Antarctic Science 19 (2), 253–266 (2007) © Antarctic Science Ltd Printed in the UK DOI: 10.1017/S0954102007000363

Ecological responses of Antarctic krill to environmental variability: can we predict the future?

LANGDON B. QUETIN[1], ROBIN M. ROSS[1], CHRISTIAN H. FRITSEN[2] and MARIA VERNET[3]

[1]*Marine Science Institute, University of California at Santa Barbara, Santa Barbara, CA 93106-6159, USA*
[2]*Desert Research Institute, 2215 Raggio Parkway, Reno, NV 89512, USA*
[3]*Scripps Institution of Oceanography, La Jolla, CA 92093-0218, USA*
Corresponding author: langdon@icess.ucsb.edu

Abstract: Antarctic krill are a key species in the Southern Ocean ecosystem, and their life cycle appears to be correlated with, and by implication dependent upon, seasonal sea ice dynamics. Moving from correlations with environmental parameters to an understanding of the mechanisms that lead to these correlations may allow predictions of the consequences of climate change on the distribution of favourable habitat for Antarctic krill. During winter cruises in 2001 and 2002 in the region west of the Antarctic Peninsula, one of the most rapidly warming regions on the planet, ice camps were established for periods of 3–9 days. Timing of sea ice advance, chlorophyll *a* concentrations in ice cores, and growth rates and pigment content of larval krill all differed significantly between winters. Growth rates and pigment content of larval krill from the same ice floe were correlated, suggesting that growth rates in winter are a function of the biomass of the sea ice microbial community. A possible mechanism underlying the correlation between recruitment success and timing of ice advance is proposed. In conjunction with other postulated habitat requirements, this proposed mechanism allows for speculation about future changes in the geographic location of favourable habitat for Antarctic krill.

Received 1July 2006, accepted 19 April 2007

Key words: climate change, larval krill, Palmer LTER, sea ice dynamics, Southern Ocean GLOBEC

Introduction

Antarctic krill (*Euphausia superba* Dana) serve as both an important grazer (Quetin *et al.* 1996, Ross *et al.* 1998, Walsh *et al.* 2001) and a critical prey item for the reproductive success of seals and seabirds (Croxall *et al.* 1999, Everson 2000) in the Southern Ocean ecosystem. As a consequence, variations and/or trends in annual production and recruitment success of this key species may impact multiple levels in the ecosystem. Predicting the response of this species to climate change is thus of interest both to ecosystem monitoring efforts and to the development of management schemes for the fishery. One common difficulty in predicting ecological response to climate change is the need for long-term data in order to first detect a trend against a background of strong interannual variability, in addition to short- or long-term cycles and decadal-scale regime shifts, e.g. El Niño–Southern Oscillation (ENSO) and the Pacific Decadal Oscillation. Documentation of changes in several abundant species in the Southern Ocean with respect to changing sea ice and climate warming suggests that ecological responses are detectable, even against longer-term climate cycles, if long-term data are available. For example, long-term trends in seabird population dynamics appear to be related to sea ice extent and processes related to the Southern Oscillation Index (SOI) (Croxall *et al.* 2002, Ainley *et al.* 2005), and stocks of Antarctic krill in the south-west Atlantic have declined since the 1970s, with a correlation to sea ice cover in the winter (Atkinson *et al.* 2004).

For a robust prediction, however, an understanding of the mechanisms underlying the correlations with measures of environmental change and an awareness of the non-linearity of responses to environmental change is essential. The optimal habitat model (used in Smith *et al.* (1999) to illustrate patterns in Adélie penguin populations) is non-linear, with highest population growth in mid-range of an index of environmental characteristics (sea ice in the case of the Adélie penguin). With this model, conditions are optimal for population growth when the frequency of high sea ice coverage is neither too high nor too low. With the warming climate and changes in seasonal sea ice dynamics in the region west of the Antarctic Peninsula (WAP), sea ice advance is later, retreat earlier and the duration of ice-covered waters shorter (Parkinson 2002, Smith *et al.* 2003, Stammerjohn *et al.* in press), suggesting that geographic locations along the WAP may have shifted in their position along the spectrum of environmental conditions and thus are no longer experiencing the same frequency of ‘good’ sea ice conditions as in the past.

Atkinson *et al.* (2004), in an analysis of trawl data from 1926 through 2003, showed that stocks of Antarctic krill in the south-west Atlantic have declined since the 1970s, in some areas by over a factor of two. Confirmation of this trend may be problematic (Smetacek & Nicol 2005), but essential. Some of the difficulties in the trend analysis are technical (different trawling methods, slightly different times of year), but part of the difficulty lies in trying to detect linear trends in a species with a cycle in population abundance due to variability in recruitment (Siegel & Loeb 1995, Quetin & Ross 2003, Ross *et al.* in press). Shorter-term and smaller-space scale studies in the northern WAP show a decline in krill stocks based on net data (Siegel 2000), but more of a cycle based on acoustic data (Hewitt *et al.* 2003). Along the WAP, peak abundance during the 5–6 year cycle has declined over the last 14 years (Quetin & Ross 2003), suggesting a decrease in stocks, but a linear trend was not detectable (Ross *et al.* in press) as in Atkinson *et al.* (2004). The changes detected are probably due to changes in recruitment success, i.e. abundance or strength of a year class as it enters the population as subadults.

The correlation found between sea ice cover in the winter and krill population size in the south-west Atlantic the following summer, although relatively weak in the linear model ($r_2 = 0.21$), supports a large-scale linkage (Atkinson *et al.* 2004) between sea ice and the distribution and recruitment success of Antarctic krill - a concept first put forward and discussed decades ago (Laws 1985, Smetacek *et al.* 1990, Ross & Quetin 1991, Siegel & Loeb 1995). Presumably the microbial communities (SIMCOs) within the sea ice provide a source of food for young-of-the-year of Antarctic krill during winter when food concentrations in the water column are low (Meyer *et al.* 2002), thus enhancing their survival for the first year, and overall abundance the following summer. The stronger correlations found in smaller-scale studies (Siegel & Loeb 1995, Quetin & Ross 2003) between recruitment success of Antarctic krill and various ice parameters may be due to a more precise matching of the population and the sea ice parameter impacting a population than is possible with correlations across the entire south-west Atlantic and a population influenced by both the Antarctic Circumpolar Current from the west and the Weddell Sea gyre from the east (Atkinson *et al.* 2004).

Focused on the WAP region, the initial premise of the Palmer Long Term Ecological Research program (PAL LTER), established in 1990, was that physical forcing, e.g. seasonal sea ice dynamics, affected the structure and function of the ecosystem (Quetin & Ross 1992, Smith *et al.* 1995). Subsequently teleconnections and long-term climate change have also become recognized factors (Dierssen *et al.* 2002, Goodin & Smith 2003, Stammerjohn *et al.* 2003, Smith *et al.* 2003, Ducklow *et al.* 2007). Annual multi-disciplinary sampling occurs on a large spatial scale within a region that extends from Anvers Island to south of Adelaide Island, and from close to the continent to about 200 km offshore, about 40 km seaward of the shelf break.

Long-term datasets serve to highlight variability on multiple time scales - trends, cycles, teleconnections to the rest of the world's oceans and ecological responses to climate change. Fortuitously PAL LTER is sited in an ideal region to document ecosystem response to observed climate change. At present the maritime system is expanding southward along the WAP, replacing the colder polar system (Smith *et al.* 2003), with attendant environmental effects. In the WAP, surface air temperatures have warmed 5–6°C in the winter over the last 50 years (Vaughan *et al.* 2003). In addition, throughout the Antarctic Peninsula, ice shelves and marine glaciers are rapidly retreating (Scambos *et al.* 2003, Cook *et al.* 2005), and sea ice has decreased in concentration and duration over the satellite record both in the Peninsula region and the southern Bellingshausen Sea (Jacobs & Comiso 1997, Smith & Stammerjohn 2001, Parkinson 2002, Liu *et al.* 2004, Stammerjohn *et al.* in press).

Atmospheric teleconnections between the WAP and the rest of the world's ocean are clear (Yuan & Martinson 2000, 2001, Turner 2004). The anti-correlation of the SOI and sea ice extent in the PAL LTER region is significant (Smith *et al.* 2003). There also appears to be a positive trend in the Southern Annular Mode (SAM) that may be amplifying the high latitude response to ENSO (Marshall *et al.* 2004). A recent analysis of the linkage between seasonal sea ice dynamics, ENSO and SAM suggests that an intensification of the high latitude response to La Niña during the spring–autumn period together with increased polarity of the SAM associated with climate warming underlies the

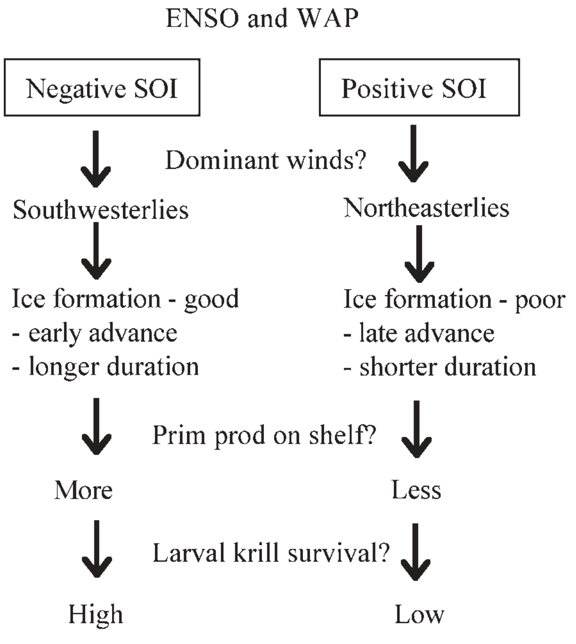

Fig. 1. Teleconnections among the Palmer LTER study region and El Niño – Southern Oscillation (ENSO) and the western Antarctic Peninsula (WAP). Predictions of conditions and linkages between positive and negative phases of the ENSO cycle, dominant winds, ice formation conditions, primary production on the shelf in summer and larval krill survival in winter along the WAP.

trends seen in the timing and advance of sea ice, both in the WAP and in the western Ross Sea (Stammerjohn personal communication 2007).

Given that the physical environment of the WAP, e.g. temperature, sea ice dynamics and snow/precipitation, is affected by strong atmospheric teleconnections to the world's ocean, we can formulate a series of predictions on how variability and trends in ENSO (and SAM) will impact krill population dynamics through effects on primary production and seasonal sea ice dynamics (Fig. 1). Conceptually, teleconnections with the WAP mean that during the warm phase of the ENSO cycle, south-westerlies (cold winds) create good conditions for ice formation, thus an early advance and longer duration of sea ice cover in the region (Yuan 2004), which in turn favour higher larval krill survival during their first winter (Quetin & Ross 2003) and higher average primary production on the shelf in summer (January/February) (Vernet unpublished data). Primary production on the shelf in summer correlates closely with the timing of sea ice retreat, e.g. the longer duration and associated later sea ice retreat bring an increased seasonal sea ice zone (SIZ) on the shelf in conjunction with the associated elevated primary production in late spring and summer (Smith *et al.* 2001, Vernet unpublished data). The reverse will be true during the La Niña phase.

The following discussion on the ecological responses of Antarctic krill to environmental variability is primarily based on results from PAL LTER and Southern Ocean Global Ocean Ecosystem Dynamics (SO GLOBEC) research. We first review recruitment processes in Antarctic krill as associated with environmental variability, then present results from two winter cruises focused on the functional linkages between the seasonal pack ice habitat and larval Antarctic krill. Long-term data (PAL LTER) combined with experiments and observations during winter process cruises (SO GLOBEC) suggested a possible mechanism underlying the correlation seen between recruitment of krill and timing of ice advance. We then review the various criteria for successful recruitment in Antarctic krill, and discuss these criteria in relation to climate change in order to speculate on future changes in the geographic location of the optimal habitat of krill. In particular, we focus on seasonal sea ice dynamics and how changing seasonal sea ice dynamics impacts the availability of food to Antarctic krill at critical times in its life cycle.

Antarctic krill – recruitment processes and the environment

Recently a more coherent picture of Antarctic krill population dynamics has emerged that describes cycles in reproductive activity and recruitment, and correlations with primary production and seasonal sea ice dynamics. Antarctic krill are relatively long-lived crustaceans, with a life span of 5–7 years in the field (Siegel & Nicol 2000). The first description of their large-scale distribution (Marr 1962) fostered the perception that this species inhabits the sea ice zone (SIZ) (Laws 1985), except around South Georgia. Highest densities are found in areas with high summer chlorophyll *a* (chl *a*) concentrations (Atkinson *et al.* 2004). The abundant population of krill in the south-west Atlantic around South Georgia, outside the seasonal sea ice zone, is unusual. One major factor affecting the abundance of krill around South Georgia is the variability in ocean currents thought to transport krill to the region from the Antarctic Peninsula and southern Scotia Sea (Murphy *et al.* 2004b, Siegel 2005), fuelling speculation that this population may not be self-sustaining.

Several key aspects of the life cycle of Antarctic krill appear to be associated with the seasonal advance and retreat of sea ice. Within the seasonal cycle of light and ice formation, the concept of timing appears to define critical periods. In the autumn, during frazil ice formation, particulate organic matter is scavenged from the water column into the sea ice and establishes the initial SIMCOs. The amount of material available to be scavenged will depend on the strength and timing of the autumn phytoplankton bloom and ice formation. Low light in winter, due to the seasonal light cycle, is further reduced in the water column by the sea ice cover and there is little or no primary production in the water column. In spring, melting sea ice conditions the water column for ice-edge blooms, stabilizing the water column and releasing SIMCOs as seed populations. Thus, there are times during the year when food is available in the water column, but available food in the winter is primarily associated with sea ice. This interplay between variability in the abundance and location of food within the water column and seasonal sea ice and the krill life cycle is one of the major conduits whereby physical factors impact the Antarctic krill population.

Reproductive cycle in Antarctic krill and seasonal sea ice dynamics

Antarctic krill initiate their reproductive cycle in the spring, but actual spawning (release of eggs) will depend on the rate of oöcyte maturation and thus energy input prior to spawning (Ross & Quetin 2000). Unlike other Antarctic euphausiids, ovarian development in krill is dependent on immediate food supplies, not stored reserves (Hagen *et al.* 2001). Thus sea ice mediates the areal extent and timing of spring food availability and, in turn, the timing of spawning. The timing and duration of the reproductive cycle appears to vary with latitude and the period of elevated primary production (Spiridonov 1995), which is linked to seasonal sea ice dynamics (Smith *et al.* 2001, Vernet unpublished data).

In both the Antarctic Marine Living Resources (AMLR) (Siegel & Loeb 1995) and PAL LTER (Quetin & Ross 2001) time series, low sea ice extent in winter and/or early retreat was associated with a delay in spawning (slower oöcyte maturation). Of even greater import to calculations of overall population fecundity, however, is that not all females of reproductive size reproduce every season (Ross & Quetin 2000). If individual females do not accumulate enough lipid stores to reach a threshold for continuing ovarian development, the strategy appears to be to delay reproduction until the following year. The intensity of reproduction, or the proportion of the females in the reproductive cycle that season, is derived from an analysis of the physiological maturity of female Antarctic krill (Cuzin-Roudy & Amsler 1991). Within the PAL LTER study region the intensity of reproduction varied interannually by nearly an order of magnitude (10–90%), and was associated with both long-term average sea ice extent and seasonal primary production in the region (Quetin & Ross 2001). Spring sea ice extent, defined as the region of 15% cover in the September–November period, represents the region affected by the retreat and melting of sea ice, and thus will be the area of enhanced primary production and food availability. Both areal extent of sea ice and the timing of the retreating ice edge, with its associated phytoplankton bloom, play a role in optimizing the habitat for krill reproduction. A balance that provides adequate food at the appropriate time for ovarian development is required. Further, the role played by the above factors in optimizing reproduction may vary within the latitudinal range of the krill population. For example, towards the northern limits of the population, krill reproduction is maximal at highest sea ice extent and late retreat. At the mid-range of the krill population, average spring sea ice extent and retreat optimize reproductive output since a later than average retreat results in lack of food at a critical time in ovarian development (Quetin & Ross 2001).

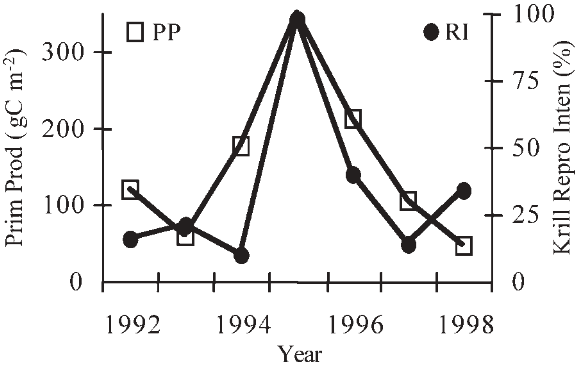

Fig. 2. Cycles of the intensity of Antarctic krill reproduction (RI) (closed circle) (% of the mature females with red thelycums of the total immature and mature females) and seasonal integrated primary production (PP) (open square) (gC m^{-2}) from the PAL LTER area between October and March over the same years (Smith *et al.* 2001 for 1992–93 and 1993–94, and Vernet unpublished data for other years). The intensity of reproduction is an index derived from an analysis of the physiological maturity stages in January, is equal to (stages 4–9) / (stages 2–10), and represents the proportion of the females reproducing that season. Stages 4–9 have red thelycums, and stages 2, 3 and 10 do not and are not in the reproductive cycle (Cuzin-Roudy & Amsler 1991).

The concept that the linkage between seasonal sea ice dynamics and krill reproduction is related to food limitation is supported by the coherence between the cycles of intensity of reproduction and seasonal integrated primary production (October–March as measured at stations near Palmer Station) (Fig. 2) (Quetin & Ross 2001, Smith *et al.* 2001, Vernet unpublished data). We conclude that for the most successful reproductive effort in the mid-WAP region, both average sea ice extent in spring (enhancing spring primary production and food availability for krill) and high summer primary production are optimal. To complete the first ovarian cycle and potentially recycle the ovary as these multiple-spawners do when food is abundant (Ross & Quetin 1983, Quetin & Ross 2001), primary production must continue to be high in summer. An early retreat is thus the worst of conditions for promoting primary production and food sources for Antarctic krill during its reproduction cycle.

Survival of larval Antarctic krill and seasonal sea ice dynamics

Recruitment success in Antarctic krill, defined as the mean abundance of one-year olds or AC1s relative to total mean abundance of post-larval krill in the study region, depends on both the population fecundity (reproductive output in the summer or the number of potential recruits) and the survival of those recruits. Larval krill hatched from embryos released in summer enter winter as late larvae, but without the energy reserves to survive the winter without eating (Quetin *et al.* 1996, Meyer & Oettl 2005). Over a decade ago, several investigators (Daly 1990, Smetacek *et al.* 1990, Ross & Quetin 1991) suggested that SIMCOs might be an essential food resource for winter survival, with pack ice the winter nursery ground for these young krill during their first winter when food availability in the water column is low. Although SIMCO production and biomass accumulation are expected to be at a minimum in winter (Dieckmann *et al.* 1998) (due to low irradiances and low temperatures), the winter SIMCO biomass is orders of magnitude greater than that in the water column (e.g. Kottmeier & Sullivan 1987, Fritsen 1996, Hoshiai 1985, Garrison & Close 1993, Garrison *et al.* 2003). Both behavioural and physiological evidence from larval and juvenile krill continues to support this concept (e.g. Marschall 1988, Stretch *et al.* 1988, Daly 1990, Quetin *et al.* 1994, Frazer *et al.* 1997, 2002, Meyer *et al.* 2002, 2003, Ju & Harvey 2004).

Thus both factors associated with recruitment success are affected by seasonal sea ice dynamics - but in separate seasons. The basic correlations have been borne out with analysis of long-term datasets both at the tip of the Antarctic Peninsula (AMLR) (Siegel & Loeb 1995, Siegel & Nicol 2000) and in the PAL LTER region (Quetin & Ross 2003, Ducklow *et al.* 2007). However, differences exist in the relationships found between recruitment success and reproduction and ice dynamics between the two study locations 450 km apart. Absolute extent of winter sea ice, duration and timing appeared to be key factors at the tip of the Antarctic Peninsula , whereas in the PAL LTER region, timing and the correspondence of an individual year to average sea ice conditions of duration and extent (22 yr average of satellite data for the LTER region between 1978 and 2001) appeared to be important (Quetin & Ross 2003). Unlike at the tip of the Peninsula, recruitment in the PAL LTER region was not well correlated with maximum extent or area in this region (Quetin & Ross 2003), suggesting that extreme conditions were not necessary for recruitment success. The contrast between the two regions may be attributable to latitudinal differences in the timing and concentration of the pack ice habitat that enhances recruitment success, leading to differences in the frequency of high recruitment years. Alternatively, differences in the pattern of recruitment success may arise because krill sampled at the tip of the Peninsula can be influenced by krill populations from the WAP and from the Weddell gyre, i.e. some years the recruitment success may be keyed to ice conditions to the east of the Peninsula which are not always synchronized with those along the WAP.

Two key correlations emerged for the PAL LTER region, neither linear. First, the recruitment index in Antarctic krill was strongly correlated with the timing of ice advance, with higher recruitment when sea ice advances earlier in the austral fall. The recruitment index decreased exponentially with later advance of sea ice ($r^2 = 0.6$) for 11 of the 13 years analysed (Fig. 3) (update of fig. 6a in Quetin & Ross 2003). Second, mean sea ice extent (a combination of duration and sea ice extent through the winter) had an impact. For context, if sea ice extent was 90% of the long-term mean extent in August, the entire PAL LTER shelf region would be covered by sea ice. A sigmoidal relationship existed between the recruitment index and the number of months the annual advance and retreat followed the monthly climatological pattern of advance and retreat between April and December for the PAL LTER study region. A specific month was scored as 'following' the climatological pattern if the sea ice extent was 90% of the climatology for that month. Recruitment was high after a threshold value of five months (fig. 6b in Quetin & Ross 2003). Thus west of the Antarctic Peninsula, the long-term mean conditions, including sea ice persisting into the spring months, but not into December, appeared to be key to recruitment success.

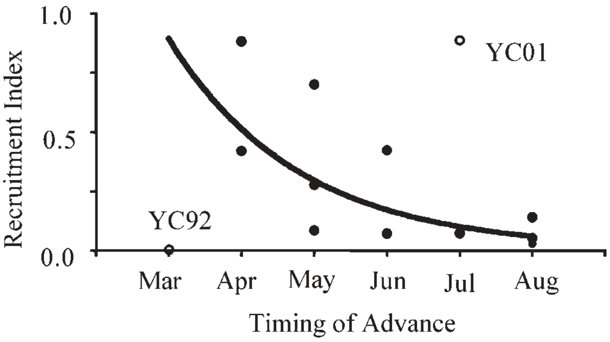

Fig. 3. Relationship between timing of sea ice advance in the PAL LTER region and recruitment index of the year class entering that winter for year classes 1991–2003 [updated with 2 more years from Quetin & Ross (2003)]. Exponential fit to 11 of the 13 years: recruitment index = $4.75\ e^{-0.56*}(\text{mo advance})$, $r^2 = 0.57$. Open circles not included are year classes 1992 and 2001.

Critical periods and teleconnections

Generally if sea ice does not advance until July in the PAL LTER region, recruitment is low. But the exceptions illustrate the role of reproductive capacity. For example, 1996 and 2001, two of the highest years of reproductive output (Quetin & Ross 2001, Ross & Quetin unpublished data, PAL LTER annual summer cruise), appear as outliers in plots of recruitment success and ice conditions that foster larval survival. For 2001, ice did not advance until mid-winter, suggesting that the ice habitat and its associated food would not be available to the larvae until after a prolonged period of low food. In 1996, there was a relatively short winter period of 'good' ice conditions of two months. In both cases autumn and winter sea ice dynamics would presumably be associated with high larval mortality due to starvation, but the high abundance of larval krill entering the winter counterbalanced and/or minimized the losses during winter to yield a high recruitment index for the year class.

Evidence suggests the first winter is a critical period for larval survival (Ross & Quetin 1991, Quetin *et al.* 1996), and larval survival during the six months of winter is a major factor in recruitment variability and thus summer population size (Atkinson *et al.* 2004). However, interannual variation in recruitment in krill appears also to be due to variation in the reproductive output of adults (Quetin & Ross 2001, 2003).

If we examine the teleconnection between krill recruitment in the PAL LTER sampling region and ENSO in light of these findings, the linkage is not with the extreme El Niño, but with neutral or moderate ENSO conditions, either El Niño or La Niña (Quetin & Ross 2003, updated time series fig. 17 in Ducklow *et al.* 2007). Extremes result in a poor year class. Thus winter sea ice conditions and their effect on survival of larval krill are not the only environmental conditions to influence the strength of a year class. Spring sea ice and its effects on food availability early in the ovarian cycle, and annual primary production and their effects on reproductive output, are also important. The primary lesson is that we should not focus exclusively on factors impacting larval survival, or we will miss part of the signal.

Winter cruises – elucidating the mechanisms underlying correlations

Most of the linkages discussed above were derived from observations during spring and summer cruises, in conjunction with satellite data on seasonal sea ice. We also need to observe and conduct experiments with larval krill in their winter habitat, e.g. the seasonal pack ice, to understand better the mechanisms underlying these correlations. In the initial stages of appreciating the role of ice in both winter survival and reproductive potential (Smetacek *et al.* 1990, Ross & Quetin 1991), variation in the degree of 'goodness' of the habitat for larval krill was not a consideration. All pack ice was 'good' habitat for krill, providing food (SIMCOs) at a time of low food availability in the water column and a refuge from predation (Smetacek *et al.* 1990, Ross & Quetin 1991, Daly 1990). Recent evidence from synthesis of historical data and collaborative studies during SO GLOBEC suggests that the situation is more complex, and that the pack ice is of varying habitat quality, e.g. food availability, both within and between winters. We suggest that timing of ice formation is key to habitat quality. 'Good' krill habitat is pack ice that forms early, increasing the probability of longer exposure to light and scavenging phytoplankton from autumn phytoplankton blooms in the water column (Garrison *et al.* 1983, 1989), and growing a higher algal biomass before winter darkness than if pack ice forms late (Melnikov 1998, Fritsen unpublished data). The higher algal biomass would lead to higher ingestion and growth rates in larval krill.

Survival in larval marine fish appears to be directly related to growth rates in the pre-recruit stage (Ottersen & Loeng 2000, Pepin 1991, Takahashi & Watanabe 2004). The assumption is that slower growing individuals are more likely to die before recruitment into the adult population than faster growing individuals (Pepin 1989), i.e. food limitation simultaneously affects both growth rates and survivorship. Similar linkages among food limitation, growth rates, survival and ultimately recruitment success may underlie the correlation found between timing of ice advance and recruitment success of krill. For larval krill, a lack of sea ice and/or the variation in the amount or availability of SIMCOs could lead to food limitation during the winter, and variability in growth rates.

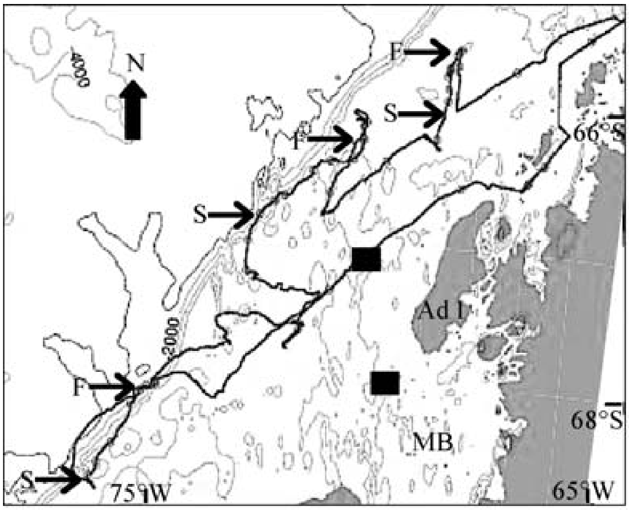

Fig. 4. Southern Ocean GLOBEC study region, location of ice camps. Two ice camps during the 2001 cruise followed a meandering course within the filled squares. The tracks of the three ice camps during the 2002 cruise are marked with start (S) and finish (F) arrows. The dark solid line is the cruise track during winter 2002. Lighter lines are bathymetry with the 2000 and 4000 m isobaths labelled. Adelaide I. (Ad I) and Marguerite Bay (MB).

Until recently, published growth rates of larval krill in winter were rare (Daly 1990, Ross & Quetin 1991), and analysis of food limitation in winter difficult, but several studies of winter growth have recently been published (Quetin *et al.* 2003, Daly 2004, Ross *et al.* 2004, Massom *et al.* 2006). An analysis of autumn and winter (April–September) *in situ* growth rates of larval krill west of the Antarctic Peninsula from multiple years showed a strong

Table I. Southern Ocean GLOBEC ice camps: dates, number, duration, number of stations at which samples were taken for integrated chlorophyll *a* in ice cores, *in situ* growth rates of larval Antarctic krill and pigment content of larval Antarctic krill.

	2001	2002
	28 Jul to 22 Aug	7 Aug to 9 Sep
Number of ice camps	2	3
Duration of ice camp	5–9 Aug 16–18 Aug	13–17 Aug 23–28 Aug 1–9 Sep
No. ice cores, from ice camps and other stations	114	127
No. stations growth experiments (individual growth increments)	6 (114) (10 expts)	5 (132) (12 expts)
No. stations pigment content (grazing on autotrophs index)	3 (30 determinations of 6 groups krill)	2 (70 determinations from 15 groups krill)
No. groups krill both pigment content and growth increment	3	5

seasonal cycle in the growth that overrode interannual variability with a minimum of near zero in early winter (Quetin *et al.* 2003), implying a within-year variation in the amount of food available in the pack ice habitat. The low growth rates suggest that food concentrations available during most of the winter were below the concentration needed for maximum growth found for young-of-the-year in austral spring (Ross *et al.* 2000).

Southern Ocean GLOBEC ice camps - measurements and experiments

To understand better the dynamics between sea ice processes and the physiological condition of larval krill, ice camps supported by the ARSV *Laurence M. Gould* were set up during winters of 2001 and 2002, in various locations on the shelf and shelf break west of the Antarctic Peninsula, generally west of Marguerite Bay (Fig. 4). Both winter cruises were in August, a month with little historical information. The ice camps were in good krill habitat (over-rafted ice), and set up on relatively small ice floes for periods of up to a week (Table I). During 2001, the ice camps were on the inner and mid-shelf, and the floes traced a meandering path during occupation (Ross *et al.* 2004), whereas in 2002, the ice camps were on the outer shelf, and generally moved toward the northeast during occupation (Fig. 4). In October 2001, the RVIB *N.B. Palmer* conducted a study in this same general region. The anomalous atmospheric conditions were reflected in multiple aspects of the ecosystem, including larval krill growth rates (Massom *et al.* 2006).

Ice cores were taken at multiple stations by the *L.M. Gould* and *N.B. Palmer* throughout the study region (including the ice camps) with a 10 cm diameter Kovacs ice core barrel. Cores were immediately sectioned and transferred into cleaned Nalgene jars. Ice core samples were melted slowly at 4°C in the dark. Immediately upon melting, the ice core meltwater was filtered through glass fibre filters (GF/F) that were then extracted in cold 90% acetone to determine chl *a* via fluorometric methods (e.g.

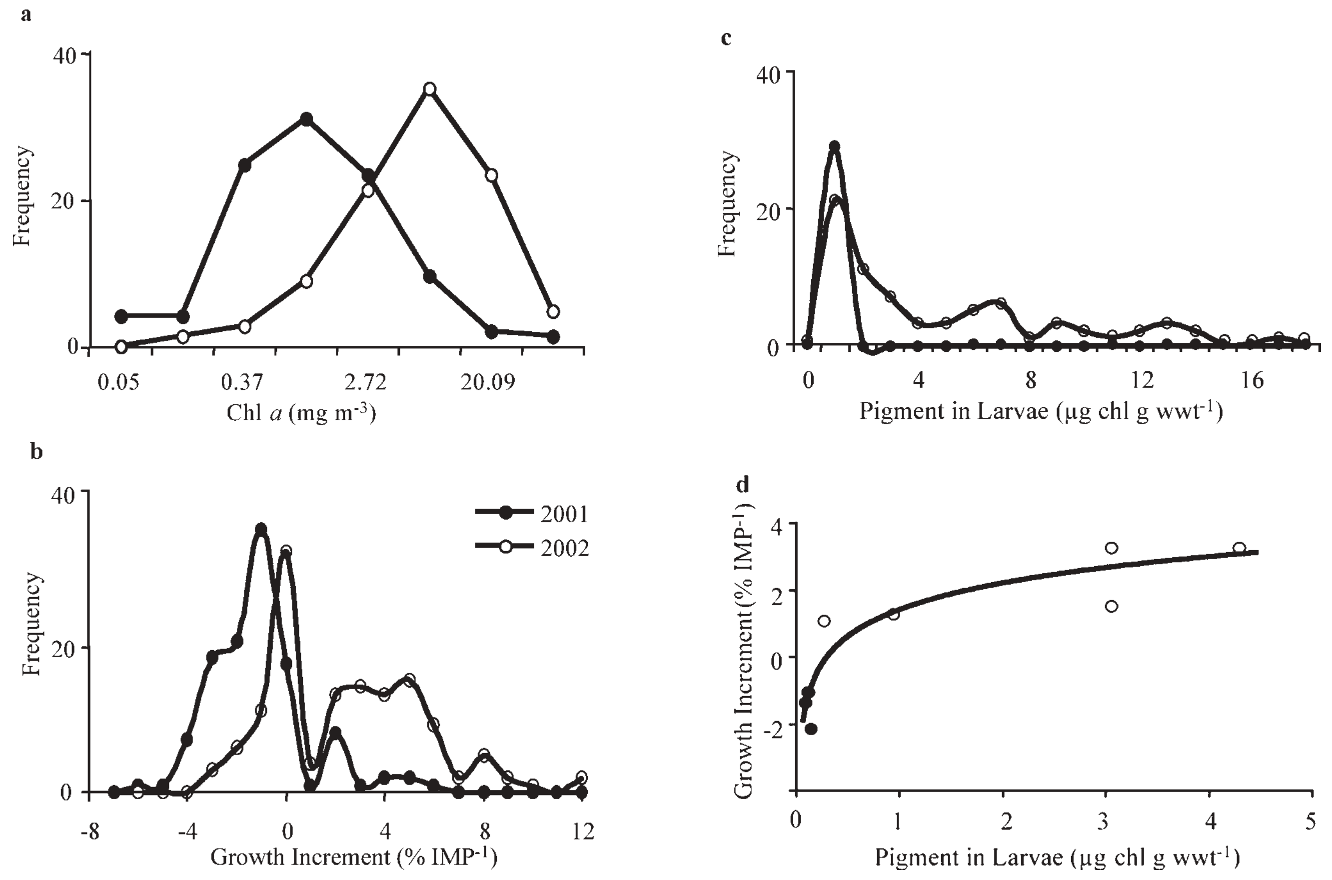

Fig. 5. Comparison of data on ice cores and larval krill from two winters, 2001 (closed circles) and 2002 (open circles). **a.** Distribution of integrally averaged chlorophyll *a* (chl *a*) in ice cores. Log scale; 2001 n = 114; 2002 n = 127. **b.** Distribution of individual growth increments from growth rate experiments conducted with larval krill from the under-ice habitat: 2001, *n* = 114; 2002, *n* = 132. **c.** Distribution of pigment content of larval krill from the under-ice habitat: 2001, *n* = 30; 2002, *n* = 70. **d.** Non-linear relationship between average growth increment of larval krill and average pigment content of larval krill collected from the same aggregation at the same time. Curve fit by eye.

Parsons 1984). Integrated chl *a* was used as an indication of food availability for larval krill. For larval krill collected from the under-ice habitat, both the individual growth increment and the pigment content were measured as described in Ross *et al.* (2004). Instantaneous growth rate experiments (IGR) (short-term experiments conducted immediately after capture which document *in situ* growth rates) have become accepted as the best method to determine growth rates of euphausiids in the field while avoiding the multiple assumptions inherent in following a cohort with length frequency analysis (Nicol 2000). Pigment content in larval krill, determined within minutes after collection, is an index of feeding on autotrophs (Daly 1990, 1998, Ross *et al.* 2004, Meyer *et al.* 2002, Pakhomov & Froneman 2004).

Results of ice camp sampling and experiments

The winter datasets from 2001 and 2002 showed that the two years differed in many ways. The frequency distribution of the integrated chl *a* in the ice cores showed an order of magnitude difference in the mean chl *a* concentration (Fig. 5a), with a mean of 1 mg m^{-3} in 2001 compared to 10 mg m^{-3} in 2002. Larval krill either stayed the same size or shrank in 2001, but primarily either grew or stayed the same size in 2002 (Fig. 5b), with a median intermolt period of 30 days for both winters. A large proportion of larval krill had low pigment content in both years, but, in 2001, few larvae had elevated pigment content whereas in 2002 a significant proportion of the population showed evidence of feeding on autotrophic organisms (Fig. 5c). Over the two winters, there were eight stations at which both pigment content and growth increment of larval krill collected at the same time and from the same aggregation were determined. There was a significant non-linear relationship between pigment content and growth increment, with higher growth increments when the feeding index was higher, as would be predicted if the pigment content was an indicator of ingestion and thus food available for growth after metabolic costs were satisfied (Fig. 5d). Thus, interannual variability in SIMCO biomass, and pigment content and *in situ* growth rates of larval and juvenile krill suggested that the sea ice habitat varied in its ability to enhance condition (growth) in larval and juvenile krill.

Conceptual diagram of the mechanism underlying correlation between recruitment success and timing of ice advance

Based on a diagnostic algal growth and ice dynamics model (Fritsen *et al.* 1998) and analysis of scavenging potential from the water column, the accumulation of microalgal biomass is greater in sea ice that forms early, i.e. when there is more material in the water column to be scavenged and enough photosynthetically available radiation (PAR) for *in situ* growth to take place. Simulations predict that chl *a* will be higher in the pack ice in winters when ice forms early, and that even a ten day delay can cause an effect (Fritsen unpublished data). As an illustration, the mid-month day length at 68°S in March, April or May will decrease from 12.8 h to 4.4 h (Fig. 6). In 2001, sea ice did not advance in the study region until May, whereas in 2002, advance was in April (Smith *et al.* 2003). During the transition from autumn to winter, SIMCO biomass can accumulate over time in first year ice, and this rate of accumulation generally slows as the daily PAR diminishes from March to June (Hoshiai 1985, Fritsen & Sullivan 1997, Melnikov 1998). In concordance with these findings is the enhanced biomass (chl *a* >10 mg m^{-2}) found in the winter ice of the eastern Ross Sea in ice floes that had more cumulative exposure to PAR during May to June (Garrison *et al.* 2003). Thus, variation in the timing of advance of sea ice means that day length and the photosynthetically available radiation (PAR) reaching the ice algae within the sea ice will vary (Fig. 6), resulting in higher SIMCO biomass when ice advances earlier. When there is more food, larval growth rates are higher, which implies both higher survival during the winter, and potentially a higher recruitment success measured the following January. This concept illustrates a possible mechanism underlying the strong correlation found between recruitment success and timing of sea ice advance (Quetin & Ross 2003).

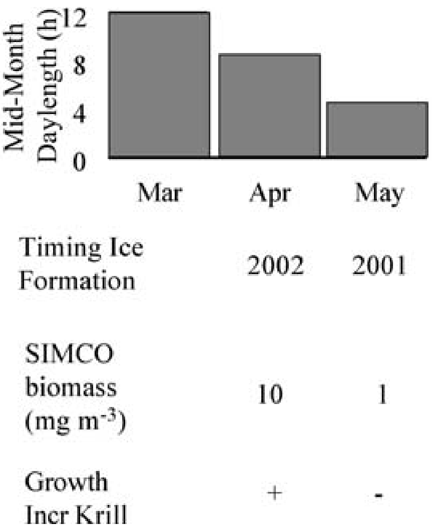

Fig. 6. Pack ice ecosystem. Relationship between differences in timing of ice formation in winters 2001 and 2002 west of the Antarctic Peninsula, light available for primary production as represented by daylength mid-month at 68°S, , accumulated sea ice microbial community (SIMCO) biomass in late winter, and growth increments in larval krill in the under-ice habitat.

Over the twenty five year period of the satellite record, ice advance in the WAP has become later in the autumn, changing from March in the late 1970s to April or May at present (Parkinson 2002). In a comparison of the satellite record before PAL LTER began and the period until now, the mean day of advance is 20–30 days later in 1992–2004 than in the 1979–91 period (Stammerjohn *et al.* in press). In the southern Bellingshausen Sea, immediately to the south of the PAL LTER study region, the day of advance is later by 54 days (± 9 d) over the 26 yr period of 1979–04 (Stammerjohn personal communication 2007). Understanding how variability in sea ice advance impacts krill recruitment success will ultimately help us predict how changes in seasonal sea ice dynamics due to global warming will affect Antarctic krill population dynamics.

Habitat requirements and regional contrast

Habitat requirements for a species are often inferred from large-scale distribution patterns. In the case of Antarctic krill, our overall understanding of the large-scale distribution has changed little since Marr (1962) described its circumpolar distribution based on the *Discovery* expeditions. The distribution is clearly asymmetrical, with 58–71% of the population in the 10°–70°W sector that includes the Scotia Sea (Atkinson *et al.* 2004), and sparse populations in some SIZ regions. The unifying characteristic of regions of high abundance appears to be high food abundance (Atkinson *et al.* 2004), due to various processes associated with seasonal sea ice dynamics, frontal zones and mixing associated with the bathymetry (Siegel 2005, Murphy *et al.* 2007). However, the inferred habitat does not necessarily give us the requirements for population persistence due to the complex interactions among animal behaviour and the confounding roles of advection and retention in maintaining population distributions in specific regions (Hofmann & Murphy 2004). We need to know how aspects of the environment (e.g. temperature, timing and abundance of food and food quality) affect individual growth, reproductive success and survival rates and thus recruitment success to fully define habitat requirements.

Frequency of successful recruitment

Priddle *et al.* (1988) calculated that a failure in recruitment in any one year could lead to a 3–4-fold variation in the density of Antarctic krill, and that recovery to initial densities might take several years of good recruitment. With a life-span of 5–7 yr, successful recruitment in Antarctic krill is not necessary every year, but long term maintenance of krill stocks requires a certain frequency of high recruitment years. Successful but variable recruitment will occur under a range of defined habitat requirements beyond which successful recruitment will not occur. Extremes in environmental conditions will lead to failure of a year class. The conditions, not the actual geographical location, define the habitat. If extreme deviations in conditions that lead to recruitment failure occur with too high a frequency then recovery to initial densities after a recruitment failure will not occur, and the population will decline.

The analysis of the several long-term datasets in the south-west Atlantic and a more detailed comparison of two long-term datasets west of the Antarctic Peninsula can help to formulate predictions of the consequences of continuing climate change. At present the maritime system of the northern WAP is shifting southward along the Antarctic Peninsula, replacing the colder continental polar system of the southern WAP (Smith *et al.* 2003). In general there is large-scale regional coherence between recruitment patterns found at the tip of the Antarctic Peninsula and the PAL LTER region midway down the western side of the Peninsula (Siegel *et al.* 2003). However, the frequency of “strong” year classes differed between the two regions in the 1990s. A “strong” year class is identified by a recruitment index of greater than 0.4, e.g. age class 1 krill are > 40% of the population the summer following hatching. At the northern tip of the Peninsula strong year classes have tended to occur only once every 5–6 yr (Siegel *et al.* 2003), whereas in the 1990s the Palmer LTER region had two sequential “strong” year classes in a 5–6 year period. The frequency of “strong” year classes at the tip of the Peninsula was less in the 1990s than in the early 1980s (Siegel & Loeb 1995, Siegel 2000, Siegel *et al.* 2003, Fraser & Hofmann 2003), but the two regions may be becoming more congruent. In the last cycle, year classes 2001 and 2002 were relatively strong in both locations (Quetin & Ross 2003, Lipsky 2005). One source of the differences in the 1990s may have been that krill populations at the tip of the Peninsula are under the influence of both the westward flowing Antarctic Circumpolar Current and the Weddell Sea gyre to the east, and that the relative influence of the two current systems varies interannually (Murphy *et al.* 2004a, 2004b, Thorpe *et al.* 2004, Siegel 2005). A second possibility is that at the more northern latitudes successful recruitment required more extreme conditions that were less frequent in the 1990s than the average conditions required mid-way down the WAP. The implication from both long-term studies, however, is that either the amplitude of the two sequential “good” recruitment years or the frequency of the “good” recruitment years may not be adequate to maintain the stocks.

Conditions for a strong year class

A suite of conditions is necessary for successful recruitment, and these conditions must occur at a high enough frequency to maintain the population. Although the common denominator is food availability, the requirements of Antarctic krill vary during different periods in their life cycle. Post-larval krill require food, both spring and summer for reproduction; larval krill require food at two critical periods, the first at metamorphosis to the first feeding stage in summer (Ross & Quetin 1989), and the second during their first winter (Ross & Quetin 1991). Thus multiple factors operating throughout the seasons will affect the timing, abundance and quality of food at critical times in the krill life cycle. The following discussion focuses on factors known to be important, such as spawning grounds, and/or that may be affected by climate change in the Antarctic, such as seasonal sea ice dynamics or increasing temperature in the water column (Clarke *et al.* 2007).

Spawning populations of krill are generally found in the surface waters over warmer deeper waters associated with the Antarctic Circumpolar Current, the Upper Circumpolar Deep Water (UCDW) (Hofmann *et al.* 1992, Hofmann & Hüsrevoglu 2003). Spawned embryos sinking into these warmer waters (Quetin & Ross 1984) develop more quickly (Ross *et al.* 1988), and ascend to the surface to feed in a shorter time than if embryos were released in regions without UCDW. This putative reproductive strategy results in less metabolic cost before metamorphosis to the first feeding stage, allowing for longer survival on stored reserves until food must be available, the first critical period for the larvae (Ross & Quetin 1989). Reproductive success of the population is thus enhanced. Greater distances between the position of summer spawning habitat and winter nursery grounds, due to changes in seasonal sea ice dynamics, may decrease the viability of present spawning regions due to sea ice extent and associated food not extending to the source of larval krill.

The quality and quantity of food available affects growth rates, and presumably rates of reproduction, of Antarctic krill (Ross *et al.* 2000, Atkinson *et al.* 2006). Changes from diatom-dominated to cryptomonad-dominated phytoplankton communities, associated with regional warming (Moline *et al.* 2004), may lead to reduced food quality in regions of the Southern Ocean impacted by warming, and thus reduced production in krill in that habitat.

In a study of the effects of food, temperature, and sex on growth rates of krill, Atkinson *et al.* (2006) found growth decreased above a temperature optimum of 0.5°C, suggesting that krill populations probably experience thermal stress at the northern limits of their range. Warming oceans (Gille 2002, Meredith & King 2005) will increase the region of potential thermal stress and restrict the current habitat range.

Given the linkage between seasonal sea ice dynamics and food availability during these two key periods of the life cycle of Antarctic krill - to fuel reproduction in the spring/summer and to feed the larval krill during their first winter - changes/trends in the timing of sea ice advance and retreat will impact the timing of food availability at critical times.

There are other variables affecting primary production, such as latitudinal variation in light, the interaction between environmental conditions and ice physical structure that influences ice algal growth and thus the seeding of the water column by melting sea ice and even the deposition of iron through ice melt (and dust deposition) (Murphy *et al.* 2007). Of importance too is the possibility that, with climate change, conditions for maximum reproductive output and maximum larval krill survival may not occur in the same reproductive cycle, thus the best available habitat will be in a region with some compromise between the two processes, ultimately producing more or fewer total recruits to the population. Any prediction as to the response of Antarctic krill to climate change contains many caveats. But for the sake of simplicity we focus on the two factors we consider most critical for predictions: changes in seasonal sea ice dynamics and the light regime associated with any changes in latitude of optimal sea ice conditions.

The krill populations from the Scotia Sea to the Bellingshausen and Amundsen seas, moving from lower to higher latitudes, can be seen as being influenced by a continuum of seasonal sea ice dynamics. Since extremely long or short sea ice seasons are not associated with strong year classes, we suggest that the greatest frequency of strong year classes lies somewhere along this continuum, not at either end, i.e. an optimal habitat model. Implied is a changing frequency with latitude in the occurrence of the specific pattern(s) of sea ice dynamics that foster high recruitment success. Atkinson *et al.* (2004) found that krill stocks have significantly declined in the south-west Atlantic, potentially through lack of food in the winter for larval krill. Although evidence from nets and from acoustics at the tip of the Peninsula are not in total agreement (Loeb *et al.* 1997, Hewitt *et al.* 2003), both at the tip of the Peninsula and in the Palmer LTER region further south (Quetin & Ross 2003) some evidence suggests that krill stocks are declining. The evidence suggests that the effect of the current seasonal sea ice dynamics on recruitment is not enough to maintain the population. However, further south and west in the Bellingshausen or eastern Amundsen seas, the observed change in ice conditions is from the extreme of perennial sea ice to more of a seasonal sea ice zone. Are these regions south and west of the Palmer LTER region now more favourable krill habitat?

One important aspect of the environment that changes with latitude is the seasonal cycle of light, and variation in the timing and amount of energy input into the ecosystem. Results from the SO GLOBEC cruises imply that timing of ice formation at a specific latitude is crucial to the amount of food available to larval krill in the winter ice habitat. However, due to the differences in day length and sun angle, the amount of energy reaching the surface from the sun is significantly less in autumn and winter at higher latitudes than lower latitudes. For a latitudinal gradient inclusive of the PAL LTER study region, the decrease with increasing latitude is ~ 8% for spring/summer, but over 50% for autumn/winter (Fig. 7) (calculated according to Brine & Iqbal 1983). For biota or an ecosystem that can survive the autumn and winter with some light, but not complete darkness, this decrease in light input could be critical. With

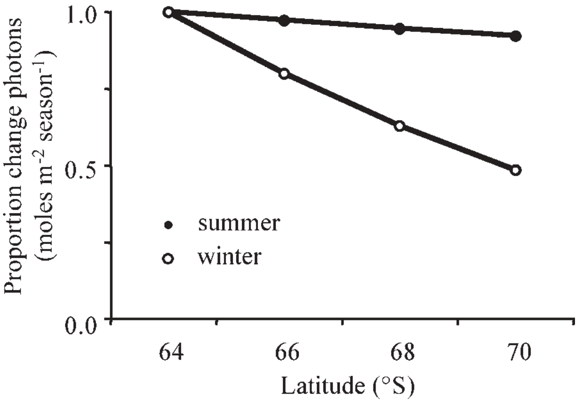

Fig. 7. Proportional change in light at wavelength of 435 nm reaching the upper atmosphere in summer and winter with latitude. The absolute value calculated for 64°S is 36.0 moles photons m^{-2} in summer, and 1.9 moles photons m^{-2} in winter.

current climate change scenarios, the timing of advance is later at the same latitude, and at some point further south ice advance will occur at the same chronological time as it did at the lower latitude previously, but under lower energy input conditions. For example, with the same chronological timing the amount of ice algal growth possible in seasonal sea ice forming at 70°S is less than in ice formed at 66°C, suggesting that food availability and larval survival will decrease with the same timing at more southerly latitudes, a change that may severely impact the krill population.

Another potential impact on the krill population moving south in response to regional warming is the direct impact of the changing seasonal cycle of light on krill physiology. We mention this here because the impact on the krill population is not often considered and little work has been done in this area. We do know that over the latitudinal range where Antarctic krill are found, there are definite differences in such behaviours as diel vertical migration (Watkins 2000) and physiological processes such as initiation of production of oöcytes (Spiridonov 1995). Although the exact signal for the initiation of ovarian development is unknown, it is likely to be some aspect of the light cycle that varies with latitude. Thus the light signal influencing the phenology of Antarctic krill may be restricted by latitude, making a shift to the highest latitudes detrimental to population success. Other studies have found phenological responses to climate change differ across trophic levels which may disrupt the synchrony between food availability and reproductive requirements of higher trophic levels, as found in examples from birds to plankton (Stenseth & Mysterud 2002, Edwards & Richardson 2004, Visser & Both 2005).

In addition to the appropriate timing and duration of the seasonal sea ice cycle at a latitude with enough light to foster winter production of SIMCOs, the krill life cycle may need to occur where the influence of Antarctic Circumpolar Current and warmer deep water and the seasonal sea ice zone overlap (Siegel 2005). The perennial sea ice of the Weddell Sea does not appear to favour high reproductive output (Siegel 2005), but if a significant seasonal sea ice zone appeared at the lower latitudes of the Weddell Sea in greater proximity to the Antarctic Circumpolar Current, the habitat might improve. Krill are currently found within the Ross Sea gyre (Azzali & Kalinowski 2000, Siegel 2005), particularly within the marginal sea ice zone where Marr (1962) was unable to sample, leading to the previous conclusion that krill stocks were low in the region. All these factors combined suggest, at least in the near term, that the lower latitudes of the seasonally ice-covered oceans in the Amundsen and Ross seas may become increasingly important as reservoirs for krill and warrant further investigation. Whether the physiology and behavior of Antarctic krill can adapt to warmer temperatures, life without ice and new food sources, is presently beyond our ability to predict.

Acknowledgements

We would like to express our appreciation to the Captain and crew of the ASRV *Laurence M. Gould* for their skill and attention to safety during both the summer and winter cruises. Staff of Raytheon Polar Services Compamy also contributed significantly to our ability to conduct research under winter conditions. We would particularly like to mention the contributions of T. Newberger, C. Boch, K. Johnston, J. Watson, J. White, A. Willis, SCUBA divers 'par excellence', who were essential to the underwater collection of larval krill. W. Kozlowski and K. Sines, F. Stewart, J. Memmott, S. Marshall, P. Adkins, L. Cunningham, M. Blees, A. Gibson, S. Dovel and P. Hartshough were valued members of the team that produced the biomass data. We would also like to thank S. Stammerjohn for her intellectual input, both in the analysis of sea ice data and the long discussions about the variability in sea ice dynamics. The original draft of this paper was considerably improved by the comments and suggestions from three anonymous reviewers. This research was supported by National Science Foundation, Office of Polar Programs, grant Nos. OPP-9909933 and OPP-0217282 to Ross, Quetin and Vernet, ANT05-29087 to Quetin and Ross, ANT05-28728 to Vernet, and OPP-9910098 and ANT-0529666 to Fritsen for research within the Southern Ocean GLOBEC and PAL LTER programs. PAL LTER Contribution No. 291.

References

AINLEY, D.G., CLARKE, E.D., ARRIGO, K.R., FRASER, W.R., KATO, A., BARTON, K.J. & WILSON, P.R. 2005. Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. *Antarctic Science*, **17**, 171–182.

ATKINSON, A., SIEGEL, V., PAKHOMOV, E.A. & ROTHERY, P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, **432**, 100–103.

Atkinson, A., Shreeve, R.S. & Hirst, A.G. 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.

Azzali, M. & Kalinowski, J. 2000. Spatial and temporal distribution of krill *Euphausia superba* biomass in the Ross Sea (1989–1990 and 1994). *In* Faranda, F.M., Guglielmo, L. & Ianora, A., *eds. Ross Sea ecology.* Berlin: Springer, 433–455.

Brine, D.T. & Iqbal, M. 1983. Diffuse and global solar spectral irradiance under cloudless skies. *Solar Energy*, **30**, 447–453.

Clarke, A., Murphy, E.J., Meredith, M.P., King, J.C., Peck, L.S., Barnes, D.K.A. & Smith, R.C. 2007. Climate change and the marine ecosystem of the western Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London*, **B362**, 149–166.

Cook, A.J., Fox, A.J., Vaughan, D.G. & Ferrigno, J.G. 2005. Retreating glacier fronts on the Antarctic Peninsula over the past half-century. *Science*, **308**, 541–544.

Croxall, J., Prince, P. & Reid, K. 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology Progress Series*, **177**, 115–131.

Croxall, J.P., Trathan, P.N. & Murphy, E.J. 2002. Environmental change and Antarctic seabird populations. *Science*, **297**, 1510–1514.

Cuzin-Roudy, J. & Amsler, M.O. 1991. Ovarian development and sexual maturity staging in Antarctic krill, *Euphausia superba* Dana (Euphausiacea). *Journal of Crustacean Biology*, **11**, 236–249.

Daly, K.L. 1990. Overwintering development, growth, and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. *Limnology and Oceanography*, **35**, 1564–1576.

Daly, K.L. 1998. Physioecology of juvenile Antarctic krill (*Euphausia superba*) during spring in ice-covered seas. *Antarctic Research Series*, **73**, 183–198.

Daly, K.L. 2004. Overwintering growth and development of larval *Euphausia superba*: an interannual comparison under varying environmental conditions west of the Antarctic Peninsula. *Deep-Sea Research II*, **51**, 2139–2168.

Dieckmann, G.S., Eicken, H., Haas, C., Garrison, D.L., Gleitz, M., Lange, M., Nöthig, E.-M., Spindler, M., Sullivan, C.W., Thomas, D.N. & Weissenberger, J. 1998. A compilation of data on sea ice algal standing crop from the Bellingshausen, Amundsen, and Weddell seas from 1983 to 1994. *Antarctic Research Series*, **73**, 85–92.

Dierssen, H.M., Smith, R.C. & Vernet, M. 2002. Glacial meltwater dynamics in coastal waters west of the Antarctic Peninsula. *Proceedings of the National Academy of Sciences*, **99**, 1790–1795.

Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernet, M. & Fraser, W.R. 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London*, **B362**, 67–94.

Edwards, M. & Richardson, A.J. 2004. The impact of climate change on the phenology of the plankton community and trophic mismatch. *Nature*, **430**, 881–884

Everson, I. 2000. Role of krill in marine food webs: the Southern Ocean. *In* Everson, I., *ed. Krill: biology, ecology and fisheries.* Oxford: Blackwell Science, 194–201.

Fraser, W.R. & Hofmann, E.E. 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series*, **265**, 1–15.

Frazer, T.K., Quetin, L.B. & Ross, R.M. 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. 1996. *Ecology of pack ice microbial communities*. PhD thesis, University of Southern California.

Fritsen, C.H., Ackley, S.F., Kremer, J.N. & Sullivan, C.W. 1998. Flood-freeze cycles and microalgal dynamics in Antarctic pack ice. *Antarctic Research Series*, **73**, 1–21.

Fritsen, C.H. & Sullivan, C.W. 1997. Distributions and dynamics of microbial communities in the pack of the western Weddell Sea, Antarctica. *In* Battaglia, B., Valencia, J. & Walton, D.W.H., *eds. Antarctic communities: species, structure and survival.* Cambridge: Cambridge University Press, 101–106.

Garrison, D.L. & Close, A.R. 1993. Winter ecology of the sea ice biota in Weddell Sea pack ice. *Marine Ecology Progress Series*, **96**, 17–31.

Garrison, D.L., Ackley, S.F. & Buck, K.R. 1983. A physical mechanism for establishing algal populatins in frazil ice. *Nature*, **306**, 363–365.

Garrison, D.L., Close, A.R. & Reimnitz, E. 1989. Algae concentrated by frazil ice: evidence from laboratory and field measurements. *Antarctic Science*, **1**, 313–316.

Garrison, D.L., Jeffries, M.O., Gibson, A., Coale, S.L., Neenan, D., Fritsen, C.H., Okolodkov, Y.B. & Gowing, M.M. 2003. Development of sea ice microbial communities during autumn ice formation in the Ross Sea. *Marine Ecology Progress Series*, **259**, 1–15.

Gille, S.T. 2002. Warming of the Southern Ocean since the 1950s. *Science*, **295**, 1275–1277.

Goodin, D.G. & Smith, R.C. 2003. Century to millennial timescale - synthesis. *In* Greenland, D., Goodin, D.G. & Smith, R.C., *eds. Climate variability and ecosystem response at Long-Term Ecological Research sites.* New York: Oxford University Press, 384–388.

Hagen, W., Kattner, G., Terbrüggen, A. & van Vleet, E.S. 2001. Lipid metabolism of Antarctic krill *Euphausia superba* and its ecological implications. *Marine Biology*, **139**, 95–104.

Hewitt, R., Demer, D.A. & Emery, J.H. 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 1991/92 through 2001/2002. *Aquatic Living Resources*, **16**, 205–213.

Hofmann, E.E. & Husrevoglu, Y.S. 2003. A circumpolar modeling study of habitat control of Antarctic krill (*Euphausia superba*) reproductive success. *Deep-Sea Research II*, **51**, 1323–1331.

Hofmann, E.E. & Murphy, E.J. 2004. Advection, krill and Antarctic marine ecosystems. *Antarctic Science*, **16**, 487–499.

Hofmann, E.E., Capella, J.E., Ross, R.M. & Quetin, L.B. 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.

Hoshiai, T. 1985. Autumnal proliferation of ice-algae in Antarctic sea-ice. *In* Siegfried, W.R., Condy, P.R. & Laws, R.M., *eds*. *Antarctic nutrient cycles and food webs*. Berlin: Springer, 89–92.

Jacobs, S.S. & Comiso, J.C. 1997. Climate variability in the Amundsen and Bellingshausen seas. *Journal of Climate*, **10**, 697–709.

Ju, S.-J. & Harvey, H.R. 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. & Sullivan, C.W. 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.

Laws, R.M. 1985. The ecology of the Southern Ocean. *American Scientist*, **73**, 26–40.

Lipsky, J.D. 2005. *AMLR 2004/2005 Field season report - objectives, accomplishments, and tentative conclusions.* La Jolla, CA: NMFS Southwest Fisheries Science Center, 167 pp.

Liu, J., Curry, J.A. & Martinson, D.G. 2004. Interpretation of recent Antarctic sea ice variability. *Geophysical Research Letters*, **31**, 10.1029/2003GL018732.

Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W. & Trivelpiece, S. 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature*, **387**, 897–900.

Marschall, H.-P. 1988. The overwintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. *Polar Biology*, **2**, 245–250.

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

Marshall, G.J., Stott, P.A., Turner, J., Connolley, W.M., King, J.C. & Lachlan-Cope, T.A. 2004. Causes of exceptional atmospheric circulation changes in the Southern Hemisphere. *Geophysical Research Letters*, **31**, 10.1029/2004GL019952.

Massom, R.A., Stammerjohn, S.E., Smith, R.C., Pook, M.J., Iannuzzi, R.A., Adams, N., Martinson, D.G., Vernet, M., Fraser, W.R., Quetin, L.B., Ross, R.M., Massom, Y. & Krouse, H.R. 2006. Extreme anomalous atmospheric circulation in the West Antarctic Peninsula region in austral spring and summer 2001/02, and its profound impact on sea ice and biota. *Journal of Climate*, **19**, 3544–3571.

Melnikov, I. 1998. Winter production of sea ice algae in the western Weddell Sea. *Journal of Marine Systems*, **17**, 195–205.

Meredith, M.P. & King, J.C. 2005. Rapid climate change in the ocean west of the Antarctic Peninsual during the second half of the 20th century. *Geophysical Research Letters*, **32**, 10.1029/2005GL024042.

Meyer, B. & Oettl, B. 2005. Effects of short-term starvation on composition and metabolism of larval Antarctic krill *Euphausia superba*. *Marine Ecology Progress Series*, **292**, 263–270.

Meyer, B., Atkinson, A., Blume, B. & Bathmann, U.V. 2003. Feeding and energy budgets of larval Antarctic krill *Euphausia superba* in summer. *Marine Ecology Progress Series*, **257**, 167–177.

Meyer, B., Atkinson, A., Stübing, D., Oettl, B., Hagen, W. & Bathmann, U.V. 2002. Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter - I. Furcilia III larvae. *Limnology and Oceanography*, **47**, 943–952.

Moline, M.A., Claustre, H., Frazer, T.K., Schofield, O. & Vernet, M. 2004. Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. *Global Change Biology*, **10**, 1973–1980.

Murphy, E.J., Thorpe, S.E., Watkins, J.L. & Hewitt, R. 2004a. Modeling the krill transport pathways in the Scotia Sea: spatial and environmental connections generating the seasonal distribution of krill. *Deep-Sea Research II*, **51**, 1435–1456.

Murphy, E.J., Watkins, J.L., Meredith, M.P., Ward, P., Trathan, P.N. & Thorpe, S.E. 2004b. Southern Antarctic Circumpolar Current Front to the northeast of South Georgia: horizontal advection of krill and its role in the ecosystem. *Journal of Geophysical Research*, 109 (C1), art. C01029.

Murphy, E.J., Watkins, J.L., Trathan, P.N., Reid, K., Meredith, M.P., Thorpe, S.E., Johnston, N.M., Clarke, A., Tarling, G.A., Collins, M.A., Forcada, J., Shreeve, R.S., Atkinson, A., Korb, R., Whitehouse, M.J., Ward, P., Rodhouse, P.G., Enderlein, P.L., Hirst, A.G., Martin, A.R., Hill, S.L., Staniland, I.J., Pond, D.W., Briggs, D.R., Cunningham, N.J. & Fleming, A.H. 2007. Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. *Philosophical Transactions of the Royal Society*, **B362**, 113–148.

Nicol, S. 2000. Understanding krill growth and aging: the contribution of experimental studies. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**(Suppl. 3), 168–177.

Ottersen, G.A. & Loeng, H. 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.

Pakhomov, E.A. & Froneman, P.W. 2004. Zooplankton dynamics in the eastern Atlantic sector of the Southern Ocean during the austral summer 1997/1998; Part 2: Grazing impact. *Deep-Sea Research II*, **51**, 2617–2631.

Parkinson, C.L. 2002. Trends in the length of the southern Ocean sea ice seasons, 1979–1999. *Annals of Glaciology*, **34**, 435–440.

Parsons, T.R., Maita, Y. & Lalli, C.M. 1984. *A manual of chemical and biological methods for seawater analysis.* Oxford: Pergamon Press, 173 pp.

Pepin, P. 1989. Using growth histories to estimate larval fish mortality rates. *Rapport Procedes-verbaux Réunion des Conseil Internationale Exploration de la Mer*, **191**, 324–329.

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.

Priddle, J., Croxall, J.P., Everson, I., Heywood, R.B., Murphy, E.J., Prince, P.A. & Sear, C.B. 1988. Large-scale fluctuations in distribution and abundance of krill – a discussion of possible causes. *In* Sahrhage, D., *ed. Antarctic resources and variability.* Berlin: Springer, 169–182.

Quetin, L.B. & Ross, R.M. 1984. Depth distribution of developing *Euphausia superba* embryos, predicted from sinking rates. *Marine Biology*, **79**, 47–53.

Quetin, L.B. & Ross, R.M. 1992. A Long-Term Ecological Research strategy for polar environmental research. *Marine Pollution Bulletin*, **25**, 233–238.

Quetin, L.B. & Ross, R.M. 2001. Environmental variability and its impact on the reproductive cycle of Antarctic krill. *American Zoologist*, **41**, 74–89.

Quetin, L.B. & Ross, R.M. 2003. Episodic recruitment in Antarctic krill, *Euphausia superba*, in the Palmer LTER study region. *Marine Ecology Progress Series*, **259**, 185–200.

Quetin, L.B. & Ross, R.M. & Clarke, A. 1994. Krill energetics: seasonal and environmental aspects of the physiology of *Euphausia superba*. *In* El-Sayed, S., *ed. Southern Ocean ecology: the BIOMASS perspective.* Cambridge: Cambridge University Press, 165–184.

Quetin, L.B., Ross, R.M., Frazer, T.K., Amsler, M.O., Wyatt-Evens, C. & Oakes, S.A. 2003. Growth of larval krill, *Euphausia superba*, in fall and winter west of the Antarctic Peninsula. *Marine Biology*,**143**, 833–843.

Quetin, L.B., Ross, R.M., Frazer, T.K. & Haberman, K.L. 1996. Factors affecting distribution and abundance of zooplankton, with an emphasis on Antarctic krill, *Euphausia superba*. *Antarctic Research Series*, **70**, 357–371.

Ross, R.M. & Quetin, L.B. 1983. Spawning frequency and fecundity of the antarctic krill *Euphausia superba*. *Marine Biology*, **77**, 201–205.

Ross, R.M. & Quetin, L.B. 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.

Ross, R.M. & Quetin, L.B. 1991. Ecological physiology of larval euphausiids, *Euphausia superba* (Euphausiacea). *Memoirs of the Queensland Museum*, **31**, 321–333.

Ross, R.M. & Quetin, L.B. 2000. Reproduction in Euphausiacea. *In* Everson, I., *ed. Krill: biology, ecology and fisheries.* Oxford: Blackwell Science, 150–181.

Ross, R.M., Quetin, L.B., Baker, K.S., Vernet, M. & Smith, R.C. 2000. Growth limitation in young *Euphausia superba* under field conditions. *Limnology and Oceanography*, **45**, 31–43.

Ross, R.M., Quetin, L.B. & Haberman, K.L. 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., Quetin, L.B. & Kirsch, E. 1988. Effect of temperature on developmental times and survival of early larval stages of *Euphausia superba* Dana. *Journal of Experimental Marine Biology and Ecology*, **121**, 55–71.

Ross, R.M., Quetin, L.B., Newberger, T. & Oakes, S.A. 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.

Ross, R.M., Quetin, L.B., Martinson, D.G., Iannuzzi, R., Stammerjohn, S.S. & Smith, R.C. In press. Palmer LTER: patterns of distribution of major zooplankton species west of the Antarctic Peninsula over a twelve year span. *Deep-Sea Research II*.

Scambos, T., Hulbe, C. & Fahnestock, M. 2003. Climate-induced ice shelf disintegration in the Antarctic Peninsula. *Antarctic Research Series*, **79**, 79–92.

Siegel, V. 2000. Krill (Euphausiacea) demography and variability in abundance and distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**(Suppl. 3), 151–167.

Siegel, V. 2005. Distribution and population dynamics of *Euphausia superba*: summary of recent findings. *Polar Biology*, **29**, 1–22.

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

Siegel, V. & Nicol, S. 2000. Population parameters. *In* Everson, I., *ed. Krill: biology, ecology and fisheries.* Oxford: Blackwell Science Ltd, 103–149.

Siegel, V., Ross, R.M. & Quetin, L.B. 2003. Krill (*Euphausia superba*) recruitment indices from the western Antarctic Peninsula: are they representative of larger regions? *Polar Biology*, **26**, 672–679.

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

Smetacek, V., Scharek, R. & Nothig, E.-M. 1990. Seasonal and regional variation in the pelagial and its relationship to the life history cycle of krill. *In* Kerry, K.R. & Hempel, G., *eds. Antarctic ecosystems: ecological change and conservation.* Berlin: Springer, 103–114.

Smith, R.C. & Stammerjohn, S.E. 2001. Variations of surface air temperature and sea-ice extent in the western Antarctic Peninsula region. *Annals of Glaciology*, **33**, 493–500.

Smith, R.C., Fraser, W.R. & Stammerjohn, S.E. 2003. Climate variability and ecological response of the marine ecosystem in the Western Antarctic Peninsula (WAP) region. *In* Greenland, D., Goodin, D.G. & Smith, R.C., *eds. Climate variability and ecosystem response at Long-Term Ecological Research sites.* New York: Oxford University Press, 158–173.

Smith, R.C., Baker, K.S., Dierssen, H.M., Stammerjohn, S.E. & Vernet, M. 2001. Variability of primary production in an Antarctic marine ecosystem as estimated using a multi-scale sampling strategy. *American Zoologist*, **41**, 40–56.

Smith, R.C., Ainley, D.G., Baker, K., Domack, E., Emslie, S., Fraser, W.R., Kennett, J., Leventer, A., Mosley-Thompson, E., Stammerjohn, S.E. & Vernet, M. 1999. Marine ecosystem sensitivity to climate change. *BioScience*, **49**, 393–404.

Smith, R.C., Baker, K.S., Fraser, W.R., Hofmann, E.E., Karl, D.M., Klinck, J.M., Quetin, L.B., Prézelin, B.B., Ross, R.M., Trivelpiece, W.Z. & Vernet, M. 1995. The Palmer LTER: A Long-Term Ecological Research program at Palmer Station, Antarctica. *Oceanography*, **8**(3), 77–86.

Spiridonov, V.A. 1995. Spatial and temporal variability in reproductive timing of Antarctic krill (*Euphausia superba* Dana). *Polar Biology*, **15**, 161–174.

Stammerjohn, S.E., Drinkwater, M.R., Smith, R.C. & Liu, X. 2003. Ice-atmosphere interactions during sea-ice advance and retreat in the western Antarctic Peninsula region. *Journal of Geophysical Research*, 108(C10), 10.1029/2002JC001543.

Stammerjohn, S.E., Martinson, D.G., Smith, R.C. & Iannuzzi, R.A. In press. Sea ice in the Palmer LTER region: spatio-temporal variability from ecological and climate change perspectives. *Deep-Sea Research II*.

Stenseth, N.C. & Mysterud, A. 2002. Climate, changing phenology, and life history traits: nonlinearity and match-mismatch to the environment. *Proceedings of the National Academy of Sciences USA*, **99**, 13 379–13 381.

Stretch, J.J., Hamner, P.P., Hamner, W.M., Michel, W.C., Cook, J. & Sullivan, C.W. 1988. Foraging behavior of antarctic krill *Euphausia superba* on sea ice microalgae. *Marine Ecology Progress Series*, **44**, 131–139.

Takahashi, M. & Watanabe, Y. 2004. Growth rate-dependent recruitment of Japanese anchovy *Engraulis japonicus* in the Kuroshio-Oyashio transitional waters. *Marine Ecology Progress Series*, **266**, 227–238.

Thorpe, S.E., Heywood, K.J., Stevens, D.P. & Brandon, M.A. 2004. Tracking passive drifters in a high resolution ocean model: implications for interannual variability of larval krill transport to South Georgia. *Deep-Sea Research*, **51**, 909–920.

Turner, J. 2004. The El Niño-Southern Oscillation and Antarctica. *International Journal of Climatology*, **24**, 1–31.

Vaughan, D.G., Marshall, G.J., Connolley, W.M., Parkinson, C., Mulvaney, R., Hodgson, D.A., King, J.C., Pudsey, C.J. & Turner, J. 2003. Recent rapid regional climate warming on the Antarctic Peninsula. *Climatic Change*, **60**, 243–274.

Visser, M.E. & Both, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society*, **B272**, 2561–2569.

Walsh, J.J., Dieterle, D.A. & Lenes, J. 2001. A numerical analysis of carbon dynamics of the Southern Ocean phytoplankton community: the roles of light and grazing in effecting both sequestration of atmospheric CO2 and food availability to larval krill. *Deep-Sea Research I*, **48**, 1–48.

Watkins, J.L. 2000. Aggregation and vertical migration. *In* Everson, I., *ed. Krill: biology, ecology, and fisheries.* Oxford: Blackwell Science, 80–102.

Yuan, X. 2004. ENSO-related impacts on Antarctic sea ice: a synthesis of phenomenon and mechanisms. *Antarctic Science*, **16**, 415–425.

Yuan, X. & Martinson, D.G. 2000. Antarctic sea ice extent variability and its global connectivity. *Journal of Climate*, **13**, 1697–1717.

Yuan, X. & Martinson, D.G. 2001. The Antarctic Dipole and its predictability. *Geophysical Research Letters*, **28**, 3609–3612.