FOUNDATIONS FOR ECOLOGICAL RESEARCH WEST OF THE ANTARCTIC PENINSULA
ANTARCTIC RESEARCH SERIES, VOLUME 70, PAGES 199-217

DISTRIBUTION OF ANTARCTIC KRILL AND DOMINANT ZOOPLANKTON WEST OF THE ANTARCTIC PENINSULA

Robin M. Ross and Langdon B. Quetin

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

Cathy M. Lascara

Center for Coastal Physical Oceanography, Old Dominion University, Norfolk, Virginia

The horizontal and vertical distributions of selected taxa that dominate the pelagic zooplankton community (> 0.2 mm) within the Palmer Long-Term Ecological Research (LTER) study region are described. In addition to a synthesis of existing published descriptions for euphausiids, salps, and copepods, two newly available datasets are analyzed. Recent observations (1991-1994) obtained as part of the Palmer LTER program are used to provide new information on the seasonal and interannual distribution and abundance of the salp, *Salpa thompsonii*. Acoustic data collected during a series of twelve cruises conducted in the late 1980s are used to describe seasonal differences in the geographic distribution and the dimensional character (length, height, volume, depth) of krill (*Euphausia superba*) aggregations along the west coast of the Antarctic Peninsula.

1. INTRODUCTION

Zooplankton, particularly those > 0.2 µm in length, are the main trophic link between primary producers and apex predators in the Southern Ocean. In this chapter we will focus on the dominant groups of these larger zooplankton. Biomass and distribution of these zooplankters can change vertically and horizontally with season, life cycle, and year. The degree of interannual and seasonal variability in spatial distribution is important to ecosystem function at multiple trophic levels, since many of these zooplankton species both graze on phytoplankton and are prey items for predators. The existence and numerical abundance of the smaller zooplankters and their link to the microbial loop is not in question, but is not within the scope of this chapter.

One initial task of a long-term ecological research program is the selection of the parameters and species that will be the best indicators or representatives of that ecosystem. Since one objective of a long-term program is to collect a data base for analyzing trends or cycles in ecosystem dynamics or composition, choices must be based on current knowledge of interactions and critical components within that ecosystem. These choices may not all be correct, but it is neither logistically nor financially feasible to measure everything. A species originally considered pivotal from the results of a short study may be an ephemeral member of the community and have little impact on the overall dynamics from a long-term perspective. Alternatively, dominant components or species may not be the only determinants of ecosystem dynamics, and as understanding of the interactions between species or functional groups grows, additional representatives may need to be added. For polar ecosystems, where many of the zooplankters are long-lived and thus population changes are not quickly seen, initial choices are important since it may be several years before the 'invisible present' [*Magnuson*, 1990] can be placed in a long-term perspective.

In the Southern Ocean, and the waters west of the Antarctic Peninsula in particular, one species of herbivorous euphausiid, *Euphausia superba* or Antarctic krill, often dominates zooplankton assemblages. *E. superba* is an obvious target species. Not only can it be 75 to 90% of the biomass in this area [*Hopkins*, 1985; *Schnack-Schiel and Mujica*, 1994], but the importance of krill in the diet of seabirds and seals in the region make it a keystone species [*Laws*, 1985]. One important characteristic of Antarctic krill is its strong tendency to form aggregations. Aggregations are often divided into swarms (no parallel orientation of krill) or schools (with parallel orientation). Extensive acoustic observations have documented that krill aggregations occur in many different physical forms [*Witek et al.*, 1981, 1988; *Macaulay et al.*, 1984; *Kalinowski and Witek*, 1985; *Watkins et al.*, 1986]. *Murphy et al.* [1988] placed krill aggregations into a classification scheme with a hierarchy of levels based on the spatial and temporal scale with which aggregations interact with the environment. The heterogeneous distribution of krill across multiple spatial scales is of ecological importance to krill population studies [*Siegel and Kalinowski*, 1994], and affects both the distribution of pelagic phytoplankton upon which krill primarily grazes, and of vertebrate predators which depend on krill as their primary food source. In particular the fine-scale patchiness of krill differentially impacts the foraging strategy and thus potential feeding success of these predators [*Greene et al.*, 1994; *Murphy*, 1995].

In addition to Antarctic krill, we have identified some abundant copepod species and salps as important to the ecosystem within the Palmer Long-Term Ecological Research (LTER) region. These choices are based on both the function of these species in the ecosystem, and on their abundance. Even though krill are abundant, other species can comprise over 25% of zooplankton biomass [*Brinton and Antezana*, 1984], and their role as grazers on the phytoplankton community as well as prey may be significant at times [*Smith and Schnack-Schiel*, 1990]. During a workshop with broad objectives for Southern Ocean GLOBEC (Global Ocean Ecosystem Dynamics), *E. superba* was one of the chosen species, but representatives from taxonomic groups including euphausiids, salps, copepods and chaetognaths were also identified as warranting consideration in broadly based ecosystem studies [*Hofmann and Huntley*, 1991].

In this chapter, our goal is to review the horizontal and vertical distribution of the dominant zooplankton > 0.2 mm that occur, at least seasonally, in the upper 300 m of the water column of the Palmer LTER study region. The Palmer LTER study region, a grid 900 km alongshore by 200 km offshore, Figure 1 in *Stammerjohn and Smith* [this volume], is west of the Antarctic Peninsula and extends from western Bransfield Strait to south of Marguerite Bay. Our approach is two-fold, involving the synthesis of existing published descriptions and the presentation of new data. In the next section, we review previous research on zooplankton communities relevant to the Palmer LTER study. As little information was available on the distribution of salps, the review is augmented by recent observations on the distribution of the salp, *Salpa thompsoni*, obtained as part of the Palmer LTER program. The third section of this chapter is devoted to an analysis of unpublished data describing the distribution and dimensional characteristics of Antarctic krill aggregations detected with acoustic techniques during a series of cruises within the northern reaches of the LTER study region during the late 1980s.

2. PREVIOUS RESEARCH IN THE LTER REGION

The waters west of the Antarctic Peninsula are a physically complex environment, influenced by several major water masses and the annual advance and retreat of the seasonal ice pack [*Hofmann et al.*, this volume; *Stammerjohn and Smith*, this volume]. Most of the Palmer LTER study region is over the shelf break and relatively deep continental shelf, and belongs to two of the major functional subdivisions delineated by *Treguer and Jacques* [1992], the coastal and continental shelf zone (CCSZ) and seasonal ice zone (SIZ). The continental shelf is cut by valleys and characterized by inshore depressions [*Andriashev*, 1965], creating an environment with water depths > 400 m in the immediate vicinity of the coast.

2.1. *Zooplankton Provinces*

Smith and Schnack-Schiel [1990] divide the Southern Ocean into a Subantarctic Zone, from about 40°S to the Polar Front, and an Antarctic Zone south of the Polar Front. The Polar Front forms a biogeographical boundary. *Siegel and Piatkowski* [1990] describe three distinct provinces for zooplankton assemblages in the Antarctic Zone: oceanic, neritic and transitional (mixing zone with both oceanic and neritic species). Classifications with nearly identical species assemblages and geographic locations to those of *Siegel and Piatkowski* have also been defined by other investigators [*Jazdzewski, et al.*, 1982; *Rakusa-Suszczewski*, 1983; *Hempel*, 1985; *Piatkowski*, 1985, 1989; *Witek, et al.*, 1985]. The provinces are defined by variations in abundance rather than by distinct indicator species. Only the oceanic community has clear indicator species, the hyperiid amphipod, *Vibilia antarctica*, and the polychaete, *Tomopteris carpenteri*, [*Piatkowski*, 1989]. The location of these provinces can shift to some extent, although it is not clear whether the movement is a seasonal or interannual shift.

The oceanic province is generally in areas where the water is deeper than 2000 m, and is rich in mesozooplankton [*Siegel and Piatkowski*, 1990]. The zooplankton assemblage is characterized by phytophagous copepods, pteropods, chaetognaths, tomopterid polychaetes, siphonophores, the amphipod *Themisto gaudichaudii*, and salps. The neritic province includes parts of the broad southwest shelf south of Anvers Island, and most of the Bransfield Strait. The dominant species include *E. superba*, *Euphausia crystallorophias*, and fish larvae. The transitional zone, encompassing the outer shelf, the shelf break and the western and central Bransfield Strait, generally has significantly lower volumes of plankton [*Jazdżewski et al.*, 1982; *Witek et al.*, 1985], and is a mixture of these groups. There appear to have been very few investigations of biodiversity in this region, but in one study, species diversity was highest in the transitional zone (Bransfield Strait) [*Piatowski*, 1985].

2.2. *Euphausiacea*

Of the eleven species of euphausiids in the Subantarctic and Antarctic Zones, only five or six are routinely found south of the Polar Front, i.e., in the Antarctic Zone [*Mauchline*, 1980a, b]. *E. superba* and *Thysanoessa macrura* are the most abundant euphausiid species within the Palmer LTER region and have the broadest regional coverage, covering the entire region from the coastline to the Polar Front. The maximum abundance of *E. superba* shifts with season, and is closer to shore in the fall. *T. macrura*, with maximum abundances south of the Polar Front [*Siegel*, 1987] is found throughout the Palmer LTER region, although less frequently at shelf and inshore stations where *E. superba* dominates. Two species have restricted distributions. *E. crystallorophias*, the ice krill, occurs in waters immediately adjacent to the coastline. *Euphausia triacantha* is found beyond the northern limit of the pack ice with maximum abundances around the Polar Front or in adjacent waters to the south, as is also true for *Euphausia frigida* [*Siegel*, 1987]. *E. triacantha* is rare within the Palmer LTER region, even at offshore stations. *E. frigida*, however, has a similar distribution (not maximum abundance) to that of *E. superba*, and has been found in lower numbers in the shelf waters south of Anvers Island [*Kittel et al.*, 1985], and in Croker Passage, Gerlache Strait, and shelf waters of the Palmer LTER (R. Ross, L. Quetin, personal communication, 1986-1994). The two

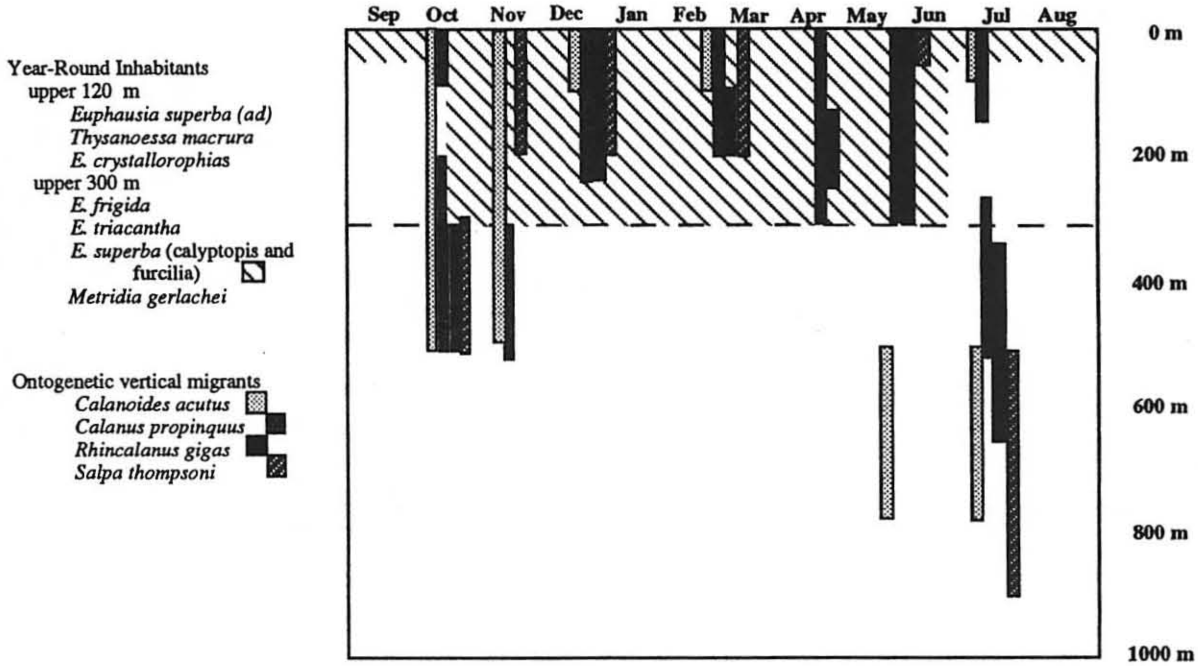

Fig. 1. Composite diagram of seasonal vertical distribution of the dominant meso- and macrozooplankton from nearshore to 200 km west of the Antarctic Peninsula. Year-round inhabitants of the upper 300 m are divided into those in the upper 120 m and those in the upper 300 m. Ontogenetic vertical migrants (fall and winter) are shown in the appropriate depth horizon.

species of *Thysanoessa* in the Antarctic, *T. macrura* and the smaller *Thysanoessa vicina*, are difficult to distinguish [*Mauchline*, 1980a]. However, in two studies, *T. vicina* was found only north of 60°S, and not in the Bransfield Strait [*Weigmann-Haas and Haas*, 1980; *Siegel*, 1986], suggesting it may not inhabit the Palmer LTER region. Although the distribution of the larvae of these species is less well known, larvae of Antarctic krill occur in all three provinces.

Although several feeding modes have been observed in Antarctic krill, both *E. superba* and *E. crystallorophias* are known to be predominantly herbivores. *Thysanoessa* spp. are characterized as omnivores, but the trophic position is not clear for either *E. frigida* or *E. triacantha*. One important aspect of the biology of Antarctic krill is the tendency to form aggregations, as do many other species of euphausiids [*Mauchline*, 1980b; *Mauchline and Fisher*, 1969]. Of the euphausiids found in the Palmer LTER region, there is clear evidence that at least three species, *E. superba*, *E. crystallorophias*, and *T. macrura*, form aggregations. Schooling and aggregation formation is better known in *E. superba* [*Marr*, 1962; *Hamner et al.*, 1983; *Siegel and Kalinowski*, 1994] than in the other species. Aggregations of *E. crystallorophias* have been observed under the ice [*Everson*, 1987; *O'Brien*, 1987], inferred from high concentrations [*Kittel*, 1980; *Piatowski*, 1985], and documented in the Palmer LTER region (R. Ross, L. Quetin, personal communication, 1993). Large surface swarms of *T. macrura* have been documented [*Kittel et al.*, 1985], and aggregations inferred from the presence of this species in whale stomachs [*Mauchline*, 1980b]. Even the smallest species south of the Polar Front, *E. frigida*, occurs in high enough concentrations that swarm formation is suspected [*Mauchline*, 1980b].

The timing of the reproductive season for these different species varies [*Makarov*, 1979a; *Quetin et al.*, this volume], creating seasonal differences in the occurrence of specific larval stages. All Antarctic euphausiids release their embryos into the water column. After a short embryonic period, embryos hatch into a typical crustacean nauplius, and go through a long and complex period of larval development: nauplius, metanauplius, calyptopis, and furcilia. Development proceeds during the spring and summer, and in many cases involves an ontogenetic migration. For most species, young animals spawned earlier in the season have reached the post larval stage by early winter, but *E. superba* winters as furcilia larvae [*Fraser*, 1936].

All six euphausiid species found in the Antarctic Zone are year-round inhabitants of the upper 300 m of the water column, with several species, including *E. superba*, remaining in the upper 120 m year round (Figure 1). Distinct diel vertical migrations have been observed for *E. crystallorophias* [*Everson*, 1987; *O'Brien*, 1987] within the top 120 m, *E. frigida* from mid-depths to the surface [*Piatowski*, 1985; *Kittel et al.*, 1985], and *E. triacantha* also from mid-depth to the surface [*Piatowski*, 1985]. Within the upper layers, the vertical distribution of larval *E. superba* is shallower (upper 100 m) in the winter than the summer (100-250 m) [*Fraser*, 1936]. Inconsistent evidence for diel vertical migration in *E. superba* is discussed in section 2.

Many Antarctic euphausiids undergo an ontogenetic migration in the spring and summer. One of the basic characteristics in the development of larvae of *E. superba*, *E. frigida*, and *T. macrura* is ontogenetic migration. The embryos sink and hatch at depth, and the earliest stages (nauplii) occupy a deeper layer than the more advanced larvae which reach the surface via a developmental ascent [*Marr*, 1962; *Makarov*, 1975, 1977, 1979b; *Makarov and Maslennikov*, 1981]. In contrast, in *E. crystallorophias* both the early and late larvae are found in surface waters, 0-25 m [*Makarov and Maslennikov*, 1981].

2.3. Copepoda

Three of the four most abundant species of copepods in the upper 300 m were identified as target species for Southern Ocean GLOBEC: the two herbivores, *Calanoides acutus* (total length about 4 mm), *Calanus propinquus*, and the omnivore *Metridia gerlachei* (total length about 2.5 mm). Both *C. propinquus* and *Rhincalanus gigas*, typical Antarctic Circumpolar Current species that are sometimes abundant [*Zmijewska and Yen*, 1993], are suspected to be omnivores at times [*Schnack-Schiel and Hagen*, 1994]. The two calanoid copepods have contrasting life cycles, although both reproduce in the austral spring. *M. gerlachei*, the most typical species of high latitudes and the most abundant of the copepods in the upper 300 m, undergoes a strong diel vertical migration within the upper 400 m [*Zmijewska and Yen*, 1993]. Although *M. gerlachei* does shift to the upper 100 m in winter, occupying the place previously occupied by the herbivores, it is a year-round inhabitant of the upper 300 m of the water column [*Vervoort*, 1965; *Zmijewska and Yen*, 1993]. For the herbivorous copepods, the evidence for a standard diel vertical migration is contradictory, with the most consistent evidence for a weak diel vertical migration in *C. propinquus* [*Hopkins and Torres*, 1988; *Mackintosh*, 1937; *Zmijewska and Yen*, 1993].

In addition to the summer ontogenetic vertical migration of some euphausiids, four other species, three copepods and the salp, *S. thompsoni*, undergo ontogenetic vertical migrations. But in these species, most of the population lives deeper than 300 m in the winter months (Figure 1). Voronina's theory of asynchronic life cycles in three species of copepods has been confirmed west of the Antarctic Peninsula in several recent studies [*Atkinson and Peck*, 1990; *Marin and Schnack-Schiel*, 1993; *Schnack-Schiel and Hagen*, 1994; *Zmijewska and Yen*, 1993]. *C. acutus* undergoes a diapause, has the strongest ontogenetic vertical migration of the three and is the first to move into the upper 200 m of the water column in the early spring. Copepodid IVs start the descent in April, overwintering in Circumpolar Deep Water deeper than 500 m where water depths permit. In shallow coastal areas, part of the population remains in the surface waters [*Schnack-Schiel and Hagen*, 1994]. *C. propinquus* does not appear to have a diapause, but under some conditions does have a shallower, seasonal ontogenetic vertical migration [*Zmijewska and Yen*, 1993] (Figure 1). Thus *C. propinquus* does not winter in waters as deep as *C. acutus*, although still below 300 m (Figure 1). Migration to the surface begins in mid-November, with the majority of the population gradually moving to the top 50 m by January. Although there is a tendency to migrate below 300 m a few weeks after *C. acutus*, the majority of the population remains in the surface layers for the winter [*Zmijewska and Yen*, 1993]. The third species, *R. gigas*, is not a permanent constituent of high-latitude waters, and starts its seasonal migration last of the three copepods. In the winter *R. gigas* lives at depths between those of the deeper living portions of the populations of *C. acutus* and *C. propinquus* (Figure 1). In summer *R. gigas* is more widely dispersed than the other 2 herbivorous copepods but is generally in the upper 100 m [*Zmijewska and Yen*, 1993]. By late autumn, only the early larval stages are still in the surface waters, with copepodid Vs and females deep in the water column. *M. gerlachei* does not undergo either an ontogenetic vertical migration or a diapause.

2.4. Salpidae

Salps are herbivores, and high population growth rates are often associated with small phytoplankton cells or low standing stocks [*Harbison et al.*, 1986]. Because the rate of population increase in salps is much higher than in either copepods or euphausiids, they can respond quickly to improved environmental conditions. Thus their grazing impact can be strong and ephemeral. Two different species of salps have been identified west of the Antarctic Peninsula. *Salpa gerlachei* and *S. thompsoni* are considered clinal forms of the same species [*Soest*, 1974], and are difficult to distinguish, especially in areas of overlapping distributions. *S. gerlachei* is mainly found in the Bellingshausen (extreme southern part of the Palmer LTER region) [*Foxton*, 1966]. The second species, *Idhlea racovitzai*, has been identified in the northern Bransfield Strait [*Nishikawa et al.*, 1995]. All share a life history characterized by alternating sexual and asexual (budding) generations, and a spring or summer maximum in abundance. By late winter the small population is dominated by the solitary (asexual) form. These solitary forms were <10 mm upon release the previous season, and can grow slightly in the winter. When environmental conditions are right, budding from the stolon creates the aggregate form. In the aggregate form, individuals form chains. Individuals within the chain also grow during the season. The aggregate form dominates when the population is at its maximum. Sexual reproduction occurs in the aggregate form, with the release of the embryo at some point after the individuals in the aggregate are 25-30 mm long. The 3-4 mm embryo absorbs the placenta and eleoblast, and begins the cycle as the solitary form. Mortality of the aggregate form is heavy in the fall and winter, leading to dominance of the solitary form again. In the winter, budding and embryo production cease [*Foxton*, 1966].

Both *Foxton* [1966] and *Piatowski* [1985] have reported that *S. thompsoni* undergoes a diel vertical migration within the upper 300 m and is found at depths greater than 100 m during the day and at relatively shallow depths during the night. *Foxton*'s [1966] data also suggest that depth distributions change seasonally, with small solitaries deeper in the fall and winter, from 250 to 2000 m. Aggregates were rarely found in the deeper tows.

2.4.1. The distribution and abundance of S. thompsoni in the Palmer LTER study region.

TABLE 1. Dates and locations for Palmer LTER cruises during the first three field seasons.

Year	Dates	Transect lines	No. 2 m tows
1991	Nov 12 - 20	700, 600, 500	20
1993	Jan 8 - Feb 6	600, 500, 400, 300, 200, Palmer Basin	115
1993	Mar 29 - May 9	900, 800, 700, 600, 500, 400, 300, 200, 100, 000, selected stations	120
1993	Aug 30 - Sept 17	600, 500, 400, 300	27
1994	Jan 11 - Feb 6	600, 500, 400, 300, Palmer Basin	58

During the first three field seasons for the Palmer LTER, there were two summer cruises (January), and three cruises covering spring (November 1991), fall (March-May 1993), and late winter (August-September 1993) that covered segments of the LTER Peninsula grid (Table 1). Standard alongshore transects (perpendicular to the shore) were 100 km apart, and stations on transects were spaced 20 km apart from the coast to 200 km offshore. Macrozooplankton were collected at each station with a 2 m square Metro net (1000 μm mesh, 500 μm mesh in codend). Ice cover limited the geographical range in both November 1991 and August/September 1993. The net was rigged with an General Oceanics flowmeter to measure volume filtered, and a Time-Depth-Recorder to record the maximum depth of tow. Standard tows were oblique from the surface to 120 m. In January 1993 and the first 2 weeks of March 1993, the flow meters did not operate properly. The volume filtered for these tows was estimated from tow duration and the relationship between tow duration and volume filtered in January 1994.

The catch was poured from the cod-end into a 50 liter tub filled with seawater. All salps were removed from the catch, the volume of salps measured in a graduated cylinder, and representatives from each size class preserved for later taxonomic identification. Wet volume was chosen instead of number to represent salp abundance because the size range of salps is so large, from 10 to > 90 mm. Selected salps from the preserved samples were stained with bengal rose to help with inspection of the muscle bands. Only *S. thompsoni* was found in these samples.

2.4.2. Results of Palmer LTER cruises, 1991-1994. Seasonal, geographical and interannual differences were seen in the distribution and abundance of *S. thompsoni* throughout the Palmer LTER grid. Highest volumes, up to 2500 ml · 1000 m^{-3} water filtered, were found in the southwest Bransfield Strait (the northern sector of the Palmer LTER grid) in the fall (Figure 2). Salps were spread throughout the entire grid in March 1993, generally more abundant on the northern transects, and at shelf break stations than inshore. Inshore stations on the southern most transect lines and stations inside the Biscoe Islands had no salps. The previous summer, salps were found at very few stations, and volumes were much lower. Except for three stations on the outer shelf (600.200, 600.180 and 400.160), the volume of salps never exceeded 5 ml ·1000 m^{-3}. The following summer (January 1994), however, salps were found at the majority of stations, with highest volumes in Palmer Basin and at outer stations of all but the 500 transect line (Figure 2). Although these volumes were not as high as in the previous fall in the southwest Bransfield, they were higher than both the previous fall and summer within the region between Anvers and Adelaide Islands, about 1200 ml · 1000 m^{-3}.

Both late winter and spring were times of low salp abundance. Although in late winter/early spring 1993, salps were widespread, volumes were less than 18 ml ·1000 m^{-3} except at the innermost station on the northern transect (Figure 3). During an earlier spring, salps were only found at about one-third of the stations, and in small numbers and volumes (< 7 ml · 1000 m^{-3}).

2.4.3. Seasonal and interannual variability in S. thompsoni. Initial sampling by the Discovery Expeditions in the 1930s [*Foxton*, 1966] covered the entire Southern Ocean, and investigated seasonal patterns of abundance of the alternating solitary and aggregate forms in the life cycle. Sexual reproduction occurs in the aggregate form at the end of swarm formation. The solitary form produced is capable of budding and growing quickly in both individual size and chain length under the appropriate environmental conditions. Thus we expect to see significant variations in abundance on short time scales of weeks during the potential growth season, and interannual variation in any one location depending on environmental conditions.

Foxton [1966] found that peak abundance of the aggregate salp form occurs in February and is followed by a marked decline in March. This general pattern was seen during the first three field seasons for the Palmer LTER: low abundances in the winter and spring, variable in the summer, with a maximum in the fall. Salp abundance in general was higher in the northern part of the grid and the offshore stations, corresponding to areas influenced by the Antarctic Circumpolar Current and dominated by oceanic communities.

Most data on salp distribution and abundance west of the Antarctic Peninsula in the last fifteen years is for regions outside the Palmer LTER grid, in the region of the South Shetland Islands and northern Bransfield Strait [*Siegel and Piatowski*, 1990]. Numerous studies have been conducted in this region, e.g., the international BIOMASS (Biological Investigations of Marine Antarctic Systems and Stocks) program in the early 1980s, FIBEX (First International BIOMASS Experiment) in 1981, SIBEX (Second International BIOMASS Experiment) in 1984, and the annual AMLR program (Antarctic Marine Living Resources) sampling of the Elephant Island area instituted in 1992 [*Loeb and Siegel*, 1993, 1994].

In the Elephant Island area, both 1993 and 1994 were years in which salp abundance was high, and high concentrations of salps were found in nearly all tows in both January and February. Maximum volumes in 1994 were 33.5 liters. The situation in the Palmer LTER grid was somewhat different. Only in the summer of 1994 were salps in high abundance, and maximum volumes were only 2.5 liters · 1000 m^{-3}. In 1993, salps did not reach high abundances until late fall. Some of the differences in these

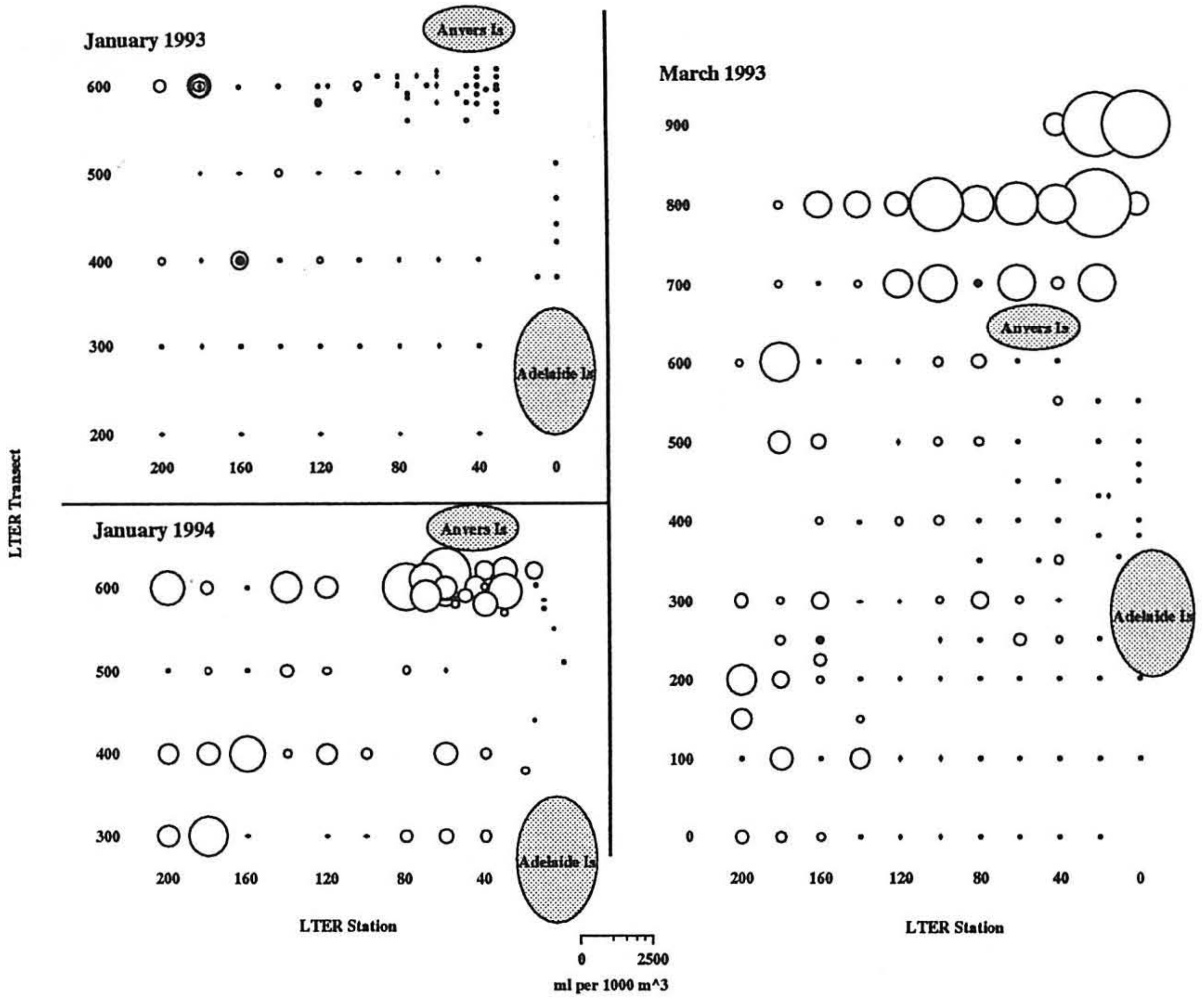

Fig. 2. *Salpa thompsoni* abundance and distribution in summer (January 1993 and January 1994) and fall (March-May, 1993) west of the Antarctic Peninsula in Palmer LTER Peninsula grid [*Waters and Smith*, 1992]. Transect lines are perpendicular to the coastline, and stations run from 0 near the mainline to 200 km offshore. The size of the bubble indicates volume of salps per 1000 m^3; filled bubble means a net tow was done, but no salps were found.

two regions can be explained by looking at relative timing of salp swarm formation. In 1993, in the AMLR region, the peak in salp abundance was later, whereas in 1994 abundances decreased by 50% with advancing season. The same relative timing, i.e., salp swarm formation later in 1992/1993 than in the 1993/1994 summer, appeared to occur in the Palmer LTER grid, but swarm formation in both years was later in the season. In 1993, salps peaked in the fall, whereas in 1994 the bloom was early in the summer. At the higher latitudes of the Palmer LTER, January is early enough in the season's succession that we cannot tell from summer data alone whether it will be a year of high salp abundance or not.

Siegel and Loeb [1995] established correlations between salp density in spring/summer and ice concentration in winter (negative) and duration of ice free conditions (positive) west of the Antarctic Peninsula [*Stammerjohn and Smith*, this volume]. They suggest that after a winter of low or no ice, asexual reproduction (budding) will start earlier and there will be a longer period of population growth. There are also several hypotheses about optimal environmental conditions for rapid population growth in salps that revolve around composition and concentration of food available (see *Quetin et al.* [this volume]), which in turn may be correlated with the effects of winter ice on phytoplankton production. And it is these factors which may ultimately explain the variation in timing and in maximum abundance found both in the Palmer LTER and northern Bransfield Strait regions.

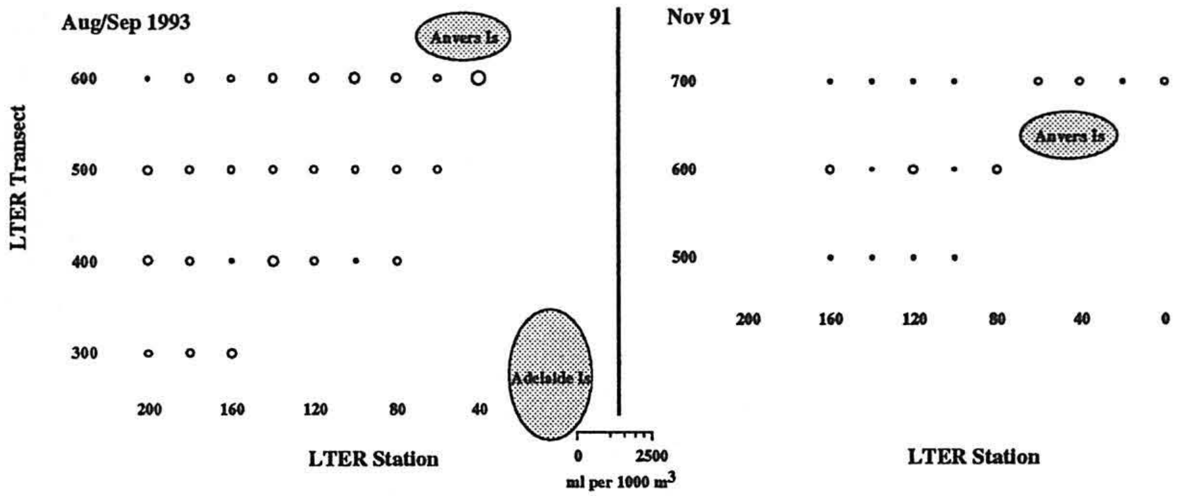

Fig. 3. *Salpa thompsoni* abundance and distribution in winter (August/September 1993) and spring (November 1991) west of the Antarctic Peninsula in Palmer LTER Peninsula grid. Transect lines are perpendicular to the coastline, and stations run from 0 near the mainline to 200 km offshore. Bubble size is proportional to volume of salps per 1000 m^3; filled bubble means a net tow was done, but no salps were found.

2.5. *Other Taxa*

Of the remaining herbivores, the shelled pteropod *Limacina helicina* deserves mention, as it can occur at abundances > 50 · 1000 m^{-3}. Most of the carnivorous zooplankters are found in low abundance. Carnivorous pteropods (*Clione* spp.) are rare (< 1 · 1000 m^{-3}) and the maximum abundance of chaetognaths is < 80 · 1000 m^{-3}. Most amphipods are also rare, although *T. gaudichaudii* is known to form dense surface aggregations, and has been found at abundances of 810 · 1000 m^{-3} [*Piatkowski*, 1985].

3. THE DISTRIBUTION AND DIMENSIONS OF KRILL AGGREGATIONS WEST OF THE ANTARCTIC PENINSULA

One important aspect of the biology and ecology of Antarctic krill is the formation of aggregations. *Everson and Miller* [1994] reviewed questions of the mesoscale distribution and abundance of Antarctic krill, and the application of acoustic technology to determine its biomass during the BIOMASS expeditions (FIBEX and SIBEX). Improved target strength determinations over the last several years have changed biomass estimates from the BIOMASS cruises [*Trathan et al.*, 1995], and continued refinement of target strength estimates is clearly necessary. Both *Miller and Hampton* [1989a] and *Siegel and Kalinowski* [1994] have reviewed the smaller-scale distribution of Antarctic krill and its aggregation dynamics. In particular *Siegel and Kalinowski* [1994] discuss the methods used since the introduction of acoustic technology in the mid-1970s, and the potential causes and advantages of aggregation formation. In the following section, we present observations on krill aggregations collected on a series of cruises conducted west of the Antarctic Peninsula.

3.1. *Material and Methods*

In the late 1980s, a series of 12 cruises took place west of the Antarctic Peninsula to investigate aspects of the physiology of adult and larval krill. Multiple cruises in spring and summer, and single cruises in fall and winter over 4.5 years provided seasonal coverage (Table 2 and Figure 4).

A Simrad 50 kHz echosounder mounted in the hull of the R/V *Polar Duke* was used to locate krill aggregations. The chart record from the Simrad echosounder provided a routine source of information on the distribution and characteristics of aggregations of krill, and variability with season and year. Each cruise was within regions historically abundant in krill, although the same region was not necessarily a dependable source every year. Although the cruise track was a variable search pattern for krill, many of the same locations were visited repeatedly over the years, allowing qualitative and quantitative comparisons of the distribution and characteristics of krill aggregations. Earlier cruises on the R/V *Hero* also used a 50 kHz echosounder to find and sample krill aggregations; observations from these cruises are qualitative and used only to evaluate the generality of these results.

At a minimum of hourly intervals the date, time, position (latitude and longitude), ship speed (over ground), and ship heading were recorded. Any change in ship speed or heading was recorded on the acoustic paper trace with date, time and position. Changes during the hourly intervals were incorporated into the calculations of aggregation dimensions and location. The length of the cruise track was calculated from the hourly position information (Table 2). Time and position of detected aggregations were interpolated between recorded times and positions. The frequency (50 kHz) of the Simrad echosounder and cruising speed (5-10 kts) imposed limitations on the detection and

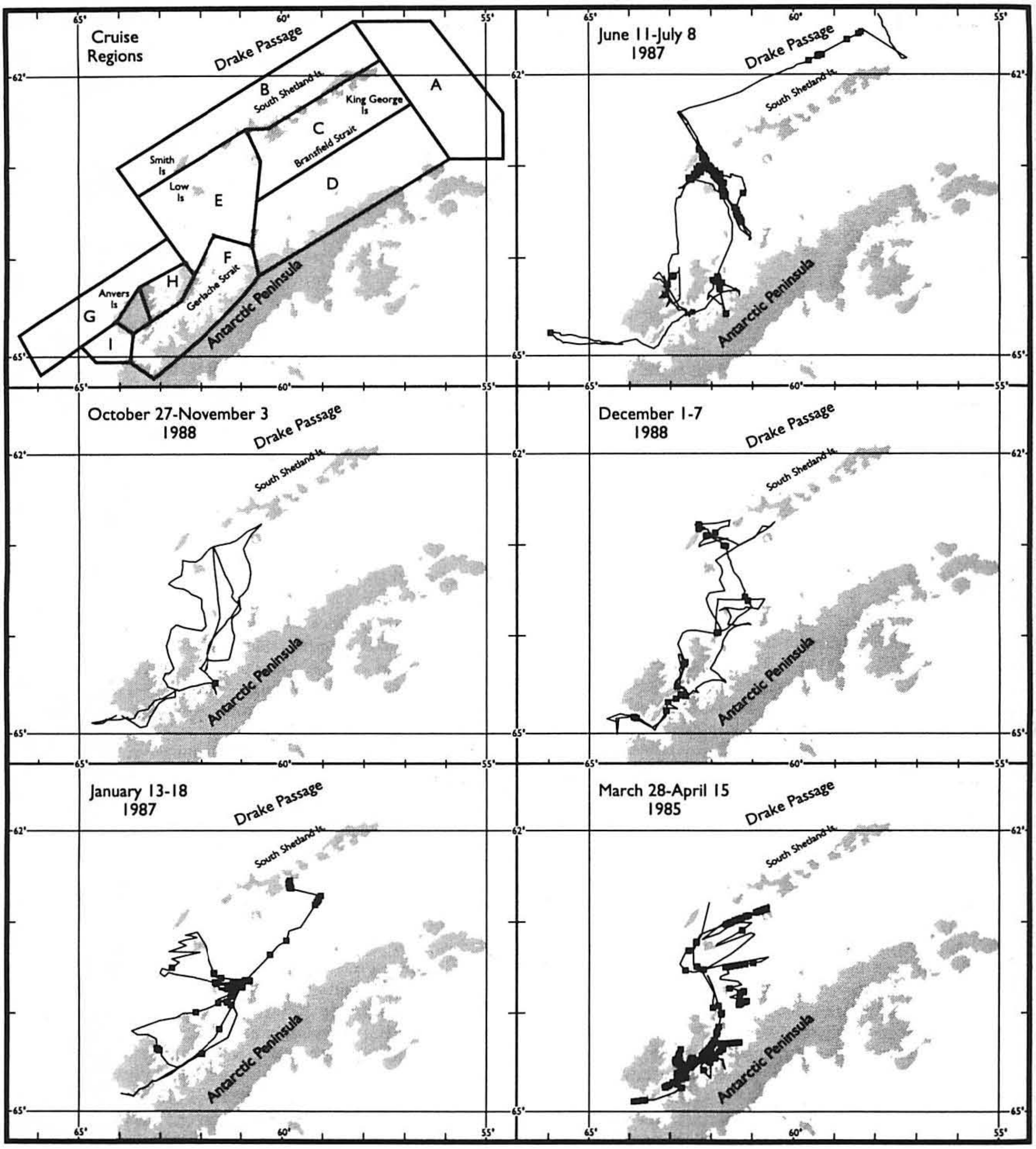

Fig. 4. Cruise regions west of the Antarctic Peninsula (upper left) for all 12 cruises and cruise tracks and aggregation locations for 5 representative cruises. Cruise regions are: A, northeast Bransfield Strait; B, outside South Shetland Islands; C, northern Bransfield; D, Southern Bransfield; E, southwest Bransfield; F, Gerlache Strait; G, west of Anvers Island; H, Dallmann Bay; and I, Palmer Basin. Black lines are the cruise track, each square represents an aggregation.

TABLE 2. Research cruises (n = 12) from February 1985 to December 1988 on the R/V *Polar Duke* west of the Antarctic Peninsula: date, total distance travelled on the cruise track, number of aggregations detected, number of aggregations detected per unit distance, and location. Locations (Figure 1): A, northeast Bransfield Strait; B, outside South Shetland Islands; C, inside South Shetland Islands, northern Bransfield Strait; D, near Antarctic Peninsula, southern Bransfield Strait; E, southwest Bransfield Strait; F, Gerlache Strait; G, west of Anvers Island; H, Dallmann Bay; I, Palmer Basin. sm = only small amount of region investigated.

Season	Year	Dates with Echo Traces	Cruise Trk (km)	No. Schls	Schls per 100 km	Location
Spr	1988	Oct 27 - Nov 3	1415	1	0.1	C (sm), E, F, H, I
Spr	1988	Dec 1 - 7	1701	36	2.1	C (sm), E, F, H, I
Spr	1985	Dec 8 - 16	1898	76	4.0	A, B, C, D, E, F, G, I
Spr	1986	Dec 12 - 14	664	36	5.4	E, F, H, I
Sum	1986	Jan 5 - 13	2144	108	5.0	A, C, D, E, F, G
Sum	1987	Jan 13 - 18	2452	54	2.2	C, E, F, H, I
Sum	1986	Feb 2 - 6, 10 - 13	1168	182	15.6	C, D, E, F
Sum	1985	Feb 23 - 27	1258	224	17.8	A, C, E, F
Sum	1985	Mar 3 - 8	1356	305	22.5	C, E, F, H, I
Fall	1985	Mar 28 - Apr 5	1598	350	21.9	E, F, I, H
Win (mid)	1987	Jun 11 - Jul 8	2865	117	4.1	B, E, F, G, H, I
Win (late)	1985	Aug 24 - Sep 17	1831	131	7.2	D, E, F, G, H, I & sw of Anvers

detectable size of aggregations, respectively. The depth range for detection was 300 m. In practical terms, for the technology available on the R/V *Polar Duke* during these cruises, aggregations less than about 25 m in horizontal dimension could not be distinguished from background noise when cruising at 10 knots. Therefore a lack of detectable krill aggregations along a cruise track in this study does not mean there are no krill in the water column, only that they may be dispersed, of small size and thus more difficult to detect, or in small aggregations less than 25 m across. Several aggregations 25 m across in sequence would be seen as a larger aggregation. Because *Miller and Hampton* [1989b] found a high proportion of krill swarms in this size range, this detection limit also limits our ability to infer that a lack of aggregations means a lack of krill, but does not detract from our ability to examine patterns for krill aggregations larger than 25 m. This data set is unique in that it provides a series of consistent observations from a well-defined region over many years and all seasons. Note that the same echosounder was used throughout this series of cruises. Both chart recorder speed and ship speed were necessary to calculate maximum horizontal dimension and volume from the measured length of an aggregation on the chart paper.

Aggregation characteristics extracted from the echosounder chart recording included: aggregation depth (minimum, maximum, average depth), maximum vertical and horizontal dimension, and inter-aggregation distance if the aggregation was part of a group. An aggregation was defined as part of a group if the inter-aggregation distance was < 5 km. This criteria was based on a frequency plot of inter-aggregation distance for aggregations detected on three cruises. The distribution was highly skewed, with most aggregations within 1 km of each other, a decreasing proportion between 1 and 5 km apart, and the remainder at greater distances (Figure 5). Aggregation volume was based on a cylinder with a height equal to maximum vertical dimension and a diameter equal to maximum horizontal dimension. Only the first pass over an area was used to characterize krill aggregations to avoid including the same aggregation twice in the data base.

One potential source of error lies in our ability to classify acoustic returns as either krill or non-krill. Several criteria were applied before an echo trace was identified as a krill aggregation. Multiple abiotic factors, such as ice at the surface, snow, high wind speeds, ship thrusters and second returns from the bottom, can create returns. Ship and trawl logs were used to separate this abiotic 'noise' from biotic returns. Biotic sources included krill, phytoplankton, salps, and on rare occasions, diving penguins or whales. Targeted net tows along these transects verified general distributions. We also eliminated all aggregations with characteristics similar to echotraces proven with targeted tows to be salps, phytoplankton or salp/*Thysanoessa* spp. mixtures. Krill aggregations were a distinct blotch with definite edges and mild undulations (see *Miller and Hampton* [1989b] for examples). Phytoplankton, on the other hand, tended to be found in more continuous fuzzy strips of lesser vertical extent; and long, steeply wavy traces with a diffuse lower boundary were usually composed of salps. Ground truthing of these criteria was primarily from targeted tows of traces with partic-

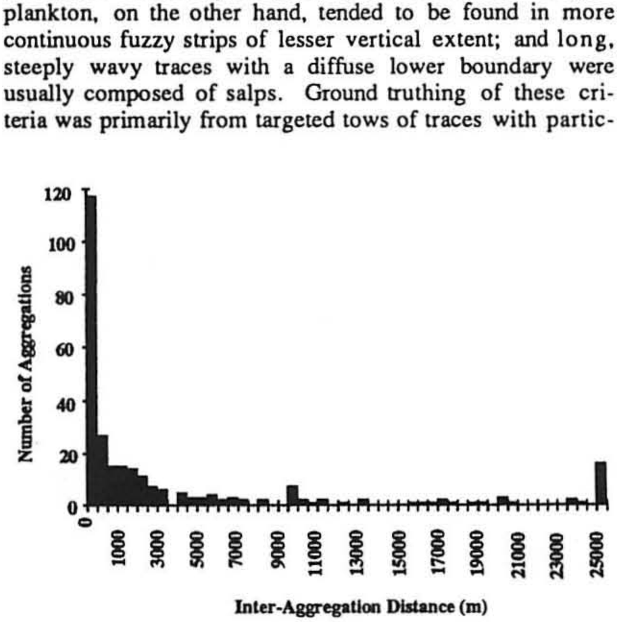

Fig. 5. Antarctic krill aggregations. Frequency distribution for inter-aggregation distances measured on three cruises: December 1986, January 1987, and February 1985.

TABLE 3. Aggregation dimensions for aggregations detected on 12 cruises from February 1985 to December 1988 west of the Antarctic Peninsula: N, median and ranges for vertical and horizontal dimensions (in meters) and volume calculated as a cylinder (10^5 m^3). Dimensions include: minimum (with absolute range), maximum, and mid-depth, vertical extent (with range) and horizontal extent (with range), and volume. The depth of the transducer (5 m) was taken as the zero depth.

Year	Cruise Dates with Echo Traces	N vert	Min Depth (m)	Max Depth (m)	Mid-Depth (m)	Vert Extent (m)	N horz	Horiz Extent (m)	Vol (10^5 m^3)
1988	Oct 27 - Nov 3	1	7	11	9	5	0	nd	nd
1988	Dec 1 - 7	34	29 (0-99)	38	33 (4-92)	11 (2-50)	20	62 (32-947)	0.33 (0.05-47)
1985	Dec 8 - 16	62	49 (0-110)	61	55 (10-95)	13 (3-47)	62	98 (37-1334)	1.07 (0.09-397)
1986	Dec 12 - 14	36	43 (0-110)	58	50 (7-105)	11 (3-41)	36	69 (36-229)	0.41 (0.03-9.49)
1986	Jan 5 - 13	100	28 (0-115)	42	35 (1-105)	17 (2-45)	99	98 (48-977)	1.17 (0.03-10,025)
1987	Jan 13 - 18	51	8 (0-102)	25	17 (4-90)	16 (4-65)	50	104 (49-1989)	2.61 (0.35-1694)
1986	Feb 2 - 6, 10 - 13	180	12 (0-123)	30	20 (3-116)	13 (5-38)	178	54 (23-442)	0.29 (0.03-59)
1985	Feb 23 - 27	218	23 (0-128)	41	32 (6-122)	16 (3-93)	213	71 (32-888)	0.55 (0.03-103)
1985	Mar 3 - 8	226	18 (0-139)	33	25 (5-135)	13 (5-192)	225	72 (20-11,600)	0.59 (0.03-15,702)
1985	Mar 28 - Apr 5	343	0 (0-185)	20	10 (4-179)	14 (3-43)	329	102 (29-2790)	1.35 (0.05-816)
1987	Jun 11 - Jul 8	39	25 (0-120)	70	50 (5-100)	33 (3-92)	39	396 ($57\text{-}143 \cdot 10^3$)	31.86 ($0.41\text{-}1.6 \cdot 10^6$)
1985	Aug 24 - Sep 17	63	5 (0-120)	27	18 (4-87)	18 (2-48)	53	211 (24-4437)	9.99 (0.04-4904)

ular characteristics, but information on krill caught in the seawater intake screen of the ship or visual sightings of aggregations amongst ice floes or at the surface were helpful when aggregations were in the upper 10 m.

3.2. *Results*

3.2.1. Horizontal distribution and abundance of krill aggregations. Most cruises were seven to ten days long with cruise track distances from 1200 to 2200 km. Although cruise tracks differed in exact location, during most cruises data was collected from several regions including the southern Bransfield, Dallmann Bay, Gerlache Strait and Palmer Basin (Figure 4, regions C, E, F, H and I, Table 2). In early spring (Figure 4, middle left panel), only one aggregation was observed in over 1400 km of cruise track. Aggregations were detected more frequently, 2-5 per 100 km, during the five cruises conducted in late spring and early summer (December and January); however, the distribution was patchy with aggregations absent from some portion of the transect each cruise, although the region without aggregations was not the same during all cruises. The highest aggregation counts per 100 km were observed during the late summer, early fall (February through April) and these cruises were characterized by aggregations throughout most of the regions sampled with high abundances in Gerlache Strait. During mid-winter (June/July), most of the aggregations were detected in the low ice or no ice conditions observed for the southwest Bransfield Strait and northern Gerlache Strait (Figure 4, upper right). In the heavy pack ice regions sampled during the mid-winter cruise, aggregations were not detected with the exception of a single aggregation south of Anvers Island. In late winter/early spring of 1985, krill aggregations were found predominantly in the nearshore areas (areas I, H, and F) with a few in the southeastern Bransfield (area D); they were not associated with heavy pack ice.

Seasonal differences were observed in the number of aggregations and the total cross-sectional area of these aggregations normalized by the length of the cruise track (Figure 6*a, b*). The peak in the maximum number of aggregations per km occurred before the peak in total cross-sectional area. The median cross-sectional area (Figure 6*c*) was very similar throughout the year with the exception of winter observations when the aggregations were consis-

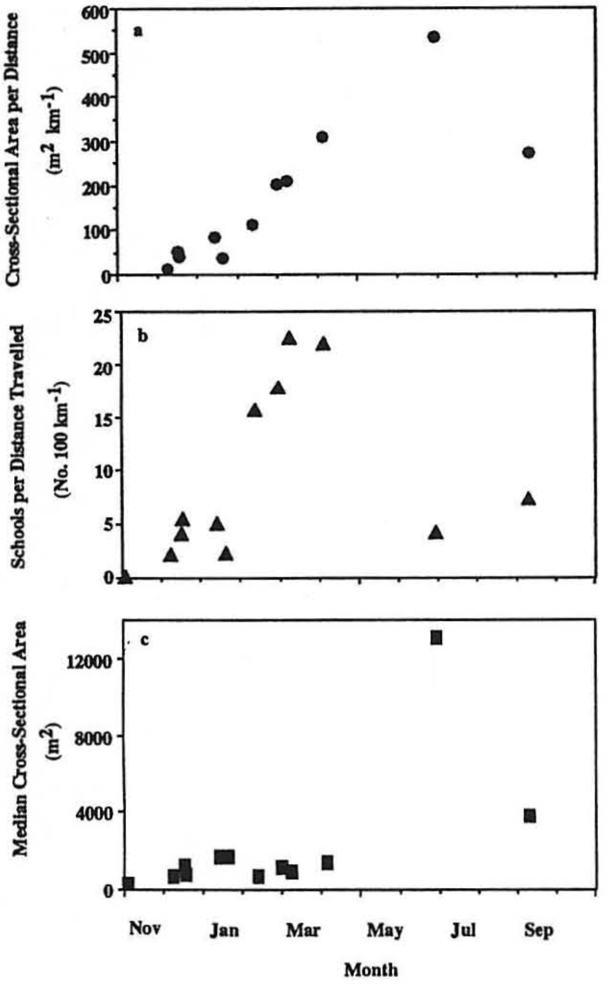

Fig. 6. Antarctic krill aggregations. Cruise aggregation statistics normalized to total distance traveled: (*a*) vertical cross-sectional area (m^2) detected per km over the seasons (n=11 cruises); (*b*) number of aggregations detected per km over the seasons (n=12 cruises) ; and (*c*) median cross-sectional area from a single cruise (n=12 cruises).

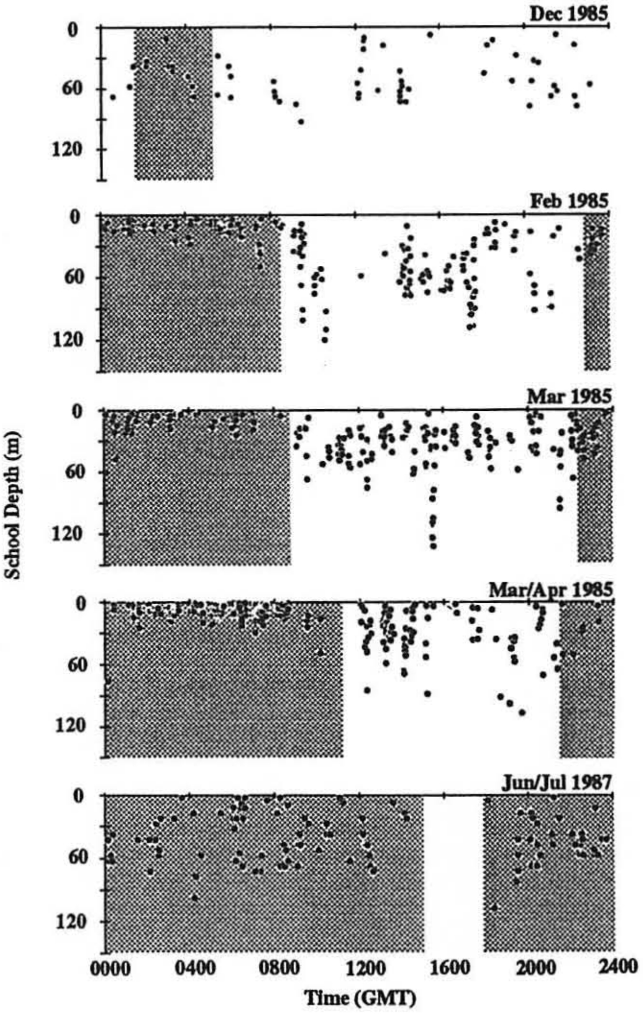

Fig. 7. Antarctic krill aggregations. Vertical distribution of average aggregation depth throughout the day for 5 cruises west of the Antarctic Peninsula from late spring to mid-winter. The shaded area is from sunset to sunrise for 64°S (latitude of Palmer Station). Time is in GMT (Greenwich Mean Time) which is 3 hours ahead of local time in spring and summer, 4 in fall and winter. Zero depth is the depth of the transducer.

tently much larger. The steady increase in total cross-sectional area between spring and fall is thus due primarily to the increase in the number of aggregations detected. Though no quantitative data are available, a rapid increase in aggregation count during the early spring was observed in 1983 aboard the R/V *Hero* when no aggregations were detected on the first transect through Palmer Basin in December, yet ten days later several aggregations were detected and sampled. This increase in aggregations in the same area during spring was quantitatively demonstrated for 1988 (Figure 4, middle left and right).

3.2.2. Vertical distribution of krill aggregations. Krill aggregations were found in the upper 120 m of the water column during all cruises (Table 3, depth range), with the exception of a few aggregations found between 120 and 185 m during the two March cruises. Median mid-depth of aggregations ranged between 9 and 55 m, with no apparent seasonal trend (Table 3). For depth of the aggregation in the water column, distributions were not strongly skewed, and median (Table 3) and mean depth (Figure 7) were very similar.

The mean depth of krill aggregations within a 24 h period followed a seasonal pattern, as represented by five cruises (Figure 7). Around the solstices (December and June/July) when daylength is either very long (> 20 h) or very short (< 4 hours), aggregations were dispersed evenly throughout the upper 90 m during the entire 24 h, with a few deeper aggregations (Figure 7, upper and bottom panels). However, when periods of light and dark are of similar length, as in late February, March and April, aggregations were found in a narrow shallow (top 30 m) layer at night, and dispersed throughout the upper 120 m of the

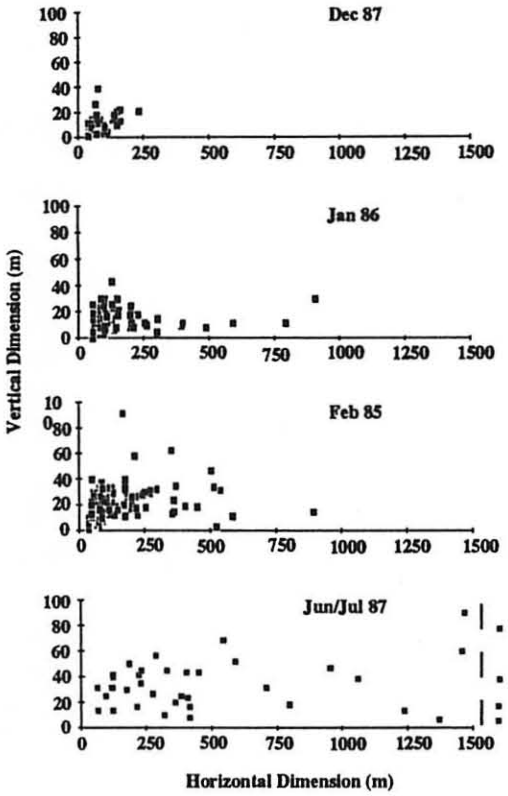

Fig. 8. Antarctic krill aggregations. Paired horizontal and vertical dimension of aggregations detected during four of the 12 cruises: December 1986 (36 aggregations), January 1986 (99 aggregations), February 1985 (213 aggregations), and June/July 1987 (39 aggregations, 4 large and very large aggregations off horizontal scale).

water column during the day (Figure 7, middle three panels). The period of dispersal correlated closely with sunrise, while the formation of a narrow shallow layer was associated with sunset.

Although daylight dispersal was the general trend when all aggregations were plotted, the depth distribution of aggregations was not as greatly dispersed nor as deep in the water column on all daylight segments of any one cruise. For example, for the first five days of the January 1986 cruise, 87% of the aggregations (n = 30), regardless of time of day, were between 0 and 30 m (79% of daylight aggregations were in the top 30 m.). These daytime observations are similar to nighttime distributions during times of a strong diel signal. For the entire cruise only 45% had mid-depths < 30 m (41% of daylight aggregations), similar to the overall pattern found for times during the year when the diel light signal is weak. This variability in the depth distribution of aggregations was common and would obscure a diel vertical migration pattern.

3.2.3. Dimensional characteristics of aggregations. The cruise track during the winter of 1987 (Figure 4, upper right) also paralleled the ice edge north of the South Shetland Islands. The longest, continuous trace on the echosounder was detected in this area as a 143 km long band between 10 and 20 m deep along the ice edge. Due to the length of the band we hesitate to term it an aggregation. Four net tows at intervals along the length of the band verified that it was composed exclusively of larval *E. superba*. Due to the magnitude and anomalous nature of this band of krill, both in dimension and in content, it was not used in our analysis of aggregation dimensions.

As was true for previous investigations [*Kalinowski and Witek*, 1981; *Miller and Hampton*, 1989b], the distribution of the horizontal dimensions of aggregations is strongly positively skewed, with median values (Table 3) less than the mean. The vertical dimension of aggregations did not vary greatly, either within a cruise or among the spring and summer cruises. However, the vertical dimension of mid-winter aggregations was at least twice that of aggregations from all other cruises. The range was commonly between 2 m and about 50 m, with individual aggregations of greater vertical extent found only during the three cruises in late February, early March and June/July (Table 3). The maximum horizontal dimension was more variable, increasing over the seasons from 20 m to 5 km, with the greatest range in fall and winter (Table 3, Figure 8).

A seasonal pattern of maximum aggregation size in mid-winter, decreasing in late winter, with smaller sizes in spring and summer includes both the vertical and hori-

TABLE 4. Degree of grouping in aggregations detected on 12 research cruises from February 1985 to December 1988 west of the Antarctic Peninsula: Date, number of aggregations and groups, number and percent of aggregations in any size group, percent of aggregations in groups of 2 and > 5 aggregations.

Year	Cruise Dates with Echo Traces	No. Aggr	No. Groups	No. Aggr in Groups	% Aggr Groups n = 2 - 59	% Aggr Group n = 2	% Aggr Group n > 5
1988	Oct 27 - Nov 3	1	0	0	0	0	0
1988	Dec 1 - 7	36	7	20	56	43	0
1985	Dec 8 - 16	76	15	51	67	53	20
1986	Dec 12 - 14	36	7	26	72	29	14
1986	Jan 5 - 13	108	22	84	78	41	18
1987	Jan 13 - 18	54	8	33	61	25	38
1986	Feb 2 - 6, 10 - 13	182	18	166	91	28	50
1985	Feb 23 - 27	224	37	195	87	38	32
1985	Mar 3 - 8	305	41	267	88	29	37
1985	Mar 28 - Apr 5	350	25	305	87	8	56
1987	Jun 11 - Jul 8	117	16	82	70	25	38
1985	Aug 24 - Sep 17	131	14	66	50	43	29

zontal dimension (Figure 8), and was seen in median cross-sectional area (Figure 6c), in median volume (Table 3), and in the frequency distribution of aggregation volumes by season (Figure 9). Small aggregations are missing from the mid-winter distribution. Large aggregations (> 1 km in horizontal dimension) were found at all times of year except spring. However, less than 1.5% of aggregations detected during late spring and summer cruises (December-February) were greater than 1 km in horizontal dimension, with 2% in fall (March-April) and 15% in winter (June-September) (Figure 8). Numbers of large aggregations detected per km also increased over the season, from < 1 (range 0 to 1.6) in spring and summer to 3.7 (2.5 to 5.2) in fall and 3.0 (2.7 to 3.1) per 1000 km in winter. For those three summer cruises (of a total of seven) with large aggregations, the proportion of large aggregations is similar to that found in fall or late winter, but the abundance (number per 1000 km) is less than either fall or winter by a factor of 2 or 3.

The frequency distributions of aggregation volume in spring/summer and fall are very similar, with most of the aggregations smaller than 10 · 10^5 m^3. Large aggregations (100 to 1000 · 10^5 m^3) represented a much larger proportion of all aggregations during the mid- and late winter compared to all other seasons. Very large aggregations (1000 to 10,000 · 10^5 m^3) were absent from or rarely found during cruises extending from October through April. This size category, however, represented 12 and 2% of all aggregations observed during the mid-winter and late winter, respectively.

Concentrations of krill can be viewed as individual large aggregations or groups of smaller aggregations, where aggregations are in a group where inter-aggregation distance is < 5 km. For these cruises, median inter-aggregation distance within a group ranged from 300 to 1500 m throughout the year, with no clear seasonal pattern. The degree of grouping, as represented by the proportion of aggregations found within a group, increased from a low in late spring to a maximum in February, decreasing throughout the fall and winter to late winter/early spring values close to those in December (Table 4). The size of the group varied from 2 to 59 aggregations, but the size of the groups tended to increase throughout the spring and summer, from about half in small groups of 2 early in the summer to half in groups of greater than 5 by fall (Table 4).

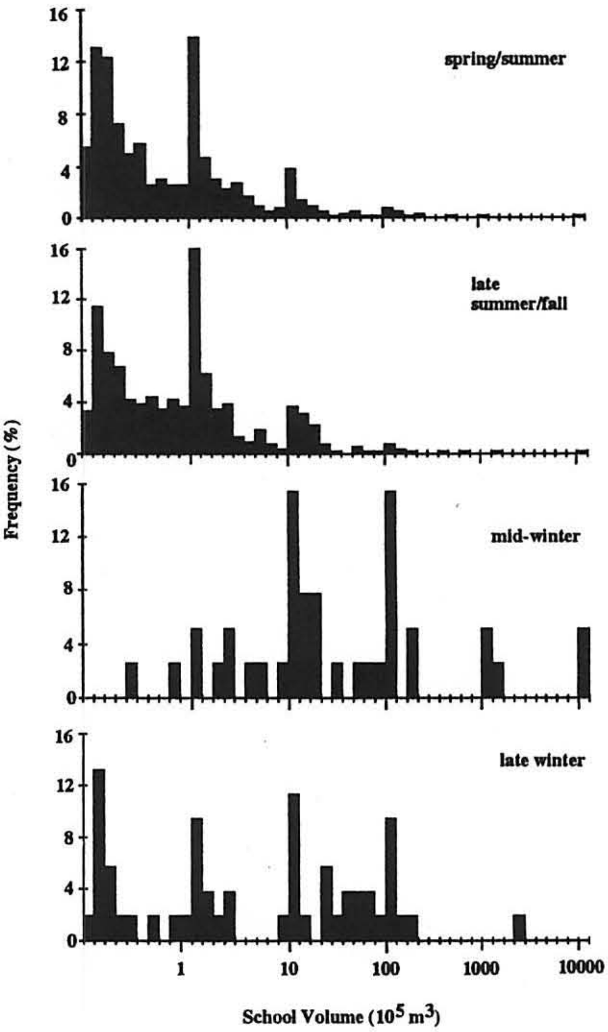

Fig. 9. Antarctic krill aggregations. Volume (in 10^5 m^3) frequency distribution of aggregations at different times of year. Volume categories increase logarithmically. The 12 cruises are grouped into: spring and summer (December- February, 7 cruises, 658 aggregations), late summer and fall (March-April, 2 cruises, 551 aggregations), mid-winter (June-July, 1 cruise, 39 aggregations), and late winter (August/September, 1 cruise, 53 aggregations).

3.3. *Discussion*

3.3.1. General data considerations. The collection methods used to obtain the acoustic observations described in this paper may be considered antiquated in comparison to current acoustic technology. The frequency employed, 50 kHz, is lower than that commonly used today and so smaller sized organisms may have been less detectable. The backscattering data was logged ping-by-ping only to the chart recorder so post-processing was manual and not computer automated. Estimates of the vertical dimensions (maximum height, minimum, maximum and mid-depth) of identified krill aggregations from echotraces were straightforward, whereas measurements of horizontal dimensions (maximum length, distance between schools) were sensitive to the speed of the ship. The impact of these apparent limitations of the dataset, however, was greatly reduced as a result of the consistency with which the dataset was collected and post-processed. Care was taken to ensure that all observations used in this study were obtained using a single set of echosounder configuration parameters over a narrow range of ship speeds (5 to 10 kts). Part of the value of this data set is that it provides a series of consistent observations from a well defined region over many years and all seasons, a major objective of long-term ecological research.

3.3.2. Seasonal variability. The general seasonal pattern synthesized from the acoustic observations is that the number of aggregations detected per km increases from low values in the spring to a maximum in late summer, early fall and then decreases through the winter. The total cross-sectional area of these aggregations follows a similar pattern but the maximum is observed during the winter.

The increase in the number of aggregations is not a function of large aggregations splitting into more numerous smaller ones, as the median size of individual aggregations remains about the same throughout the period spring to fall. During the winter, the median cross-sectional area was much larger and aggregations of extensive cross-sectional area (> 1000 · 10^5) were observed predominantly during the winter. The maximum in total cross-sectional area observed during the winter may be explained by two alternative mechanisms. First, more of the krill population may be within aggregations of detectable size, i.e., around 25 m for the ship speeds used in this study. Second, the number of krill within an aggregation may be the same, but interkrill distances may change with season, changing the density (gm m^{-3}) within an aggregation. With greater interkrill distances in winter than in summer, aggregations with the same number of krill will have a greater cross-sectional area in winter.

The acoustic observations also support the hypothesis of *Siegel* [1987, 1989] of post-summer movement of krill aggregations into inshore areas along the Antarctic Peninsula. The inner shelf was consistently sampled throughout most of the cruises. Horizontal movement inshore in the fall would increase the number of krill aggregations detected in the Gerlache Strait and other nearshore areas, as observed (Figure 4, January versus March/April, bottom panels) and would also increase the number of aggregations detected per distance traveled and the total cross-sectional area detected in the late summer and fall, as observed (Figure 6).

3.3.3. Interannual variability. Variability between years, for a given season, in the general patterns of krill distribution and abundance, has been well documented. The region north of Elephant Island and in the Bransfield Strait has historically been considered an area abundant in krill throughout the summer based on observations from the Discovery Expeditions, and from more recent BIOMASS and AMLR cruises [*Hewitt and Demer*, 1994]. During the first series of SIBEX cruises during summer 1983/1984, Antarctic krill were scarce in this region, with salps dominating the biomass of macrozooplankton. Our observations over the same time period in 1983/1984 indicate that krill were found consistently in Gerlache Strait over the entire season, and, moreover, that reproducing krill were actually inshore that year, another abnormal situation [*Hofmann et al.*, 1992] (L. Quetin, personal communication, 1984). The next year Antarctic krill were found in abundance in late March 1985 (second SIBEX cruise) in both the Bransfield and Gerlache Straits [*Siegel and Kalinowski*, 1994]. As would be predicted by a fall horizontal migration, no krill were detected in either the offshore or inshore region south of Anvers Island (central Palmer LTER region) [*Siegel and Kalinowski*, 1994]. Thus, in the same year and season, numbers of Antarctic krill aggregations detected on the mesoscale can change from 'many' forming 'concentrations' to undetectable. With only a year separating the two surveys of the Bransfield/Elephant Island region, recruitment failure and immediate replacement does not appear to be a reasonable mechanism to explain interannual regional variability in this long-lived animal.

Large scale changes in circulation patterns have been postulated as a mechanism to explain these distribution changes [*Sahrhage*, 1988]. Interannual shifts in atmospheric pressure centers likely cause frontal regions and the associated water masses and eddies to shift geographically. This interpretation is supported by stock densities of Antarctic krill in the Elephant Island area that increase by a factor of 10 between 1981 and 1982, only to decrease the following year by a factor of 5 [*Siegel and Loeb*, 1995]. In another example, acoustic estimates of krill biomass in the same region decreased by a factor of three from 1984 to 1985, then increased by nearly a factor of 10 by 1987 [*Hewitt and Demer*, 1994]. Such large swings in population size are not likely to be the results of recruitment failure or local predation pressure [*Murphy*, 1995], but more likely to large scale changes in atmospheric and connected oceanic circulation patterns [*Priddle et al.*, 1988].

3.3.4. Winter/spring aggregations, dispersal and formation. Since data on aggregations of krill in the water column in the winter are scarce, the results from the two winter cruises reported here provide important additional observations. Krill aggregations were detected in the water column west of the Antarctic Peninsula (Figure 4, Table 2), under regional winter conditions of light ice cover (late winter 1985) and heavy ice cover (mid winter 1987), but in areas of either open pack or open water on the shelf and in the straits. In contrast [*Siegel*, 1989] detected almost no aggregations in the open-water zone offshore of the pack ice along the Antarctic Peninsula in 1986 and 1987 [*Sahrhage*, 1988] until the pack ice began to retreat in the spring. More recently, on a small spatial scale, acoustic measurements made with an ADCP in the Gerlache Strait during the winter of 1992 showed the presence of euphausiid aggregation distributions which were similar in character to those observed during the summer and fall in this region, and no evidence for abundant aggregations immediately below surface sea ice [*Zhou et al.*, 1994].

Results from acoustic studies in the Weddell Sea relevant to the influence of the pack ice on krill aggregations also show variability. During an AMERIEZ (Antarctic Marine Ecosystem Research in an Ice Edge Zone) spring cruise in the northern Weddell Sea, krill aggregations were seen both in open water and under the retreating pack ice [*Daly and Macaulay*, 1988], in contrast to the first EPOS (European *PolarStern* cruise) leg slightly earlier in the season when no clear aggregation was observed [*Siegel et al.*, 1990]. Later that same spring, on the second EPOS leg in December, few and small aggregations were detected in the ice, with increasing numbers and larger aggregations observed in more open water [*Cuzin-Roudy and Schalk*, 1989]. The variability in observations of distribution and abundance in winter may be partially a result of the interplay of ice and proximity to inshore regions. For example, aggregations which migrate inshore during the fall and stay through the winter would increase the abundance of aggregations coincident with the region of seasonal ice cover in comparison to the open water zone offshore.

3.3.5. Aggregation dimensional charac-

teristics. Most previous studies suggest that krill have a tendency to form small, compact swarms [*Macaulay et al.*, 1984; *Miller and Hampton*, 1989a, b; *Siegel and Kalinowski*, 1994; *Watkins et al.*, 1986], a result confirmed in this study for the summer months, but not for the winter months. In the Antarctic Peninsula region during SIBEX, the maximum horizontal dimensions of krill aggregations ranged from 9 to 1800 m, with a median value of about 45 m, and mean vertical dimensions of about 11 m [*Kalinowski and Witek*, 1985; *Siegel and Kalinowski*, 1994]. These dimensions correspond well to aggregation dimensions found in this study during the spring and summer. However, on three cruises, the range in horizontal dimensions far exceeded those found in summer. These large aggregations found in fall and winter, however, cannot really be classified as 'super swarms' according to the definition in *Kalinowski and Witek* [1985], because the vertical dimensions were not within the range of those usually considered typical of a 'super swarm'.

An increase in aggregation size from spring to mid-summer (January) was observed in the Scotia and Weddell Seas from November to January, in contrast to the situation west of the Antarctic Peninsula (Figure 6c). In the Weddell and Scotia Seas, larger aggregations were more commonly found in open waters than ice-covered areas [*Sprong and Schalk*, 1992]. But during this time frame, the increase in aggregation size was linked to a decrease in the numbers of swarms, indicating a merging of numerous small aggregations into fewer larger aggregations. The difference here may partially be a function of the minimum size aggregation detected. In this study, very small aggregations would not have been detected, so a decrease in their number would also have gone undetected.

West of the Antarctic Peninsula, large aggregations form a larger proportion of aggregations in fall and winter, and also increase in absolute abundance by a factor of two or three. There are three basic alternative explanations for this pattern: foraging, migration or predation. The formation of the large aggregations, however, could be driven by different processes in different seasons. *Antezana and Ray* [1983] suggested that foraging was more efficient in small aggregations, and that small schools would be associated with horizontal movement as the krill searched for food. Once food was discovered, large semi-stationary aggregations would form as the small aggregations joined. The large aggregations found on some cruises in spring and summer may be 'feeding' aggregations, and more research on the characteristics of such aggregations is clearly merited. *Antezana and Ray* [1983] also suggested that when the food resources became depleted, the large aggregation would break up and the process of searching for a new food source would begin again. Under this hypothesis, the aggregation patterns would be a function of the foraging abilities and requirements of the krill themselves.

Antarctic krill from offshore are thought to migrate inshore in the fall [*Siegel*, 1987, 1989], but it is not known if they migrate in small or large aggregations. They also have a suite of winter-over mechanisms that allows them to survive the winter without eating [*Quetin et al.*, this volume], so they would not have to forage. The presence of large aggregations inshore in the fall and winter and the frequent occurrence of large and very large aggregations in winter is consistent with the concept of small summer foraging aggregations collapsing into large aggregations coincident with the disappearance of summer food. Breakup and dispersal to search for a food source is not necessary. The degree of grouping and large number of aggregations in a group also support this coalescing of small groups of small aggregations into larger groups of small aggregations to one larger aggregation. The peak in grouping corresponds with the peak in number detected per km in the fall, post movement onshore, and prior to the actual merging of aggregations into the large winter aggregations. However, in late winter and early spring, large aggregations would start to break up and disperse coincident with an increasing energy requirement for seasonal reproduction [*Quetin et al.*, this volume].

Alternatively this pattern may be an evolutionary remnant of the time when whales were the dominant predator. Whales forage best on large aggregations, so in the summer in areas where whales are feeding on krill, a large aggregation would not confer the same degree of protection as a small one. The advent of fall coincides with the departure of the whales and the general inshore shift in the abundance and size of aggregations. Under these conditions we might predict that aggregation size will vary with both predation pressure and type of predator. Vertical migration is another possible response to predators as discussed below.

3.3.6. Vertical distribution of krill. Generalizations about vertical migration in adult *E. superba* have been difficult, and evidence is as contradictory as for herbivorous copepods (see section 2.3). Although diel vertical migration appears to be common [*Mauchline and Fisher*, 1969; *Croxall et al.*, 1985; *Godlewska and Klusek*, 1987; *Loeb and Schulenberger*, 1987; *Fraser et al.*, 1989; *Demer and Hewitt*, 1995], it is by no means a consistent pattern [*Everson*, 1983; *Lancraft et al.*, 1989; *Schulenberger et al.*, 1984]. Some of this inconsistency may be a function of the fact that results were from individual cruises isolated in space and time that spanned all seasons and hydrographic regimes.

With this series of cruises throughout the seasons we can look for general patterns in the vertical distribution of krill aggregations. Throughout much of the year most aggregations were within the top 120 m. Although there was no obvious seasonal trend in mid-depth of aggregations, the range was somewhat greater in late summer and fall than in either mid-summer or winter when most aggregations were in the upper 90 m (Figure 7, Table 3). This summer/winter contrast is not the same as in the Weddell Sea, where krill aggregations tended to be shallower in winter [*Lancraft et al.*, 1989].

Of particular importance is the observation that when periods of day and night are a similar length, krill aggregations definitely are shallower at night. In mid-summer and mid-winter, when days are either very long or very short, this diel shallowing was not apparent. When a diel shallowing does occur, sunset and sunrise appear to be the signal for initiating either the upward movement or the downward dispersal. Regardless of season, aggregations are still dispersed throughout the water column during the daylight hours. From the data available it is not clear whether the signal required for night time shallowing is a contrast between day and night light intensities or a sustained period of time of either day or night light levels. Since aggregations in the winter were also dispersed throughout the water column, the former appears more likely.

Seasonal or oceanographic conditions such as temperature, nutrition and optical conditions may play an important role in the vertical distribution of krill. Many euphausiids seek a preferred isolume [*Mauchline and Fisher*, 1969], suggesting that the extent of daylight dispersal may be a function of the transparency of the water column. Other investigators have suggested that vertical distribution patterns may be a response to a thermocline or even to feeding conditions or predation pressure (reviewed by *Siegel and Kalinowski* [1994]). Daytime light levels in the water column are altered not only by surface irradiance, but also by the transparency of water, itself a function of glacial melt, phytoplankton blooms, and other particulates in the water column. For example, *Arimoto et al.* [1979] observed day/night differences in vertical migration of *E. superba* during a cruise in late December, but a month later in the same area most aggregations were below 50 m and there was no day/night variation. One difference was the appearance of a bloom of *Thalassiothrix antarctica* that discolored the water; and the authors suggested the cause was that krill are rarely found in waters with high concentrations of *T. antarctica*. However, if *E. superba* was responding solely to light levels, the dense phytoplankton bloom could have created a light environment similar to that in winter when day and night light levels are the same, and krill are dispersed in the water column day and night.

Antarctic krill may also alter vertical distribution patterns in response to predators, as do some species of zooplankton [*Bollens and Frost*, 1989; *Bollens and Frost*, 1991]. During the mid-winter cruise (1987), although the overall vertical distribution pattern did not show a day/night difference (Figure 7), in an area of loose pack ice with large concentrations of fur seals and an abundance of seabirds the depth distribution of two aggregations over a period of nearly a day in the western Bransfield Strait showed a distinct movement from daytime depths of about 100 m to about 10 m at night [*Fraser et al.*, 1989]. This observed diel vertical migration may be an alteration in the behavior of krill in the presence of abundant visual predators. Generally, the complex patterns we see in the vertical distribution of Antarctic krill will only be totally understood when we understand which environmental cues krill sense and the levels necessary to elicit a response and simultaneously observe biotic factors like phytoplankton composition and predation pressure.

For larval krill, diel vertical distributions are documented with net tows, not hydroacoustic surveys, and as a result data are scarce. However, in the few early studies, strong diel vertical migrations from 200 or 300 m to the surface were documented for larval stages from calyptopis to adolescent in summer [*Fraser*, 1936; *Nast*, 1978] (L. Quetin, R. Ross, personal communication, 1988). In addition, either a portion of the population does not migrate daily or the timing of the diel migration varies for groups within the population as some larvae were always found in the surface layers even in daylight. Many standard oceanographic programs tow from 0-200 m for larval krill [*Loeb and Schulenberger*, 1987]; if the larvae are at 200-250 m in the day as observed in some locations, then the net will not be fishing at the appropriate depths in the day, miss at least a portion of the population, and underestimate larval abundances by an unknown amount.

Conditions in winter and spring appear to differ from those in summer. In a June visit to the ice edge by the R/V *Discovery*, larval krill were in a shallow layer close to the surface day and night [*Fraser*, 1936], as was also seen outside the South Shetland Islands in winter 1987 (this study). In spring (October/November), larval and adolescent forms dominated the catch along the ice edge, and also were almost always at the surface. Larval and adult krill therefore may occur at different depths in some locations and some seasons. South of Elephant Island in summer 1976, *Nast* [1978] found that adult and larval krill were both vertically migrating, and although the extent of the diel vertical migration was somewhat greater in adults, the two groups were occupying nearly the same depth horizon day and night. However, further south in the Bransfield and Gerlache Straits, where aggregations of adult krill were between 0 and 120 m day or night, larvae were found to undergo a diel vertical migration from about 250 m to the surface in the late summer, but appeared to be restricted to a narrower surface layer in winter and spring (L. Quetin, R. Ross, personal communication, 1988). West of the Antarctic Peninsula, although both adult and larval krill distributions are linked to the seasonal ice, only the larval population has been observed closely coupled to the under ice surface in winter [*Quetin et al.*, 1994; *Quetin et al.*, this volume]. This habitat segregation in winter, with larvae linked to the under ice surface and adults away from the ice surface, has been attributed to 'risk balancing', i.e., balancing the relative strength of the requirement for food and the need to avoid predation [*Quetin et al.*, this volume].

4. SUMMARY

This chapter integrates both historical data and newly analyzed data to present a description of the horizontal and vertical distribution of several dominant zooplankton taxa that have been selected by the Palmer LTER program as representatives of the pelagic marine ecosystem along the west coast of the Antarctic Peninsula. These descriptions represent historical accounts that will be compared to datasets collected by the Palmer LTER program, and that will provide a context for initial analyses and interpretations. Used wisely, these historical data sets will prove to be a valuable asset that will extend the spatial-temporal scales of Palmer LTER analyses. Both new and old data discussed in this chapter further illustrate the requirement for long-term data sets collected with consistent methods. Without such data sets, studies of the biology and ecology of both long-lived zooplankton and short-lived zooplankton, that appear to require specific environmental conditions to flourish, will suffer from the short-term approach and the inability to put results in the context of the 'invisible present'.

Past and current international and national efforts outside the Palmer LTER region will provide valuable data sets for comparative analyses (e.g., BIOMASS and BOFS (British Ocean Flux Study), RACER (Research on Antarctic Coastal Ecosystem and Rates), AMERIEZ, and CCAMLR (Committee for the Conservation of Antarctic Marine Living Resources)). Information on the seasonal and interannual variability of these same taxa living in somewhat different habitats or under different environmental regimes will help us understand the mechanisms behind such variability. For example, the northern tip of the Antarctic Peninsula and the Bransfield Strait area was a focus for the BIOMASS program, with historical results that have been recently reviewed in *Southern Ocean Ecology - The BIOMASS Perspective* [*El Sayed,* 1994]. The AMLR program (United States National Ocean and Atmospheric Association) is a long-term study oriented around food web dynamics in the Elephant Island region, an area with a long history of oceanographic research. These two long-term sites have significant differences in both hydrographic and sea ice regimes, yet many of the same zooplankton taxa are present. The AMLR program, sampling in these more northerly latitudes and in more oceanic waters, will prove an intriguing comparison to the primarily neritic and transitional zone Palmer LTER.

Acknowledgments. Data on krill aggregations were collected on a series of cruises funded by Office of Polar Programs through several grants to Quetin and Ross (DPP82-18356, DPP85-18872, DPP88-20589, and OPP91-17633). Data on salp abundance and distribution were collected on Palmer LTER cruises, also funded through Office of Polar Programs (OPP90-11927). Numerous volunteers and students participated on these cruises. Without their hard work and enthusiasm the data would not exist, and they deserve our hearty thanks. A special acknowledgment goes to D. Martin who extracted the data on krill aggregations from the chart records with efficiency, consistency, and unfailing good nature. D. Steinberg and C. Wyatt were particularly helpful at different junctures in the krill data analysis. P. Hopkinson was instrumental in analysis of the salp data. These cruises would not have been possible without the support of the captains and crews of the R/V *Polar Duke* (all cruises except fall 1993), the captain and crew of the R/V *Nathaniel B. Palmer* in fall 1993, and the logistical support of Antarctic Services (1985-1989), and Antarctic Support Associates (1990-1994). Comments from three reviewers (V. Siegel, J. Watkins and one anonymous reviewer) improved the organization and the content of this chapter. This is Palmer LTER Publication No. 85.

REFERENCES

Andriashev, A.P., A general review of the Antarctic fish fauna, in *Biogeography and Ecology in Antarctica*, edited by P.V. Oye and J. Van Mieghem, pp. 491-550, Junk Publishers, The Hague, 1965.

Antezana, T., and K. Ray, Aggregation of *Euphausia superba* as an adaptive group strategy to the Antarctic ecosystem, in *On the Biology of Krill, Euphausia superba,* Berichte zur Polarforschung, 4, edited by S.B. Schnack, pp. 199-215, Alfred-Wegener-Institute for Polar Research, Bremerhaven, 1983.

Arimoto, T., K. Matuda, E. Hamada, and K. Kanda, Diel vertical migration of krill swarm in the Antarctic Ocean, *Trans. Tokyo Univ. Fish.*, *3*, 93-97, 1979.

Atkinson, A., and J.M. Peck, The distribution of zooplankton in relation to the South Georgia shelf in summer and winter, in *Antarctic Ecosystems: Ecological Change and Conservation*, edited by K.R. Kerry and G. Hempel, pp. 159-165, Springer-Verlag, Berlin, 1990.

Bollens, S.M., and B.W. Frost, Predator-induced diel vertical migration in a planktonic copepod, *J. Plankton Res.*, *11*, 1047-1065, 1989.

Bollens, S.M., and B.W. Frost, Diel vertical migration in zooplankton: rapid individual Response to predators, *J. Plankton Res.*, *13*, 1359-1365, 1991.

Brinton, E., and T. Antezana, Structures of swarming and dispersed populations of krill (*Euphausia superba*) in Scotia Sea and South Shetland waters during January-March 1981, determined by Bongo nets, *J. Crust. Biol.*, *4*, 45-66, 1984.

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 Cycling and Food Webs*, edited by W.R. Siegfried, P.R. Condy, and R.M. Laws, pp. 516-533, Springer-Verlag, Berlin, Heidelberg, New York, Tokyo, 1985.

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, Abundance and distribution of krill in the ice edge zone of the Weddell Sea, austral spring 1983, *Deep-Sea Res.*, *35*, 21-41, 1988.

Demer, D.A., and R.P. Hewitt, 1995, Bias in acoustic biomass estimates of *Euphausia superba* due to diel vertical migration, *Deep-Sea Res.*, *42*, 455-475, 1995.

Everson, I., Zooplankton, in *Antarctic Ecology*, edited by R.M. Laws, pp. 463-490, Academic Press, London, New York, 1984.

Everson, I., Some aspects of the small scale distribution of *Euphausia crystallorophias*, *Polar Biol.*, *8*, 9-15, 1987.

Everson, I., and D.G.M. Miller, Krill mesoscale distribution and abundance: results and implications of research during the BIOMASS program, in *Southern Ocean ecology: The BIOMASS Perspective*, edited by S.Z. El-Sayed, pp. 129-143, University Press, Cambridge, Bremerhaven, Germany, 1994.

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., R.L. Pitman, and D.G. Ainley, Seabird and fur seal responses to vertically migrating winter krill swarms in Antarctica, *Polar Biol.*, *10*, 37-41, 1989.

Godlewska, M., and Z. Klusek, Vertical distribution and diurnal migrations of krill - *Euphausia superba* Dana - from hydroacoustical observations, SIBEX, December 1983/January 1984, *Polar Biol.*, *8*, 17-22, 1987.

Greene, C., H.P.H. Wiebe, and J.E. Zamon, Acoustic visualization of patch dynamics in oceanic ecosystems, *Oceanography*, 7, 4-12, 1994.

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.*, *31*, 371-382, 1986.

Hempel, G., On the biology of polar seas, particularly the Southern Ocean, in *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*, edited by J.S. Gray and M.E. Christiansen, pp. 3-33, Wiley, Chichester, 1985.

Hewitt, R.P., and D.A. Demer, Acoustic estimates of krill biomass in the Elephant Island area: 1981-1993, *CCAMLR Science*, *1*, 1-5, 1994.

Hofmann, E.E., J.E. Capella, R.M. Ross, and L.B. Quetin, Models of the early life history of *Euphausia superba*--Part I. Time and temperature dependence during the descent-ascent cycle, *Deep-Sea Res.*, *39*, 1177-1200, 1992.

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., The zooplankton community of Croker Passage, Antarctic Peninsula, *Polar Biol.*, *4*, 161-170, 1985.

Hopkins, T.L., and J.J. Torres, The zooplankton community in the vicinity of the ice edge, western Weddell Sea, March 1986, *Polar Biol.*, *9*, 79-87, 1988.

Jazdzewski, K., W. Kittel, and K. Lotocki, Zooplankton studies in the southern Drake Passage and in the Bransfield Strait during the austral summer (BIOMASS-FIBEX, February-March 1981), *Pol. Polar Res.*, *3*, 203-242, 1982.

Kalinowski, J., and Z. Witek, The physical parameters of krill aggregations in the western Antarctic, *ICES Biol. Oceanogr. Cttee CM 1981/L*, *19*, 1-4, 1981.

Kalinowski, J., and Z. Witek, Scheme for classifying aggregations of Antarctic krill, *BIOMASS Handbook*, *27*, 12, 1985.

Kittel, W., Populational studies on *Euphausia superba* Dana, 1852 (Euphausiacea, Crustacea) in waters of the Admiralty Bay during Antarctic summer of 1978, *Pol. Arch. Hydro. Biol.*, *27*, 267-272, 1980.

Kittel, W., Z. Witek, and H. Czykieta, Distribution of *Euphausia frigida*, *Euphausia crystallorophias*, *Euphausia triacantha* and *Thysanoessa macrura* in the southern part of Drake Passage and in the Bransfield Strait during the 1993-1984 austral summer (BIOMASS-SIBEX), *Pol. Polar Res.*, *6*, 133-149, 1985.

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.

Loeb, V.J., and E. Schulenberger, Vertical distributions and relations of euphausiid populations off Elephant Island, March 1984, *Polar Biol.*, *7*, 363-373, 1987.

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.

Macaulay, M.C., T.S. English, and O.A. Mathisen, Acoustic characterization of swarms of Antarctic krill (*Euphausia superba*) from Elephant Island and Bransfield Strait, *J. Crust. Biol.*, *4*, 16-44, 1984.

Mackintosh, N.A., The seasonal circulation of the Antarctic macroplankton, *Discovery Rep.*, *16*, 365-412, 1937.

Magnuson, J.J., Long-term ecological research and the invisible present, *BioScience*, *40*, 495-508, 1990.

Makarov, R.R., Vertical distribution of euphausiid's eggs and larvae at northeastern inshore waters of South Georgia, *Oceanologia*, *15*, 1101-1106, 1975. (In Russian)

Makarov, R.R., Larval distribution and some questions of reproductive ecology of *Euphausia frigida* Hansen (1911) in the southern part of the Scotia Sea, *Oceanologia*, *17*, 324-332, 1977. (In Russian)

Makarov, R.R., Spawning terms of Antarctic euphausiids, *Biol. Morya, Vladivostok*, *3*, 30-38, 1979a. (In Russian)

Makarov, R.R., Larval distribution and reproductive ecology of *Thysanoessa macrura* (Crustacea: Euphausiacea) in the Scotia Sea, *Mar. Biol.*, *52*, 377-386, 1979b.

Makarov, R.R., and V.V. Maslennikov, Some data on vertical distribution of euphausiid larvae on the Antarctic Peninsula shelf, *BIOMASS Newsletter*, *3*, 7-9, 1981.

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.

Mauchline, J., Key for the identification of Antarctic euphausiids, *BIOMASS Handbook*, *5*, 4, 1980a.

Mauchline, J., Studies on patches of krill, *Euphausia superba* Dana, *BIOMASS Handbook*, *6*, 36, 1980b.

Mauchline, J., and L.R. Fisher, The biology of euphausiids, *Adv. Mar. Biol.*, *7*, 1-454, 1969.

Miller, D.G.M., and I. Hampton, Biology and ecology of the Antarctic krill (*Euphausia superba* Dana): a review, *BIOMASS Scientific Series*, *9*, 166, 1989a.

Miller, D.G.M., and I. Hampton, Krill aggregation characteristics: spatial distribution patterns from hydro-acoustic observations, *Polar Biol.*, *10*, 125-134, 1989b.

Murphy, E.J., Spatial structure of the Southern Ocean ecosystem: predator-prey linkages in Southern Ocean food webs, *J. An. Ecol.*, *64*, 333-347, 1995.

Murphy, E.J., D.J. Morris, J.L. Watkins, and J. Priddle, Scales of interaction between Antarctic krill and the environment, in *Antarctic Resources and Variability*, edited by D. Sahrhage, pp. 120-130, Springer-Verlag, Berlin, Heidelburg, 1988.

Nast, F., The vertical distribution of larval and adult krill (*Euphausia superba* Dana) on a time station south of Elephant Island, South Shetlands, *Meeresforsch.*, *27*, 103-118, 1979.

Nishikawa, J., M. Naganobu, T. Ichii, H. Ishii, M. Terazaki, and K. Kawaguchi, Distribution of salps near the South Shetland Islands during austral summer, 1990-1991 with special reference to krill distribution, *Polar Biol.*, *15*, 31-59, 1995.

O'Brien, D.P., Direct observations of the behavior of *Euphausia superba* and *Euphausia crystallorophias* (Crustacea: Euphausiacea) under pack ice during the Antarctic spring of 1985, *J. Crust. Biol.*, *7*, 437-448, 1987.

Piatkowski, U., Distribution, abundance and diurnal migration of macrozooplankton in Antarctic surface waters, *Meereforsch.*, *30*, 264-279, 1985.

Piatkowski, U., Macroplankton communities in Antarctic surface waters: spatial changes related to hydrography, *Mar. Ecol. Prog. Ser.*, *55*, 251-259, 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, Heidelburg, 1988.

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, University Press, Cambridge, Bremerhaven, Germany, 1994.

Quetin, L.B., R.M. Ross, T.K. Frazer, and K.L. Haberman, Factors Affecting Distribution and Abundance of Zooplankton, With an Emphasis on Antarctic Krill, *Euphausia superba*, this volume.

Rakusa-Suszczewski, S., The relationship between the distribution of plankton biomass and plankton communities in the Drake Passage and the Bransfield Strait (BIOMASS-FIBEX, February-March 1981), in *Proceedings of the BIOMASS Colloquium in 1982*, edited by T. Nemoto and T. Matsuda, pp. 77-83, National Institute of Polar Research, Tokyo, 1983.

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, Heidelberg, New York, London, Paris, Tokyo, 1988.

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.

Schulenberger, E., J.H. Wormuth, and V.J. Loeb, A large swarm of *Euphausia superba*: overview of patch structure and composition, *J. Crust. Biol.*, *4*, 1984.

Siegel, V., Structure and composition of the Antarctic krill stock in the Bransfield Strait (Antarctic Peninsula) during the Second International BIOMASS Experiment (SIBEX), *Arch. FischWiss.*, *37*, 51-72, 1986.

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

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

Siegel, V., B. Bergstrom, J.O. Stromberg, and P.H. Schalk, Distribution, size frequencies and maturity stages of krill, *Euphausia superba*, in relation to sea-ice in the northern Weddell Sea, *Polar Biol.*, *10*, 549-557, 1990.

Siegel, V., and J. Kalinowski, Krill demography and small-scale processes: a review, in *Southern Ocean Ecology: the BIOMASS Perspective*, edited by S.Z. El-Sayed, pp. 145-163, University Press, Cambridge, England, 1994.

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.

Siegel, V., and U. Piatkowski, Variability in the macrozooplankton community off the Antarctic Peninsula, *Polar Biol.*, *10*, 373-386, 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.

Soest, R.W.M.V., A revision of the genera Salpa Forskal, 1775, Pegea Savigny, 1816, and Ritteriella Metcalf, 1919 (Tunicata, Thaliacea), *Beaufortia*, *22*, 153-191, 1974.

Sprong, I., and P.H. Schalk, Acoustic observations on krill spring-summer migration and patchiness in the northern Weddell Sea, *Polar Biol.*, *12*, 261-268, 1992.

Stammerjohn, S.E., and R.C. Smith, Spatial and Temporal Variability in West Antarctic Sea Ice Coverage, this volume.

Trathan, P.N., E. Everson, D.G.M. Miller, J.L. Watkins, and E.J. Murphy, Krill biomass in the Atlantic, *Nature*, *373*, 201-202, 1995.

Treguer, P., and G. Jacques, Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean, *Polar Biol.*, *12*, 149-162, 1992.

Vervoort, W., Notes on the biogeography and ecology of free-living marine copepods, in *Biogeography and Ecology in Antarctica*, edited by J.V. Miegham and P.V. Oye, pp. 381-400, Junk Publishers, The Hague, 1965.

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.

Watkins, J.L., D.J. Morris, C. Ricketts, and J. Priddle, Differences between swarms of Antarctic krill and some implications for sampling krill populations, *Mar. Biol.*, *93*, 137-146, 1986.

Weigmann-Haass, R., and G. Haass, Geographische verbreitung der Euphausiacea (Crustacea) wahrend der Expedition 1975/76, *Meeresforsch.*, *28*, 19-31, 1980.

Witek, Z., J. Kalinowski, A. Grelowski, and N. Wolnomiejski, Studies of aggregations of krill (*Euphausia superba*), *Meeresforsch.*, *28*, 228-243, 1981.

Witek, Z., J. Kalinowski, and A. Grelowski, Formation of Antarctic krill concentrations in relation to hydrodynamic processes and social behaviour, in *Antarctic Resources and Variability*, edited by D. Sahrhage, pp. 237-244, Springer-Verlag, Berlin, Heidelburg, 1988.

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.

Zhou, M., W. Nordhausen, and M. Huntley, ADCP measurements of the distribution and abundance of euphausiids near the Antarctic Peninsula in winter, *Deep-Sea Res.*, *41*, 1425-1445, 1994.

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), *Oceanologia*, *35*, 101-127, 1993.

R.M. Ross and L.B. Quetin, Marine Science Institute, University of California at Santa Barbara, Santa Barbara, CA 93106 and C.M. Lascara, Center for Coastal Physical Oceanography, Crittenton Hall, Old Dominion University, Norfolk, VA 23529.

(Received June 16, 1995; accepted October 27, 1995.)