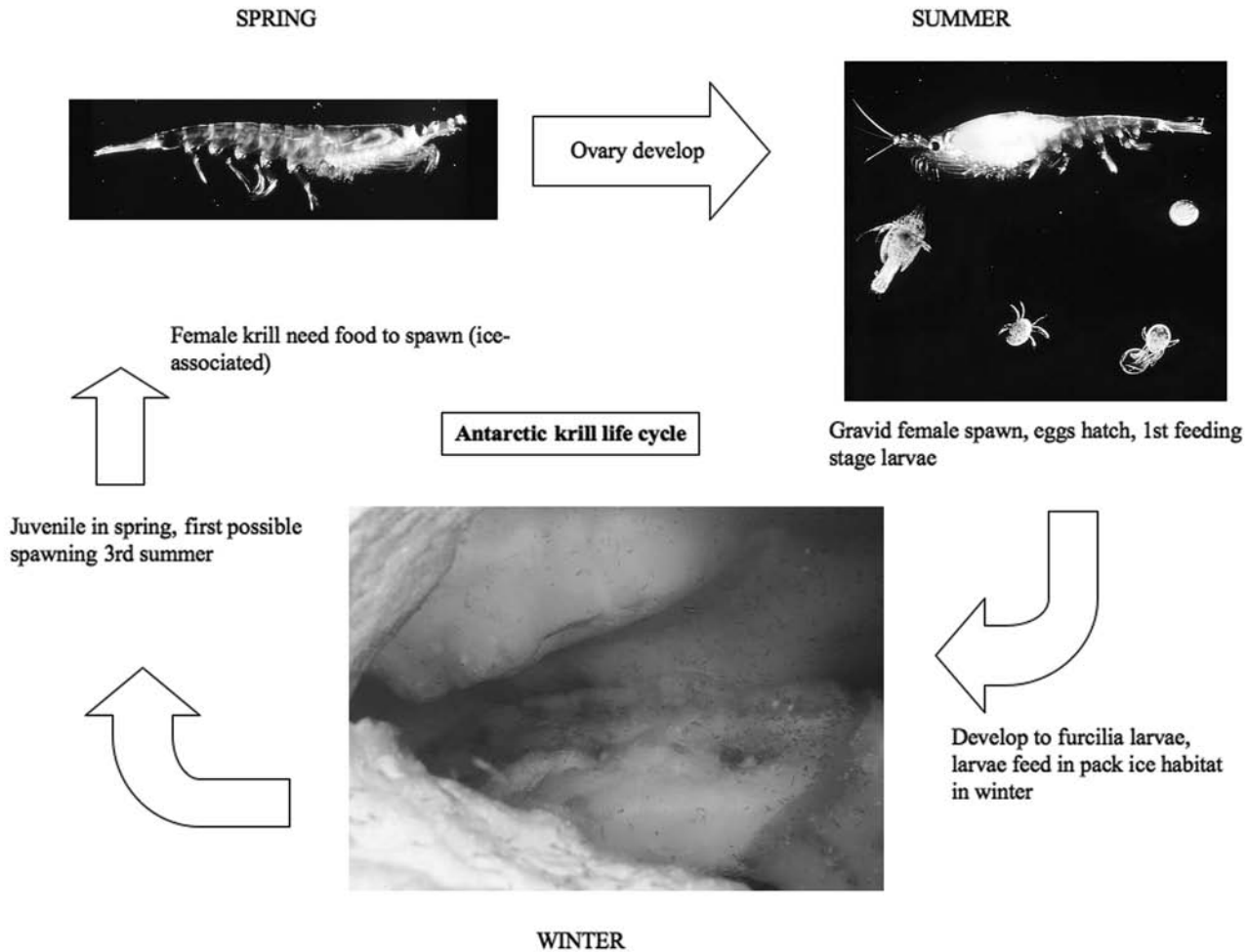


FIGURE 1. Life cycle of Antarctic krill with three critical periods; two are directly influenced by seasonal sea ice dynamics: ovarian development in the austral spring and survival during the first winter.

Variability in the environment, including seasonal sea ice dynamics, impacts food available to the Antarctic krill during these critical periods and is a primary factor driving variability in recruitment success or year class strength. Recruitment in this species shows high interannual variability as illustrated by two long-term research programs in the region of the Antarctic Peninsula—Antarctic Marine Living Resources (AMLR), Siegel and Loeb (1995), and Palmer Long Term Ecological Research (LTER), Quetin and Ross (2003)—and by shorter series in other regions (Watkins, 1999; Siegel 2000, 2005). Within the Palmer LTER study region, recruitment has been episodic with two sequential high years followed by two to three years of low or zero recruitment (Quetin and Ross, 2003), a 5–6 year cycle. Further north, with a longer time series, the frequency of high recruitment years has not been as repetitive (Siegel and Loeb, 1995; Siegel, 2005), although there is a rough correspondence between successful recruitment years between the two regions 800 km apart (Siegel et al., 2003; Ducklow et al., 2007). However, with several possible reproductive summers, Antarctic krill would not need successful recruitment every year, and models suggest that several years of low to zero recruitment would not preclude recovery of the stock (Priddle et al., 1988).

These results provide the opportunity to use correlations with environmental variability to formulate potential mechanisms that drive the variability (Siegel and Loeb, 1995; Quetin and Ross, 2003; Quetin and Ross, 2001). From these long-term studies, correlations have been found between both reproduction and recruitment success and various aspects of seasonal sea ice dynamics, including timing, duration, and maximum extent, with the dominant parameter varying with the study region and/or latitude. Evidence from two long-term studies suggests that timing and extent of sea ice in winter and/or spring impact the reproductive cycle (Siegel and Loeb, 1995; Loeb et al., 1997; Quetin and Ross, 2001). We will use examples from the Palmer LTER¹ as illustrations of the correlations found and potential mechanisms suggested.

Our first example illustrates the impact of the timing of sea ice retreat in the spring on the reproductive cycle. The most important factor in estimates of population fecundity (numbers of larvae produced in a region during the season) is the intensity of reproduction (percentage female krill in the reproductive cycle for a season), an index that can vary by a factor of 10 interannually (Quetin and Ross, 2001). The intensity of reproduction correlated with both dynamics of sea ice in spring and with annual primary production, which are both environmental factors associated

with food availability, as seasonal sea ice dynamics mediates the availability of food in the austral spring. Intensity of reproduction was consistently low when sea ice retreat was either early (August) or late (November), and highest when retreat occurred around the climatological mean for the region (Quetin and Ross, 2001). We emphasize here that the timing of retreat influences the timing of the food available for ovarian development, critical for a successful reproductive season. As discussed by Cuzin-Roudy (1993), Cuzin-Roudy and Labat (1992), and Quetin and Ross (2001), accumulation of stores in the “fat body” by late spring is hypothesized to be necessary for continued ovarian development. If development does not or cannot continue because of lack of adequate food in the spring, then the intensity of reproduction is low.

In the second example, we examine recruitment success and timing of sea ice advance. Our measure of recruitment success, the recruitment index, R_1 , is a consequence of both the numbers of larval krill entering the winter (reproductive output in the summer) and larval mortality during the winter (availability of winter food sources), and thus reflects two critical periods in the life cycle. From catches of krill from each station during the summer cruise, we calculate a recruitment index for the year, the proportion of one-year-old krill of the entire population one-year and older, as described in Quetin and Ross (2003). For the time series to date (Quetin and Ross, 2003; Ducklow et al., 2007) R_1 decreases exponentially with delay in sea ice advance. With advance in April, R_1 is greater than 0.4 (defined as a high recruitment year; Ducklow et al., 2007), but if advance is delayed until May or June, then R_1 is usually below 0.4. The suggestion is that if sea ice does not advance until late in the fall, that is, May, then recruitment tends to be low. However, the outliers or exceptions also provide insight into the mechanisms involved, in this instance the year classes of 1992 and 2001, as detailed in Quetin and Ross (2003). For the year class of 1992, although sea ice advanced early (March), retreat was also early (July), so SIMCOs were not available as an alternate food source in later winter, and presumably larval mortality was high. For the year class of 2001, sea ice did not advance until July, yet the R_1 (0.9) indicated a very successful year class. In this year, we had observed a strong reproductive output in the summer, leading to high numbers of larval krill entering the winter, so even with presumed high mortality due to a lack of SIMCOs early in the winter, enough larvae survived for a strong year class. This latter point emphasizes the importance of understanding the reproductive cycle and population fecundity, as well as mortality during the first year.

DIVING IN THE PACK ICE

The above examples illustrate how seasonal sea ice dynamics is correlated with the population dynamics of Antarctic krill. What have we learned about the interaction between Antarctic krill and the pack ice habitat from entering the habitat itself?

Historical Overview

The pack ice environment is dynamic—on both seasonal and shorter time scales—which creates challenges for investigators. In the early 1960s, biologists began to realize that sea ice presents a variety of different modes and contains distinct communities of plants and animals (Fogg, 2005). Scuba diving with observations of both the habitat and its inhabitants has played a key role in revealing the mysteries of the seasonal pack ice habitat, and scuba diving has become a key tool in investigations of the pack ice environment. Bunt (1963) used scuba diving to examine sea ice algal communities in situ and suggested ice algae could add appreciably to primary production in the Southern Ocean. He gave one of the earliest hints of the possible importance of sea ice algae as a food source for grazers. Early observations of the pack ice habitat were infrequent due to the lack of dedicated ice-capable research vessels. This limitation was relieved with the introduction of the RVIB *Polarstern*, commissioned in 1982 and operated by the Alfred Wegener Institute of Germany, and shortly thereafter, the MV *Polar Duke*, which began operations for the National Science Foundation of the USA in 1985. The advent of dedicated, ice-worthy research vessels led to a proliferation of studies in ice-covered waters (Ross and Quetin, 2003).

Some of the earliest observations of Antarctic krill under the pack ice were made by U.S. Coast Guard (USCG) scuba divers during spring (November 1983) and fall (March 1986) cruises in the Weddell Sea for the Antarctic Marine Ecosystem Ice Edge Zone (AMERIEZ) program (Daly and Macaulay, 1988; 1991). Subsequently, in late winter 1985 west of the Antarctic Peninsula during the first of a series of six winter cruises (WinCruise I, Quetin and Ross, 1986), divers investigating the SIMCOs associated with the underside of the ice (Kottmeier and Sullivan, 1987) observed larval krill in the under-ice habitat. Quetin and Ross (1988) began research on the physiology and distribution of larval krill found on the underside of the ice with WinCruise II in 1987; recently Quetin and Ross (2007) published detailed protocols, based on their experience, for diving in pack ice under various conditions that

included a table of the year and month of their pack ice diving activities (Table 1). O'Brien (1987) observed both Antarctic krill and ice krill (*Euphausia crystallorophias*) in the under-ice habitat in austral spring of 1985. Hamner et al. (1989) found larval krill in austral fall 1986 associated with newly forming sea ice. In all cases, the investigators observed larval krill in higher abundance associated with the sea ice than with the water column, and observed larval krill feeding on the sea ice algae (Table 1). Investigators made complementary observations onboard ships both west of the Antarctic Peninsula (Guzman, 1983) and in the Weddell Sea in spring (Marschall, 1988).

Gains from Diving Activities

Distinct advances in our understanding of the interaction of Antarctic krill and the pack ice environment emerged from diving activities. Not only were larval krill observed directly feeding on sea ice algae (as detailed above), but scuba observations also documented that a clear habitat segregation existed between adult and larval krill in winter (Quetin et al., 1996), with adult krill away from the underside of the pack ice, and larval krill coupled to the underside of the pack ice. These observations led to the concept of “risk-balancing” as put forth by Pitcher et al. (1988) for these two life stages of krill in winter; for example, the degree of association with the under-ice surface and its SIMCOs (food source) is a balance between the need to acquire energy and the need to avoid predation. The two life stages differ in both starvation tolerance and vulnerability to predation. The smaller larvae appear to have a refuge in size (Hamner et al., 1989), as most vertebrate predators ingest primarily adults (Lowry et al., 1988; Croxall et al., 1985). Thus, the risk of predation for the adults is higher near the pack ice that is used as a platform for many upper-level predators. Quantitative surveys also revealed that larval krill occurred in over-raftered pack ice and not smooth fast ice, and that they were more commonly found on the floors of the “caves” formed by the over-raftering pack ice than the walls or ceilings (Frazer, 1995; Frazer et al., 1997; 2002). Not only were gains made in our understanding of the natural history and habitat use of Antarctic krill in winter, but also the ability to collect krill directly from the habitat has advantages over other collection methods such as towing through ice. First, the gentle collection of specimens by scuba divers with aquarium nets yields larval krill in excellent physiological conditions for experiments, for example, growth and grazing. Second, this method allows for immediate processing of larval krill for time-dependent indices such as pigment

TABLE 1. Diving projects at Palmer Station and on cruises in the Southern Ocean, 1983–2005.

Palmer Station	Year	Cruises												Ship	
		Fall			Winter			Spring			Summer				
		A	M	J	J	A	S	O	N	D	J	F	M		
	1983								AZ						
	1984														
	1985					W	W		O'B						PD
	1986	H	AZ												PD (H)
	1987			W	W										PD
	1988														
	1989				W										PD
	1990									K					PD
L	1991		K				W								PD
L	1992														
L	1993	L	L	W			L								PD
L	1994			W	W										PD
L	1995														
L	1996														
L	1997														
L	1998														
	1999			L											LMG
L	2000										A	A			NBP
L	2001				G	G	L	L							LMG (G) NBP (L)
L	2002					G	G								LMG
L	2003														
L	2004														
L	2005														

AZ–AMERIEZ, W–WinCruise krill studies to Ross and Quetin, K–krill studies to Ross and Quetin, H–krill studies to Hamner, O'B–krill studies to O'Brien, L–Palmer Long-Term Ecological Research project, A–Antarctic Pack Ice Seals research project, G–Southern Ocean GLOBEC, PD–M/V *Polar Duke*, LMG–ARSV *Laurence M Gould*, NBP–RVIB *Nathaniel B. Palmer*.

content, an index of feeding on ice algae in situ (Ross et al., 2004). Entry into the under-ice habitat also meant that larval krill and their food resource (SIMCOs on the bottom surface of the pack ice) could be collected simultaneously, allowing for close temporal/spatial linkages.

PROCESS CRUISES—SOUTHERN OCEAN GLOBEC

ICE CAMPS

With the correlations that suggested mechanisms and the scuba diving protocols in place, the next step was to move beyond the correlations and explore and test mechanisms consistent with the observations. The evolution of pack ice diving is far from complete, however. Although long-term ice camps have been occupied in the perennial ice of the Weddell Sea on floes of much greater dimension than we describe below (Melnikov and Spiridonov 1996),

shorter term ice camps on smaller floes west of the Antarctic Peninsula had not been attempted. On some recent cruises with both the Palmer LTER and U.S. Southern Ocean GLOBEC (Global Ocean Ecosystem Dynamics) programs, we pulled together many historical observations of ways to cope with the dynamics of the pack ice environment west of the Antarctic Peninsula, and developed the ability to dive from small (>50 m) consolidated floes west of the Antarctic Peninsula repeatedly for periods up to nine days (Ross et al., 2004; Quetin et al., 2007). These ice camps entailed sampling from consolidated pack ice floes occupied for periods of days using the research vessel to stage operations (Quetin and Ross, 2007). Diving on floes for days at a time enabled us to explore local variability in the pack ice community associated with an individual floe over time as the floe drifted within the pack ice. Scuba diving was not the only activity that occurred at these ice camps. In fact, the ability to do simultaneous sampling both from the topside and underside of the ice

floes made for efficient sampling and better linkage between data sets.

During ice camps on two winter cruises for Southern Ocean GLOBEC west of the Antarctic peninsula in 2001 and 2002 (methods and results described in Quetin et al., 2007), total integrated chlorophyll *a* in multiple ice cores (Fritsen et al., 2008) was measured on the same ice floes where larval krill were collected by scuba divers. The amount of chlorophyll *a* in the ice cores was used as a proxy for the SIMCOs available as food to the larval krill living on the underside of the pack ice. Some of the larval krill were used immediately for an index of feeding (pigment content) (as described in Ross et al., 2004), while others were used in instantaneous growth rate experiments (in situ growth rate estimates as described in Ross and Quetin, 1991; Quetin et al., 2003; Ross et al., 2004). Growth of larval krill in their winter habitat reflects their feeding history over the past three weeks to one month, and may be an indicator of their ability to survive, that is, better growth indicates higher survivorship than lower growth. Evidence for similar linkages has been found for larval fish; larvae in better condition will have lower mortality rates and hence lead to stronger year classes, all else being equal (Pepin, 1991; Ottersen and Loeng, 2000; Takahashi and Watanabe, 2004).

CONTRAST TWO YEARS

The contrast in the results for total integrated chlorophyll *a* in ice cores, pigment content in larval krill, and the in situ growth rates of larvae for 2001 and 2002 was marked (Table 2) (fig. 5 in Quetin et al., 2007). Generally, in 2002 the ice cores contained an order of magnitude more chlorophyll *a* than in 2001 (Fritsen et al., 2008), leading us to suggest that more food was available to larval krill in 2002 than 2001. The median pigment content and in situ growth rates were also higher in larval krill in 2002 than in 2001. In both years, the distribution of pigment content was skewed to the left, but in 2002 more than 70% of the samples showed higher pigment content than those of larval krill collected from under the ice in 2001. A similar difference in distribution occurred for the in situ growth rates (Table 2). In 2002, more than 60% of the growth increments were positive, whereas in 2001 only 13% were positive.

The hypothesis that high concentrations of ice algae lead to higher growth rates is supported by a comparison of the in situ growth rates in the larvae and an index of feeding for larvae collected from the same place and at the same time. For this comparison, in situ growth rates

TABLE 2. Comparison of data from ice camps in 2001 and 2002 during two winter process cruises west of the Antarctic Peninsula near Marguerite Bay: median values of integrated chlorophyll *a* in ice cores, pigment content in larval krill, and in situ growth rates in larval krill. Ranges are in parentheses below median values; n = number of samples. Data in graph form in Quetin et al. (2007).

Data type (unit) and statistic	2001	2002
Integrated Chl <i>a</i> (mg m ⁻³)	1	10
Pigment Content	0.148	2.594
(median µg chl <i>a</i> gwwt ⁻¹)	(0.074–0.226)	(0.088–16.615)
n	29	71
In situ Growth Rate	–1.31	1.54
(% intermolt period ⁻¹)	(–6.10–5.13)	(–3.23–11.69)
n	114	132

in units of percent per intermolt period (the growth increment) were converted to growth in units of mm d⁻¹. For larvae that molted we used the median intermolt period of 30 d found for both years (Quetin et al., 2007), and individual growth increments and total lengths to estimate growth in mm d⁻¹:

$$(\text{total length (mm)} \cdot \% \text{ IMP}^{-1}) / (\text{IMP (d)})$$

The relationship between growth and the index of feeding for the eight in situ growth experiments from both years for which we have complimentary pigment content data is exponential, similar to a functional response curve with a maximum growth rate above a threshold feeding intensity or pigment level (Figure 2). The different symbols for the two years illustrate that data from ice camps from one year alone would not have yielded as comprehensive an illustration of the relationship between the feeding index and growth rates. Larvae with very low pigment content and negative growth rates were those from 2001, whereas larvae with a range of pigment content above 0.2 µg chl *a* g wwt⁻¹ and with positive growth rates were those from 2002. Thus, the combined data presents strong evidence that larval krill with a higher feeding index are growing at higher rates than those with lower feeding indices, and that the relationship holds at the large scale of the entire cruise (Table 2), and at the smaller scale of ice camps (Figure 2) with simultaneously collected data sets. This relationship and the difference between years in the chlorophyll *a* in the ice cores gives support to the infer-

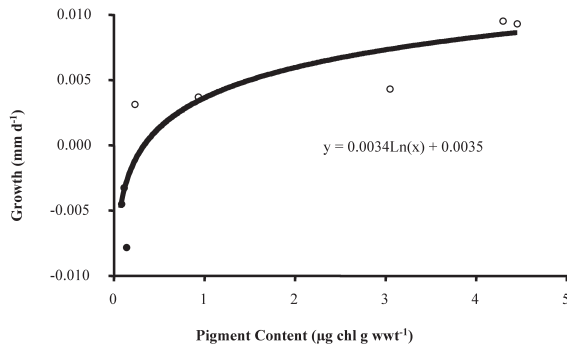


FIGURE 2. Growth rate (mm d^{-1}) of larval krill as a function of feeding index (pigment content, $\mu\text{g chl g ww}^{-1}$) of krill from same school. Growth rate is average for an experiment, with $n = 3$ to 14 individual measurements per experiment. Pigment content is average of 3 to 6 subsamples of larvae from same school, with 15–20 larvae per subsample. Filled circles = 2001, open circles = 2002. Exponential equation, $r^2 = 0.81$.

ence that larval krill have higher growth rates during years when there is more ice algae in the pack ice.

INTERACTION OF KRILL POPULATION DYNAMICS AND SEA ICE DYNAMICS

CONCEPTS DEVELOPED

One of the major concepts developed from these results and from the results of a diagnostic algal growth and ice dynamics model (Fritsen et al., 1998) is that not all pack ice has the same value as habitat for larval krill. Not only have we learned that larval krill appear to prefer over-raftered pack ice in preference to fast ice or un-raftered pack ice, but we have learned that there is significant variability in the quality of the habitat that the over-raftered pack ice habitat affords larval krill. What causes these differences in habitat quality for larval krill? The hypothesis is that the timing of ice formation in the austral fall impacts two aspects of production in SIMCOs and thus food available: (1) the amount of material in the water column to be scavenged and incorporated into the forming ice, or the base standing stock, and (2) the amount of photosynthetically available radiation (PAR) for in situ growth of the ice algae to take place integrated over the time between ice formation and mid-winter darkness. In general the rate of accumulation of SIMCO biomass slows during the transition from fall to winter as the daily PAR decreases (Hoshiai, 1985; Fritsen and Sullivan, 1997; Melnikov, 1998), following the decrease in day length.

Simulations predict that in winters when ice forms early, chlorophyll *a* will be higher in the pack ice due to both factors. Even a 10-day delay may cause an effect (C. H. Fritsen, unpublished data). Timing of ice formation is critical since the earlier ice forms, the higher the probability of incorporation of high abundances of phytoplankton from fall blooms into the ice lattice, and earlier ice formation also means more total light available for the ice algae to grow before mid-winter when light levels are too low for net primary production at most latitudes. The variation in PAR is significant, as illustrated by the decrease by more than 50% in the day length from March to April to May: 12.8 h to 9.2 h to 5.6 h at 66°S (Figure 3) and 12.8 h to 4.4 h at 68°S (Quetin et al. 2007). For our two-year comparison, the sea ice advance was a month earlier in 2002 than in 2001, April versus May. Thus, day length at the time of sea ice advance was about twice as long in 2002, 9 h versus 5 h, possibly one of the factors leading to the order of magnitude difference in the biomass of ice algae in the ice cores between the years (Table 2).

Thus, in mid-winter when larval krill need to feed, earlier forming ice will have higher concentrations of ice algae than later forming ice. Ultimately with later forming ice, lower food concentrations of ice algae leads to less food available for the larval krill, lower growth rates, and lower predicted survivorship rates (Figure 3). We suggest that this mechanism underlies the correlation seen between the timing of sea ice advance and recruitment success in the Palmer

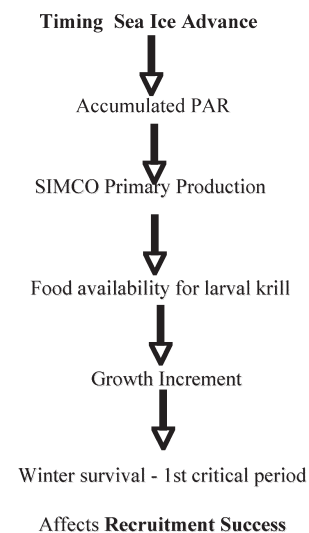


FIGURE 3. Concept of mechanism underlying the correlation found between timing of ice advance and recruitment in Antarctic krill (Siegel and Loeb, 1995; Quetin and Ross, 2003).

LTER study region (Quetin and Ross, 2003; Quetin et al., 2007). When ice does not form until May or June there is little in the water column to scavenge and PAR is near or at the minimum for the year. Thus, net primary production from ice formation to mid-winter will be low, and as a consequence so will food for larval krill.

POTENTIAL IMPACT OF CLIMATE CHANGE

The development of this conceptual view of the mechanism(s) underlying the correlation found between timing of sea ice advance and recruitment success in the Palmer LTER study region west of the Antarctic Peninsula underscores the importance of sea ice in the life cycle of Antarctic krill, and enhances our ability to predict how climate changes might impact krill population dynamics (Quetin et al., 2007). In a recent paper, Quetin et al. (2007) discuss the various scenarios and combinations of sea ice, light regime, and presence of Antarctic Circumpolar Deep Water that would create an optimal habitat for Antarctic krill.

The Palmer LTER study region is situated in one of the fastest warming regions of the world, with the other two in the northern hemisphere, the Svalbard Island group and the Bering Sea. The evidence of warming west of the Antarctic Peninsula comes from multiple studies: the air temperatures are rapidly warming, with an increase in winter temperatures over the last 50 years of about 6°C (Smith and Stammerjohn, 2001; Vaughan et al., 2003); there is a warming of ocean temperatures at both surface and sub-surface depths (Gille, 2002; Meredith and King, 2005); and ice shelves and marine glaciers are retreating (Scambos et al., 2003; Cook et al., 2005). With the warming climate, the duration of winter sea ice is shorter, but perhaps more importantly the timing is changing—sea ice advance is now later and retreat earlier (Parkinson, 2002; Smith et al., 2003; Stammerjohn et al., 2008). Sea ice advance west of the Antarctic Peninsula is now usually in April or May, whereas in the late 1970s sea ice advanced in March (Parkinson, 2002). In a recent analysis of the 25-year satellite record for sea ice, Stammerjohn found that the mean day of advance is 20–30 days later in the latter half of that period (1992–2004) than in the earlier half (1979–1991) (Stammerjohn et al., 2008). From the model simulations of Fritsen (1998), the impact of the 20- to 30-day delay in advance on accumulated SIMCO biomass in the sea ice between ice formation and mid-winter is likely to be substantial.

Do we have any evidence of changes in the Antarctic krill population concurrent with this regional warming?

Two studies to the north of the Palmer LTER study region suggest that populations of Antarctic krill are in decline. Atkinson et al. (2004) collated and compared trawl data from diverse studies in the Southern Ocean between 1926–2003, and concluded that stocks of Antarctic krill in the southwest Atlantic have declined since the 1970s by a factor of two. Shorter-term and smaller-space scale studies at the northern tip of the Antarctic Peninsula have included both net and bioacoustic data. The net data suggest a decline in krill stocks (Siegel, 2000) whereas the acoustic data suggest a cycle (Hewitt et al., 2003). One of the difficulties in the analysis of these time-series data is that detecting a linear trend in data that exhibit a repetitive cycle will take many years. In the Palmer LTER study region, where we have shown that the pattern of episodic recruitment leads to a five- to six-year cycle in the abundance of Antarctic krill (Quetin and Ross, 2003), a linear trend was not detectable in the 12-year time series (Ross et al., 2008). In this last section, we show the same data (methods and results in Quetin and Ross (2003) and Ross et al. (2008) from a different perspective, incorporating our understanding of the predictability of the cycle in the population dynamics and interannual variability in the pattern of abundance. With the five- to six-year cycle and two sequential years of successful recruitment followed by several years of low to no recruitment (Quetin and Ross 2003) in the LTER study region, the peak biomass in the cycle will appear in the January following the second good year class—in the time-series to date, in January of 1997 and 2003 (Figure 4). We can also look at the trend in the abundance during the fourth January: 1993, 1998 and 2004 (Figure 4). In both instances (year of maximum abundance, year 4 in cycle) the abundance

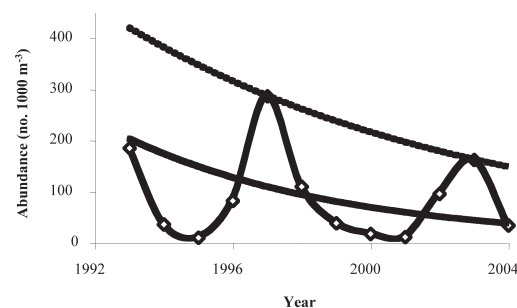


FIGURE 4. Mean abundance of Antarctic krill within the Palmer LTER study region from 1993 to 2004, calculated with equations of the delta distribution as detailed in Ross et al. (2008). The dotted line follows the year of maximum abundance within the 5–6 yr cycle, and the solid line follows the fourth year within the cycle.

has declined by 40%–45% (Figure 4). We suggest that this analysis provides preliminary evidence from the Palmer LTER study region that populations of Antarctic krill are declining in this region in concert with the change in timing of advance of sea ice. However, to date, the analysis only encompasses two full cycles; an additional cycle may yield a different trend.

SUMMARY

Scuba diving research during the past 30 years has enhanced our understanding of the linkages between Antarctic krill and sea ice. We have been able to make key observations and conduct experiments on the dependency of larval Antarctic krill on the SIMCOs in the pack ice habitat. Our conceptual understanding of the ecology of the pack ice habitat and the intricacies of the interactions has greatly increased due to these activities.

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NOTE

1. Since 1993 the Palmer LTER, a multidisciplinary program focused on the pelagic ecosystem west of the Antarctic Peninsula (Smith 1995), has conducted research cruises in January/February, sampling a geographical area from the southern end of Anvers Island to Marguerite Bay to the south. The sampling grid is composed of five transect lines extending approximately 200 km offshore, with stations every 20 km, and 100 km apart alongshore, and covers an area of nearly 80,000 km².

LITERATURE CITED

- Atkinson, A., R. S. Shreeve, and A. G. Hirst. 2006. Natural Growth Rates in Antarctic Krill (*Euphausia superba*): II. Predictive Models Based on Food, Temperature, Body Length, Sex, and Maturity Stage. *Limnology and Oceanography*, 51:973–987.
- Atkinson, A., V. Siegel, E. A. Pakhomov, and P. Rothery. 2004. Long-Term Decline in Krill Stock and Increase in Salps within the Southern Ocean. *Nature*, 432:100–103.
- Atkinson, A., and R. Snýder. 1997. Krill-Copepod Interactions at South Georgia, Antarctica, I. Omnivory by *Euphausia superba*. *Marine Ecology Progress Series*, 160:63–76.
- Barrera-Oro, E. 2002. The Role of Fish in the Antarctic Marine Food Web: Differences between Inshore and Offshore Waters in the Southern Scotia Arc and West Antarctic Peninsula. *Antarctic Science*, 14:239–309.
- Bunt, J. S. 1963. Diatoms of Antarctic Sea Ice as Agents of Primary Production. *Nature*, 199:1255–1257.
- Cadée, G. C., H. González, and S. B. Schnack-Schiel. 1992. Krill Diet Affects Faecal String Settling. *Polar Biology*, 12:75–80.
- Cook, A. J., A. J. Fox, D. G. Vaughan, and J. G. Ferrigno. 2005. Retreating Glacier Fronts on the Antarctic Peninsula over the Past Half-Century. *Science*, 308:541–544.
- Croxall, J. P. 1984. “Seabirds.” In *Antarctic Ecology*, ed. R. M. Laws, pp. 533–616. London: Academic Press.
- Croxall, J. P., P. A. Prince, and C. Ricketts. 1985. “Relationships between Prey Life Cycles and the Extent, Nature, and Timing of Seal and Seabird Predation in the Scotia Sea.” In *Antarctic Nutrient Cycling and Food Webs*, ed. W. R. Siegfried, P. R. Condy, and R. M. Laws, pp. 516–533. Berlin: Springer-Verlag.
- Cuzin-Roudy, J. 1993. Reproductive Strategies of the Mediterranean Krill, *Meganyctiphanes norvegica* and the Antarctic Krill, *Euphausia superba* (Crustacea, Euphausiacea). *Invertebrate Reproduction and Development*, 23:105–114.
- . 2000. Seasonal Reproduction, Multiple Spawning and Fecundity in Northern Krill, *Meganyctiphanes norvegica*, and Antarctic Krill, *Euphausia superba*. Proceedings of the Second International Krill Symposium, Santa Cruz, California, August 1999. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(Suppl. 3):6–15.
- Cuzin-Roudy, J., and J. P. Labat. 1992. Early Summer Distribution of Antarctic Krill Sexual Development in the Scotia-Weddell Region: A Multivariate Approach. *Polar Biology*, 12:65–74.
- 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 Research*, 35:21–41.
- . 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.
- Daniels, R. M., T. L. Richardson, and H. W. Ducklow. 2006. Food Web Structure and Biogeochemical Processes during Oceanic Phytoplankton Blooms: An Inverse Model Analysis. *Deep-Sea Research II*, 53:532–554.
- Dayton, P. K. 1972. “Toward an Understanding of Community Resilience and the Potential Effects of Enrichments to the Benthos at McMurdo Sound, Antarctica.” In *Proceedings of the Colloquium on Conservation Problems in Antarctica*, ed. B. C. Parker, 81–96. Lawrence, Kan.: Allen Press.
- Ducklow, H. W., K. Baker, D. G. Martinson, L. B. Quetin, R. M. Ross, R. C. Smith, S. E. Stammerjohn, M. Vernet, and W. Fraser. 2007. Marine Pelagic Ecosystems: The West Antarctic Peninsula. *Philosophical Transactions of the Royal Society B*, 362:67–94.

- Eicken, H. 1992. The Role of Sea Ice in Structuring Antarctic Ecosystems. *Polar Biology*, 12:3–13.
- Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliot, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of Foundation Species: Consequences for the Structure and Dynamics of Forested Ecosystems. *Frontiers in Ecology and the Environment*, 3:479–486.
- Everson, I. 2000. "Role of Krill in Marine Food Webs: The Southern Ocean." In *Krill: Biology, Ecology and Fisheries*, ed. I. Everson, pp. 194–201. Oxford: Blackwell Science Ltd.
- Fogg, G. E. 2005. *A History of Antarctic Science*. Cambridge, U.K.: Cambridge University Press.
- Fowler, S. W., and L. F. Small. 1972. Sinking Rates of Euphausiid Fecal Pellets. *Limnology and Oceanography*, 17:293–296.
- Frazer, T. K. 1995. On the Ecology of Larval Krill, *Euphausia superba*, during Winter: Krill–Sea Ice Interactions. Ph.D. diss., University of California, Santa Barbara.
- Frazer, T. K., L. B. Quetin, and R. M. Ross. 1997. "Abundance and Distribution of Larval Krill, *Euphausia superba*, Associated with Annual Sea Ice in Winter." In *Antarctic Communities: Species, Structure and Survival*, ed. B. Battaglia, J. Valencia, and D. W. H. Walton, pp. 107–111. Cambridge, U.K.: Cambridge University Press.
- . 2002. Abundance, Sizes and Developmental Stages of Larval Krill, *Euphausia superba*, during Winter in Ice-Covered Seas West of the Antarctic Peninsula. *Journal of Plankton Research*, 24:1067–1077.
- Fritsen, C. H., S. F. Ackley, J. N. Kremer, and C. W. Sullivan. 1998. "Flood-Freeze Cycles and Microalgal Dynamics in Antarctic Pack Ice." In *Antarctic Sea Ice—Biological Processes, Interactions and Variability*, ed. M. P. Lizotte and K. R. Arrigo, pp. 1–21. Washington, D.C.: American Geophysical Union.
- Fritsen, C. H., J. C. Memmott, and F. J. Steward. 2008. Interannual Sea Ice Dynamics and Micro-Algal Biomass in Winter Pack Ice: Marguerite Bay, Antarctica. *Deep-Sea Research, Part II*, 55, doi:10.1016/j.dsr2.2008.04.034.
- Fritsen, C. H., and C. W. Sullivan. 1997. "Distributions and Dynamics of Microbial Communities in the Pack of the Western Weddell Sea, Antarctica." In *Antarctic Communities: Species, Structure and Survival*, ed. B. Battaglia, J. Valencia, and D. W. H. Walton, pp. 101–106. Cambridge, U.K.: Cambridge University Press.
- Garibotti, I. A., M. Vernet, M. E. Ferrario, R. C. Smith, R. M. Ross, and L. B. Quetin. 2003. Phytoplankton Spatial Distribution Patterns along the Western Antarctic Peninsula (Southern Ocean). *Marine Ecology Progress Series*, 261:21–39.
- Gille, S. T. 2002. Warming of the Southern Ocean since the 1950s. *Science*, 295:1275–1277.
- González, H. E. 1992. The Distribution and Abundance of Krill Faecal Material and Oval Pellets in the Scotia and Weddell Seas (Antarctica) and Their Role in Particle Flux. *Polar Biology*, 12:81–91.
- Guzman, O. 1983. "Distribution and Abundance of Antarctic Krill (*Euphausia superba*) in the Bransfield Strait." In *On the Biology of Krill Euphausia superba*, ed. S. B. Schnack, pp. 169–190. Bremerhaven, Germany: Alfred-Wegener-Institute for Polar Research.
- Hagen, W., G. Kattner, A. Terbrüggen, and E. S. van Vleet. 2001. Lipid Metabolism of Antarctic Krill *Euphausia superba* and Its Ecological Implications. *Marine Biology*, 139:95–104.
- Hamner, W. M., P. P. Hamner, B. S. Obst, and J. H. Carleton. 1989. Field Observations on the Ontogeny of Schooling of *Euphausia superba* Furcilliae and Its Relationship to Ice in Antarctic Waters. *Limnology and Oceanography*, 34:451–456.
- 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.
- Hewitt, R., D. A. Demer, and J. H. Emery. 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.
- Hewitt, R. P., J. L. Watkins, M. Naganobu, V. Sushin, A. S. Brierley, D. Demer, S. Kasatkina, Y. Takao, C. Goss, A. Malyshko, M. Brandon, S. Kawaguchi, V. Siegel, P. Trathan, J. Emery, I. Everson, and D. Miller. 2004. Biomass of Antarctic Krill in the Scotia Sea in January/February 2000 and Its Use in Revising an Estimate of Precautionary Yield. *Deep-Sea Research II*, 51:1215–1236.
- Hoddell, R. J., A. C. Crossley, R. Willimas, and G. W. Hosie. 2000. The Distribution of Antarctic Pelagic Fish and Larvae (CCAMLR division 58.4.1). *Deep-Sea Research II*, 47:2519–2541.
- Hofmann, E. E., J. E. Capella, R. M. Ross, and L. B. Quetin. 1992. Models of the Early Life History of *Euphausia superba*—Part I: Time and Temperature Dependent Dependence during the Descent-Ascent Cycle. *Deep-Sea Research*, 39:1177–1200.
- Hopkins, T. L. 1985. The Zooplankton Community of Croker Passage, Antarctic Peninsula. *Polar Biology*, 4:161–170.
- Hopkins, T. L., and J. J. Torres. 1988. The Zooplankton Community in the Vicinity of the Ice Edge, Western Weddell Sea, March 1986. *Polar Biology*, 9:79–87.
- Hoshiai, T. 1985. Autumnal Proliferation of Ice-Algae in Antarctic Sea Ice. In *Antarctic Nutrient Cycles and Food Webs*, ed. W. R. Siegfried, P. R. Condy, and R. M. Laws, pp. 89–92. Berlin: Springer.
- Ikedda, T., and P. Dixon. 1982. Body Shrinkage as a Possible Over-Wintering Mechanism of the Antarctic Krill, *Euphausia superba*. *Journal of Experimental Marine Biology and Ecology*, 62:143–151.
- Ju, S.-J., and H. R. Harvey. 2004. Lipids as Markers of Nutritional Condition and Diet in the Antarctic Krill *Euphausia superba* and *Euphausia crystallorophias* during Austral Winter. *Deep-Sea Research II*, 51:2199–2214.
- 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. *Marine Ecology Progress Series*, 36:287–298.
- Lancraft, T. M., T. L. Hopkins, J. J. Torres, and J. Donnelly. 1991. Oceanic Micronektonic Macrozooplanktonic Community Structure and Feeding in Ice-Covered Antarctic Waters during the Winter (AMERIEZ 1988). *Polar Biology*, 11:157–167.
- 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 Biology*, 9:225–233.
- Laws, R. M. 1984. "Seals." In *Antarctic Ecology*, ed. R. M. Laws, pp. 621–716. London: Academic Press.
- . 1985. The Ecology of the Southern Ocean. *American Scientist*, 73:26–40.
- Loeb, V., V. Siegel, O. Holm-Hansen, R. Hewitt, W. Fraser, W. Trivelpiece, and S. Trivelpiece. 1997. Effects of Sea-Ice Extent and Krill or Salp Dominance on the Antarctic Food Web. *Nature*, 387:897–900.
- Loots, C., P. Koubbi, and G. Duhamel. 2007. Habitat Modeling of *Electrona antarctica* (Myctophidae, Pisces) in Kerguelen by Generalized Additive Models and Geographic Information Systems. *Polar Biology*, 30:951–959.
- Lowry, F. F., J. W. Testa, and W. Calvert. 1988. Notes on Winter Feeding of Crabeater and Leopard Seals near the Antarctic Peninsula. *Polar Biology*, 8:475–478.
- Marr, J. W. S. 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*, 2:245–250.
- Melnikov, A. A., and V. A. Spiridonov. 1996. Antarctic Krill under Perennial Sea Ice in the Western Weddell Sea. *Antarctic Science*, 8: 323–329.

- Melnikov, I. 1998. Winter Production of Sea Ice Algae in the Western Weddell Sea. *Journal of Marine Systems*, 17:195–205.
- Meredith, M. P., and J. C. King. 2005. Rapid Climate Change in the Ocean West of the Antarctic Peninsula during the Second Half of the 20th Century. *Geophysical Research Letters*, 32: L19604, doi: 10.1029/2005GL024042.
- Meyer, B., and B. Oettl. 2005. Effects of Short-Term Starvation on Composition and Metabolism of Larval Antarctic Krill *Euphausia superba*. *Marine Ecology Progress Series*, 292:263–270.
- Miller, D. G. M., and I. Hampton. 1989. *Biology and Ecology of the Antarctic Krill (Euphausia superba Dana): A Review*. Cambridge, U.K.: Scientific Committee on Antarctic Research and Scientific Committee on Oceanic Research of the International Council of Scientific Unions.
- Moline, M. A., H. Claustre, T. K. Frazer, O. Schofields, and M. Vernet. 2004. Alterations of the food web along the Antarctic Peninsula in response to a regional warming trend. *Global Change Biology*, 10: 1973–1980.
- Morales-Nin, B., I. Palomera, and S. Schadwinkel. 1995. Larval Fish Distribution and Abundance in the Antarctic Peninsula Region and Adjacent Waters. *Polar Biology*, 15:143–154.
- Nicol, S. 1994. “Antarctic Krill: Changing Perceptions of Its Role in the Antarctic Ecosystem.” In *Antarctic Science—Global Concerns*, ed. G. Hempel, pp. 144–166. Berlin: Springer-Verlag.
- Nicol, S., A. J. Constable, and T. Pauly. 2000. Estimates of Circumpolar Abundance of Antarctic Krill Based on Recent Acoustic Density Measurements. *CCAMLR Science*, 7:87–99.
- 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. *Journal of Crustacean Biology*, 7:437–448.
- Ottersen, G. B., and L. H. Loeng. 2000. Covariability in Early Growth and Year-Class Strength of Barents Sea Cod, Haddock and Herring: The Environmental Link. *ICES Journal of Marine Science*, 57: 339–348.
- Parkinson, C. L. 2002. Trends in the Length of the Southern Ocean Sea Ice Seasons, 1979–1999. *Annals of Glaciology*, 34:435–440.
- Pepin, P. 1991. The Effect of Temperature and Size on Development and Mortality Rates of Pelagic Life History Stages of Marine Fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 48:503–518.
- Pitcher, T. J., S. H. Lang, and J. A. Turner. 1988. A Risk-Balancing Trade-Off between Foraging Rewards and Predation Hazard in a Shoaling Fish. *Behavioral Ecology and Sociobiology*, 22:225–228.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the Quest for Keystones. *BioScience*, 46:609–620.
- Priddle, J., J. P. Croxall, I. Everson, R. B. Heywood, E. J. Murphy, P. A. Prince, and C. B. Sear. 1988. “Large-Scale Fluctuations in Distribution and Abundance of Krill—A Discussion of Possible Causes.” In *Antarctic Resources and Variability*, ed. D. Sahrhage, pp. 169–182. Berlin: Springer-Verlag.
- Quetin, L. B., and R. M. Ross. 1984. Depth Distribution of Developing *Euphausia superba* Embryos, Predicted from Sinking Rates. *Marine Biology*, 79:47–53.
- . 1986. Summary of Cruise 85–5 of the Polar Duke to the Antarctic Peninsula during August and September. *Antarctic Journal of the United States*, 21:192–193.
- . 1988. Summary of WinCruise II to the Antarctic Peninsula during June and July 1987. *Antarctic Journal of the United States*, 23: 149–151.
- . 2001. Environmental Variability and Its Impact on the Reproductive Cycle of Antarctic Krill. *American Zoologist*, 41:74–89.
- . 2003. Episodic Recruitment in Antarctic Krill, *Euphausia superba*, in the Palmer LTER Study Region. *Marine Ecology Progress Series*, 259:185–200.
- . 2007. “Pack Ice Diving.” In *Proceedings of the International Polar Diving Workshop*, ed. M. A. Lang and M. D. J. Sayer, pp. 111–131. Washington, D.C.: Smithsonian Institution.
- Quetin, L. B., R. M. Ross, T. K. Frazer, M. O. Amsler, C. Wyatt-Evens, and S. A. Oakes. 2003. Growth of Larval Krill, *Euphausia superba*, in Fall and Winter West of the Antarctic Peninsula. *Marine Biology*, 143:833–843.
- Quetin, L. B., R. M. Ross, T. K. Frazer, and K. L. Haberman. 1996. “Factors Affecting Distribution and Abundance of Zooplankton, with an Emphasis on Antarctic Krill, *Euphausia superba*.” In *Foundations for Ecological Research West of the Antarctic Peninsula*, ed. R. M. Ross, E. E. Hofmann, and L. B. Quetin, pp. 357–371. Washington, D.C.: American Geophysical Union.
- Quetin, L. B., R. M. Ross, C. H. Fritsen, and M. Vernet. 2007. Ecological Responses of Antarctic Krill to Environmental Variability: Can We Predict the Future? *Antarctic Science*, 19:1–14.
- Robison, B. 2003. What Drives the Diel Vertical Migrations of Antarctic Midwater Fish? *Journal of the Marine Biological Association of the United Kingdom*, 83:639–642.
- 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. *Journal of Experimental Marine Biology and Ecology*, 133:103–127.
- . 1991. Ecological Physiology of Larval Euphausiids, *Euphausia superba* (Euphausiacea). *Memoirs of the Queensland Museum*, 31: 321–333.
- . 2000. “Reproduction in Euphausiacea.” In *Krill: Biology, Ecology and Fisheries*, ed. I. Everson, pp. 150–181. Cambridge, U.K.: Blackwell Science.
- . 2003. Working with Living Krill: The People and the Places. *Marine and Freshwater Behaviour and Physiology*, 36:207–228.
- Ross, R. M., L. B. Quetin, and M. O. Amsler. 1985. *Euphausia superba*: A Preliminary Report on Three Areas of Investigation. *Antarctic Journal of the United States*, 19:153–155.
- Ross, R. M., L. B. Quetin, K. S. Baker, M. Vernet, and R. C. Smith. 2000. Growth Limitation in Young *Euphausia superba* under Field Conditions. *Limnology and Oceanography*, 45:31–43.
- Ross, R. M., L. B. Quetin, and K. L. Haberman. 1998. Interannual and Seasonal Variability in Short-Term Grazing Impact of *Euphausia superba* in Nearshore and Offshore Waters West of the Antarctic Peninsula. *Journal of Marine Systems*, 17:261–273.
- Ross, R. M., L. B. Quetin, D. G. Martinson, R. Iannuzzi, S. S. Stammerjohn, and R. C. Smith. 2008. Palmer LTER: Patterns of Distribution of 5 Dominant Zooplankton Species in the Epipelagic Zone West of the Antarctic Peninsula, 1993–2004. *Deep-Sea Research, Part II*, 55, doi:10.1016/j.dsr2.2008.04.037.
- Ross, R. M., L. B. Quetin, T. Newberger, and S. A. Oakes. 2004. Growth and Behavior of Larval Krill (*Euphausia superba*) under the Ice in Late Winter 2001 West of the Antarctic Peninsula. *Deep-Sea Research II*, 51:2169–2184.
- Scambos, T., C. Hulbe, and M. Fahnestock. 2003. “Climate-Induced Ice Shelf Disintegration in the Antarctic Peninsula.” In *Antarctic Peninsula Climate Variability: Historical and Paleoenvironmental Perspectives*, ed. E. Domack, A. Burnett, A. Leventer, P. Conley, M. Kirby, and R. Bindschadler, pp. 79–92. Washington, D.C.: American Geophysical Union.
- Schmidt, K., A. Atkinson, K.-J. Petzke, M. Voss, and D. W. Pond. 2006. Protozoans as a Food Source for Antarctic Krill, *Euphausia superba*: Complementary Insights from Stomach Contents, Fatty Acids, and Stable Isotopes. *Limnology and Oceanography*, 51: 2409–2427.
- Siegel, V. 2000. Krill (Euphausiacea) Life History and Aspects of Population Dynamics. Proceedings of the Second International Krill Symposium, Santa Cruz, California, August 1999. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(Suppl. 3):130–150.

- . 2005. Distribution and Population Dynamics of *Euphausia superba*: Summary of Recent Findings. *Polar Biology*, 29:1–22.
- Siegel, V., and V. Loeb. 1995. Recruitment of Antarctic Krill (*Euphausia superba*) and Possible Causes for Its Variability. *Marine Ecology Progress Series*, 123:45–56.
- Siegel, V., R. M. Ross, and L. B. Quetin. 2003. Krill (*Euphausia superba*) Recruitment Indices from the Western Antarctic Peninsula: Are They Representative of Larger Regions? *Polar Biology*, 26: 672–679.
- Smetacek, V., P. Assmy, and J. Henjes. 2004. The Role of Grazing in Structuring Southern Ocean Pelagic Ecosystems and Biogeochemical Cycles. *Antarctic Science*, 16:541–558.
- Smetacek, V., R. Scharek, and E.-M. Nothig. 1990. “Seasonal and Regional Variation in the Pelagial and Its Relationship to the Life History Cycle of Krill.” In *Antarctic Ecosystems: Ecological Change and Conservation*, ed. K. R. Kerry and G. Hempel, pp. 103–114. Berlin: Springer-Verlag.
- Smith, R. C., W. R. Fraser, and S. E. Stammerjohn. 2003. “Climate Variability and Ecological Response of the Marine Ecosystem in the Western Antarctic Peninsula (WAP) region.” In *Climate Variability and Ecosystem Response at Long-Term Ecological Research Site*, ed. D. Greenland, D. G. Goodin, and R. C. Smith, pp. 158–173. New York: Oxford University Press.
- Smith, R. C., and S. E. Stammerjohn. 2001. Variations of Surface Air Temperature and Sea-Ice Extent in the Western Antarctic Peninsula Region. *Annals of Glaciology*, 33:493–500.
- Stammerjohn S. E., D. G. Martinson, R. C. Smith, and R. A. Iannuzzi. 2008. Sea Ice in the Western Antarctic Peninsula Region: Spatio-Temporal Variability from Ecological and Climate Change Perspectives. *Deep-Sea Research, Part II*, 55, doi:10.1016/j.dsr2.2008.04.026.
- Takahashi, M., and Y. Watanabe. 2004. Growth Rate-Dependent Recruitment of Japanese Anchovy *Engraulis japonicus* in the Kuroshio-Oyashio Transitional Waters. *Marine Ecology Progress Series*, 266: 227–238.
- Turner, J. T. 2002. Zooplankton Fecal Pellets, Marine Snow and Sinking Phytoplankton Blooms. *Aquatic Microbial Ecology*, 27:57–102.
- Vaughan, D. G., G. J. Marshall, W. M. Connolley, C. Parkinson, R. Mulvaney, D. A. Hodgson, J. C. King, C. J. Pudsey, and J. Turner. 2003. Recent Rapid Regional Climate Warming on the Antarctic Peninsula. *Climatic Change*, 60:243–274.
- Vernet, M., D. Martinson, R. Iannuzzi, S. Stammerjohn, W. Kozlowski, K. Sines, R. Smith, and I. Garibotti. 2008. Primary Production within the Sea-Ice Zone West of the Antarctic Peninsula: Sea Ice, Summer Mixed Layer, and Irradiance. *Deep-Sea Research, Part II*, 55, doi:10.1016/j.dsr2.2008.05.021.
- Ward, P., S. Grant, M. Brandon, V. Siegel, V. Sushin, V. Loeb, and H. Griffiths. 2004. Mesozooplankton Community Structure in the Scotia Sea during the CCAMLR 2000 Survey: January–February 2000. *Deep-Sea Research II*, 51:1351–1367.
- Watkins, J. 1999. A Composite Recruitment Index to Describe Interannual Changes in the Population Structure of Antarctic Krill at South Georgia. *CCAMLR Science*, 6:71–84.