FOUNDATIONS FOR ECOLOGICAL RESEARCH WEST OF THE ANTARCTIC PENINSULA
ANTARCTIC RESEARCH SERIES, VOLUME 70, PAGES 357-371

FACTORS AFFECTING DISTRIBUTION AND ABUNDANCE OF ZOOPLANKTON, WITH AN EMPHASIS ON ANTARCTIC KRILL, *EUPHAUSIA SUPERBA*

Langdon B. Quetin, Robin M. Ross,
Thomas K. Frazer, and Karen L. Haberman

Marine Science Institute, University of California at Santa Barbara

Variation in the abundance and distribution of zooplankton is an inherent characteristic of pelagic marine ecosystems. In this chapter, we discuss how patterns of abundance and distribution are affected by the life cycle characteristics of some of the predominant macrozooplankton west of the Antarctic Peninsula. Because of the importance of Antarctic krill, *Euphausia superba*, within this region, some aspects of its ecology are given special attention. Of particular relevance to current hypotheses is the association of krill and sea ice, and new evidence is presented for winter habitat segregation between adult and larval stages. Subsequent discussion focuses on strategies for winter survival, and variation in recruitment. Finally, we discuss the effects of abiotic factors such as frontal shifts, and biotic factors such as food composition, as they relate to abundance and distribution of zooplankton.

1. INTRODUCTION

Processes underlying the temporal and spatial variation observed in abundance and distribution of zooplankton west of the Antarctic Peninsula [*Ross et al.*, this volume] are not well understood. Total zooplankton biomass in the upper 2000 m of the Southern Ocean appears to be constant on large temporal and spatial scales (decadal, entire Southern Ocean) [*Foxton*, 1956; *Hopkins*, 1971; *Kawamura*, 1986]. However, both biomass and community composition in the epipelagic zone varies significantly on smaller scales: within regions, with season, and with year [*Kawamura*, 1986; *Ross et al.*, this volume]. Changes in the abundance of zooplankton may indicate a trend, or may be part of a natural cycle. If we are to begin to understand the causal mechanisms underlying these differences, more information will be necessary on how various processes operate on multiple scales and interact to impact distribution patterns. One process of particular interest is the seasonal advance and retreat of annual sea ice, a physical phenomena affecting large areas of the Soutern Ocean. Several current hypotheses suggest that interannual variability in the timing and extent of ice cover may either impact zooplankton populations directly or be an indicator of processes that cause changes in distribution patterns on the mesoscale.

In this chapter we evaluate our current understanding of specific processes influencing the ecology and population dynamics of some of the most abundant meso- and macrozooplankton. A complete review of the ecophysiology and biological/physical interactions of these organisms and their oceanic environment is beyond the scope of this chapter. We have chosen to review a number of related topics identified as critical areas for future investigations. Antarctic krill, *Euphausia superba*, is the keystone species, and often the most abundant macrozooplankton species within the Palmer LTER region. The role of annual sea ice in the ecology of *E. superba* has received particular attention, and our understanding of this interaction is used at several points in this review to illustrate the processes involved.

First, we discuss the impact of life cycle characteristics on seasonal patterns of distribution and abundances in some of the dominant zooplankton. Specific life cycle characteristics discussed are life span, ontogenetic migration, and the reproductive cycle. This section ends with a discussion of the impact of life history stage on winter habitat and distribution in *Euphausia superba*. Second, we review strategies used by zooplankters to survive the winter period of low food availability in the water column, and discuss variability in recruitment. Since many of the abundant zooplankton are thought to be primarily herbivores, low light levels and attendant low primary production in winter are environmental factors of importance to these species. We conclude with a discussion of abiotic and biotic factors that impact distribution and abundance. Abiotic factors include the Polar Front and the Southern Ocean Oscillation, biotic factors include food availability and composition. Our purpose here is to synthesize previously published research, and reference several recent reviews for additional detail.

2. LIFE CYCLE CHARACTERISTICS

There are general trends in the abundance and distribution of meso- and macrozooplankton in the upper 300 m throughout the year that are primarily due to life cycle characteristics of specific zooplankters. Timing and vertical extent of ontogenetic migration, and timing, duration and predictability of reproduction greatly impact seasonal pat-

TABLE 1. Life cycle characteristics of four mesozooplanktonic copepods: life span, ontogenetic migration, timing and duration of spawning, and winter strategy and depth. Information from *Schnack-Schiel and Hagen* [1994] unless otherwise indicated. a [*Marin*, 1988], b [*Drits et al.*, 1993], c [*Zmijewska*, 1987], d [*Marin and Schnack-Schiel*, 1993], e [*Atkinson*, 1991], f [*Atkinson and Peck*, 1988], g [*Huntley and Escritor*, 1992], h [*Zmijewska and Yen*, 1993], i [*Lopez et al.*, 1993].
* in shallow water *C. acutus* winters near the surface

Species	Life span	Ontogenetic Migration	Spawning	Copepodite I appearance	Winter
Calanoides acutus	1 year	strong	early spring (Oct - Nov) short	late spring (Dec)	diapause; as late stage copepodites (CIV-CVI) > 500 m *
Calanus propinquus	1 [a] or 2 [b]	partial	late spring to early summer, extended	summer (Feb)	active, no diapause; disperse <500 m [h]
Rhincalanus gigas (largest)	1 or 2 [a]	partial	fall [a], [d] spring & fall [e] Dec [c]	fall	active, no diapause; mid-depth
Metridia gerlachei	unknown	no [f]	spring/summer, extended (Nov-Jan) [c], [g]	summer/fall	active; surface

terns in horizontal and vertical distribution. For example, in several copepod species, ontogenetic migration dictates that specific larval stages inhabit both a different depth strata and a different temporal frame than the adults. Whereas for many of the euphausiids, both adults and larvae inhabit the upper layer and may overlap in space and time. Questions about the extent of the association of the life cycle of krill and sea ice have been asked since *Marr* [1962] first noticed the coincidence of the distributional range of *E. superba* and the area covered by the annual advance and retreat of the sea ice. In this section, winter distribution patterns of Antarctic krill are discussed in the context of differences in the ecology of two life stages, adults and larvae..

Two seasonal surface maxima in total zooplankton, spring and late summer, have been observed in several areas [*Smith and Schnack-Schiel*, 1990], although the timing varies in different geographical regions and with latitude. The spring abundance peak has been attributed to the migration of the overwintering populations of copepods to the upper water layers. The fall peak is explained by the appearance of the new generations of copepods and euphausiids in mid to late summer (Tables 1 and 2).

2.1. *Ontogenetic Migration and Life Span*

For copepods, the timing and strength of ontogenetic migration varies (Table 1). Of the three calanoid copepods with documented ontogenetic vertical migrations, *Calanoides acutus* migrates to the deepest depths, and ascends first from depth in the spring. Both *Calanus propinquus* and *Rhincalanus gigas* exhibit a partial ontogenetic migration, either dispersing throughout the midwater or inhabiting an intermediate depth. They ascend and descend sequentially after *C. acutus*. No ontogenetic migration is found in *Metridia gerlachei*. This species is found closer to the surface in winter than in summer. Euphausiids as a group do not show ontogenetic migrations.

Salps (Tunicata: Salipidae) do show a distinct and deep ontogenetic migration. In general, the solitary form, not the aggregate form, is found in the deeper layers of the water column [*Foxton*, 1966]. One possible scenario is that the ontogenetic vertical migration occurs after sexual reproduction (Figure 1), and is undertaken by the solitary form to depths from 250 to 1500 m in the fall [*Foxton*, 1966; *Ainley et al.*, 1991], leaving the aggregate form in the surface waters. The observation of aggregate forms under the ice by SCUBA divers in both early and later winter (T. Frazer, L. Quetin, personal communication) and the widespread presence of *Salpa thompsoni* in low numbers across the Palmer LTER region in winter 1993 [*Ross et al.*, this volume] supports the suggestion that only solitary forms, and not the total population, participate in the ontogenetic migration. Timing in the reproductive cycle is thus going to determine when the vertical maximum in the salp population moves from the upper 250 m to below 250 m. The wide vertical distribution of *S. thompsoni* found in the Scotia Sea in austral spring and in the Weddell Sea in austral fall [*Lancraft et al.*, 1989], for example, may result from sampling during times of year when both solitary and aggregate forms are present and ontogenetic migration is anticipated. Unfortunately in most studies the aggregate and solitary forms have not been distinguished.

Within taxonomic groups, the strength of the seasonal peak(s) in abundance varies widely, partially as a function of whether a species has an annual, biannual or longer life cycle (Tables 1, 2). Seasonal abundances in the surface layer are expected to fluctuate less in longer-lived organisms that do not undergo an ontogenetic vertical migration and have multiple age groups within the population, such as euphausiids, than in shorter lived organisms, such as copepods with annual or biannual life cycles,

TABLE 2. Life span, timing of spawning, larval occurrence, and total length at about 1 yr for euphausiid species found west of the Antarctic Peninsula. Reference number in parentheses: (1) [*Hempel and Marschoff*, 1980]; (2) [*Brinton*, 1984]; (3) [*Makarov*, 1977]; (4) [*Baker*, 1959]; (5) [*Siegel*, 1986]; (6) [*Harrington and Thomas*, 1987]; (7) [*Fevolden*, 1980] (Weddell); (8) [*Hempel et al.*, 1979] (Bransfield); (9) [*Stepnik*, 1982] (max gravids); (10) [*Makarov*, 1980]; (11) [*Brinton and Townsend*, 1991].

Species (life span, yr)	Spawn	Calyptopis	Furcilia	Total Length at 1 yr (mm)
E. superba (6 - 7 yr)	Dec - Mar	Jan	late Feb	20-24 (Jan)
E. crytallorophias (4 yr males; 5 yr females)	1 Nov (6, 7, 8, 11)	Jan (11)	Mar early furcilia & F3 (7, 11)	12.6 (Oct)
E. frigida (2 yr)	1 Oct (5)	Nov/Dec (1)	late Nov, first (2) Dec/Jan, most (3)	12? (winter tl)
E. triacantha (3 yr)	1 Sept (4)		Nov (4) 6.2 mm	19? (5) (winter)
T. macrura (4 yr)	1 Sept (9)	Oct (10)	Feb F3, 5 mm	J, 6.3 mm (Oct) 9 mm (Nov) (9)

especially those which do migrate ontogenetically [*Ross et al.*, this volume]. However, the duration of the reproductive season in annual or biannual organisms will also affect the strength of the seasonal peak. In *M. gerlachei* and *R. gigas*, for example, most stages are found in the surface waters all summer long [*Marin, 1988; Zmijewska and Yen*, 1993], spreading out the peak in abundance over time.

2.2. *Reproductive Cycle*

2.2.1. ***Copepods.*** Timing of the seasonal peak in abundance due to the new generation will be affected by variability in both initiation and duration of the reproductive cycle. For example, different species of copepods have different patterns of reproduction (Table 1) that lead to broader or sharper peaks in abundance. Three of the four macrozooplanktonic calanoid copepods in the LTER region reproduce in the late spring or early summer, but one does not reproduce until late summer or early fall. *C. acutus* spawns over a relatively brief period in December, creating a well-defined cohort [*Schnack-Schiel and Mujica*, 1994]. Although the major spawning period for *C. propinquus* is also in December, this species can spawn as early as October/November, and continues spawning longer than *C. acutus* [*Schnack-Schiel and Hagen*, 1994]. Thus the new generation of *C. propinquus* appears over a broader temporal range. *M. gerlachei*, an omnivore, also has a protracted spawning period, beginning in November and continuing through January [*Huntley and Escritor*, 1992]. *R. gigas* does not spawn until March [*Marin and Schnack-Schiel*, 1993; *Schnack-Schiel and Mujica*, 1994].

The energy source for reproduction can be winter stores (see *3.1 Strategies for Winter Survival*) or food from that spring and summer season. Egg production of *C. acutus* does not appear to depend on surrounding food concentrations; this suggests that egg production is fueled primarily by winter stores [*Huntley and Escritor*, 1992]. Thus, for *C. acutus*, timing and duration of the reproductive season will be a function of the previous summer's food intake, and the appearance of the next generation will be more predictable than for species whose egg production depends on availability of food in the spring. *C. propinquus*, on the other hand, continues to feed in summer, fall and winter [*Schnack-Schiel and Hagen*, 1994], supplying the energy for a longer spawning period.

2.2.2. ***Euphausiids.*** Initiation of spawning and timing of appearance of larval stages for most euphausiids west of the Antarctic Peninsula occurs earlier than for copepods. Herbivorous euphausiids appear to spawn later than either omnivores or carnivores (Table 2). For example, *Thysanoessa macrura* spawns in early austral spring [*Nordhausen*, 1994], well before the phytoplankton bloom. *E. superba* feeds primarily as an herbivore, and is the last of the euphausiids to spawn; initiation of its spawning season can vary by a month (early December to early January), and last from 1.5 to 3.5 months depending on the year [*Fraser*, 1936; *Ross and Quetin*, 1986], a period that encompasses the period of reproduction for most copepods. Initiation of spawning for *E. superba* often co-occurs with a phytoplankton bloom.

Like copepods, herbivorous euphausiids that spawn in late spring before the summer phytoplankton bloom must either depend on energy stores laid down the previous summer or exploit alternative food sources like ice algae or the early ice-edge blooms in spring. The correspondence of minimum lipid content and the beginning of spawning in *E. crystallorophias* suggests that this herbivore depends primarily on lipid stores from the previous summer to fuel gonadogenesis [*Clarke*, 1985; *Littlepage*, 1964]. For *E. superba* the minimum in lipid occurs in September (L. Quetin, R. Ross, personal communication), several months before spawning, implying that Antarctic krill depend on spring and summer food supplies for reproduction.

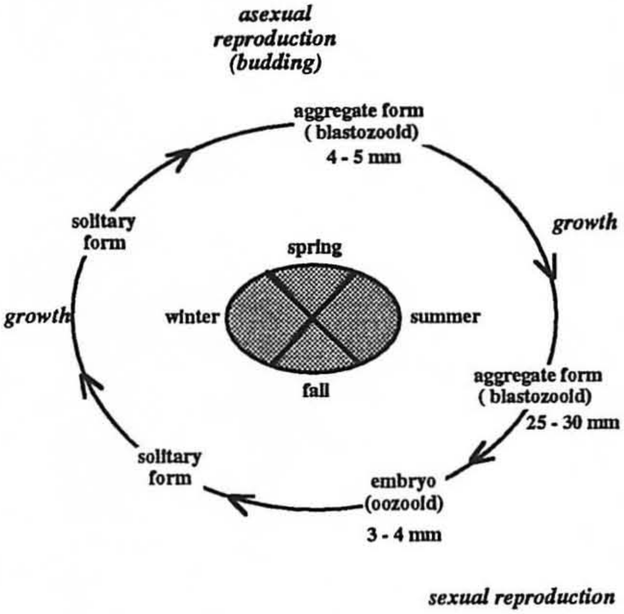

Fig. 1. Conceptual life cycle of salps, with alternating generations of solitary and aggregate forms. Based on seasonal data of *Foxton* [1966].

2.2.3. Salps. The life cycle of the Salpidae is complex, and consists of alternating sexual (production of embryos) and asexual (budding) generations (Figure 1). In the solitary form, chains of the aggregate form are produced by budding from the stolon. Individuals (blastozooids) in a recently released aggregate chain are only 4-5 mm long. These hermaphroditic individuals continue to grow. Once they are about 25-30 mm long, each individual releases a fertilized embryo (oozooid) 3-4 mm in total length, and then functions as a male. The seasonal pattern of these alternating generations is understood on broad scales [*Foxton*, 1966]. Budding, release of aggregates and swarm production are zero in winter, and the aggregate form is at minimum abundance. In winter, solitary individuals are also generally small, but some growth can occur. In the spring, there is an increase in the relative proportion of aggregate forms, with a maximum in summer or fall. The aggregate form dominates when swarms are found. Sexual reproduction occurs at the end of a salp bloom. *Foxton* [1966] originally described an aggregate maximum in February. However, *S. thompsoni* can clearly dominate the zooplankton assemblage during other months. For example, in the Antarctic spring/summer season, *S. thompsoni* was numerically dominant in the Scotia Sea in November-December 1983 [*Lancraft et al.*, 1989], in the Palmer LTER region in January 1994 [*Ross et al.*, this volume], and sometimes in the fall, as found in the Palmer LTER region in 1993 [*Ross et al.*, this volume]. There also appears to be a latitudinal gradient, with blooms of salps occuring earlier at more northern latitudes [*Ross et al.*, this volume].

Under favorable environmental conditions, salps can rapidly reproduce by asexual budding (Figure 1). Environmental conditions that favor salp swarm development are not well understood, although low chlorophyll concentrations and small, rather than large food, particles appear to foster blooms [*Harbison et al.*, 1986]. The feeding apparatus of salps may become irreversibly clogged at phytoplankton concentrations at or above $3\ \mu g\ l^{-1}$ (calculated from *Harbison* [1986] with a carbon:chlorophyll ratio of 50:1), with potential consequences for growth and survival. In at least one case, a rapid increase in the number of *S. thompsoni*, was followed by a collapse in their population in conjunction with a phytoplankton bloom [*Perissinotto and Pakhomov*, 1995; E. Pakhomov, personal communication, 1995].

2.3. Antarctic Krill: Adult and Larval Habitat Segregation in Winter

The association of Antarctic krill with sea ice has been inferred by the coincidence of the distributional range of this species with the area covered by the seasonal advance and retreat of sea ice [*Marr*, 1962; *Laws*, 1985], but details of this association and variation with life stage are not well known. *Smetacek et al.* [1990] discussed early qualitative observations with a remotely operated vehicle (ROV) [*Marschall*, 1988] with respect to the association of Antarctic krill with sea ice during its life cycle, and suggested that adult krill retreat to the ice habitat during winter. Since then, however, observations from other geographical regions during the winter, and both qualitative and quantitative observations of the under ice population by SCUBA divers have become available. The view that both adult and larval krill are closely linked to the sea ice during the entire winter must be revised in light of this new information.

2.3.1. Spatial and temporal scale of new observations. Our understanding of the association of Antarctic krill with sea ice west of the Antarctic Peninsula is based on observations between 1985 and 1994 during a series of cruises that occurred from late May to late September (Figure 2). From 1985-1989, areas surveyed were in the northern region of the Palmer LTER Peninsula grid [*Waters and Smith*, 1992] and immediately north of the grid (from 50 km south of Anvers Island to the northern Shetland Islands and Bransfield Strait). Since 1991 the research effort has focused on the area south of Anvers Island and north of Marguerite Bay. Early observations by SCUBA divers established that under-ice diving is essential for sampling the larval krill population in winter (WinCruise I, 1985, WinCruise II, 1987) [*Kottmeier and Sullivan*, 1987; *Quetin and Ross*, 1988]. On subsequent cruises (1991-1993), standardized, quantitative surveys were used to estimate krill abundances (see *Frazer et al.* [1995] for larval abundances).

2.3.2. Observations by SCUBA divers. During WinCruise III (1989), ice cover within the sampling area was extremely low, and diving under ice was only possible in some of the bays close to the Antarctic Peninsula. Neither adults nor larvae were found associated with the ice. In winter 1992, *Nordhausen* [1994] inspected the underside of the ice in nearby bays with a video camera on an ROV, and also found no krill associated with the ice. Six cruises, (n=136 dives), oc-curred during winters with adequate ice-cover to allow for a reasonable number of

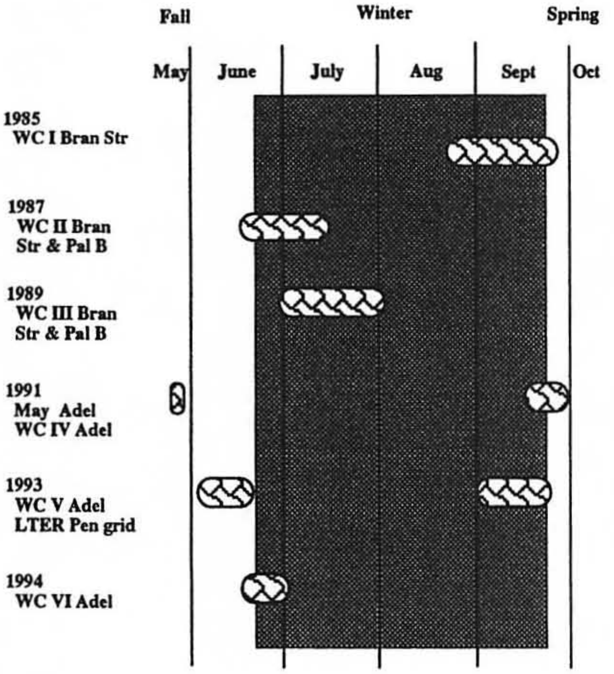

Fig. 2. Timing of research cruises on winter ecology of Antarctic krill west of the Antarctic Peninsula on the R/V *Polar Duke*. WC = WinCruise, with year. Cruise locations are Bran Str (Bransfield Strait), Pal Basin (Palmer Basin, 20 km south of Anvers Island), off Adel (Adelaide Island), and LTER grid (Palmer LTER Peninsula Grid transect lines from Anvers Island to south of Adelaide Island (600, 500, 400, 300, and 200) [*Waters and Smith*, 1992].

under-ice observations; pre-sence or absence of larval and adult krill within 1 m of the ice surface, and aggregation size(s) were noted. Larvae were generally less than 15 mm in total length; juveniles were rarely found during the winter; adults were generally greater than 26 mm in total length (L. Quetin, R. Ross, personal communication).

Observations of adult krill associated with sea ice, either as individuals or in aggregations, are relatively rare compared to larvae (Table 3). The distinction between life stages made during the cruises is important, since differences in the physiology of adults and larvae may underlie differences in distribution patterns [*Ross and Quetin*, 1991]. Larvae were observed on every cruise and during the majority of the dives (52 to 93% of the dives per cruise). In contrast, adults were observed on only one early winter cruise. Adults were sighted only 11 to 47% of the time in late winter (September) and their numbers were low. When adults were sighted, larvae were also present in the ice habitat.

Both larvae and adults occurred in aggregations, but adults under the ice were primarily seen either as individuals or in small groups (< 10) mixed with larval aggregations (56% of total observations of adults). Large numbers (aggregations of 100-200) of adult krill were seen only on 4 dives, all in closed pack and 40-60 km seaward of Adelaide Island. Larvae were frequently found in much larger aggregations, i.e., 100s to 1000s of individuals. Very large aggregations, with 10,000 larvae or more, were seen only on one late winter cruise. Individual larvae and aggregations of less than 10 were only a small proportion of the larval aggregations seen in winter.

2.3.3. Winter distribution patterns in adult and larval krill. Our observations suggest that adult krill are not tightly coupled to the undersides of the sea ice during winter. This lack of close association with the under-ice surface does not mean, however, that adult krill were not in the region. During several winter cruises (WinCruise I-III) (1985-1989), adult krill were detected with acoustics and collected with nets from the water column in ice-covered regions [*Ross et al.*, this volume]. Adult krill have also been detected with acoustics and nets in the water column below sea ice in the Weddell Sea [*Daly and Macaulay*, 1991; *Lancraft et al.*, 1991]. However, adults were concentrated near the ice edge in winter, not under the ice [*Daly and Macaulay*, 1991]. Comparable winter surveys with direct observations by divers have not been reported for the Weddell Sea area, although aggregations of adults have been seen with an ROV closely associated with sea ice in the Weddell Sea during spring (October/November) [*Marschall*, 1988].

If adult krill are not coupled to the under surface of sea ice, where are they during the winter west of the Antarctic Peninsula? Adults may: (1) migrate downward seasonally and assume a benthopelagic existence; (2) maintain schools in the water column, either under the ice or away from the ice and the ice edge; (3) disperse into aggregations too small to detect acoustically; and (4) migrate horizontally out of the region. Winter distributions may include all of the above.

Under some circumstances adult krill have been seen either with remotely operated video cameras on the bottom [*Gutt and Siegel*, 1994] or collected in light traps [*Kawaguchi et al.*, 1986] near the bottom in a shallow shelf region. These findings emphasize that krill occupy habitats other than the water column in winter, but the importance of a benthopelagic existence to the population as a whole and whether it is a re-sponse to only winter conditions has not been thoroughly evaluated. In summer, krill aggregations have been detected with acoustics in depressions within Arthur Harbor, near Palmer Station on Anvers Island (R. Ross, L. Quetin, T. Newberger, personal communication, 1993, 1994). Krill aggregations also have been observed with an ROV near the glacier face at the back of Arthur Harbor (G. Ashley, personal communication, 1994). These observations, coupled with those of krill in the stomachs of starfish [*Fratt and Dearborn*, 1984], suggest that some portion of the krill population may occupy a benthopelagic habitat at all times of year. Krill may more often exist benthopelagically where their preferred depth in the water column intersects with the bottom, such as inner shelf locations < 100 m deep.

West of the Antarctic Peninsula, adult krill are often found in aggregations in the water column near the MIZ during winter [*Guzman*, 1983; *Ross et al.*, this volume]. Adults have presumably migrated inshore in the fall [*Siegel*, 1989], leaving the open water beyond the continental slope void of post-larval krill. This pattern appears to change with the onset of spring. In late winter or early spring, *Huntley et al.* [1994] suggest that krill move toward the marginal ice zone and take advantage of both the

TABLE 3. Under-ice observations of larval and adult Antarctic krill, *E. superba* in winter. Cruises ordered by time in season. Number of dives per cruise, and percent of dives larvae and adults observed. *WinCruise III was unusual as the dives were on smooth fast ice in the bays, versus pack ice with a degree of overrafting as on other cruises.

Cruise, dates & Location	No. Dive	% dives Lar	% dives Ad
May 1991	6	83	0
WinCruise V	20	95	25
WinCruise VI	21	52	0
WinCruise II	12	67	0
WinCruise III	4	0	0
LTER Aug 1993	45	93	47
WinCruise IV	27	93	11

algae in the ice and released by melting ice to supply energy for growth. By October, both in the Weddell Sea [*Marschall*, 1988] and west of the Antarctic Peninsula (T. Frazer, L. Quetin, and R. Ross, personal communication, 1988, 1990), adults can be found in the water column both in the open ocean and under the ice, and sometimes closely linked with the ice surface. During a late spring (December) cruise on the R/V *Polarstern* in the Weddell Sea, a progression in krill school size and depth was seen moving from ice to open water. Few schools were detected in the water column under ice, small shallow schools occurred in the MIZ, and large schools were detected at greater depths in open water [*Cuzin-Roudy and Schalk*, 1989].

The sum of these observations suggests that although the distribution of both adults and larvae is linked with sea ice, larval populations are more closely coupled to the under-ice surface. This pattern is consistent with the hypothesis that the degree of association with the under-ice surface and its ice biota (food source) is a balance between the need to acquire energy and the need to avoid predation [*Quetin and Ross*, 1991; *Quetin et al.*, 1994]. The differing balance between the two life stages, i.e., adults and larvae, is a result of differences in starvation tolerance and vulnerability to predation. Most vertebrate predators ingest primarily adults [*Lowry et al.*, 1988; *Croxall et al.*, 1985]. The smaller size of the larvae likely provides a 'refuge in size' [*Hamner et al.*, 1989], and allows them to inhabit the underside of the ice and encounter relatively little predation from the large vertebrates compared to adults. Adélie penguins, for example, spend the winter on the seasonal pack ice with access to the under ice habitat through leads [*Fraser and Trivelpiece*, this volume], and crabeater seals and Minke whales are also associated with pack ice in winter [*Ribic et al.*, 1991]. Since these predators are important consumers of adult krill during the summer, predation pressure is expected to be high in winter as well. Of greater importance to the larvae, however, may be the availability of ice-associated algae for food. Young larval stages can survive only a matter of weeks without food [*Elias*, 1990]; adults have survived over 211 days [*Ikeda and Dixon*, 1982]. We suggest these differences lead to the observed habitat segregation between larval and adult krill during winter.

Interannual, interregional and within life cycle differences in this balance could affect the degree of habitat segregation. For example, energy requirements for reproduction in krill are high [*Ross and Quetin*, 1986]. Although food is not necessary for winter survival in adults, initiation of the reproductive cycle in September does require energy at a time when phytoplankton concentrations in the water column are low. The change in energy requirements with the coming of spring may be the reason adults are sometimes found in closer association with the under-ice habitat in the spring, or perhaps predation pressure is less near the ice in spring. If the requirement for food or the ease of getting food outweighs the risk, we would predict that even large adults would be associated with the under-ice environment. "Risk-balancing" such as hypothesized above has been demonstrated for minnows in the laboratory. Minnows avoided areas where predators had previously been encountered when food was equal, but risked predator encounters for higher food rewards [*Pitcher et al.*, 1988].

3. ECOPHYSIOLOGY OF MESO- AND MACROZOOPLANKTON

Polar zooplankton exhibit several physiological characteristics that appear to be adaptations to or consequences of the cold water and extreme seasonality in food availability [*Clarke and Peck*, 1991]. For Antarctic crustaceans these characteristics include: low metabolic rates, low annual growth rates, high lipid stores, long life spans, and delayed reproductive maturity. In contrast, low lipid stores in carnivores (cteno-phores, chaetognaths and polychaetes) [*Smith and Schnack-Schiel*, 1990] may be a consequence of their zooplankton food source which is less seasonal than phytoplankton. Although annual growth rates of polar zooplankton are low, in areas of high primary productivity the instantaneous growth rates of herbivores can be seasonally high [*Clarke and Peck*, 1991]. An additional aspect of growth in both euphausiids and some gelatinous zooplankton is that they can use their body tissues during periods of low food availability, resulting in shrinkage or 'degrowth'.

Clarke and Peck [1991] note that gelatinous zooplankton occupy a special niche in the pelagic ecosystem. Because gelatinous zooplankton are nearly neutrally buoyant, their metabolic costs are generally less than those for crustaceans. Thus when food conditions are favorable, populations of some gelatinous zooplankton can grow and reproduce very rapidly. Peaks in abundance for gelatinous zooplankton, such as salps, will be higher and occur on shorter time scales than those for crustaceans. It is important to realize, however, that 'blooms' of gelatinous zooplankton are interspersed with longer periods of low population abundance.

The advance and retreat of pack ice each year is often discussed as affecting food availability for macrozooplankton, whether directly as a source of ice biota or indirectly by creating conditions suitable for ice-edge blooms [*Ross and Quetin*, 1986; *Smetacek et al.*, 1990]. However, quantitative information on the relative importance of various food sources for polar macrozooplankton

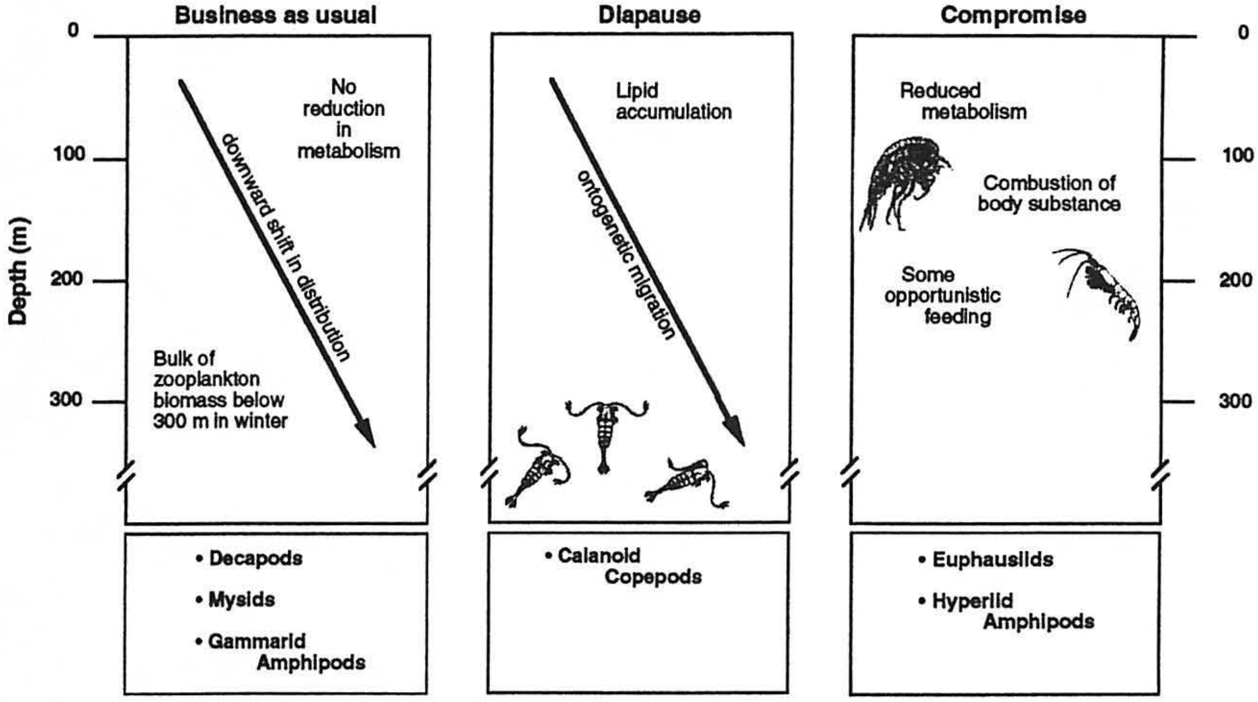

Fig. 3. Winter-over strategies for pelagic crustaceans in the Southern Ocean. Drawn from description in *Torres et al.* [1994].

is generally scarce and more information is needed, particularly in the context of winter-over mechanisms.

3.1. Strategies for Winter Survival

Several strategies for winter survival have been proposed for Antarctic zooplankton and evaluated for several groups, including Antarctic krill and copepods [*Quetin and Ross*, 1991; *Schnack-Schiel and Hagen*, 1994; *Torres et al.*, 1994] (Figure 3). Identification of the strategy used by any one species is based on the following: (1) seasonal changes in metabolic rates, (2) type and amount of lipid reserve, (3) seasonal changes in water and lipid content indicating mobilization of internal tissues, (4) indicators of net production such as growth and reproduction, and (5) indicators of ingestion such as stomach fullness and contents and rates of ingestion in the field.

3.1.1. 'Business-as-usual'. *Torres et al.* [1994] suggest that one extreme for zooplankton would be a 'business-as-usual' strategy where metabolic activity remains the same and the energy requirement during the winter months would be satisfied by opportunistic feeding combined with some combustion of tissue. This option is open to carnivores and omni-vores. Winter survival strategies may not be as essential for carnivores and omnivores because the presence of zooplankton provides a year-round food source. One species known to use this strategy is *M. gerlachei*, an omnivorous copepod that feeds actively in the winter in the upper layers of the water column, has a moderate lipid content (both wax esters and triacylglycerols), and does not enter a period of diapause [*Schnack-Schiel and Hagen*, 1994]. Such a strategy is also used by species that live below the epipelagic zone, such as gammarid amphipods, decapods, and mysids [*Torres et al.*, 1994] where the food supply is not significantly affected by season. In winter these crustaceans have access to the bulk of the zooplankton biomass which is generally deeper than 300 m, particularly in those areas where the water is deep, e.g., the MIZ of the Scotia Sea [*Hopkins et al.*, 1993].

3.1.2. Lipid stores and diapause. One strategy used by herbivorous copepods is to accumulate a large lipid reserve, generally wax esters, and in winter enter a diapause or dormant state triggered by photoperiod [*Hagen*, 1988]. In the Antarctic, one copepod, *C. acutus*, clearly follows this strategy, with a strong ontogenetic migration downward in winter, high stores of wax esters and a definite diapause [*Schnack-Schiel and Hagen*, 1994]. *R. gigas* may follow this same strategy, although the evidence is not definitive [*Schnack-Schiel and Hagen*, 1994].

3.1.3. Compromise between 'business-as-usual' and 'shut-down'. The third alternative is a mixture of the above strategies. Metabolic activity decreases to some degree either because of starvation or an environmental cue, and energy requirements are met through a combination of opportunistic feeding and mobilization of body tissue. This strategy is made possible by the metabolic flexibility of some taxonomic groups, and is not true dormancy. As groups, both hyperiid amphipods and euphausiids appear to follow this compromise strategy. Both show evidence of compositional depletion during winter [*Torres et al.*, 1994]. *C. propinquus* has been observed feeding during summer, fall and winter [*Schnack-*

Schiel and Hagen, 1994], is active in winter and does not enter a period of diapause. The lack of phytoplankton as a food source in winter, however, leads us to suggest that *C. propinquus* may follow the compromise strategy.

For antarctic krill, *Euphausia superba*, the species for which we have the most complete energetic information [*Quetin and Ross*, 1991; *Quetin et al.*, 1994; *Ross and Quetin*, 1991; *Torres et al.*, 1994], the winter-over strategy for larvae and adults appears to differ. Larvae shift their habitat from the water column to the ice to take advantage of ice biota, algae in particular, as a food source, and adults use a suite of winter-over mechanisms that allow them to compromise between completely 'shut-down' and 'business as usual'.

Winter-over strategies documented for *Euphausia superba* include shrinkage [*Ikeda and Dixon*, 1982; *Quetin and Ross*, 1991], metabolic reduction [*Kawaguchi et al.*, 1986; *Quetin and Ross*, 1991; *Torres et al.*, 1994], and lipid storage and depletion [*Quetin and Ross*, 1991; *Torres et al.*, 1994]. *Huntley et al.* [1994] are the only investigators to suggest that adult krill follow the 'business as usual' rather than the 'compromise' strategy. These authors conclude that adult krill feed carnivorously during winter. The conclusions of *Huntley et al.* [1994] are based, in part, on measurements (C:N and N:P ratios, rates of ammonia and phosphate excretion) that do not differ statistically among groups of laboratory starved and fed krill [*Ikeda and Dixon*, 1982], and their interpretation warrants caution. Better measures, with more direct interpretations for looking at winter-over strategies, would be oxygen consumption as a measure of total metabolism, and growth as an indication of net production. Unfortunately, *Huntley et al.* [1994] may have been partly mislead by a typographical error in the legend of Figure 6 in *Quetin and Ross* [1991] that compares winter and summer metabolic rates (VO_2) with krill length (TL). Though the lines representing the data in the figure are correct, the equation describing winter metabolism should be changed from:

$$\log VO_2\ (\mathrm{ml\ h^{-1}}) = 0.0285\ \mathrm{TL\ (mm)} - 2.2258 \text{ to}$$

$$\log VO_2\ (\mathrm{ml\ h^{-1}}) = 0.0285\ \mathrm{TL\ (mm)} - 2.7873.$$

The correct equation gives the winter metabolic rates that are approximately one-third of summer rates based on total length, as described in *Quetin and Ross* [1991]. These winter rates are similar to those found by others [*Kawaguchi et al.*, 1986; *Torres et al.*, 1994] and would have led the authors to very different conclusions.

3.2. *Interannual Variability in Abundance*

Interannual variation in recruitment for annual and long-lived species will impact their respective population sizes differently. In organisms with an annual life cycle, the impact of a recruitment failure should be immediately apparent, but in long-lived species such as *E. superba*, several year class failures in succession will be necessary to create a similar and detectable difference in absolute abundance [*Priddle et al.*, 1988]. Recruitment depends on the number of embryos spawned, referred to as recruitment potential, and their subsequent survival throughout larval development to maturity, referred to as larval survival. Recruitment potential depends on conditions that promote the abundance of the spawning population and its fecundity, whereas larval survival depends on conditions that promote growth and development of larval stages with minimal mortality. Conditions that promote recruitment potential and larval survival are not always the same, and maximal recruitment success may depend on a succession of optimal conditions. Recruitment for annual species depends on a succession of conditions within a single year, but for long-lived species, the best recruitment years will be the culmination of a succession of optimal conditions over many years.

E. superba provides a good example of how processes involved in interannual variability in recruitment can lead to changes in patterns of distribution and abundance. Observations from the winter cruise series prior to 1990 were key to the development of the following initial Palmer LTER hypotheses on the winter strategy for *Euphausia superba* (L. Quetin, R. Ross, 1990; [*Ross and Quetin*, 1991]).

Hypothesis 1: In winters with a greater extent in pack ice cover, larval and juvenile krill (young-of-the-year) in waters west of the Antarctic Pen-insula will be in better physiological condition, have higher growth and development rates, and higher winter-over survival than in winters of low ice cover. The greater ice extent implies availability of ice biota and food for development and growth, whereas larvae in the water column will experience near-starvation conditions, and are predicted to have lower survival rates.

Hypothesis 2: In years with greater food availability, reproductive output of adult krill will be higher. Abundance and duration of food availability will be greater after winters with a greater extent in pack ice cover than after winters of low ice cover.

There are distinct times when critical interactions with the environment occur during the life cycle of Antarctic krill (Figure 4), influencing both recruitment potential and larval survival. The spawning season for Antarctic krill west of the Antarctic Peninsula normally begins in mid-December and lasts through part of March [*Ross and Quetin*, 1986; *Quetin et al.*, 1994]. Depending on growth rates during the previous two years, a small proportion of female krill will reproduce during their third growing season (AC2). Minimum size at spawning is about 33 mm [*Cuzin-Roudy*, 1987], although most spawning individuals are 38 to 50 mm [*Ross and Quetin*, 1983]. Age classes 3 through 6 are characterized as sexually mature (Figure 4), since individuals in this size range (35 to 60 mm) have developed gonads and will reproduce under favorable environmental conditions. Oocytes begin to develop in September, with rates of development dependent on spring and summer food sources. Food intake required for fecundities observed west of the Antarctic Peninsula is high [*Ross and Quetin*, 1986], suggesting that a combination of ice biota, ice-edge blooms and open water phytoplankton blooms may be necessary to meet the spring and summer food requirements of reproducing female krill. Food availability is a factor not only in the timing of reproduction, but also in the proportion of the population that reproduces

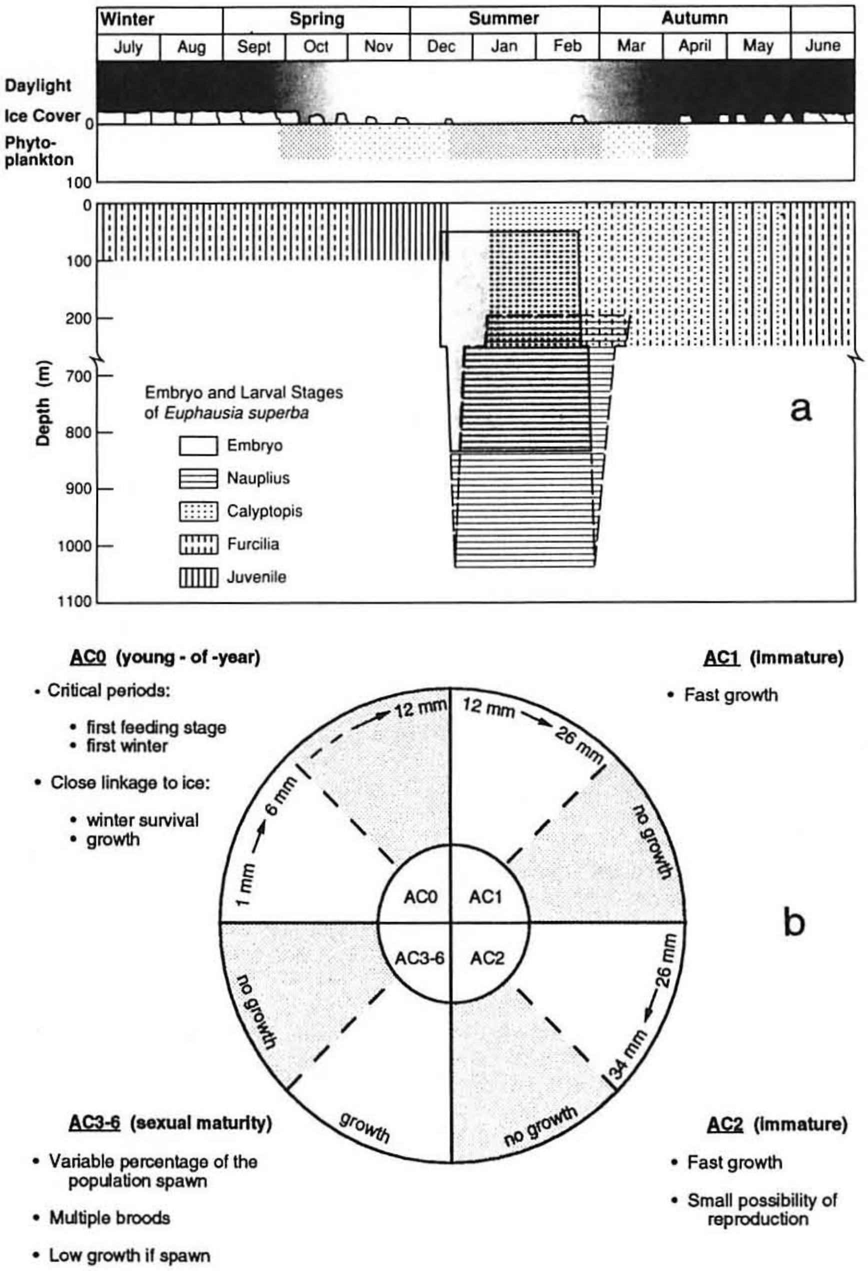

Fig. 4. Life cycle of Antarctic krill, *Euphausia superba*: (a) Vertical distribution and timing of early life history stages in relation to seasonal cycles of daylight, ice cover, and phytoplankton concentrations (from *Quetin and Ross*, [1991]); (b) Pattern of growth and reproduction with age: ACO (young-of-year) is age class 0 from January to September, AC1 and AC2 (immature) are age classes 1 and 2, AC3-6 (reproductive) includes age classes 3 through 6. The two growth periods for ACO are January to June and June to September. For age classes 1 through 6, growth periods are divided into spring/summer (October through March, white area) and fall/winter (April through September, shaded area). Characteristics of each age group(s) are to the side.

and the number of broods per female [*Quetin et al.*, 1994]. Calculations of the energetic cost of egg production based on direct measurements of gravid and spent female krill support the premise that multiple spawning requires above average phytoplankton concentrations [*Nicol et al.*, 1995].

There are several critical periods for larval survival (Figure 4). The first feeding stage, calyptopis 1, initially appears in the surface waters in January, and may continue to appear for the next 4 to 5 months (Table 2). Immediately after reaching the surface, there is a critical period when the calyptopis 1s (C1s) must find adequate food within 10 to 14 days or die [*Ross and Quetin*, 1989]. The first winter in the life cycle of krill is another critical period because larvae cannot survive the prolonged winter period of very low food availability in the water column without an alternate food source [*Ross and Quetin*, 1991]. Larvae grow from 1 to 6 mm in average total length during their first summer and fall [*Fraser*, 1936]. In winters with extensive sea ice cover larvae continue to grow, reaching an average of 12 mm by September [*Fraser*, 1936] (see Figure 4) with maximum lengths of 16 mm (Table 1). In winters with no sea ice cover, larval growth rates are zero or negative [*Ross and Quetin*, 1991]. Larval krill feed primarily as herbivores in the water column prior to exploiting ice-algae throughout the winter, as is evidenced by stable nitrogen isotope ratios in animals collected during winter sampling periods (T. Frazer, personal communication, 1995). If we think of the seasonal ice cover as winter pasture for krill larvae, then winters when pack ice covers a large spatial area for a long period of time will provide an extensive food source for larvae during a critical period, enabling a higher percentage of the original recruits to continue to grow and survive. Growth rates of krill during their second growing season (end of AC0, and AC1, Figure 4) are generally rapid, and average total lengths increase from approximately 12 mm in September to 26 mm the following fall [*Siegel*, 1987] (R. Ross, L. Quetin, personal communication, 1993, 1994). After the first two growing seasons, immature and mature adult krill do not grow throughout the winter, but either shrink or stay the same size, using a suite of winter-over mechanisms to survive the period of low food availability [*Quetin and Ross*, 1991]. Their nutritional history and growth rates during the spring and summer will be an important factor in whether or not they first join the spawning stock in their third or fourth summer.

When the Palmer LTER was first established and the hypotheses proposed, evidence existed for both significant interannual variability in recruitment potential [*Brinton et al.*, 1986; *Brinton et al.*, 1987] and for differences in recruitment success after the winter [*Siegel*, 1988] for *E. superba* in the region west of the Antarctic Peninsula. *Ross and Quetin* [1991] suggested that both recruitment potential and the critical period of larval survival during winter varied from year to year, and that both are dependent on ice conditions during the winter and early spring. However, the two factors affecting recruitment are not always in phase because recruitment potential reflects environmental conditions before the spawning season, and winter survival reflects conditions the following winter [*Ross and Quetin*, 1991].

Recently *Siegel and Loeb* [1995] analyzed historical data on krill stocks and length frequencies, and concurrent environmental data from 1977-1994 just north of the Antarctic Peninsula, from a perspective similar to the Palmer LTER hypotheses. For the fourteen years of data, significant differences exist in recruitment, and in general 'good' and 'bad' years prior to 1985 correspond to years of low recruitment potential as identified previously by *Brinton et al.* [1986, 1987].

Siegel and Loeb [1995] found a positive correlation between recruitment and both the duration and extent of ice cover. In addition, they found a positive correlation between the proportion of females in an advanced stage of maturity in mid-summer and mean ice cover the previous winter. Their suggestion that the long duration of heavy sea ice cover leads to an earlier start to the spawning season should be considered in the context of evidence presented in this paper and in *Quetin and Ross* [1991] that adult krill do not depend on ice algae in winter for survival or reproduction. It may be more likely that greater values for mean ice cover in winter will result in greater spatial distribution and temporal duration of ice algae released from melting ice and of possible areas where ice-edge blooms can develop, providing more food in spring to fuel reproduction, as stated in Hypothesis 2 above.

4. ABIOTIC AND BIOTIC FACTORS AFFECTING DISTRIBUTION PATTERNS

4.1. Abiotic Factors

Interannual mesoscale shifts in environmental conditions may impact patterns of distribution or abundance of meso- and macrozooplankton over longer temporal and larger spatial scales. Of particular relevance to macrozooplankton within the LTER study area is variation in the location of the Polar Front. This feature may move 100s of kilometers north or south over a period of weeks [*Whitworth*, 1980], and shift with it populations associated with frontal systems. This movement primarily affects the surface layers [*Whitworth*, 1980]. Smaller features such as gyres, both permanent and temporary, meanders and eddies [*Hofmann et al.*, this volume] also may serve to redistribute populations of macrozooplankton in a particular geographical location over shorter time periods.

Some species are not permanent members of the macrozooplanktonic community in high latitudes. For example, *Zmijewska and Yen* [1993] suggest that seasonal pulses of *R. gigas* in the shelf waters west of the Antarctic Peninsula are a function of the interaction of ontogenetic migration in this species and seasonal changes in ocean circulation patterns. Thus some changes in macrozooplankton distribution and abundance are not caused by population changes, but by circulation acting directly on individuals in the population. On a larger scale, meteorological conditions worldwide, such as the Southern Ocean Oscillation, may also affect oceanic conditions and change patterns of macrozooplankton populations.

Various authors have suggested that variations in atmospheric circulation can lead to changes in the Weddell Sea Confluence, and that these changes could explain the paucity of krill around South Georgia in certain years, e.g., *Sahrhage* [1988]. Carleton (in *Sahrhage* [1988]) found a relationship between summer ice anomalies and antecedent regional atmospheric circulation, linking atmospheric circulation, oceanic circulation and ice anomalies. Thus fluctuations in the mesoscale abundance of Antarctic krill which occur on the order of twice per decade are usually attributed to redistribution of krill by physical forces, not to intrinsic features of krill biology [*Sahrhage*, 1988]. Years of low krill abundance and coincident poor breeding success in the land-based predators often follow strong ENSO events, for example in 1977/78 and 1983/84 [*Croxall et al.*, 1988] or winters of low ice cover [*Rakusa-Suszczewski*, 1988]. Although krill abundance was low in northern waters, krill were still found near Anvers Island (L. Quetin, R. Ross, personal communication, 1983-1984), suggesting a southward displacement of the population. *Rakusa-Suszczewski* [1988] indicated that krill are more abundant around the South Shetland Islands and in the northern Bransfield Strait after winters of heavy ice cover.

In contrast, years when salps are abundant appear to follow strong ENSO events [*Hofmann and Huntley*, 1991], creating an alternating dominance between krill and salps. The 1983/84 season of high salp abundance [*Huntley et al.*, 1989; *Mujica and Asencio*, 1985; *Nast*, 1986; *Rakusa-Suszczewski*, 1988; *Witek et al.*, 1985] followed the intense 1982/83 El Niño. The 1992/93 and 1993/94 seasons of high salp abundance in the Elephant Island area [*Loeb and Siegel*, 1993; *Loeb and Siegel*, 1994] also followed a very long ENSO event that began in 1991/92. Coincident with abundant salp years is a change in the distribution of the other macrozooplankton taxa [*Mujica and Asencio*, 1985], resulting in a change in community composition. This change in community composition can be visualized partially as a shift in dominance between the 'oceanic' community as represented by salps, and the shelf and shelf-break community as dominated by Antarctic krill. This shift in community composition demonstrably affects the apex predators in the system [*Croxall et al.*, 1988] (W. Fraser and W. Trivelpiece, personal communication, 1995), and will affect other aspects of trophic dynamics, including the dominant pathways for carbon transfer throughout the food web and carbon flux to the benthos.

4.2. Biotic Factors - Food Availability and Composition

While hydrographic conditions clearly influence krill distribution, adult *E. superba* is able to move horizontally against currents and to form aggregations independent of hydrography [*Kanda et al.*, 1982; *Trathan et al.*, 1993]. Patterns of krill distribution may reflect their ability to detect and exploit patchy phytoplankton resources [*Antezana et al.*, 1982; *Hamner et al.*, 1983]. Movement of euphausiids toward concentrations of phytoplankton on the order of a few meters has been demonstrated in the laboratory [*Price*, 1989; *Strand and Hamner*, 1990]; however, the ability of krill to effectively locate phytoplankton at larger spatial scales is not known.

Comparisons of phytoplankton and krill distribution throughout the Antarctic have yielded both positive and negative correlations, depending upon sampling methods, spatial scale, types of analyses and time of year. Studies employing discontinuous sampling at widely spaced stations tend to show a negative relationship between adult *E. superba* and net phytoplankton [*Kopczynska*, 1992; *Witek et al.*, 1982] or chlorophyll a [*Hosie and Cochran*, 1994]. In contrast, in a study where both krill and surface chlorophyll a were sampled continuously along a transect, *Weber and El-Sayed* [1985] found a positive correlation between maximum swarm biomass and phytoplankton biomass. *Weber and El-Sayed* [1985] also found an overall positive correlation between mean krill density and chlorophyll a, but these were negatively correlated when temperature and water column stability were taken into account in multivariate analysis. Using the same data, but applying spectral analysis techniques, *Weber et al.* [1986] found the strongest positive correlation between phytoplankton and krill on scales between 2-5 kilometers.

Interpretation of distribution data is severely limited without additional temporal information. Positive associations between krill and phytoplankton could reflect the influence of the physical environment. For example, a particular set of hydrographic conditions might promote phytoplankton growth, and at the same time, facilitate krill aggregation. Alternatively, these positive associations could indicate active movement of krill into areas with phytoplankton. Negative associations might indicate the inability of krill to find rich phytoplankton sources, and could also indicate that phytoplankton (or a specific group of phytoplankton) and krill tend to be concentrated in different hydrographic regimes. Low phytoplankton levels in krill-dominated areas might also reflect the ability of krill to quickly and effectively exploit the food resource. In support of this hypothesis, *Antezana and Ray* [1984] recorded a sharp chlorophyll gradient coinciding with actively feeding *E. superba*. Monitoring krill and phytoplankton in one region over time, at spatial scales corresponding to krill schools and algal patches, is necessary for elucidating these phytoplankton-krill interactions.

In addition to the potential influence of phytoplankton biomass on zooplankton distribution patterns, phytoplankton community composition may also affect these patterns. Differences in size and nutritional worth of various taxonomic groups such as diatoms and prymnesiophytes may impact distribution directly for mobile organisms that can search out food patches, and indirectly through effects on population dynamics and recruitment success for non-mobile organisms. Even small species may alter their vertical distributions in response to phytoplankton community composition. *Schnack et al.* [1985] sampled the top 100 m of the Bransfield Strait in an area dominated by *Phaeocystis* sp. (a prymnesiophyte), and found low copepod biomass. But in an adjacent region near Joinville Island, in an area dominated by diatoms, they found relatively high copepod biomass. The investigators suggested that copepods in the *Phaeocystis* sp.-dominated area migrated vertically to deeper water to avoid *Phaeocystis* sp.

The majority of studies which address grazing by copepods on *Phaeocystis* sp. suggest that *Phaeocystis* is not a suitable food source for herbivorous copepods, although there is much conflicting evidence (reviewed by *Davidson and Marchant* [1992]). *Phaeocystis* sp. has several different forms, including single cells and a wide range of colony sizes and shapes, and these forms should be considered separately when assessing grazing on *Phaeocystis*. *Schnack et al.* [1985] found fragments of *Phaeocystis* colonies attached to the feeding appendages of copepods, and suggested that grazing would be inhibited by these obstructions. The physiological state of phytoplankton cells may be another factor affecting consumption or ingestion by zooplankton. For example, in preliminary studies of grazing by *E. superba* on *Phaeocystis*, krill ingested 100-µm diameter colonies that were actively dividing, but did not ingest similar-sized colonies in stationary phase [*Haberman et al.*, 1993, K. Haberman, personal communication, 1995]. Given the abundance of *Phaeocystis* in the Southern Ocean [*Bidigare et al.*, this volume], its edibility and influence on grazers merits further study.

5. SUMMARY

Several important factors, both biotic and abiotic, that affect the patterns of distribution and abundance in the zooplankton west of the Antarctic Peninsula have been identified. Life history characteristics such as ontogenetic migration, life span, and timing and duration of the reproductive cycle affect the population dynamics of zooplankton, and can explain much of the observed seasonal variability. Winter-over strategies have been discussed from an ecophysiological perspective to illustrate the various mechanisms used by zooplankton groups to adapt to the long polar winter. Interannual variability in recruitment influences patterns of abundance and distribution of zooplankton, and can be caused by interactions of biological and physical processes. Recruitment variation in *E. superba* provides insight into the complexities of these interactions. Other abiotic and biotic factors also affect patterns of zooplankton distribution and abundance, e.g., variability in oceanic circulation features like the Polar Front and in differences in food availability and food composition, but our understanding of their combined effects is still in its infancy.

Acknowledgements. The series of WinCruises would not have been possible without the assistance of volunteer divers and field assistants too numerous to identify individually. The captains and crews of the R/V *Polar Duke*, the support of Antarctic Services (1985-1989), and Antarctic Support Associates (1990-1994) were greatly appreciated. Special thanks are due to two outstanding research associates: M. O. Amsler (1984-1992), and C. Wyatt (1992-1995). Research and synthesis was supported by NSF grants DPP82-18356, DPP88-20589 and OPP91-17633 to Quetin and Ross, DPP85-18872 to Ross and Quetin, and OPP90-11927 to Ross, Quetin, and Smith. This is Palmer LTER Publication No. 86.

REFERENCES

Ainley, D.G., W.R. Fraser, W.O. Smith, Jr., T.L. Hopkins, and J.J. Torres, The structure of upper level pelagic food webs in the Antarctic: Effect of phytoplankton distribution, *J. Mar. Sys.*, *2*, 111-122, 1991.

Antezana, T., and K. Ray, Active feeding of *Euphausia superba* in a swarm north of Elephant Island, *J. Crust. Biol.*, *4*, 142-155, 1984.

Antezana, T., K. Ray, and C. Melo, Trophic behavior of *Euphausia superba* Dana in laboratory conditions, *Polar Biol.*, *1*, 77-82, 1982.

Atkinson, A., Life cycles of *Calanoides acutus*, *Calanus simillimus* and *Rhincalanus gigas* (Copepoda:Calanoida) within the Scotia Sea, *Mar. Biol.*, *109*, 79-91, 1991.

Atkinson, A., and J.M. Peck, A summer-winter comparison of zooplankton in the oceanic area around South Georgia, *Polar Biol.*, *8*, 463-473, 1988.

Baker, A.C., The distribution of *Euphausia triacantha* Holt and Tattersall, *Discovery Rep.*, *29*, 309-339, 1959.

Bidigare, R.R., J.L. Iriarte, S.-H. Kang, D. Karentz, M.E. Ondrusek, and G.A. Fryxell, Phytoplankton: Quantitative and Qualitative Assessments, this volume.

Brinton, E., Observations of plankton organisms obtained by bongo nets during the November-December 1983 ice-edge investigations, *Antarct. J. U.S.*, *19*, 113-115, 1984.

Brinton, E., M. Huntley, and A.W. Townsend, Larvae of *Euphausia superba* in the Scotia Sea and Bransfield Strait in March 1984. Development and abundance compared with 1981 larvae, *Polar Biol.*, *5*, 221-234, 1986.

Brinton, E., V. Loeb, M.C. Macaulay, and E. Shulenberger, Variability of *Euphausia superba* populations near Elephant Island and the South Shetland Islands: 1981 vs 1984, *Polar Biol*, *7*, 345-362, 1987.

Brinton, E., and A.W. Townsend, Developmental rates and habitat shifts in the Antarctic neritic euphausiid *Euphausia crystallorophias*, 1986-87, *Deep-Sea Res.*, *38*, 1195-1211, 1991.

Clarke, A., Energy flow in the Southern Ocean food web, in *Antarctic Nutrient Cycles and Food Webs*, edited by W.R. Siegfried, P.R. Condy, and R.M. Laws, pp. 573-580, Springer-Verlag, Berlin, 1985.

Clarke, A., and L.S. Peck, The physiology of polar marine zooplankton, *Pro Mare Symposium on Polar Marine Ecology*, 355-369, 1991.

Croxall, J.P., T.S. McCann, P.A. Prince, and P. Rothery, Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976-1987: Implications for Southern Ocean monitoring studies, in *Antarctic Ocean and Resources Variability*, edited by D. Sahrhage, pp. 261-285, Springer-Verlag, Berlin, 1988.

Croxall, J.P., P.A. Prince, and C. Ricketts, Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea, in *Antarctic Nutrient Cycles and Food Webs*, edited by W.R. Siegfried, P.R. Condy, and R.M. Laws, pp. 516-533, Springer-Verlag, Berlin, 1985.

Cuzin-Roudy, J., Gonad history of the antarctic krill *Euphausia superba* Dana during its breeding season, *Polar Biol.*, *7*, 237-244, 1987.

Cuzin-Roudy, J., and P.H. Schalk, Macrozooplankton-Biomass, development and activity, *Berichte zur Polarforschung*, *65*, 146-171, 1989.

Daly, K.L., and M.C. Macaulay, Influence of physical and biological mesoscale dynamics on the seasonal distribution and behavior of *Euphausia superba* in the antarctic marginal ice zone, *Mar. Ecol. Prog. Ser.*, *79*, 37-66, 1991.

Davidson, A.T., and H.J. Marchant, The biology and ecology of *Phaeocystis* (Prymnesiophyceae), *Prog. in Phyc. Res.*, *8*, 1-45, 1992.

Drits, A.V., A.F. Pasternak, and K.N. Kosobokova, Feeding, metabolism and body composition of the Antarctic copepod *Calanus propinquus* Brady with special reference to its life cycle, *Polar Biol.*, *13*, 13-21, 1993.

Elias, M.C., Effects of photoperiod, phytoplankton level and temperature on the growth, development and survival of larval *Euphausia superba* (Dana), M.S. Thesis, University of California, Santa Barbara, 1990.

Fevolden, S.E., Krill off Bouvetoya and in the southern Weddell Sea with a description of larval stages of *Euphausia crystal-*

lorophias, *Sarsia*, *65*, 149-162, 1980.

Foxton, P., The distribution of the standing crop of zooplankton in the Southern Ocean, *Discovery Rep.*, *28*, 191-236, 1956.

Foxton, P., The distribution and life-history of *Salpa thompsoni* Foxton with observations on a related species, *Salpa gerlachei* Foxton, *Discovery Rep.*, *32*, 1-116, 1966.

Fraser, F.C., On the development and distribution of the young stages of krill (*Euphausia superba*), *Discovery Rep.*, *14*, 1-192, 1936.

Fraser, W.R., and W.Z. Trivelpiece, Factors Controlling the Distribution of Seabirds: Winter-Summer Heterogeneity in the Distribution of Adélie Penguin Populations, this volume.

Fratt, D.B., and J.H. Dearborn, Feeding biology of the Antarctic brittle star *Ophionotus victoriae* (Echinodermata: Ophiuroidea), *Polar Biol.*, *3*, 127-139, 1984.

Frazer, T.K., Stable isotopes as indicators of ice-associated winter food resources in the diet of larval krill, *Euphausia superba*, *J. Plankton Res.*, submitted.

Frazer, T.K., L.B. Quetin, and R.M. Ross, Abundance and distribution of larval krill, *Euphausia superba*, associated with annual sea ice in winter, in *Antarctic Communities: Species, Structure and Survival*, edited by B. Battaglia, J. Valencia, and D.W.H. Walton, Cambridge University Press, in press.

Gutt, J., and V. Siegel, Benthopelagic aggregations of krill (*Euphausia superba*) on the deeper shelf of the Weddell Sea (Antarctic), *Deep-Sea Res.*, *41*, 169-178, 1994.

Guzman, O., Distribution and abundance of antarctic krill (*Euphausia superba*) in the Bransfield Strait, in *On the Biology of Krill Euphausia superba*, edited by S. B. Schnack, pp. 169-190, Alfred Wegener-Institute for Polar Research, Bremerhaven, 1983.

Haberman, K.L., R.M. Ross, and L.B. Quetin, Palmer LTER: Grazing by the antarctic krill Euphausia superba on *Nitzschia* sp. and *Phaeocystis* sp. monocultures, *Antarct. J. U.S.*, *28*, 217-219, 1993.

Hagen, W., On the significance of lipids in Antarctic zooplankton, *Berichte zur Polarfors.*, *49*, 5-63, 92-117, 1988.

Hamner, W.M., P.P. Hamner, B.S. Obst, and J.H. Carleton, Field observations on the ontogeny of schooling of *Euphausia superba* furcilia and its relationship to ice in antarctic waters, *Limnol. Oceanogr.*, *34*, 451-456, 1989.

Hamner, W.M., P.P. Hamner, S.W. Strand, and R.W. Gilmer, Behavior of Antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling, and molting, *Science*, *220*, 433-435, 1983.

Harbison, G.R., V.L. McAlister, and R.W. Gilmer, The response of the salp, *Pegea confoederata*, to high levels of particulate material: Starvation in the midst of plenty, *Limnol. Oceanogr.*, *3*, 371-382, 1986.

Harrington, S.A., and P.G. Thomas, Observations on spawning by *Euphausia crystallorophias* from waters adjacent to Enderby Land (East Antarctica) and speculations on the early ontogenetic ecology of neritic euphausiids, *Polar Biol.*, *7*, 93-95, 1987.

Hempel, I., G. Hempel, and A. de C. Baker, Early life history stages of krill (*Euphausia superba*) in Bransfield Strait and Weddell Sea, *Meereforsch.*, *27*, 267-281, 1979.

Hempel, I., and E. Marschoff, Euphausiid larvae in the Atlantic Sector of the Southern Ocean, *Meeresforsch.*, *28*, 32-47, 1980.

Hofmann, E.E., and M.E. Huntley, GLOBEC: Southern Ocean Program: GLOBEC Workshop on Southern Ocean Marine Animal Populations and Climate Change, *U.S. GLOBEC Rep. No. 5*, 1991.

Hofmann, E.E., J.M. Klinck, C.M. Lascara, and D.A. Smith, Water Mass Distribution and Circulation West of the Antarctic Peninsula and Including Bransfield Strait, this volume.

Hopkins, T.L., Zooplankton standing crop in the Pacific sector of the Antarctic, in *Biology of the Antarctic Seas 4*, edited by G.W. Llano and I.E. Wallen, pp. 347-362, American Geophysical Union, Washington, D.C., 1971.

Hopkins, T.L., T.M. Lancraft, J.J. Torres, and J. Donnelly, Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice zone in winter (1988), *Deep-Sea Res.*, *40*, 81-105, 1993.

Hosie, G.W., and T.G. Cochran, Mesoscale distribution patterns of macrozooplankton communities in Prydz Bay, Antarctica-January to February 1991, *Mar. Ecol. Prog. Ser.*, *106*, 21-39, 1994.

Huntley, M.E., and F. Escritor, Ecology of *Metridia gerlachei* Giesbrecht in the western Bransfield Strait, Antarctica, *Deep-Sea Res.*, *39*, 1027-1055, 1992.

Huntley, M.E., W. Nordhausen, and M.D.G. Lopez, Elemental composition, metabolic activity and growth of Antarctic krill *Euphausia superba* during winter, *Mar. Ecol. Prog. Ser.*, *107*, 23-40, 1994.

Huntley, M.E., P.F. Sykes, and V. Marin, Biometry and trophodynamics of *Salpa thompsoni* Foxton (Tunicata: Thaliacea) near the Antarctic Peninsula in austral summer, 1983-1984, *Polar Biol.*, *10*, 59-70, 1989.

Ikeda, T., and P. Dixon, Body shrinkage as a possible overwintering mechanism of the Antarctic krill, *Euphausia superba*, *J. Exp. Mar. Biol. Ecol.*, *62*, 143-151, 1982.

Kanda, K., K. Takagi, and Y. Seki, Movement of the larger swarms of antarctic krill *Euphausia superba* populations of Enderby Land during 1976-77 season, *J. Tokyo Univ. Fish.*, *68*, 25-42, 1982.

Kawaguchi, K., S. Ishikawa, and O. Matsuda, The overwintering strategy of Antarctic krill (*Euphausia superba* Dana) under the coastal fast ice off the Ongul Islands in Lutzow-Holm Bay, Antarctica, *Mem. Natl. Inst. Polar Res., Spec. Issue*, *44*, 67-85, 1986.

Kawamura, A., Has marine Antarctic ecosystem changed? - A tentative comparison of present and past macrozooplankton abundances, *Mem. Natl. Inst. Polar Res., Spec. Issue*, *40*, 197-211, 1986.

Kopczynska, E.E., Dominance of microflagellates over diatoms in the Antarctic areas of deep vertical mixing and krill concentrations, *J. Plankton Res.*, *14*, 1031-1054, 1992.

Kottmeier, S.T., and C.W. Sullivan, Late winter primary production and bacterial production in sea ice and seawater west of the Antarctic Peninsula, *Mar. Ecol. Prog. Ser.*, *36*, 287-298, 1987.

Lancraft, T.M., T.L. Hopkins, J.J. Torres, and J. Donnelly, Oceanic micronektonic/macrozooplanktonic community structure and feeding in ice covered Antarctic waters during the winter (AMERIEZ 1988), *Polar Biol.*, *11*, 157-167, 1991.

Lancraft, T.M., J.J. Torres, and T.L. Hopkins, Micronekton and macrozooplankton in the open waters near Antarctic Ice Edge Zones (AMERIEZ 1983 and 1986), *Polar Biol.*, *9*, 225-233, 1989.

Laws, R.M., The ecology of the Southern Ocean, *Am. Sci.*, *73*, 26-40, 1985.

Littlepage, J.L., Seasonal variation in lipid content of two Antarctic marine Crustacea, in *Biologie Antarctique*, edited by R. Carrick, M.W. Holdgate, and J. Prevost, pp. 465-470, Actualites Scientifiques et Industrielles, Paris, 1964.

Loeb, V., and V. Siegel, AMLR program: krill and macrozooplankton in the Elephant Island area, January-March 1993, *Antarct. J. U.S. 28*, 185-188, 1993.

Loeb, V., and V. Siegel, AMLR program: krill stock structure and macrozooplankton abundance near Elephant Island, January-March 1994, *Antarct. J. U.S.*, *29*, in press, 1994.

Lopez, M.D.G., M.E. Huntley, and J.T. Lovette, *Calanoides acutus* in Gerlache Strait, Antarctica. I. Distribution of late copepodite stages and reproduction during spring, *Mar. Ecol. Prog. Ser.*, *100*, 153-165, 1993.

Lowry, F.F., J.W. Testa, and W. Calvert, Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula, *Polar Biol.*, *8*, 475-478, 1988.

Makarov, R., Larval development of the Antarctic euphausiids, *BIOMASS Handbook*, *3*, 13, 1980.

Makarov, R.R., Distribution of the larvae and some questions of the ecology of reproduction of the euphausiid *Euphausia frigida* Hansen, 1911 (Crustacea, Euphausiacea) in the southern part of the Scotia Sea, *Oceanology*, *17*, 208-213, 1977.

Marin, V., Qualitative models of the life cycles of *Calanoides acutus*, *Calanus propinquus*, and *Rhincalanus gigas*, *Polar Biol.*, *8*, 439-446, 1988.

Marin, V.H., and S.B. Schnack-Schiel, The occurrence of *Rhincalanus gigas*, *Calanoides acutus*, and *Calanus propinquus* (Copepoda: Calanoida) in late May in the area of the Antarctic Peninsula, *Polar Biol.*, *13*, 35-40, 1993.

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

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

Mujica, A.R., and V.V. Asencio, Fish larvae, euphausiids and community structure of zooplankton in the Bransfield Strait (SIBEX - Phase I) 1984, *Ser Cient INACH*, *33*, 131-154, 1985.

Nast, F., Changes in krill abundance and in other zooplankton relative to the Weddell-Scotia Confluence around Elephant Island in November 1983, November 1984, and March 1985, *Arch. FischWiss.*, *37*, 73-94, 1986.

Nicol, S., W.K. De La Mare, and M. Stolp, The energetic cost of egg production in Antarctic krill (*Euphausia superba* Dana), *Ant. Sci.*, *7*, 25-30, 1995.

Nordhausen, W., Winter abundance and distribution of *Euphausia superba*, *E. crystallorophias*, and *Thysanoessa macrura* in Gerlache Strait and Crystal Sound, Antarctica, *Mar. Ecol. Prog. Ser.*, *109*, 131-142, 1994.

Perissinotto, R., and E.A. Pakhomov, The trophic importance of the tunicate *Salpa thompsoni* in the Southern Ocean carbon flux, International Symposium, *Carbon Fluxes and Dynamic Processes in the Southern Ocean: Present and Past*, Abstracts, p. 54, 1995.

Pitcher, T.J., S.H. Lang, and J.A. Turner, A risk-balancing trade-off between foraging rewards and predation hazard in a shoaling fish, *Behav. Ecol. Sociobiol.*, *22*, 225-228, 1988.

Price, H., Swimming behavior of krill in response to algal patches: A mesocosm study, *Limnol. Oceanogr.*, *34*, 649-659, 1989.

Priddle, J., J.P. Croxall, I. Everson, R.B. Heywood, E.J. Murphy, P.A. Prince, and C.B. Sear, Large-scale fluctuations in distribution and abundance of krill - A discussion of possible causes, in *Antarctic Resources and Variability*, edited by D. Sahrhage, pp. 169-182, Springer-Verlag, Berlin, 1988.

Quetin, L.B., and R.M. Ross, Summary of WinCruise II to the Antarctic Peninsula during June and July 1987, *Antarct. J. U.S.*, *23*, 149-151, 1988.

Quetin, L.B., and R.M. Ross, Behavioral and physiological characteristics of the Antarctic krill, *Euphausia superba*, *Am. Zool.*, *31*, 49-63, 1991.

Quetin, L.B., R.M. Ross, and A. Clarke, Krill energetics: seasonal and environmental aspects of the physiology of *Euphausia superba*, in *Southern Ocean Ecology: the BIOMASS Perspective*, edited by S.Z. El-Sayed, pp. 165-184, Cambridge University Press, Cambridge, 1994.

Rakusa-Suszczewski, Differences in the hydrology, biomass, and species distribution of plankton, fishes, and birds in the Bransfield Strait and the Drake Passage during FIBEX 1981 and SIBEX 1983/84, in *Antarctic Ocean and Resources Variability*, edited by D. Sahrhage, pp. 214-218, Springer-Verlag, Berlin, 1988.

Ribic, C.A., D.G. Ainley, and W.R. Fraser, 1991, Habitat selection by marine mammals in the marginal ice zone, *Ant. Sci.*, *3*, 181-186, 1991.

Ross, R.M., and L.B. Quetin, Spawning frequency and fecundity of the antarctic krill *Euphausia superba*, *Mar. Biol.*, *77*, 201-205, 1983.

Ross, R.M., and L.B. Quetin, How productive are antarctic krill?, *BioScience*, *36*, 264-269, 1986.

Ross, R.M., and L.B. Quetin, Energetic cost to develop to the first feeding stage of *Euphausia superba* Dana and the effect of delays in food availability, *J. Exp. Mar. Biol. Ecol.*, *133*, 103-127, 1989.

Ross, R.M., and L.B. Quetin, Ecological physiology of larval euphausiids, *Euphausia superba* (Euphausiacea), *Mem. Queensland Mus.*, *31*, 321-333, 1991.

Ross, R.M., L.B. Quetin, and C.M. Lascara, Distribution of Antarctic Krill and Macrozooplankton West of the Antarctic Peninsula, this volume.

Sahrhage, D., Some indications for environmental and krill resources variability in the Southern Ocean, in *Antarctic Ocean and Resources Variability*, edited by D. Sahrhage, pp. 33-40, Springer-Verlag, Berlin, 1988.

Schnack, S.B., V. Smetacek, V.B. Bodungen, and P. Stegmann, Utilization of phytoplankton by copepods in Antarctic waters during spring, *18th European Marine Biology Symposium*, 65-79, 1985.

Schnack-Schiel, S.B., and W. Hagen, Life cycle strategies and seasonal variations in distribution and population structure of four dominant copepod species in the eastern Weddell Sea, Antarctica, *J. Plankton Res.*, *16*, 1543-1566, 1994.

Schnack-Schiel, S.B., and A. Mujica, The zooplankton of the Antarctic Peninsula region, in *Southern Ocean Ecology: the BIOMASS Perspective*, edited by S.Z. El-Sayed, University Press, Cambridge, Bremerhaven, Germany, 79-92, 1994.

Siegel, V., Untersuchungen zur Biologie des antarktischen Krill, Euphausia superba, im Bereich der Bransfield StraBe und angrenzender Gebiete, *Mitt. Inst. Seefisch.*, *38*, 1-244, 1986.

Siegel, V., Age and growth of antarctic Euphausiacea (Crustacea) under natural conditions, *Mar. Biol.*, *96*, 483-495, 1987.

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

Siegel, V., Winter and spring distribution and status of the krill stock in Antarctic Peninsula waters, *Arch. FischWiss.*, *39*, 45-72, 1989.

Siegel, V., and V. Loeb, Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability, *Mar. Ecol. Prog. Ser.*, *123*, 45-56, 1995.

Smetacek, V., R. Scharek, and E.-M. Nothig, Seasonal and regional variation in the pelagial and its relationship to the life history cycle of krill, in *Antarctic Ecosystems: Ecological Change and Conservation*, edited by K.R. Kerry and G. Hempel, pp. 103-114, Springer-Verlag, Berlin, 1990.

Smith, S.L., and S.B. Schnack-Schiel, Polar zooplankton, in *Polar Oceanography*, *Part B: Chemistry, Biology and Geology*, edited by W.O. Smith Jr., pp. 527-598, Academic Press, San Diego, 1990.

Stepnik, R., All-year populational studies of Euphausiacea (Crustacea) in the Admiralty Bay (King George Island, South Shetland Island Antarctic), *Pol. Polar Res.*, *3*, 49-68, 1982.

Strand, S.W., and W.M. Hamner, Schooling behavior of Antarctic krill (*Euphausia superba*) in laboratory aquaria: reactions to chemical and visual stimuli, *Mar. Biol.*, *106*, 355-359, 1990.

Torres, J.J., A.V. Aarset, J. Donnelly, T.L. Hopkins, T.M. Lancraft, and D.G. Ainley, Metabolism of Antarctic micronektonic Crustacea as a function of depth of occurrence and season, *Mar. Ecol. Prog. Ser.*, *113*, 207-219, 1994.

Trathan, P.N., J. Priddle, J.L. Watkins, D.G.M. Miller, and A.W.A. Murray, Spatial variability of Antarctic krill in relation to mesoscale hydrography, *Mar. Ecol. Prog. Ser.*, *98*, 61-71, 1993.

Waters, K.J., and R.C. Smith, Palmer LTER: A sampling grid for the Palmer LTER program, *Antarct. J. U.S.*, *27*, 236-239, 1992.

Weber, L.H., and S.Z. El-Sayed, Spatial variability of phytoplankton and the distribution and abundance of krill in the Indian Sector of the Southern Ocean, in *Antarctic Nutrient Cycles and Food Webs*, edited by W.R. Siegfried, P.R. Condy, and R.M. Laws, pp. 284-293, Springer-Verlag, Heidelberg, 1985.

Weber, L.H., S.Z. El-Sayed, and I. Hampton, The variance spectra of phytoplankton, krill and water temperature in the Antarctic Ocean south of Africa, *Deep Sea Res.*, *33*, 1327-1343, 1986.

Whitworth, T., Zonation and geostrophic flow of the Antarctic circumpolar current at Drake Passage, *Deep-Sea Res.*, *27*, 497-507, 1980.

Witek, Z., W. Kittel, H. Czykieta, M.I. Zmijewska, and E. Presler, Macrozooplankton in the southern Drake Passage and Bransfield Strait, *Pol. Polar Res.*, *6*, 95-115, 1985.

Witek, Z., M. Pastuszak, and A. Grelowski, Net-phytoplankton abundance in western Antarctic and its relation to environmental conditions, *Meerforsch.*, *29*, 166-180, 1982.

Zmijewska, M.I., Horizontal and vertical distribution of copepods in the southern part of Drake Passage and in the Bransfield Strait (BIOMASS-SIBEX 1983/1984), *Pol. Polar Res.*, *8*, 381-390, 1987.

Zmijewska, M.I., and J. Yen, Seasonal and diel changes in the abundance and vertical distribution of the Antarctic copepod species *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, *Metridia gerlachei* and *Euchaeta antarctica* (Calanoida) in Croker Passage (Antarctic Peninsula), *Oceanol.*, *35*, 101-127, 1993.

L.B. Quetin, R.M. Ross, T.K. Frazer, and K.H. Haberman Marine Science Institute, University of California at Santa Barbara, Santa Barbara, CA 93106.

(Received July 24, 1995; accepted October 20, 1995.)