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# Effect of Sea Ice Conditions on Physiological Maturity of Female Antarctic Krill (*Euphausia superba* Dana) West of the Antarctic Peninsula

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by

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## ABSTRACT

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The Antarctic environment is one of great seasonal extremes and high interannual variability. Several investigators have suggested that variability in the annual advance and retreat of sea ice, one of the largest physical processes in the world ocean, affects the structure and function of all levels of the food web. The physiological maturity stage of female Antarctic krill (*Euphausia superba* Dana) was examined for five austral summer research cruises in the region west of the Antarctic Peninsula. Physiological maturity stages are defined by thelycum development, ovarian morphology and developmental changes in ovarian cells. The reproductive cycle includes eight stages for ovarian development leading to egg production, and two stages for sexual regression and reorganization post-spawning. Distribution data suggested that krill segregated by physiological maturity stage, with immature females and females in initial stages of the reproductive cycle on the inner shelf, and those more advanced in the reproductive cycle on the outer shelf. This distribution implies that female krill actively migrated from the inner to the outer shelf as they progressed through the reproductive cycle. Reproductive seasons were classified with three criteria as defined by

this study: timing of spawning, percentage of females reproducing, and percentage of females recycling the ovary. Good seasons occurred when spawning was early and percentages of females reproducing and recycling were high, although a good season could occur with a low percentage of females reproducing as long as the percentage recycling remained high. Poor seasons occurred when spawning was delayed and low percentages of females were reproducing and recycling. Good seasons were associated with years of high sea ice extent and initial sea ice retreat in the early spring (late September). Poor seasons were associated with years of low sea ice extent and/or initial sea ice retreat earlier or later than the early spring. Sea ice served as a proxy for food availability, indicating that a linkage exists between food availability in the spring and reproductive condition of the krill population the following summer.

# INTRODUCTION

Antarctic krill (*Euphausia superba* Dana) are considered a key species in the Antarctic food web since all vertebrates in the Southern Ocean are directly or indirectly dependent on krill as a food source (Laws 1985). Although "krill" can refer to many different species of euphausiids, throughout this paper "krill" will refer only to the species *Euphausia superba*.

Theories on krill reproduction have gone through many iterations (Bargman 1937, 1945; Denys and McWhinnie 1982; Ikeda et al. 1985; Makarov 1975, 1979; Nicol 1989; Ross and Quetin 1983, 1986; Thomas and Ikeda 1987). The absence of adult female krill from the population between late fall and early spring led to the original theory that krill lived 2-3 years, spawned and then died (Bargman 1945). Further research suggested that krill spawned in the summer, regressed to a less developed state in the winter, redeveloped in the spring and spawned again in the summer (Makarov 1975, 1979). Subsequent laboratory studies have documented regression to a more juvenile appearance after the reproductive season (Poleck and Denys 1982; Thomas and Ikeda 1987), and resumption of sexual development after a winter rest (McWhinnie et al. 1979; Thomas and Ikeda 1987). Studies of age pigments suggest that krill live 7-8 years (Ettershank 1983, 1984) and are thus able to spawn for 4 or 5 seasons. Evidence accumulated over the last decade or so suggests that krill are able to spawn multiple times in

the same season (Cuzin-Roudy 1987; Ross and Quetin 1983, 1986) with a period of about two weeks between spawns (Denys and McWhinnie 1982; Ross and Quetin 1983). If this cycle persists throughout the entire three month reproductive season, one female would be capable of releasing 9-10 batches of eggs in one year (Ross and Quetin 1983). The recent paradigm of repeat spawning in the same season combined with the increased life-span dramatically increases fecundity estimates for individual krill. Such high fecundity requires high energy input (Miller and Hampton 1989; Nicol et al. 1995; Ross and Quetin 1986). Thus food availability should determine the physiological preparedness of the krill population for reproduction (Ross and Quetin 1986).

Antarctic krill spawn during the austral summer from mid-December to April (Makarov 1979; Mauchline and Fisher 1969; Ross and Quetin 1986; Spiridonov 1995) although there is a great deal of variability in timing and intensity of spawning between seasons and geographical areas (Spiridonov 1995). After the summer spawning season, female krill regress to a more immature reproductive state and undergo oogenesis before the winter rest (Cuzin-Roudy 1987). Ovarian development occurs in the spring (Bargman 1945). Although there is evidence that krill have lipid reserves in autumn, these have dropped significantly by the end of the winter, suggesting that these reserves are used for winter metabolism and are not able to fuel reproduction (Hagen et al. 1996). Therefore, the critical time for food availability for ovarian

development in krill is spring rather than winter. Summer food availability is likely to impact the number of batches of eggs produced.

Sea ice appears to influence spring food availability in several ways - the ice biota living in and on sea ice surfaces, the release of ice biota and organic matter during melt, and stabilization of the water column by melting sea ice, thus promoting ice edge blooms (Ross and Quetin 1986; Smetacek et al. 1990). These are all thought to be sources of food essential to high reproductive output throughout the summer (Quetin and Ross 1984). The extent of sea ice in spring and timing of retreat will influence both the magnitude and timing of phytoplankton blooms along the receding ice edge (Quetin et al. 1994; Smetacek et al. 1990). If sea ice extent is high but of short duration, blooms may occur early in the season and be dissipated by storm activity before they can be used by the krill as a concentrated source of food. Spawning earlier in the season is associated with years of high winter sea ice duration and concentration (Loeb et al. 1997; Siegel and Loeb 1995) whereas years of low sea ice area and extent are correlated with delayed spawning in krill (Loeb et al. 1997). Early spawning is more favourable to the survival of krill larvae than late spawning, as the larvae will be more likely to encounter a sufficient food supply when they arrive at the surface (first critical period, Quetin and Ross 1991), and will have more time to grow and mature before winter arrives (second critical period, Quetin and Ross 1991).

Considerable interannual variability has been documented in the reproductive cycle of Antarctic krill (Siegel and Loeb 1995; Spiridonov 1995) and in reproductive effort as seen in larval abundance (Brinton et al. 1986, 1987). Depending on environmental conditions, krill may utilize different reproductive strategies (Cuzin-Roudy 1993). Distinguishing the phases of ovarian development is therefore critical to understanding environmental effects on the reproductive biology of krill (Cuzin-Roudy and Amsler 1991).

This study examined spatial patterns (onshore/offshore, north/south) and interannual variability in distribution and abundance of female krill in different physiological maturity stages as described by Cuzin-Roudy and Amsler (1991). Analysis of physiological maturity stages also yielded information on the timing of reproduction, the degree of recycling and the percentage of the population spawning in a year. These patterns were considered in relation to sea ice dynamics and the onshore/offshore gradient in primary production. Although no direct measurements of chlorophyll were available for the spring, sea ice conditions were presumed to reflect food availability.

The research reported here was conducted as part of the Palmer (PAL) Long-Term Ecological Research (LTER) program. The PAL LTER focuses on the marine ecosystem in the seasonal sea ice zone west of the

Antarctic Peninsula, and was designed to sample at various spatial and temporal scales throughout the same area (Ross et al. 1996; Smith et al. 1995). The PAL region spans 6 degrees of latitude with strong north/south gradients in year-to-year variability of sea ice coverage (Smith et al. in press). The existence of this latitudinal gradient provides the opportunity to contrast regions which are always covered by winter sea ice (southern end) with those experiencing fluctuations in annual sea ice cover (northern end). In contrast with previous studies on the timing of reproduction in Antarctic krill (Siegel and Loeb 1995; Spiridonov 1995), the present study relies on samples from the same locations at the same time of year over the five years of this study. The long-term nature of this study and the existence of the latitudinal gradient in sea ice cover allows for meaningful comparisons between physiological maturity of the krill population and sea ice conditions.

## MATERIALS AND METHODS

Krill for this study were collected from the region west of the Antarctic Peninsula during research cruises aboard the R/V POLAR DUKE between early January and mid February from 1993 through 1997 (Table 1). The Palmer LTER grid covers an area of 900 kilometers (roughly parallel to the peninsula) by 200 kilometers (on- to offshore) (Waters and Smith 1992). Transect lines are spaced 100 kilometers apart

perpendicular to the peninsula, with stations spaced every 20 kilometers along the lines (Fig. 1). Transect lines are numbered from line 000 (furthest south) to line 900 (furthest north). Station numbers denote the distance from shore from 000 (furthest inshore) to 200 (furthest offshore). Locations within the grid are referenced using transect line number and station number separated by a decimal, e.g. 600.040. Due to irregularities in the coastline and the presence of islands along transect lines, every station between *.000 and *.200 is not present on every transect line. During the annual summer LTER cruise, net tows are done at stations along the 200, 300, 400, 500 and 600 lines. January 1994 was the exception with no sampling on the 200 line due to time constraints. Consistent winter sea ice coverage is found from the inner end of the 400 line to the outer end of the 200 line (Stammerjohn 1993).

Krill examined in this study primarily came from standard oblique net tows to 120 meters with a 2 meter square frame trawl net (700 μm mesh, 500 μm codend). The standard depth of 120 meters (water depth permitting) for the 2 meter trawl is the maximum depth range for krill schools (day or night) observed in this region during the austral summer (Ross et al. 1996). The depth of the net was estimated with the wire angle and amount of wire out during the tow and recorded with a Benthos Time/Depth Recorder attached to the net during the first two cruises (93Jan and 94Jan). During later cruises (95Jan - 97Jan) a pressure sensor attached to the net cable gave a time-depth profile of the trawl.

Rates of wire out and wire in averaged 15 meters per minute; ship speed during tows averaged 2.0 knots, resulting in tow durations of 35-40 minutes. Volume filtered was determined with a General Oceanics flow meter attached across the mouth of the net.

Occasionally krill collected with a 1 meter square frame trawl net (333 μm mesh and codend) were used for this study. These trawls were conducted at each station. The standard depth for the 1 meter trawl was 300 meters (water depth permitting). Rates of wire out and wire in averaged 30 meters per minute, with ship speeds of 2.0 knots. Average tow durations were about the same as those for the 2 meter net. Net depth and volume filtered were determined as for the 2 meter net tows.

Random samples of zooplankton from each tow were preserved in 10% formalin (90% sea water). At stations where krill were caught in sufficient numbers, a random sample of 100 krill was measured to determine length frequency distribution; females with red thelyca were also recorded. The presence of a red theylcum indicates that the animal is a mature female (MF) which has entered the reproductive cycle and will spawn that year.

At the University of California, Santa Barbara (UCSB), preserved samples for detailed analysis were selected based on trawl record data. Krill samples representative of outer shelf stations (*.160-*.200), mid-

shelf stations (*.100-*.140), and inner shelf stations (*.000-*.080) within the grid were selected for each transect line sampled during each year. Length frequency samples from 2 meter standard oblique tows were preferred over random mixed samples when they contained mature females. When length frequency samples were not available, the number of krill preserved in a random sample was a deciding factor. A sample had to contain at least 30 krill in order to provide meaningful data. If krill were caught at two or three stations within a grouping, a variety of factors were considered to decide which sample to use. If number of krill and presence of mature females were consistent between the samples, their position on the grid was the deciding factor. The *.000 (when available) or *.040 samples were preferred for the inner shelf stations, *.120 for the mid-shelf samples, and *.200 for the outer shelf stations. Samples from the 1 meter net tows were used for this study only when krill were not caught in the 2 meter tow or were caught in insufficient numbers to supply meaningful data. This occurred with only four samples, two in 1994 and two in 1997.

All krill samples were analyzed in the laboratory at UCSB. The sample was poured into a mesh funnel under a fume hood and rinsed with fresh water to remove as much formalin as possible. Krill were first sorted by sex as distinguished by the presence of secondary sexual characteristics (thelycum for females, petasma for males). Krill without secondary sexual characteristics, and/or which were less than 28 mm

total length, were reproductively immature and not relevant to this study. Numbers of female krill greater than 28 mm and other krill (males, animals less than 28 mm) were recorded for each sample. Total length (TL, tip of rostrum to end of uropods, standard length; Mauchline 1980) of each female staged was measured with Mitutoyo digital calipers . On rare occasions (n=3) total length measurements for individual krill were not possible due to their poor condition. For these animals TL was calculated from the carapace length with the relationship:

$$TL = 2.813 + 2.757 * \text{carapace length} \quad (r^2=0.926)\ n=47$$

This relationship was derived from krill sampled on an LTER cruise in November 1991. Because krill shrink when preserved in formalin, all preserved TL values were converted to fresh TL values with the relationship:

$$\text{fresh TL} = (\text{preserved TL} - 0.771)/0.925 \quad (r^2=0.976)$$

This relationship was derived from total lengths of individual krill first measured fresh and then remeasured 14 to 18 months after preservation.

A variety of different maturity keys have been developed to designate maturity stages of krill (Bargman 1945; Cuzin-Roudy and Amsler 1991; Makarov 1980; Mauchline 1968). The key developed by Cuzin-Roudy and Amsler (1991) provides the most comprehensive description of physiological reproductive status, taking into account external

morphology of the female, ovarian morphology, and types of oocytes present in the ovary. The key is applicable to both fresh and preserved krill. This key divides the reproductive cycle of Antarctic krill into ten distinct stages. A synopsis follows.

Stage 1 - Gametogenesis: These females must be dissected to determine their sex. They have no thelycum and a primitive looking-ovary containing only primary (og1) or secondary oogonia (og2). Because these females were too immature to reproduce, they were not considered in this study.

Stage 2 - Oogenesis: These are subadult females in oogenesis. They have an immature thelycum and a small ovary which may still contain og1 and og2 but is dominated by young oocytes (yoc). Females at Stage 2 in January will not reproduce during that summer.

Stages 3 and 4 - Previtellogenesis: Stage 3 females are not yet in an active reproductive cycle. The thelycum is mature but not red, and yoc and type 1 oocytes (oc1) are present in the ovary. Stage 3 females may either advance to the next stage in the reproductive cycle, or remain at stage 3 and not reproduce that year. Stage 4 is the first stage at which females are considered to be in the active reproductive cycle and committed to spawn that year. In Stage 4 the ovary expands throughout the thoracic cavity and into the first two abdominal segments, and becomes filled with oc1. Stage 4 females may have a red thelycum.

Stages 5, 6, and 7 - Vitellogenesis: All these stages have red thelyca. At Stage 5 the ovary is basically the same in size and appearance as Stage 4, but now contains both oc1 and type 2 oocytes (oc2), indicating that accumulation of lipidic yolk has begun. Stage 6 females have a swollen thorax with a large, clearly visible ovary filled with type 3 oocytes (oc3) which are rapidly accumulating yolk. At Stage 7, females are ready to spawn. The ovary is filled with type 4 oocytes (oc4, or "eggs") which have completed vitellogenesis and are full of yolk. The nucleus of the cell is no longer visible in the oc4. Ovaries of females of Stages 6 and 7 may contain other cell types in addition to the dominant oc3 or oc4.

Stage 8 - Post-spawn: The thorax is still swollen, but the thoracic cavity is filled with clear hemolymph and the ovary is small. There are two different types of Stage 8 females.

1. Stage 8 final: the ovary contains only germinal zone (GZ) cells and perhaps a few residual/resorbing oc4. These females are spent and will not spawn again that season.
2. Stage 8 continuing: the ovary contains cells of types oc1 and oc2 as well as residual oc4. These females have the potential to spawn again during the current season.

Stages 9 and 10 - Ovarian Reorganization: After spawning is complete, the reproductive system is reorganized. Stage 9 females have a mature red thelycum. If the thelycum is regressing to a more juvenile form, the female is at Stage 10.

To determine the physiological maturity stage of a female, the thelycum was first rated immature or mature. To examine the ovary, the carapace was pulled back with tweezers and the ovary located and observed for shape and size. A portion of the ovary was dissected out and gently squashed with a cover slip on a glass slide. This squash was examined under an Olympus dissecting microscope to determine which types of oocytes were present in the ovary. Types of oocytes were easily distinguishable at 64x magnification based on differences in their appearance (Cuzin-Roudy and Amsler 1991). Size ranges of different types of oocytes overlap, but the ratio of nucleus to cytoplasm and the appearance of the cytoplasm are specific to particular cell types and made it possible to distinguish between them.

General guidelines for how many females to stage per sample were:

| Number of stages present | Number of females staged |
|---|---|
| 1 | 10-15 |
| 2 | 15-20 |
| 3 | 25-30 |
| 4 | 30-35 |
| 5+ | 35-40 |

All females in a sample were measured and staged if the sample was small or if many physiological maturity stages were present. If the number of females in a sample was very large, or if few physiological maturity stages were present, a random subsample of the preserved females was measured and staged. The distribution of physiological maturity stages for females in a preserved sample was used to calculate

the number of each physiological maturity stage in the total catch of krill at that station, based on total volume of krill catch as determined from data collected during the cruise. These numbers were standardized to number of each physiological maturity stage present per 1000 $m^3$ volume filtered with the following calculation.

$$\frac{\frac{\text{\# in stage for all staged krill}}{\text{\# staged krill}} * \text{\# females >28 mm in subsample} * \text{split done on board ship}}{\text{volume filtered}}$$

This calculation ensured that only the portion of females in each catch that were large enough to reproduce were represented in the calculated numbers of each stage per 1000 $m^3$.

## RESULTS

### 1993

Most females were Stage 2 (Fig. 2), and were found at the inner stations on every grid line (Fig. 3a). Although physiological maturity stages 3-10 were present in small proportions, there were 4.5 times more Stage 4 than Stage 5 krill. These proportions characterize the population as either not reproducing or in the initial stages of the reproductive cycle (Fig. 2). Stage 3 females comprised 3.96% of the population (Fig. 2). There was no pattern apparent in their distribution (Fig. 3b). Stages 6 and 7 were almost equally abundant, and, along with the few Stage 8 females, were found only in the southern part of the grid at the furthest

stations from shore (Fig. 3e-g). All Stage 8 females were Stage 8 final. Stages 10 and 9 were found at similar percentages (Fig. 2). They were found together at two stations, but Stage 9 females were also present at outer shelf stations where no Stage 10 females were found (Fig. 3h-i).

**1994**

No krill were found at the *.200 station on any line. Most of the females were Stage 2 (Fig. 4) and were found at increasingly offshore stations from north to south on the grid (Fig. 5a). Stage 3 females comprised 9.30% of the population and showed, with the exception of a small number at station 500.180, the same distribution as Stage 2 females (Figs. 5a-b). There were twice as many Stage 5 as Stage 4 females (Fig. 4), indicating that most of the krill in the reproductive cycle had advanced beyond the initial maturity stages. Stage 4 females were found at outer shelf stations in northern and southern areas of the grid, while Stage 5 females were found from *.080 to *.180, with the largest groups at the *.180 stations on the 500 and 600 lines (Figs. 5c-d). Stage 9 females were found on all sampled lines from inner shelf to outer shelf stations (Fig. 5h). Stage 7 females were found at mid-shelf and outer shelf stations on the 300 and 400 lines (Fig. 5f). Stage 6 females represented a small percentage of the population (Fig. 4) and were found only at outer shelf stations (Fig. 5e). Stage 10 females made up less than 2% of the population and were found in small numbers at mid-shelf and outer shelf stations with a large number at 600.040 (Fig. 5i). Stage 8 females

were a very small percentage of the population (Fig. 4) and all Stage 8 females, final and continuing, were found at the same station (Fig. 5g).

**1995**

Stages 2 and 3 together comprised the majority of the population (Fig. 6). One station (600.060) contributed disproportionately to these high percentages. Stage 2 and 3 females were scattered throughout the grid but tended to be concentrated in the north (Figs. 7a-b). Stage 8 females were the only other stage present in proportions greater than 2%, and were found predominantly at outer shelf stations in the southern part of the grid (Fig. 7g). Stage 8 females comprised 4.84% of the population, with 4.01% Stage 8 final and 0.83% Stage 8 continuing. With the exception of station 300.120, Stages 6 and 7 were found at the same stations in the central and southern part of the grid (Figs. 7e-f). Stage 5 females were found on all grid lines at the mid-shelf and outer shelf stations (Fig. 7d). Stage 4 females were found at low numbers from inner shelf to outer shelf stations (Fig. 7c). Stages 9 and 10 were present at very small percentages. Stage 9 females were found at mid-shelf and outer shelf stations (Fig. 7h) while Stage 10 females were found only at one mid-shelf station (Fig. 7i).

**1996**

Stage 7 females made up the majority of the population (Fig. 8), and were found on all lines with medium to large concentrations at inner

shelf and outer shelf stations on the 600 line and a very large concentration at 500.100 (Fig. 9e). Stage 5 females were the second largest percentage of the population, and were also largely concentrated at 500.100 (Fig. 9c). All other stages were less than 2% of the females (Fig. 8). Stage 2 females, although present in much smaller numbers than other years of the study, were still scattered widely throughout the grid (Fig. 9a). Stage 8 females were found at mid-shelf or outer shelf stations on all lines except 600 (Fig. 9f), with Stage 8 continuing forming 0.16% of the total population. Stage 6 females were found only at outer shelf stations, but on all lines except the 400 (Fig. 9d). Stage 4 females were present at low percentages at inner shelf and mid-shelf stations (Fig. 9b). Stage 9 females were found at low percentages at one inner shelf and two outer shelf stations (Fig. 9g). Stages 3 and 10 were absent from the population.

**1997**

Stages 2 and 4 comprised the bulk of the population (Fig. 10). Stage 2 females were scattered throughout the entire grid from inner shelf to outer shelf stations (Fig. 11a). Stage 4 females were found throughout the grid also, but were concentrated in the northern part of the study region (Fig. 11c). Stage 3 females formed 6.13% of the population (Fig. 10) and their distribution was very similar to that of Stage 4 females (Figs. 11b-c). Stage 9 females comprised 2.59% of the population (Fig. 10) and were found at mid-shelf and outer shelf stations in the more

northern part of the grid (Fig. 11g). Stage 5 females were found from inner shelf to outer shelf stations, but in very small numbers (Fig. 11d). Of the three stations where Stage 7 females were found, two were inner shelf stations (Fig. 11e). The individuals were smaller than Stage 7 females of previous seasons (Table 2). Of the few Stage 8 females found, all were Stage 8 final (Fig. 11f). Stage 10 females were found in very small numbers and were only at station 400.060. Stage 6 females were absent from the population.

**Distribution Patterns**

In 1993 and 1994, early stages of physiological maturity (Stages 2, 3, 4) were evenly distributed from north to south, although as the females advanced in physiological maturity they were found further offshore (Figs. 12, 13). In 1995 there were still many females in early stages of physiological maturity (Stages 2 and 3), though they tended to be concentrated in the northern part of the grid. Of those females in the reproductive cycle, most were in advanced stages of physiological maturity (Stages 5, 6, 7, 8) and were found mainly at mid-shelf and outer shelf stations (Fig. 14). A small number of females were found in ovarian reorganization at mid-shelf and outer shelf stations (Stage 9) suggesting that most of the mature females were still actively reproducing. Distribution of physiological maturity stages of female krill in 1996 differed from that of other years of this study (Fig. 15), which might be expected considering that the stage composition of the

population was also very different from other years (Fig. 8). In 1996 nearly all females were in the active phase of spawning, with very few either not reproducing or in the initial stages of the reproductive cycle. The majority of the reproducing stages were found at mid-shelf and outer shelf stations. Distribution of early physiological stages in 1997 showed Stage 2 females shifted a bit south of Stages 3 and 4 which were more common in the northern part of the grid (Fig. 11a-c). The vast majority of the population was either not reproducing (Stages 2 and 3) or in the initial stages of vitellogenesis (Stage 4) (Fig. 10). Stage 4 females decreased in abundance from inner shelf to outer shelf stations (Fig. 16).

**Onshore/Offshore Gradient**

Although krill abundance varies widely among seasons, general patterns emerged. For all seasons save 1996, there is a clear trend toward higher abundances of female krill at inner shelf stations, with lower numbers at mid-shelf stations. Abundances at outer shelf stations were either lower than or about the same as mid-shelf stations (Fig. 17). In 1996 highest abundances were at mid-shelf stations on the grid, with quite low numbers at inner shelf and outer shelf stations. This is not consistent with the on/offshore gradient seen during other years of this study.

**Alongshore Gradient**

There is no clear alongshore gradient as seen in abundances of krill per

grid line per year (Fig. 18). During the three years of low krill abundance (1994, 1995, 1997), low numbers of krill were found along all lines, although in 1995 there is a dramatic increase in krill on the 600 line. In 1993, high abundances of krill occurred on the 300 and 400 lines, with lower abundances on the 500 and 600 lines. In 1996, low abundances on the 200, 300 and 400 lines contrasted with extremely high numbers of krill (mostly Stage 7) on the 500 line. Krill numbers decreased on the 600 line.

**Total Length Data**

Ranges in total length of a specific stage often overlapped with other stages (Table 2). There was considerable interannual variability in the length distribution of Stages 2, 3, 4 and 5 (Figs. 19, 20, 21, 22).

Stage 2 (Fig. 19) females are concentrated in the lower part of the size range during most years. However, in 1995 Stage 2 females are slightly larger, and in 1994 Stage 2 females are noticeably larger than in any other year. Stage 3 females (Fig. 20) are smallest in 1997, tend to be larger in 1994 and 1995, and span the entire range from 36-53 mm in 1993. Stage 4 females (Fig. 21) are abundant over a wide size range in both 1993 and 1997. They are less abundant and tend to be smaller and in a more restricted size range in 1995 and 1996. In 1994 they are also less abundant, but are larger. Stage 5 females (Fig. 22) span a wide size range in all years. In 1993 there are smaller numbers of this stage, but the

animals are in the upper part of the size range. In 1994 they are concentrated in the middle of the range and in 1995 they are concentrated in the lower part of the size range. In 1996 they tend to be concentrated in the larger part of the size range and in 1997 they span a broad range but are concentrated around 48 mm. Refer to Table 2 for size ranges and Table 7 for average TL of each stage.

There is a wide variation in size ranges of the same stage between different years. With Stage 4 females, for example, the smallest size range spans 3.99 mm (1996) and the largest 20.85 mm (1997) (Table 2). The smallest individual Stage 4 female is 36.89 mm and the largest is 57.74 mm. Similar variations in size ranges occur between other stages also. There is a great deal of overlap in sizes of different stages within the same year as is apparent from Table 2. Table 3 shows each stage which would include a female with a TL of 47.00 mm for each year. With this degree of overlap, a strong correspondence between TL and physiological maturity stage is not likely to exist.

To test whether females which were larger might be able to prepare for the reproductive season more quickly and therefore be at a higher stage of development than females which were smaller, a Kolmogorov-Smirnov chi square test was used to evaluate whether females of Stage 4 were consistently smaller than females of Stage 5 for each year. This test was used because it allows comparison of the size distribution of each

stage rather than just the mean value. Since all of the distributions were skewed in one direction or another, comparison of means would not have provided an accurate answer to this question. Stages 4 and 5 were chosen for this analysis because they are in sequence in the reproductive cycle but krill are not expected to return to Stage 4 within the same season even if they recycle their ovary. At this time of year the contrast between these two stages indicates how advanced the krill population is in the reproductive season. This test was not done on combined data from all years because of the differences in length composition of the populations. These tests gave insignificant results for all years, ($p \leq 0.3453$) indicating that larger females are not necessarily moving into the reproductive cycle more quickly than smaller ones. Previous studies suggest that larger krill are able to progress through the reproductive cycle more rapidly than smaller ones (Cuzin-Roudy and Labat 1992), but this cannot be confirmed with this data set.

## DISCUSSION

### Comparison of Maturity Keys

The advantages of the maturity key by Cuzin-Roudy and Amsler (1991) are several. Other keys based on different criteria would lead to very different results than those obtained using this key. The key by Makarov & Denys (1980) is based on relative ovarian size and thelycum development and thus cannot distinguish the growing ovary from one

which is regressing after spawning. Ovarian development based on the size of germ cells (Bargman 1945; Ruud 1932) is ambiguous, as recent studies have shown krill ovaries may contain a range of germ cell sizes (Denys and McWhinnie 1982) and types (Cuzin-Roudy 1987). In addition, histological studies have shown no direct correlation between germ cell size and development to maturity (Cuzin-Roudy 1987; Kikuno and Kawamura 1983). The strengths of the key by Cuzin-Roudy and Amsler (1991) are that it distinguishes immature females that have never reproduced (Stage 2) from those that have (Stage 10), distinguishes between mature females who will not reproduce that season (Stage 3) and those that are just entering the reproductive cycle (Stage 4), and distinguishes spent females who will (Stage 8 continuing) and will not (Stage 8 final) recycle their ovaries. One cycle of the ovary results in the release of three batches of eggs (Cuzin-Roudy 1987) so recognizing this distinction is critical to understanding the physiological condition of the females in the population. The squash technique allows accurate identification of physiological steps (gametogenesis, oogenesis, previtellogenesis, vitellogenesis, oocyte final maturation) in the reproductive cycle. This is not possible with other maturity keys and as a result multiple spawners are not detected. Recognition of multiple spawners in the population results in a better understanding of the dynamics of krill reproduction and better recognition of interannual variability.

**Distribution**

Krill distribution is influenced by many factors, including water temperature, bottom topography, water circulation patterns, and phytoplankton distribution (Daly and Macaulay 1991; Ross et al. 1996; Siegel and Loeb 1994). However, the consistent pattern found in this study of krill at less advanced physiological maturity stages being closer to shore and stages with mature eggs ready to spawn near or beyond the shelf break (Figs. 12-16) suggests that krill distribution is not determined by oceanic circulation patterns alone.

The distribution of the stages may reflect the time course of development. Ross et al. (in prep.) suggested an average development through the sequence of physiological maturity stages throughout the year. In early spring (Sept-Oct) Stages 3 and 4 are expected to be the most common. Later in the spring (November), Stages 4 and 5 comprise the bulk of the population with some Stage 6 and 7 females found in December. The actively reproducing females (Stages 4-8) are present in summer, but it is believed that Stages 5-8 are those involved in recycling the ovary. Thus, as the season progresses, all Stage 4 females will advance to Stage 5 or beyond, and Stage 9 females will begin to appear after spawning ceases and reorganization of the ovary begins. By March the population is expected to consist of mostly Stages 9 and 10, with decreasing numbers of Stages 3 and 8. Stage 3 females are expected to increase in numbers in the early spring as food becomes available and

females are able to cycle from Stage 9 or 10 (the winter resting stages) to Stage 3 (reorganizing the ovary in preparation for spawning) (Fig. 23).

Distribution of physiological maturity stages throughout the grid shows spatial variation among stages and implies that the krill segregate by stage and change their location as they progress through these stages (Fig. 24). Although generally considered planktonic, adult krill are able to swim as strongly as small fish such as anchovies (Hamner 1984; Kanda et al. 1982) and are thus capable of moving against currents and actively changing their location. Trathan et al. (1993) concluded that the distribution of krill in their study area was due in part to ontogenetic migration. Other studies suggest horizontal migration inshore in the fall, so such movements are not unprecedented (Ross et al. 1996; Siegel 1988; Lascara et al. in press). Stage distribution data from this study suggest that female krill are actively migrating during the reproductive cycle (Figs. 12-16).

One possible explanation for this distribution pattern is that krill in early stages of physiological maturity remain on the inner shelf, feeding on the elevated phytoplankton standing stocks which generally occur there (El-Sayed 1968; Smith et al. in press). When they have built up the necessary energy stores for vitellogenesis they migrate offshore to areas where Circumpolar Deep Water (CDW) is located. Spawning over CDW appears to be important to the reproductive success of the krill

(Hofmann et al. 1992; Quetin et al. 1994). Stage 9 females are often found at mid-shelf stations, suggesting that they migrate back inshore after spawning (Figs. 12-16). CDW is generally found off the shelf break in locations corresponding to the outer shelf stations of the LTER grid, but its location varies between years and it may also intrude onto the shelf through inner-shelf depressions (Smith, unpubl.). Because Stage 6 or 7 females are rarely found at mid-shelf stations, it appears likely that once a female reaches Stage 4 or 5 horizontal migration may occur. In general, Stage 7 females were only found at mid-shelf and outer shelf stations on the 300 and 400 lines during this study (Figs. 3f, 5f, 7f, 9e, 11e), but in 1996 Stage 7 females were also found not only at inner shelf stations but also on the 400, 500 and 600 lines (Fig. 9e). Stage 5 and 7 females were found in a dense aggregation at station 500.100. If CDW reached to mid-shelf near 500.100 in 1996 via the bathymetric depression in this area, appropriate conditions for spawning (CDW and deep water) would exist on the mid-shelf and account for the presence of Stage 7 female krill (Fig. 15). Stage 7 females were also found at 200.000 in 1996, a station located at the end of another inner shelf depression and conceivably a location where CDW might reach. The relationship between CDW and krill distribution remains to be explored.

One possible alternate scenario is that once an individual krill moves into its summer location, ovarian development takes place there. To achieve the observed distribution pattern with this scenario, krill at

outer shelf stations would have had to start the reproductive cycle sooner or move through it at a faster rate than those in mid-shelf or inner shelf areas. This does not seem likely for several reasons. First, chlorophyll concentrations tend to be much higher onshore than offshore (El-Sayed 1968; Smith et al. in press), so krill at offshore stations will have less food available and rate of ovarian development is likely to be slower. Also, the presence of less advanced physiological maturity stages at outer shelf stations suggests not all females enter the cycle at the same time. If krill at outer shelf stations enter the reproductive cycle earlier than those at mid-shelf or inner shelf stations, the less advanced stages would not be expected at outer shelf stations at all. Their presence suggests that some other mechanism is driving the observed distribution patterns.

If female krill feed in areas of high chl during the initial phase of ovarian development in order to maximize the rate of ovarian development and then migrate to spawn over CDW, less advanced physiological maturity stages would be more strongly associated with areas of high chl concentrations (inner shelf) than would more advanced stages. Offshore chl concentrations were very low for all years so clearly food supply was not the attraction at the outer shelf stations. In January 1996, when high concentrations of krill were found in the northern part of the grid and at mid-shelf and inner shelf stations, chlorophyll concentrations were high both on northern transects and

inshore in the grid (Table 4).

**Criteria for "Good" and "Poor" Reproductive Seasons**

In spite of considerable interannual variability as shown for this five-year period, the presence or absence of certain conditions allow reproductive seasons to be categorized as "good" or "poor." The three criteria which define these categories are timing of spawning, percentage of reproducing females in the population (Fig. 25), and an index of the proportion of females that will recycle (Stage 8 continuing/Stage 8 total) (Table 5). Timing of spawning ("delayed" or "early") is determined by comparing the ratio of Stage 5 females to total females at Stages 4 and 5 (Fig. 26). When this is high the population as a whole is in a more advanced phase of the reproductive cycle and timing of spawning is classified as early. Percentage of the population considered to be reproducing are those in Stages 4-9 (Fig. 25). Females of these stages either will spawn during the season or have already spawned.

In 1993, the high ratio of Stage 4 to Stage 5 indicates that the population as a whole is an earlier phase of the reproductive cycle (Fig. 26). The presence of Stage 8 females in low numbers suggests that a minimal spawning effort by a small group occurred in late spring or early summer, but the total number of Stage 8 females was too low to determine an index of Stage 8 continuing/total Stage 8.

The 1994 population reproductive index suggests that the population as a whole is further along in the reproductive cycle than in January 1993 (Fig. 26), and the presence of the highest percentage of Stage 9 females seen in this study indicates that a small portion of the population was able to build up enough lipids to spawn early in the season and is already reorganizing (Fig. 4). Total number of Stage 8 females was too low to determine an index of Stage 8 continuing/total Stage 8.

Stages 4, 5, 6 and 7 are all present at less than 2% in January 1995 (Fig. 6), a low value for percentage of the population reproducing (Fig. 25). However, the population reproductive index is high, suggesting that those animals that are reproducing are in a more advanced phase of the reproductive cycle (Fig. 26). Stage 8 females were present at a relatively high percentage (4.84%) (Fig. 6) and a high percentage of them had the potential for recycling of the ovary that season (Table 5).

All indications for 1996 were for a good reproductive year. The population reproductive index was the highest seen during this study (Fig. 26). Stage 7 females comprised 87.20% of the population (Fig. 9), and the index of Stage 8 continuing to total Stage 8 females was high (Table 5). The small percentage of Stage 9 females indicates that the majority of the population is still actively reproducing.

Stage 4 females comprised 33.01% of the population in 1997 (Fig. 11).

This resulted in a high percentage of the population reproducing (Fig. 25) but also placed the population at a very early point in the reproductive cycle (Fig. 26). Total number of Stage 8 females was too low to determine an index of Stage 8 continuing/total Stage 8.

Criteria for a "good" reproductive season are early spawning, and high percentages of females reproducing and recycling the ovary. These criteria lead to an increased input of eggs and presumably larvae into the population. If spawning begins in early summer, females have time for multiple spawns. With a high percentage of reproducing females, more spawning females will result in more larvae. A high proportion of Stage 8 continuing suggests females will recycle the ovary and release another three batches of eggs.

Based on these criteria, 1995 and 1996 are categorized as good reproductive seasons, and 1993, 1994 and 1997 as poor ones (Table 5). Optimal conditions would result when all three criteria are met, as in 1996. However 1995, which meets two of the three conditions, is also categorized as a good year. Although the condition of a high percentage of females reproducing in the population was not met, the condition of a high percentage of Stage 8 continuing females was. As a result, increased input of eggs/larvae would still occur even though the percentage of the females reproducing was not high. In 1993, 1994 and 1997 spawning was delayed, the percentage of the population

reproducing was low and Stage 8 females were very low in number.

**Sea Ice Data**

Sea ice data for the Palmer LTER region for summer of 1992 to winter of 1995 are from Smith et al. (in press), and for spring of 1995 through fall of 1996 are from Smith (pers. comm.). These environmental parameters are considered a proxy for nutritional conditions since sea ice incorporates ice algae and conditions the water column for spring blooms (Ross and Quetin 1986; Smetacek et al. 1990). Smith et al. (in press) calculated sea ice area and sea ice extent from passive microwave satellite data. Sea ice area is defined as the ocean area covered only by sea ice with concentrations greater than 15%. Sea ice extent is defined as the ocean area enclosed by the 15% sea ice concentration contour. Sea ice extent is thought to best represent the region influenced by the sea ice (Stammerjohn 1993). Annual sea ice extent data is compared to average sea ice extent calculated from seventeen years of satellite data collected between 1978 and 1997. This long-term average value allows an understanding of how individual years fit into long-term patterns of sea ice variability. The sea ice regimes during the period of this study showed a great deal of variability (Fig. 27), and suggest that sea ice associated food will also have varied. Because krill spawn in the austral summer, it is the previous year's sea ice regime that influences the reproductive season (i.e.: 1992 sea ice conditions affect 1993 spawners).

**Chlorophyll Data**

Smith et al. (in press) present chlorophyll biomass for January only, not the entire season (Table 4). Mean values for the 500 and 600 lines (northern grid) are compared to the 200 and 300 lines (southern grid), and mean values of onshore and offshore chlorophyll concentrations are also compared. No chlorophyll data was available for 1997.

**Sea Ice and Food Availability**

The extent of sea ice cover is not the only feature of sea ice dynamics that is important to krill. Of possibly greater importance may be the onset of sea ice formation in the fall and melting in the spring and the rates of these processes. The retreat of the sea ice leads to ice-edge phytoplankton blooms which provide the source of food the krill need to build up lipid reserves for the reproductive season. The extent of the bloom and its utility to krill is dependent on the timing of this retreat. If the sea ice retreats early a large bloom may not occur, or may occur and be dissipated by storm action too early in the season to be of use to the krill (Smith et al. in press). Consequently, the food supply is less likely to be sufficient to meet the nutritional requirements the krill need to be physiologically prepared to reproduce. If the sea ice retreats late, the bloom will occur late in the season, and the krill will get a correspondingly late start on their reproductive season. Although they still may be able to complete the cycle before the sea ice forms again, their eggs will hatch so late in the season that food may not be available

for the newly-hatched larvae which must feed within 10-14 days of reaching the surface in order to survive (Ross and Quetin 1989). Thus, even though the females may successfully spawn despite the delay, larvae from that season may not have a good chance of surviving.

The high percent of Stage 2 females in poor years (1993, 1994, 1997) is entirely consistent with the sea ice regimes. Regardless of whether conditions were poor as a result of the sea ice peaking and retreating early (1992), late (1993), or because the sea ice extent was very low (1997), the result is low food availability in spring and fewer females able to acquire the food to advance to Stage 3, either for the first time from Stage 2, or for the second season as Stage 9 and 10 females reorganize (Fig. 23). Stage 3 females are common in the spring in the northern Antarctic Peninsula region (Ross, pers. comm.), as this is generally the time when the sea ice is retreating and food becomes available. The number of females remaining at Stage 3 during the summer serves as a good index of females that acquired enough energy to reorganize the ovary but not enough to enter the cycle of previtellogenesis and vitellogenesis. With the exception of 1995, percentages of Stage 3 females are low during the years of this study. The years of high percentages of Stage 2 (1993, 1994, 1997) indicate that spring nutritional conditions were not adequate to fuel the initial maturation to Stage 3.

The presence of Stage 10 females in the population in January, as seen in

1993 and 1994 (Figs. 2, 4), also suggests that spring food availability was low and the krill were not even able to acquire enough food to reorganize the ovary in preparation for spawning. 1995 was a year of above average sea ice extent which retreated in September. The low percentage of Stage 2 females and absence from the population of Stage 3 females in the summer of 1996 suggests that food was plentiful at the right time and the females were able to acquire enough resources to move on in the reproductive cycle.

**Relationship Between Reproductive Classification and Sea Ice Dynamics**

The two years classified as "good" reproductive years for the krill both show highest sea ice extent in August (Table 6). Although 1995 and 1996 are both classified as good reproductive years, there were considerable differences in the reproductive conditions of the respective krill populations. In 1995, the majority of the population was Stages 2 and 3 with only a small percentage of the population reproducing (Fig. 25). In 1996 the vast majority of the female krill were actively reproducing. Why the difference? Both years had above average spring sea ice, but sea ice in 1995 retreated two months earlier than in 1994 (Table 6). The resulting earlier food availability enabled the majority of the population to enter the reproductive cycle in 1996. The late retreat of the sea ice in 1994 resulted in lower food availability and a smaller percentage of the population entering the reproductive cycle (Fig. 25) but the above average sea ice and high percentage of Stage 8 continuing females made

for a successful reproductive season.

Sea ice conditions in poor reproductive years seem to be characterized not so much by their similarity to each other as by how they differ from the optimal timing of retreat and sea ice extent (Table 6). In 1992 sea ice retreated beginning in August, too early to result in a bloom at a time when it would be useful to the krill. The sea ice in 1993 persisted at above average values through November, and then underwent a late and rapid retreat. The pattern in 1996 was different from all other years of the study. Sea ice extent was only above average for one month, and considerably below average during the rest of 1996. Sea ice formed late, retreated early, and was below average throughout most of the season. The food resources associated with sea ice were likely at a minimum.

**Potential Causes**

Siegel & Loeb (1995) found a correlation between high winter sea ice and high reproductive success the following summer, but this may be a result of the fact that high winter sea ice usually correlates strongly with high spring sea ice. Winter of 1992 was an exception to this rule with above average sea ice in winter and below average sea ice in spring. These conditions did not lead to a good reproductive season in 1993, suggesting that high spring sea ice rather than high winter sea ice is important to reproductive success for the krill. Timing of sea ice retreat is also important. Sea ice conditions are presumed to reflect food

availability and are used as a proxy for food availability when direct measurements are not available. If high sea ice extent persists late in the spring, this could result in an increased input of food into the system but could also result in delayed or reduced spawning effort as availability of the high concentrations of food needed for reproduction would not occur until late in the spring. The evidence suggests that retreat of the sea ice in November is too late to result in optimal food availability in the spring, and retreat of the sea ice in August is too early (Table 6).

**Total Length**

There is considerable interannual variability in the average TL and size range for a specific stage throughout the five years of this study (Table 7, Figs 19-22). This variability in length composition of the population may be attributable to sea ice conditions. Winter sea ice conditions affect winter-over survivorship of krill larvae (Quetin and Ross 1991). If winter sea ice is low or retreats early, survivorship may be much reduced and a year class may be very poor, as occurred in 1993, or even fail, as occurred in 1992 (Ross and Quetin subm.). Absence of a year class from the population would result in a "hole" in the length frequency distribution, with a truncated (either end) or bimodal distribution. The relationship between TL and age in krill varies with nutritional conditions and it becomes increasingly difficult to specify age for length as the animals get older (de la Mare 1994). Approximate size ranges for krill of different ages have been calculated however, and are used here

for comparison (de la Mare 1994).

In Jan 93, TL distribution shows no obvious departures from normal. However the effects of the failure of the 1992 year class would not surface in Jan 93 when the krill are one year old (AC1) and are not reproducing. Since this study deals only with reproductive animals, the absence of non-reproductive females has no effect on the results.

In 1994 krill from the failed year class of 1992 would have been two years old (AC2) with an approximate TL range of 32-34 mm (de la Mare 1994). In 1994 there were very few small Stage 2 females, and high numbers of extremely large Stage 2 females (Fig. 19). Although the failure of the 1992 year class may be responsible for the lack of 32-34 mm krill and thus the lack of small Stage 2 females, it cannot be the underlying cause of the high number of large Stage 2 females. Large Stage 2 females are likely the result of two sequential low sea ice years (and therefore two sequential years of low food availability), and their presence suggests that krill can delay maturity for two years in a row. These large Stage 2 females may be the same individuals that were the small Stage 2 females in 1993.

In 1995 the 1992 year class would have been in their fourth summer (AC3) and approximately 42-44 mm TL (de la Mare 1994). The length-at-age relationship becomes increasingly more variable as the krill get

older, and krill in this size range could be from age classes AC3-AC5 (de la Mare 1994). Krill are present in this size range in 1995, but overall numbers are low (Figs. 19-22), fewer than would be expected if the 1992 year class was present. Stage 2 females are still in the upper part of the size range in 1995 (Fig. 14). Since 1994 was a year of late sea ice retreat, food availability conditions in the spring might have resulted in some of the Stage 2 females from 1994 remaining non-reproductive for another season.

In 1996 the 1992 year class would have been in their fifth summer (AC4) with an approximate size range of 48-50 mm (de la Mare 1994). Length distribution data from the total population in 1996 is strongly bimodal and probably represents both the absence of the 1992 year class and the very low recruitment of the 1993 year class (Ross, pers. comm.), i.e. the lack of both AC3s and AC4s. Stage 2 females are the smallest seen during this study and there are very few that fall into the 48-50 mm size range (Fig. 19). There were no Stage 3 females in 1996 and so few Stage 4 females that it is difficult to draw any conclusions from their size range, although all were smaller than 48 mm. The smallest Stage 5 females found in 1996 were around 46 mm but there are very few smaller than 50 mm. The absence of krill in the mid-size range results in the highest average TL values for Stages 6-9 seen in this study (Table 7).

In 1997 the failed year class would have been five years old (AC5) with

an approximate size range of 54-56 mm (de la Mare 1994). All Stage 2 and 3 females are smaller than this size range (Figs. 19-20). Small numbers of females of Stages 4 and 5 are present in this range (Figs. 21-22). Average TL values for reproductive Stages 5, 7, 9 and 10 are the lowest seen in this study (Table 7). Stage 8 females were present in very small numbers, and Stage 6 females were absent from the population. These low average TL values may be attributable to the absence of the 1992 year class from the population. Many of the large reproducing females in 1996 would have been five years old or older, and, as that is approaching the limit of their life span (Ettershank 1983, 1984), may not have survived to reproduce during another season. The large krill that would have been the product of the 1992 year class are absent, resulting in a generally smaller population overall (Table 7).

## CONCLUSION

Results of this study showed strong interannual variability in physiological maturity stage composition of female Antarctic krill in the Palmer LTER region west of the Antarctic Peninsula. Physiological maturity stage composition for each year was used to characterize reproductive seasons in terms of timing of spawning, percentage of females reproducing, and percentage of females recycling the ovary. Sea ice conditions were used as a proxy for food availability, with the

variability in extent of sea ice and timing of retreat representing variability in food availability in the spring. Good conditions occurred in years with high spring sea ice extent and initial sea ice retreat in late September. Poor conditions occurred when spring sea ice extent was low or initial retreat of sea ice was earlier or later than September. The predictability of good and poor reproductive seasons from sea ice extent in spring and timing of sea ice retreat suggested that the success or failure of the reproductive effort by Antarctic krill is a function of food availability in the spring. The results obtained implied a strong coupling between sea ice conditions in the spring and the physiological maturity of the population of female Antarctic krill the following summer.

Data presented in this study were consistent with the hypothesis that female krill migrate horizontally from onshore to offshore locations as they progress through the reproductive cycle. Distribution patterns of physiological maturity stages showed segregation by stage and a clear tendency for females that are either immature or in initial stages of the reproductive cycle to be located in the inner shelf region in areas with high chl concentrations. Females in more advanced stages of the reproductive cycle tended to be located offshore in deeper water, potentially associated with the CDW which is thought to be important for successful hatching of krill eggs (Hofmann et al. 1992; Quetin et al. 1994).

The importance of long-term study to the understanding of Antarctic krill reproduction is clear from this research. Sea ice conditions, and stage composition and distribution of the populations were different for each of the five years, suggesting that the time series is not yet long enough to show either cycles or trends. Further years of study of the natural experiment created by interannual variation in sea ice conditions will be necessary to better understand the association between sea ice conditions and krill reproduction.

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Table 1: Palmer LTER research cruises: dates and transect lines sampled

| Cruise | Start Date | End Date | Lines |
|---|---|---|---|
| 93Jan | 5 Jan | 8 Feb | 200-600 |
| 94Jan | 11 Jan | 7 Feb | 300-600 |
| 95Jan | 7 Jan | 8 Feb | 200-600 |
| 96Jan | 8 Jan | 10 Feb | 200-600 |
| 97Jan | 11 Jan | 13 Feb | 200-600 |

Table 2: *Euphausia superba*. Ranges in total length for females in each physiological maturity stage (Cuzin-Roudy and Amsler 1991) for the five years of this study. n=number of female krill measured.

| Stage | 1993 | n= | 1994 | n= | 1995 | n= | 1996 | n= | 1997 | n= |
|---|---|---|---|---|---|---|---|---|---|---|
| 2 | 30.63-47.44 | 144 | 30.76-50.28 | 127 | 31.65-48.25 | 135 | 30.37-43.77 | 70 | 28.50-47.61 | 207 |
| 3 | 35.63-50.95 | 22 | 40.20-47.09 | 25 | 40.49-48.29 | 34 | Ø | 0 | 36.19-45.42 | 21 |
| 4 | 40.16-57.16 | 86 | 47.00-54.77 | 15 | 42.95-48.55 | 11 | 40.35-44.34 | 7 | 36.89-57.74 | 109 |
| 5 | 46.06-56.25 | 13 | 40.13-49.45 | 48 | 40.10-53.66 | 37 | 45.20-53.96 | 15 | 39.01-53.57 | 23 |
| 6 | 42.46-56.59 | 15 | 47.62-54.12 | 12 | 42.31-55.65 | 32 | 46.39-57.95 | 24 | Ø | 0 |
| 7 | 47.56-59.21 | 24 | 47.02-57.83 | 18 | 43.70-56.70 | 28 | 45.86-60.92 | 147 | 42.15-49.59 | 3 |
| 8 | 49.40 | 1 | 50.93-52.93 | 2 | 45.31-59.98 | 95 | 40.19-61.20 | 64 | 47.88-58.61 | 2 |
| 9 | 43.06-55.32 | 9 | 39.42-52.74 | 18 | 41.79-50.84 | 10 | 45.64-55.44 | 19 | 38.08-48.15 | 16 |
| 10 | 34.66-48.47 | 11 | 41.22-46.81 | 9 | 46.62 | 1 | Ø | 0 | 33.47 | 1 |

Table 3: *Euphausia superba*. Range of stages possible for a standard 47.00 mm female within stage size ranges for the year. Ø=no females of this stage found.

| Year | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|
| 1993 | X | X | X | X | X | | | X | X |
| 1994 | X | X | X | X | | X | | X | X |
| 1995 | X | X | X | X | X | X | X | X | |
| 1996 | | Ø | | X | X | X | X | X | Ø |
| 1997 | X | | X | X | Ø | X | | X | |

Table 4: Average chl biomass (mg Chl $m^{-3}$) during annual January/February cruises for Palmer LTER (1993-1996). Averages are for different regions within the area sampled. Data from Smith et al. (in press). Northern LTER grid is the mean of stations on transect lines 500 and 600. Southern LTER grid is the mean of stations on transect lines 200 and 300. Onshore LTER grid is the mean of the innermost stations (nearest the coast) on each transect line. Offshore LTER grid is the mean of the outermost stations (furthest from the coast) on each transect line.

| Year | Northern LTER grid (mg Chl $m^{-3}$) | Southern LTER grid (mg Chl $m^{-3}$) | North vs. South | Onshore (mg Chl $m^{-3}$) | Offshore (mg Chl $m^{-3}$) | Onshore vs. Offshore |
|---|---|---|---|---|---|---|
| 1993 | 1.36 | 0.59 | 2.30 | 1.15 | 0.36 | 3.19 |
| 1994 | 1.23 | 1.39 | 0.88 | 1.94 | 0.85 | 2.28 |
| 1995 | 2.42 | 1.07 | 2.26 | 3.46 | 0.56 | 6.18 |
| 1996 | 2.65 | 0.87 | 3.04 | 5.00 | 0.44 | 11.36 |

Table 5: Criteria for classifying reproductive season of *Euphausia superba* as good or poor.

| Year | Timing of Spawning | % of Population in Stages 4-9 | % of total Stage 8 that are continuing | Type of Season |
|---|---|---|---|---|
| 1993 | delayed | low | total # too low | poor |
| 1994 | delayed | low | total # too low | poor |
| 1995 | early | low | 17.1 | good |
| 1996 | early | high | 20.8 | good |
| 1997 | delayed | low | total # too low | poor |

Table 6: Sea ice anomalies. Month of initial ice retreat is defined as the month just prior to the first month of below average ice extent in spring (from Smith et al. in press).

| Year | Winter Ice Index | Spring Ice Index | Month of Initial Ice Retreat |
|---|---|---|---|
| 1992 | +0.4 | -1.0 | Aug |
| 1993 | -0.1 | +0.2 | Nov |
| 1994 | +0.2 | +0.5 | Nov |
| 1995 | +0.6 | +nd | Sept |
| 1996 | -nd | -nd | Aug |

Table 7: *Euphausia superba*. Average total length for females in each physiological maturity stage (Cuzin-Roudy and Amsler 1991), by year. Italicized values are from total n ≤ 3.

| Stage | 1993 | 1994 | 1995 | 1996 | 1997 |
|---|---|---|---|---|---|
| 2 | 37.49 | 43.76 | 41.18 | 34.95 | 36.77 |
| 3 | 42.48 | 46.41 | 43.81 | Ø | 40.73 |
| 4 | 48.99 | 50.65 | 45.65 | 42.66 | 47.22 |
| 5 | 51.01 | 49.11 | 47.22 | 50.42 | 48.11 |
| 6 | 50.72 | 51.39 | 49.57 | 51.77 | Ø |
| 7 | 53.98 | 52.04 | 51.84 | 54.26 | *44.68* |
| 8 | *49.40* | *51.93* | 52.92 | 54.87 | *53.25* |
| 9 | 47.45 | 46.47 | 45.29 | 50.37 | 41.62 |
| 10 | 43.55 | 45.02 | *46.62* | Ø | *33.47* |

Figure 1: Basemap of the Palmer LTER study region along the west coast of the Antarctic Peninsula. Stations (Δ) are located at 20 km intervals along ten transect lines which are spaced 100 km apart. The solid and dashed lines represent the 500- and 1000- m isobaths, respectively. Geographic locations are abbreviated as: AdI-Adelaide Island, AnI-Anvers Island, DaB-Dallman Bay, EI- Elephant Island, GeS-Gerlache Strait, MaB-Marguerite Bay, ReI-Renaud Island, SSI-South Shetland Islands.

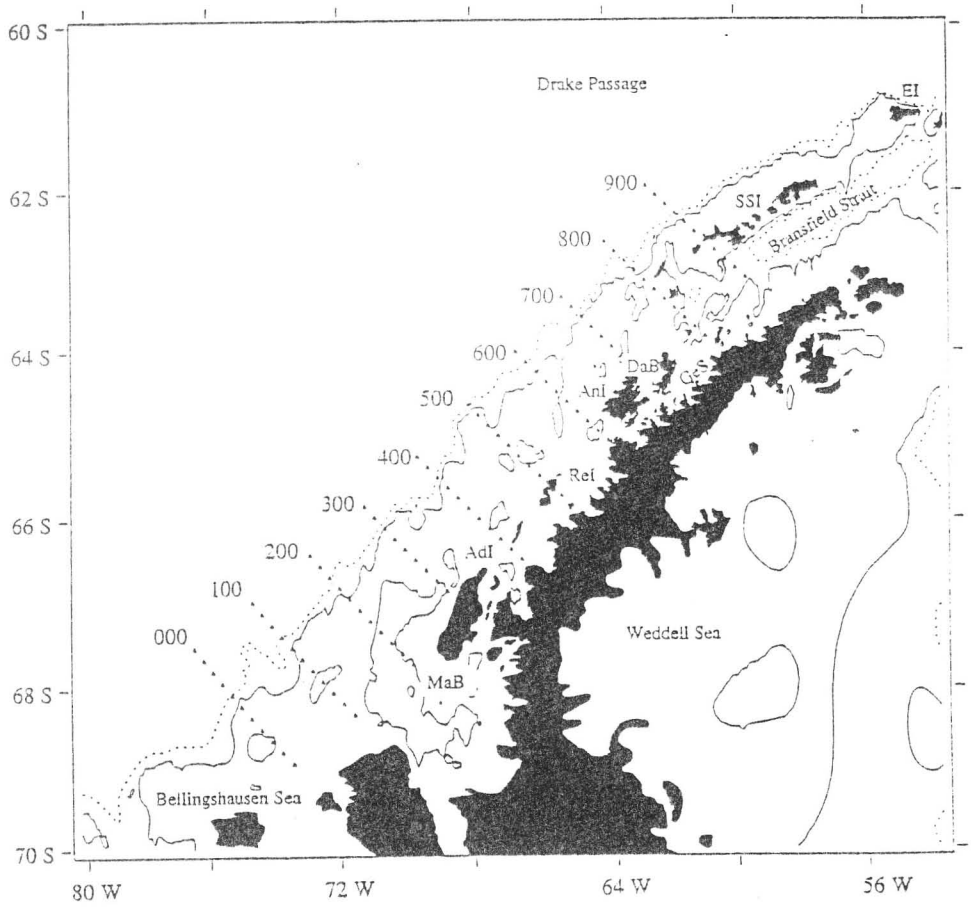

60 S
62 S
64 S
66 S
68 S
70 S
80 W
72 W
64 W
56 W
Drake Passage
EI
SSI
Bransfield Strait
900
800
700
600
500
400
300
200
100
000
DaB
GS
AnI
RoI
AdI
MaB
Weddell Sea
Bellingshausen Sea

Figure 2: *Euphausia superba.* Proportion of the female krill population in each physiological maturity stage in austral summer 1993.

# 1993

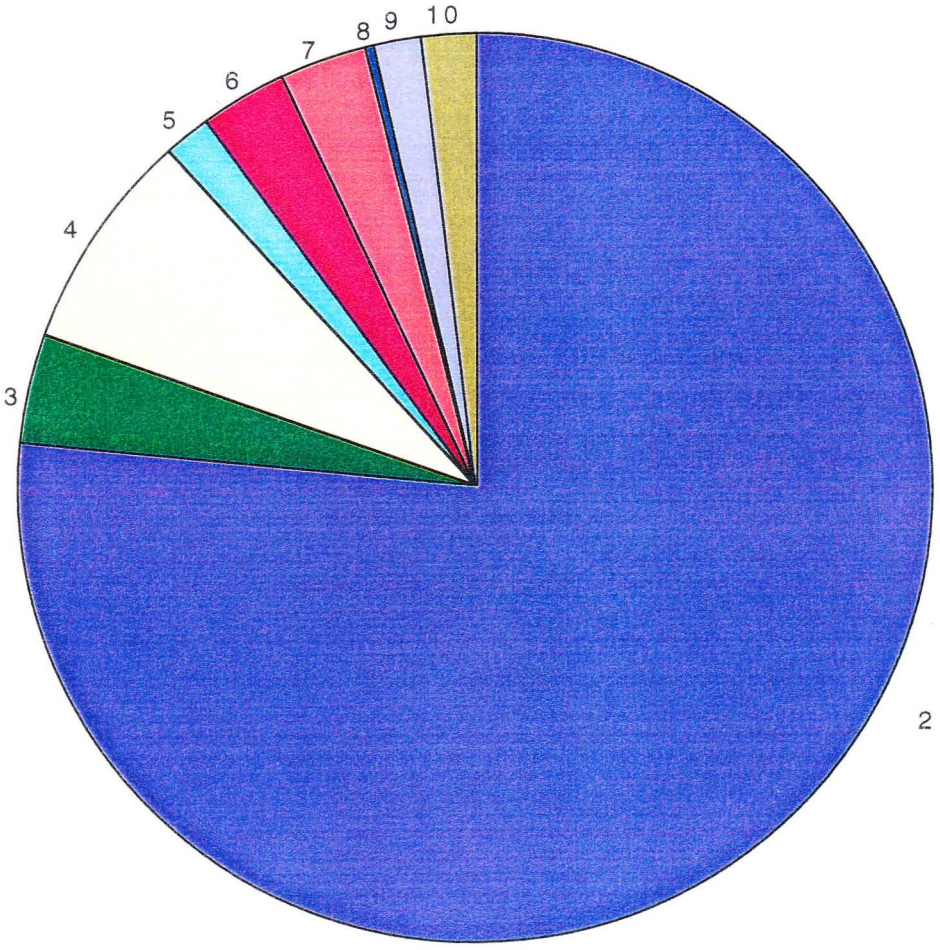
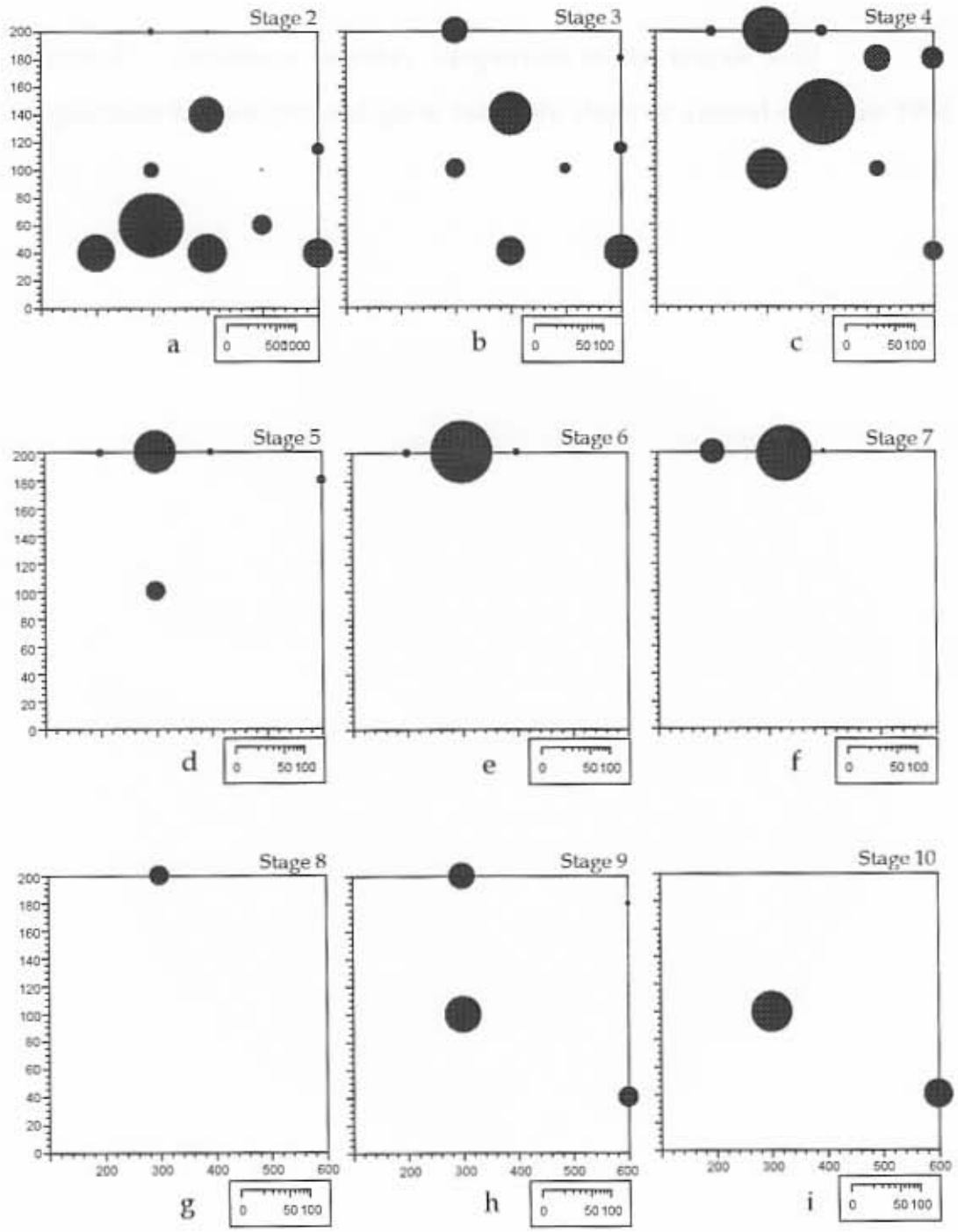


Figure 3: *Euphausia superba.* Distribution of physiological maturity stages throughout the Palmer LTER grid in austral summer 1993. Scales are linear and in number of females $10^3$ $m^{-3}$. The scale of Fig. 3a is ten times larger than the scale of the other lettered panels. LTER transects are perpendicular to the coastline, circles are centered on stations along transects. The y-axis is in kilometers from the baseline along the coast.




Palmer LTER Transects

Figure 4: *Euphausia superba.* Proportion of the female krill population in each physiological maturity stage in austral summer 1994.

**1994**

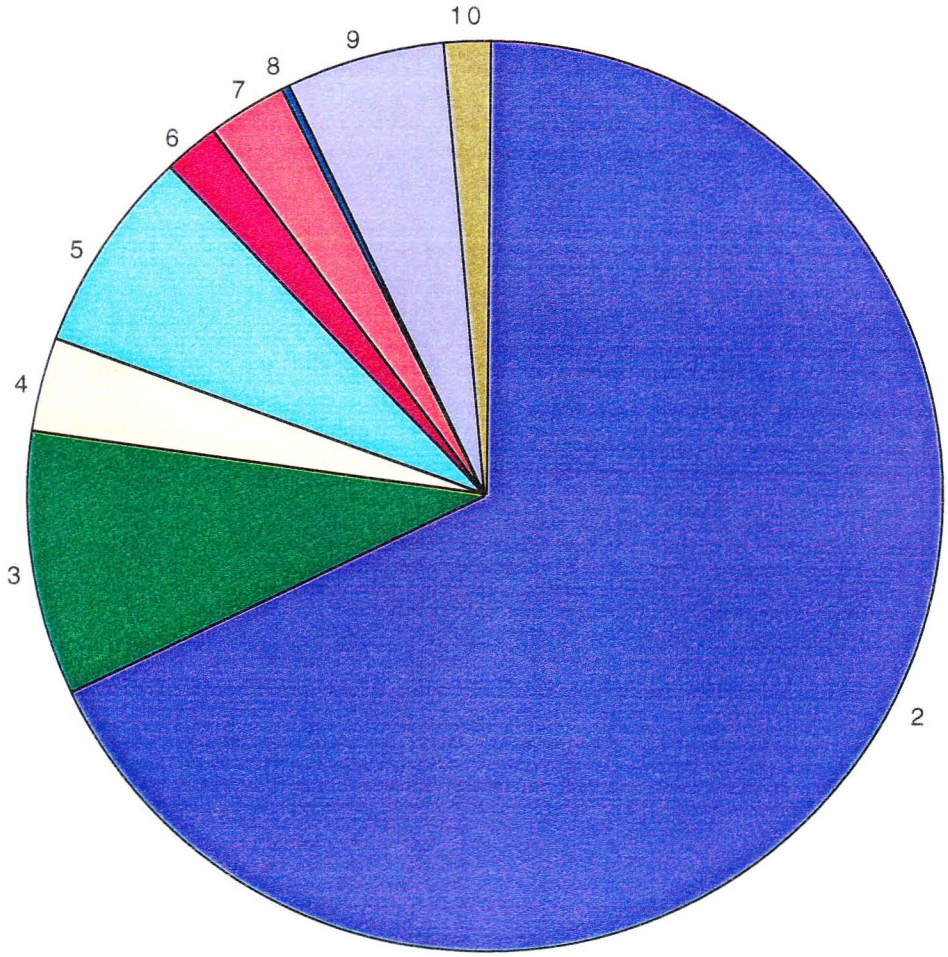
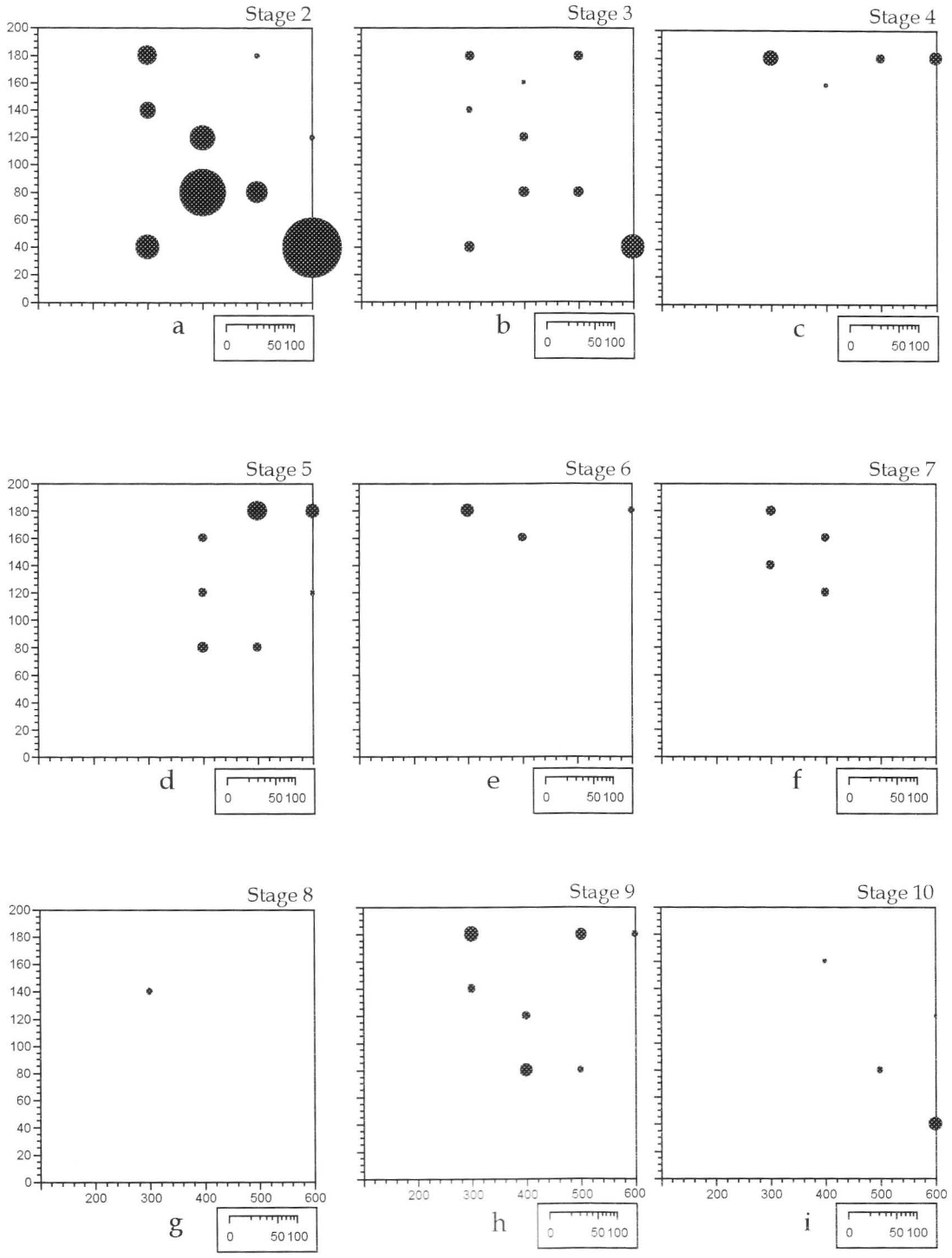


Figure 5: *Euphausia superba*. Distribution of physiological maturity stages throughout the LTER grid in austral summer 1994. Scales are linear and in number of females $10^3$ $m^{-3}$. All panels are at the same scale. LTER transects are perpendicular to the coastline, circles are centered on stations along transects. The y-axis is in kilometers from the baseline along the coast.




Palmer LTER Transects

Figure 6: *Euphausia superba.* Proportion of the female krill population in each physiological maturity stage in austral summer 1995.

**1995**

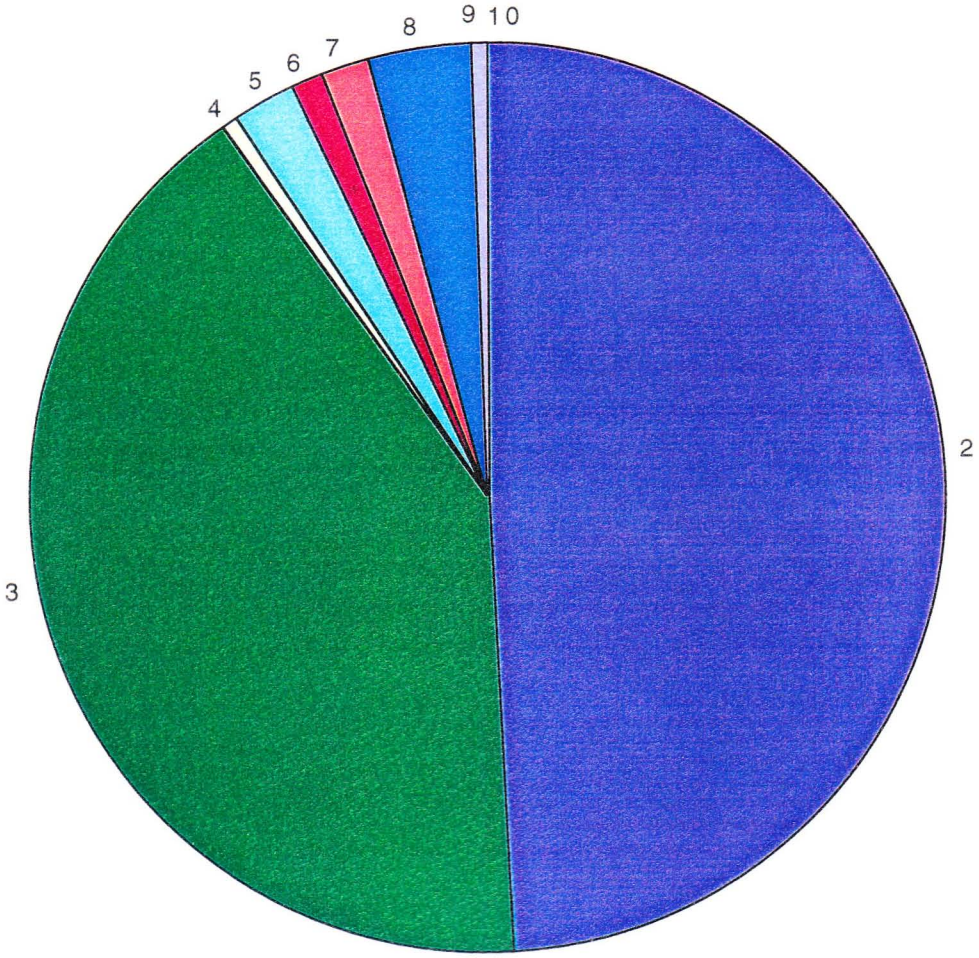
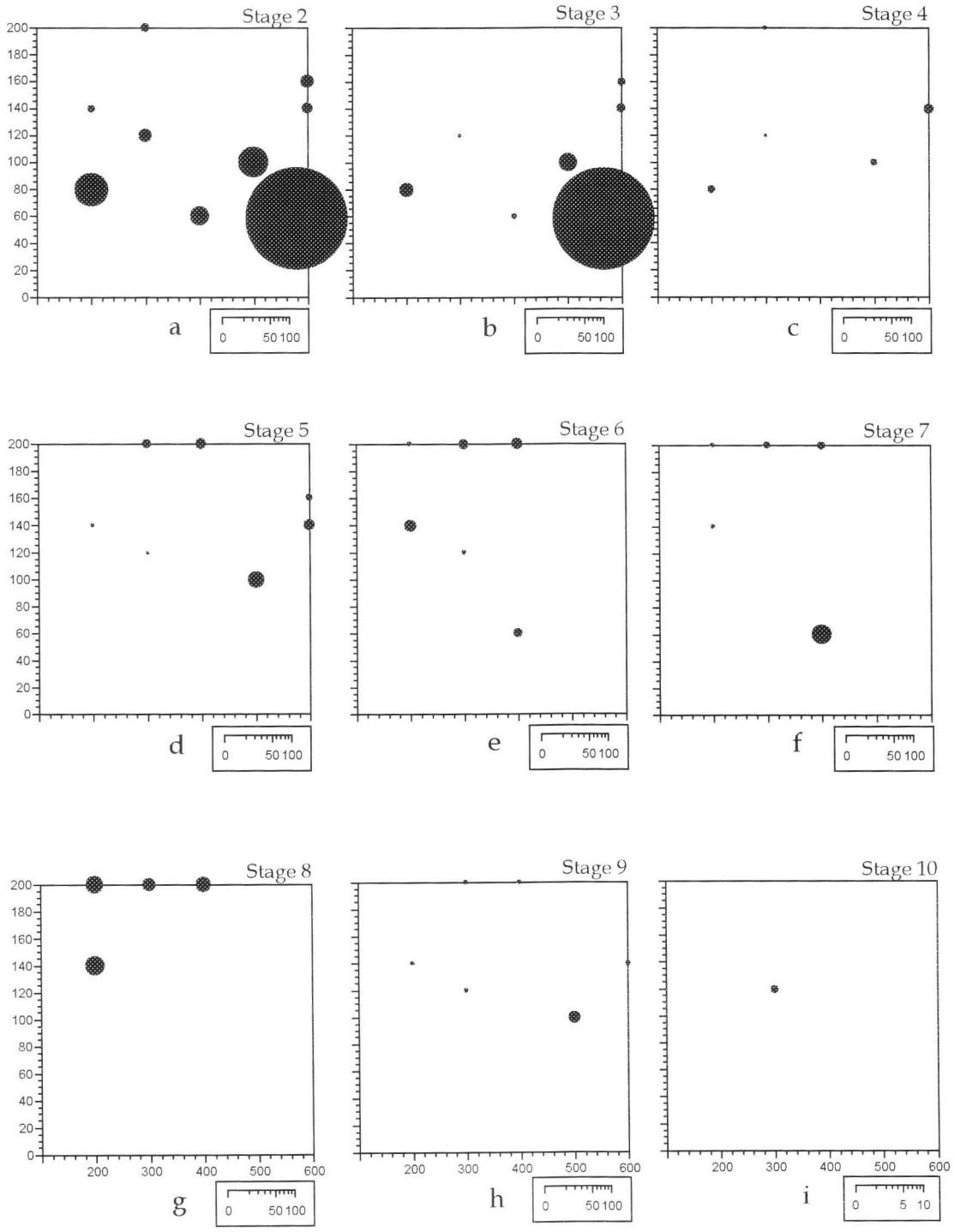


Figure 7: *Euphausia superba.* Distribution of physiological maturity stages throughout the LTER grid in austral summer 1995. Scales are linear and in number of females $10^3$ $m^{-3}$. Scale of Fig. 7i is one tenth the rest of the panels. LTER transects are perpendicular to the coastline, circles are centered on stations along transects. The y-axis is in kilometers from the baseline along the coast.




Palmer LTER Transects

Figure 8: *Euphausia superba*. Proportion of the female krill population in each physiological maturity stage in austral summer 1996.

**1996**

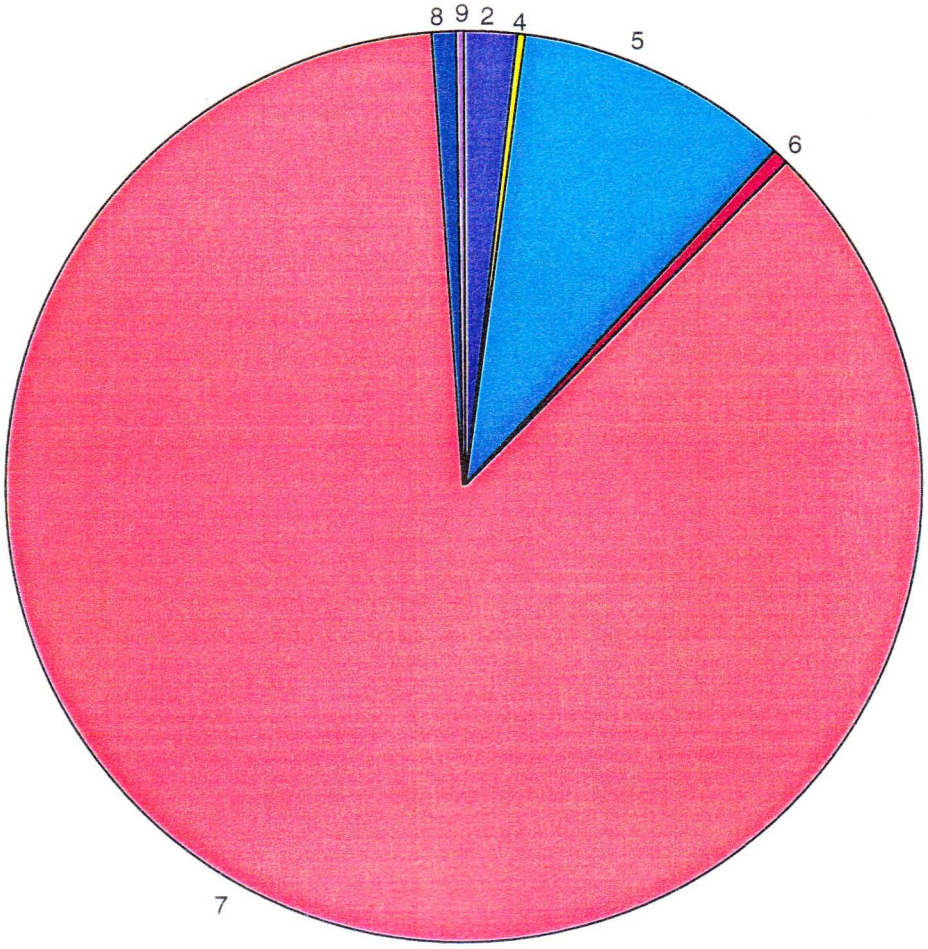
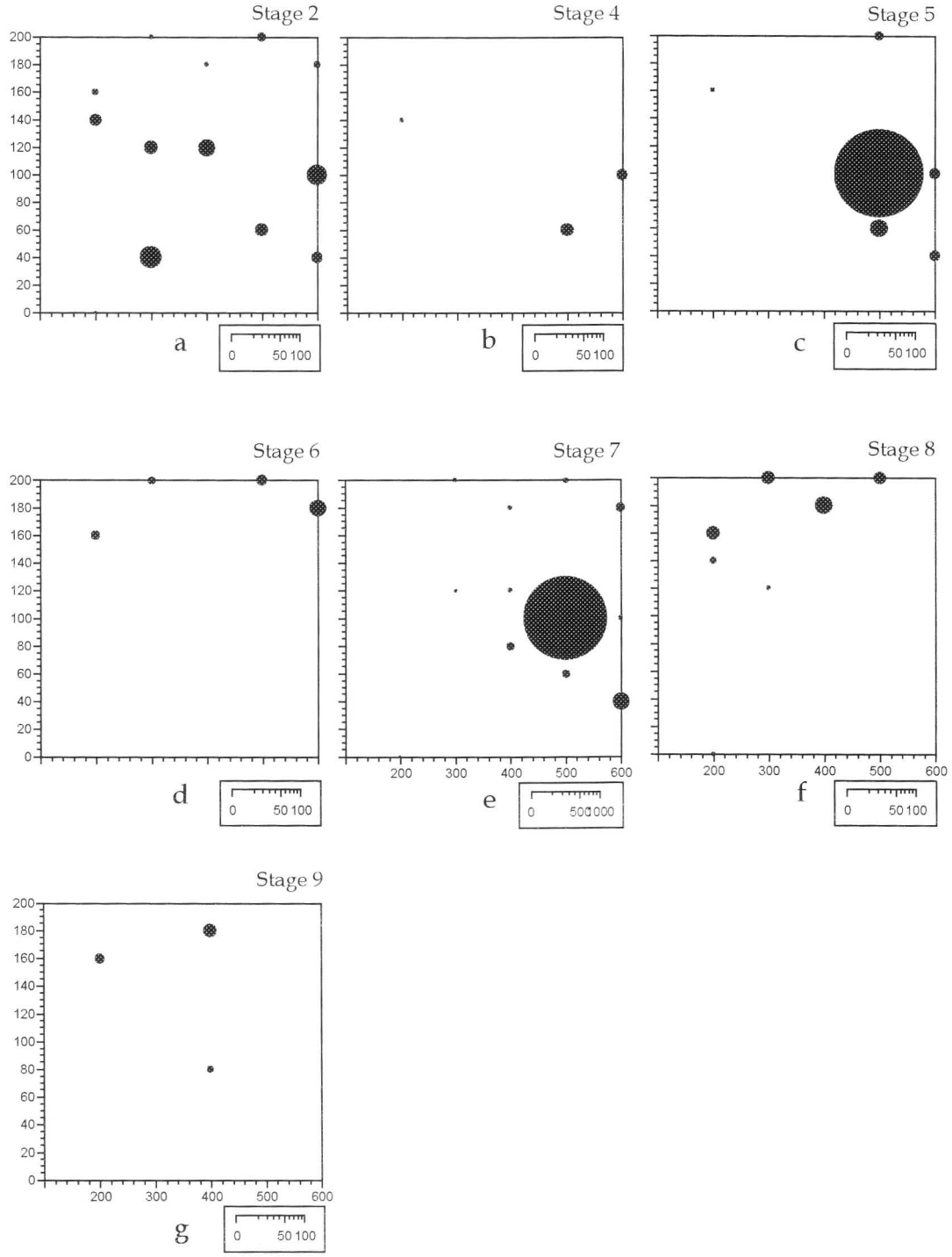


Figure 9: *Euphausia superba.* Distribution of physiological maturity stages throughout the LTER grid in austral summer 1996. Scales are linear and in number of females $10^3$ $m^{-3}$. The scale of Fig. 9e is ten times larger than the scale of the other lettered panels. There were no Stage 3 or 10 females. LTER transects are perpendicular to the coastline, circles are centered on stations along transects. The y-axis is in kilometers from the baseline along the coast.




Palmer LTER Transects

Figure 10: *Euphausia superba*. Proportion of the female krill population in each physiological maturity stage in austral summer 1997.

# 1997

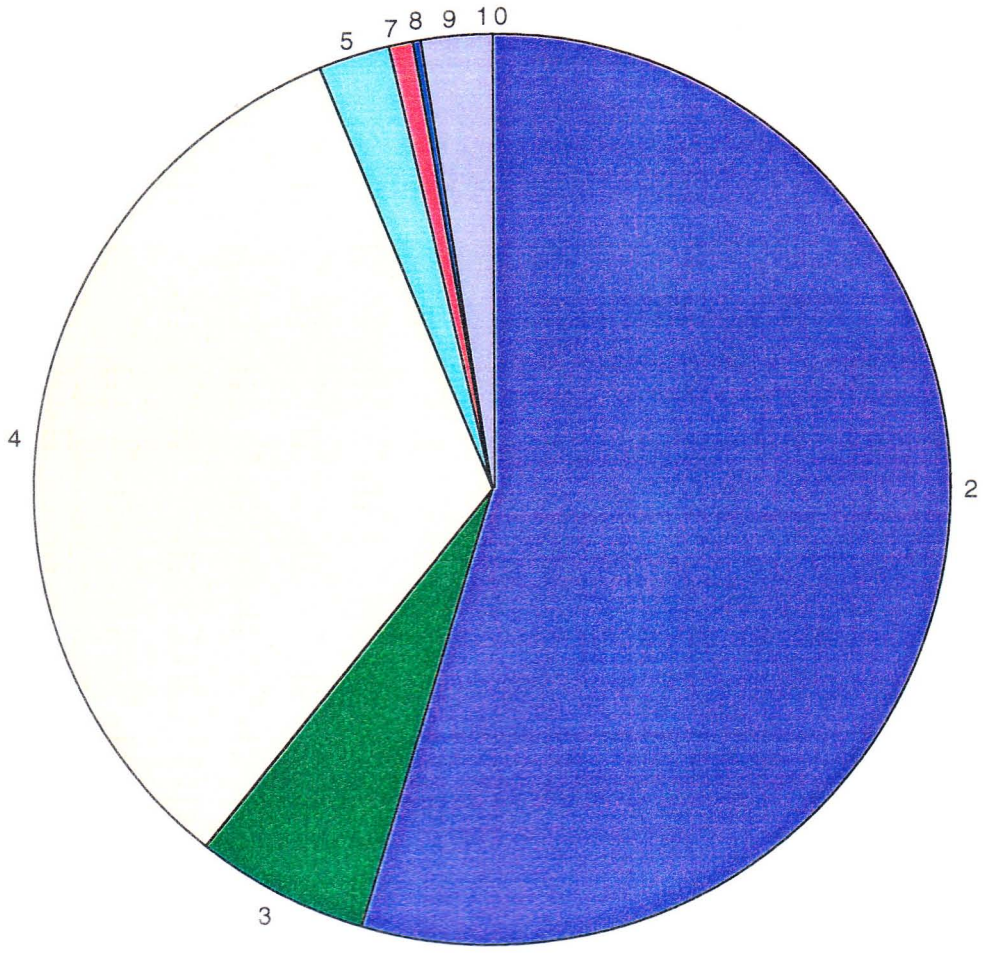
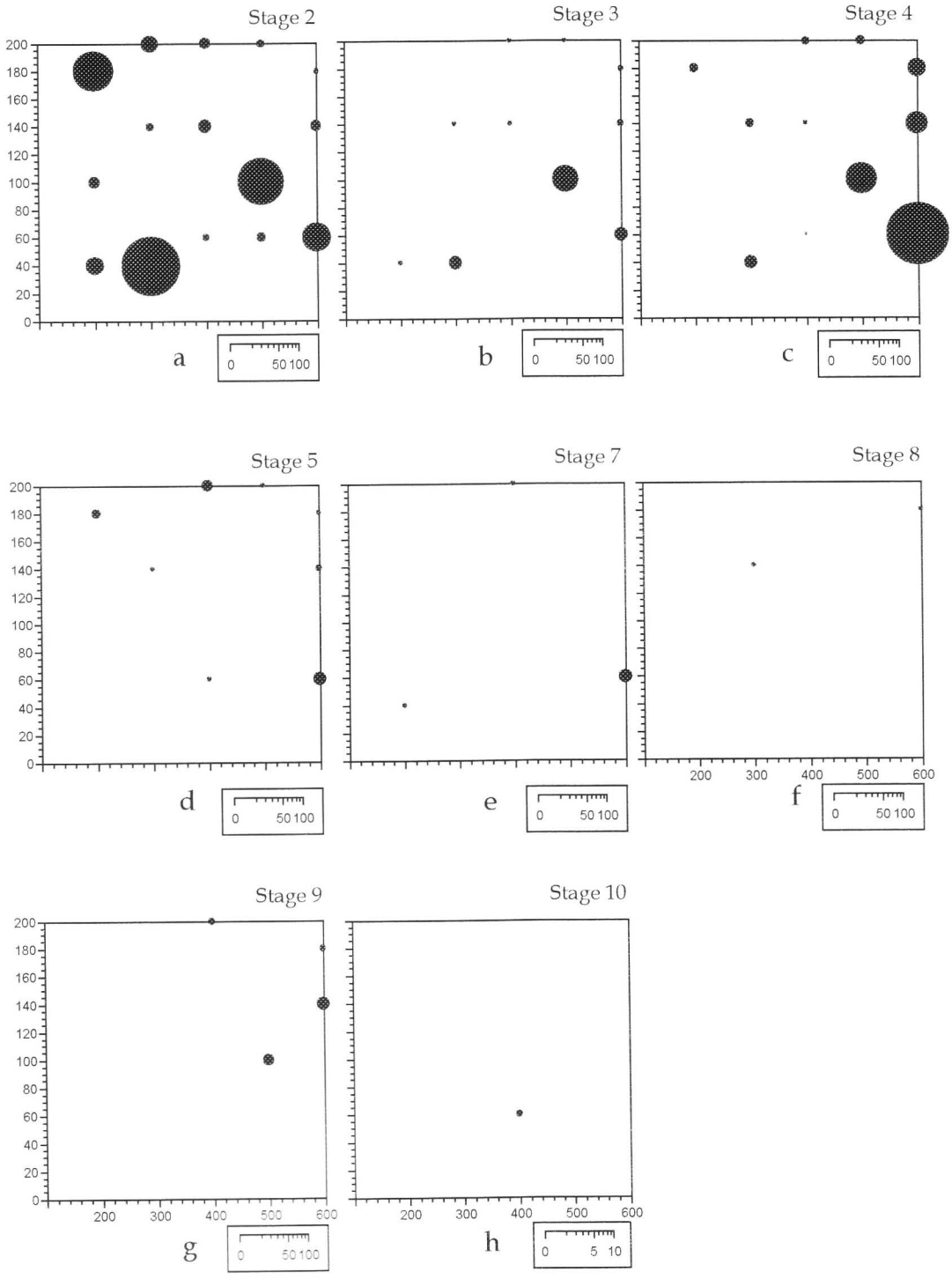
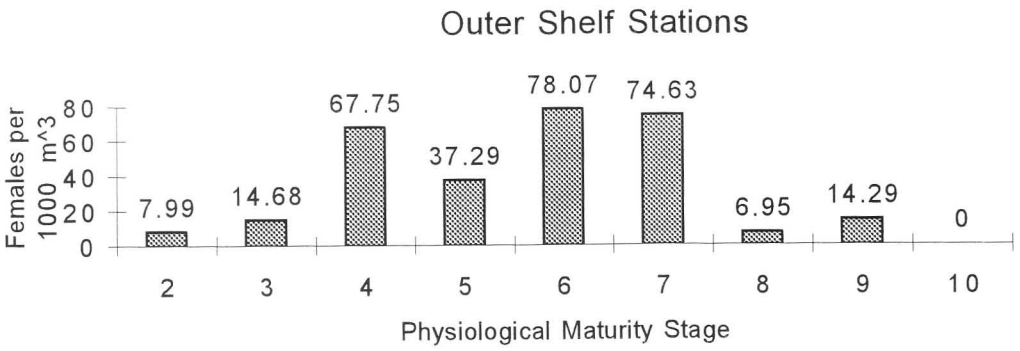


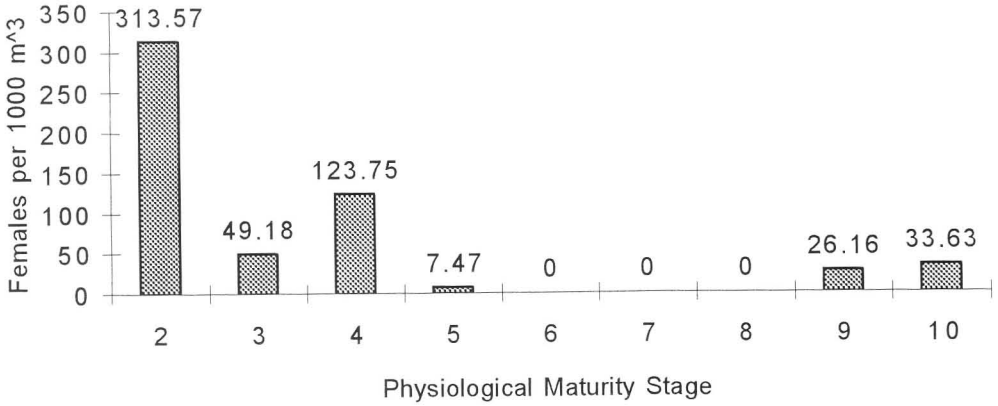
Figure 11: *Euphausia superba.* Distribution of physiological maturity stages throughout the LTER grid in austral summer 1997. Scales are linear and in number of females $10^3$ $m^{-3}$. Scale of Fig. 11h is one tenth the rest of the panels. There were no Stage 6 females. LTER transects are perpendicular to the coastline, circles are centered on stations along transects. The y-axis is in kilometers from the baseline along the coast.




Palmer LTER Transects

Figure 12: *Euphausia superba*. Number of female krill per 1000 $m^3$ in physiological maturity stages 2-10 at inner shelf (*.040-*.080), mid-shelf (*.100-*.140), and outer shelf (*.160-*.200) stations during austral summer 1993.


Outer Shelf Stations
Females per 1000 m^3
80
60
40
20
0
7.99
14.68
67.75
37.29
78.07
74.63
6.95
14.29
0
2
3
4
5
6
7
8
9
10
Physiological Maturity Stage


Mid-shelf Stations
Females per 1000 m^3
350
300
250
200
150
100
50
0
313.57
49.18
123.75
7.47
0
0
0
26.16
33.63
2
3
4
5
6
7
8
9
10
Physiological Maturity Stage

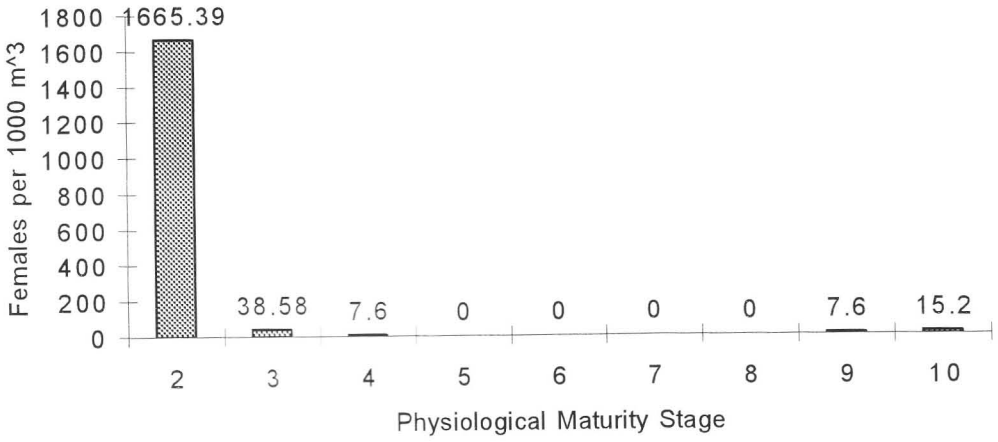
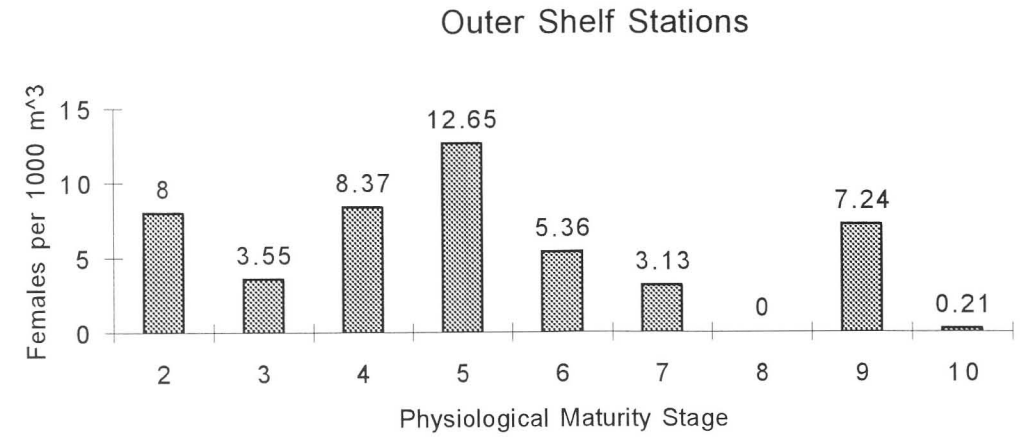
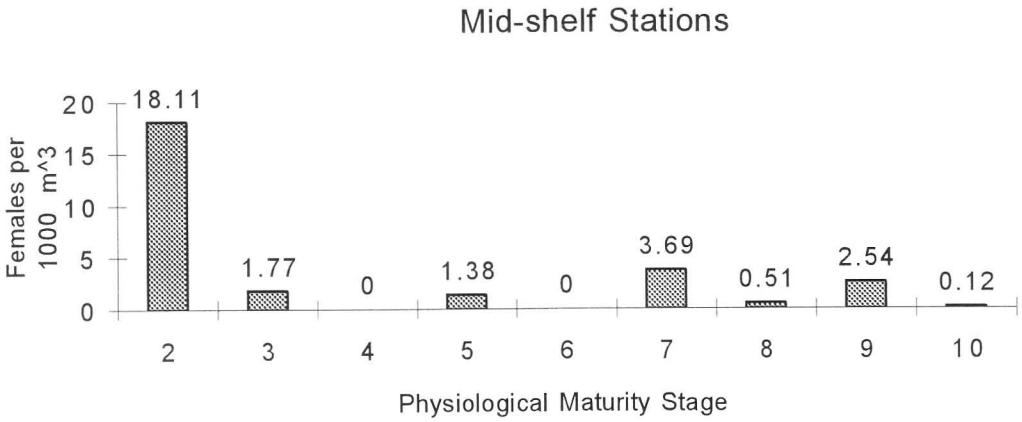

Inner Shelf Stations
Females per 1000 m^3
1800
1600
1400
1200
1000
800
600
400
200
0
1665.39
38.58
7.6
0
0
0
0
7.6
15.2
2
3
4
5
6
7
8
9
10
Physiological Maturity Stage

Figure 13: *Euphausia superba.* Number of female krill per 1000 $m^3$ in physiological maturity stages 2-10 at inner shelf (*.040-*.080), mid-shelf (*.100-*.140), and outer shelf (*.160-*.200) stations during austral summer 1994.


Outer Shelf Stations
Females per 1000 m^3
15
10
5
0
8
3.55
8.37
12.65
5.36
3.13
0
7.24
0.21
2
3
4
5
6
7
8
9
10
Physiological Maturity Stage


Mid-shelf Stations
Females per 1000 m^3
20
15
10
5
0
18.11
1.77
0
1.38
0
3.69
0.51
2.54
0.12
2
3
4
5
6
7
8
9
10
Physiological Maturity Stage

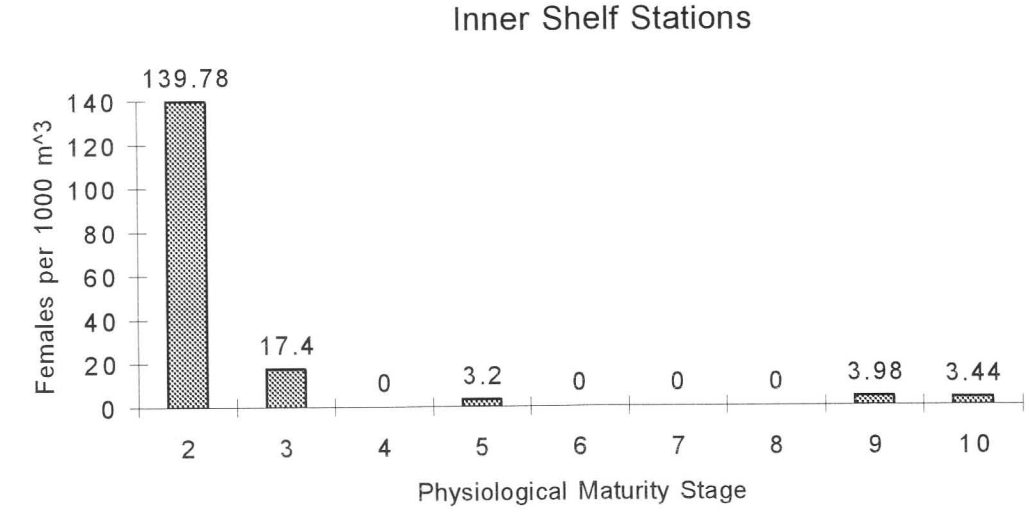
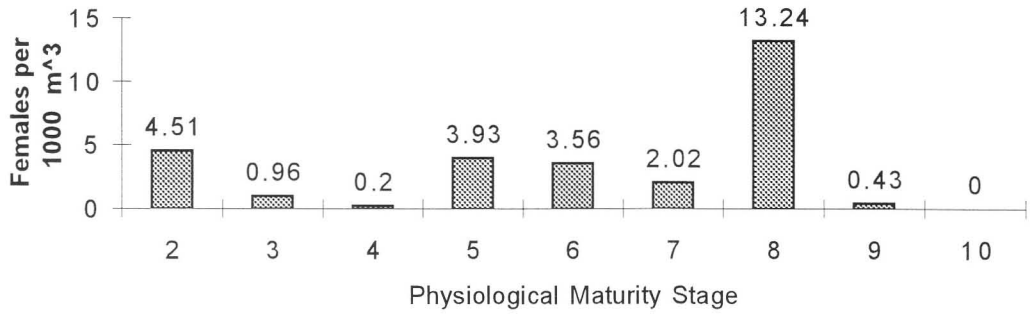
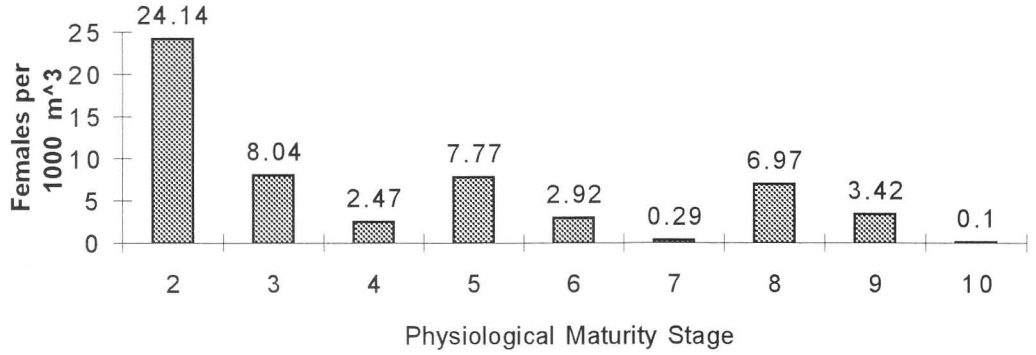

Inner Shelf Stations
Females per 1000 m^3
140
120
100
80
60
40
20
0
139.78
17.4
0
3.2
0
0
0
3.98
3.44
2
3
4
5
6
7
8
9
10
Physiological Maturity Stage

Figure 14: *Euphausia superba.* Number of female krill per 1000 $m^3$ in physiological maturity stages 2-10 at inner shelf (*.040-*.080), mid-shelf (*.100-*.140), and outer shelf (*.160-*.200) stations during austral summer 1995.

Outer Shelf Stations




Mid-shelf Stations




Inner Shelf Stations

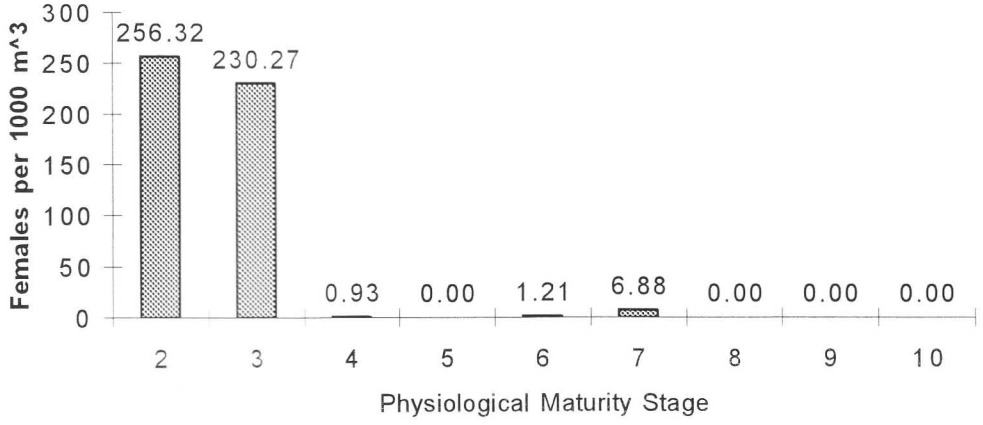
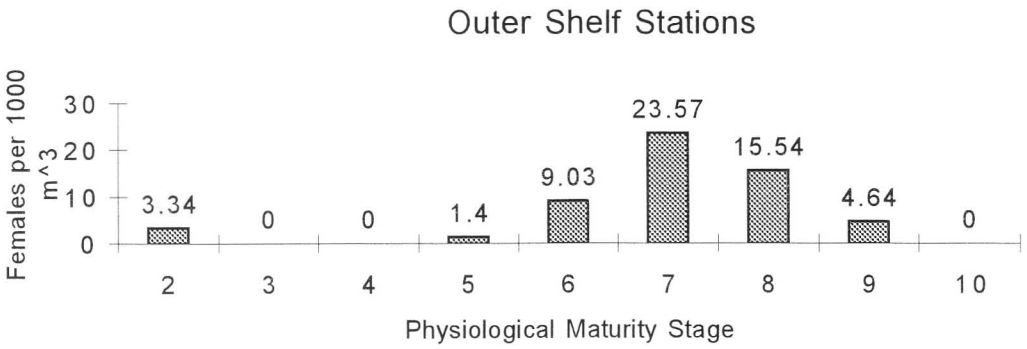
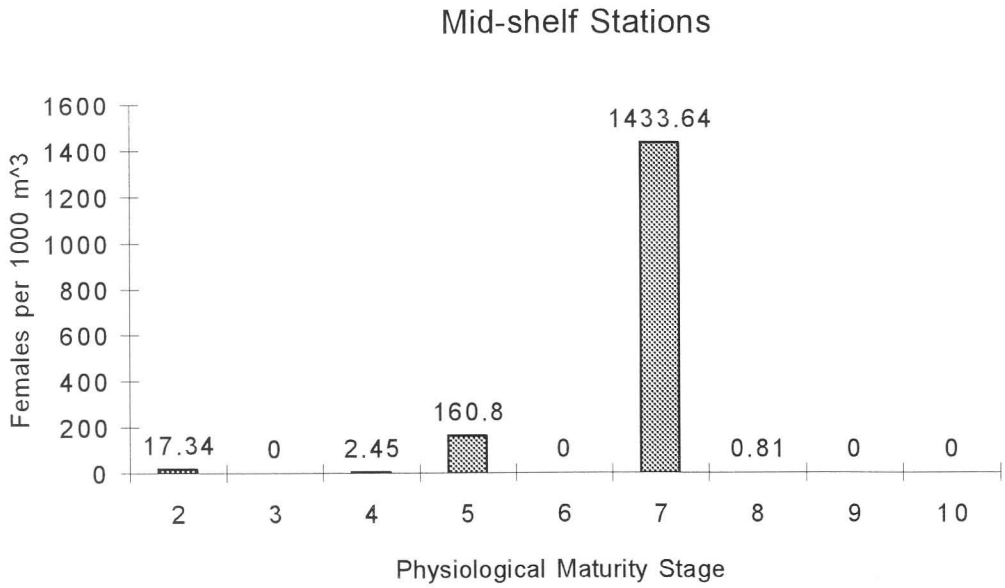


Figure 15: *Euphausia superba*. Number of female krill per 1000 $m^3$ in physiological maturity stages 2-10 at inner shelf (*.000-*.080), mid-shelf (*.100-*.140), and outer shelf (*.160-*.200) stations during austral summer 1996.


Outer Shelf Stations
Females per 1000 m^3
30
20
10
0
3.34
0
0
1.4
9.03
23.57
15.54
4.64
0
2
3
4
5
6
7
8
9
10
Physiological Maturity Stage


Mid-shelf Stations
Females per 1000 m^3
1600
1400
1200
1000
800
600
400
200
0
17.34
0
2.45
160.8
0
1433.64
0.81
0
0
2
3
4
5
6
7
8
9
10
Physiological Maturity Stage

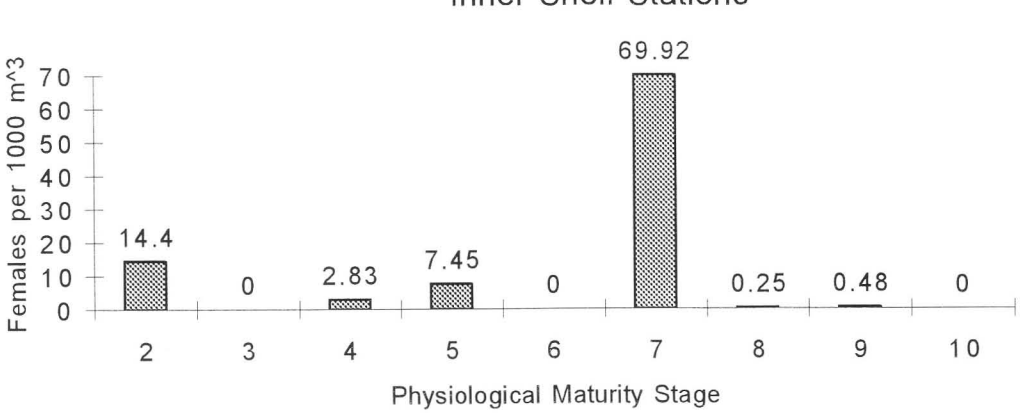
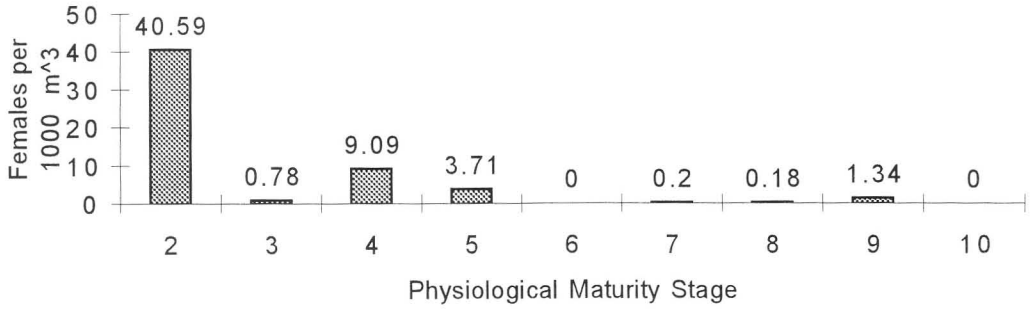
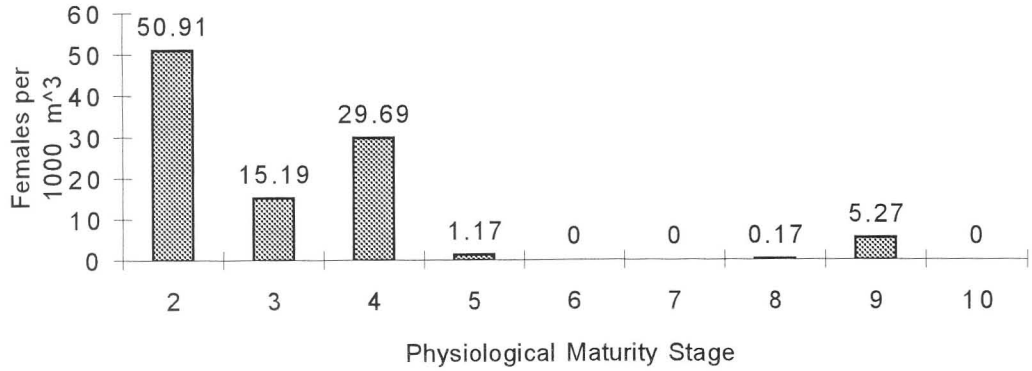

Inner Shelf Stations
Females per 1000 m^3
70
60
50
40
30
20
10
0
14.4
0
2.83
7.45
0
69.92
0.25
0.48
0
2
3
4
5
6
7
8
9
10
Physiological Maturity Stage

Figure 16: *Euphausia superba.* Number of female krill per 1000 $m^3$ in physiological maturity stages 2-10 at inner shelf (*.000-*.080), mid-shelf (*.100-*.140), and outer shelf (*.160-*.200) stations during austral summer 1997.

## Outer Shelf Stations




## Mid-shelf Stations




## Inner Shelf Stations

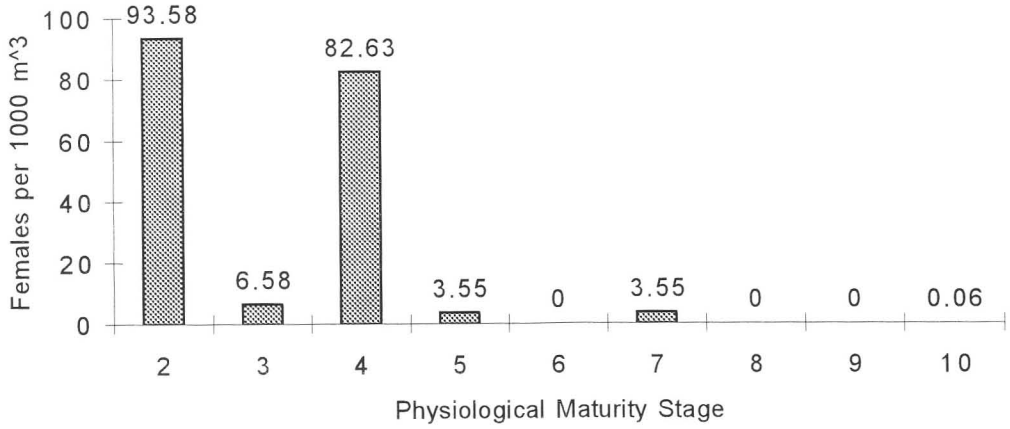


Figure 17: *Euphausia superba*. Onshore/Offshore gradient in total number of females per 1000 $m^3$ found at inner shelf, mid-shelf, and outer shelf stations during the austral summer research cruise for each year of this study.

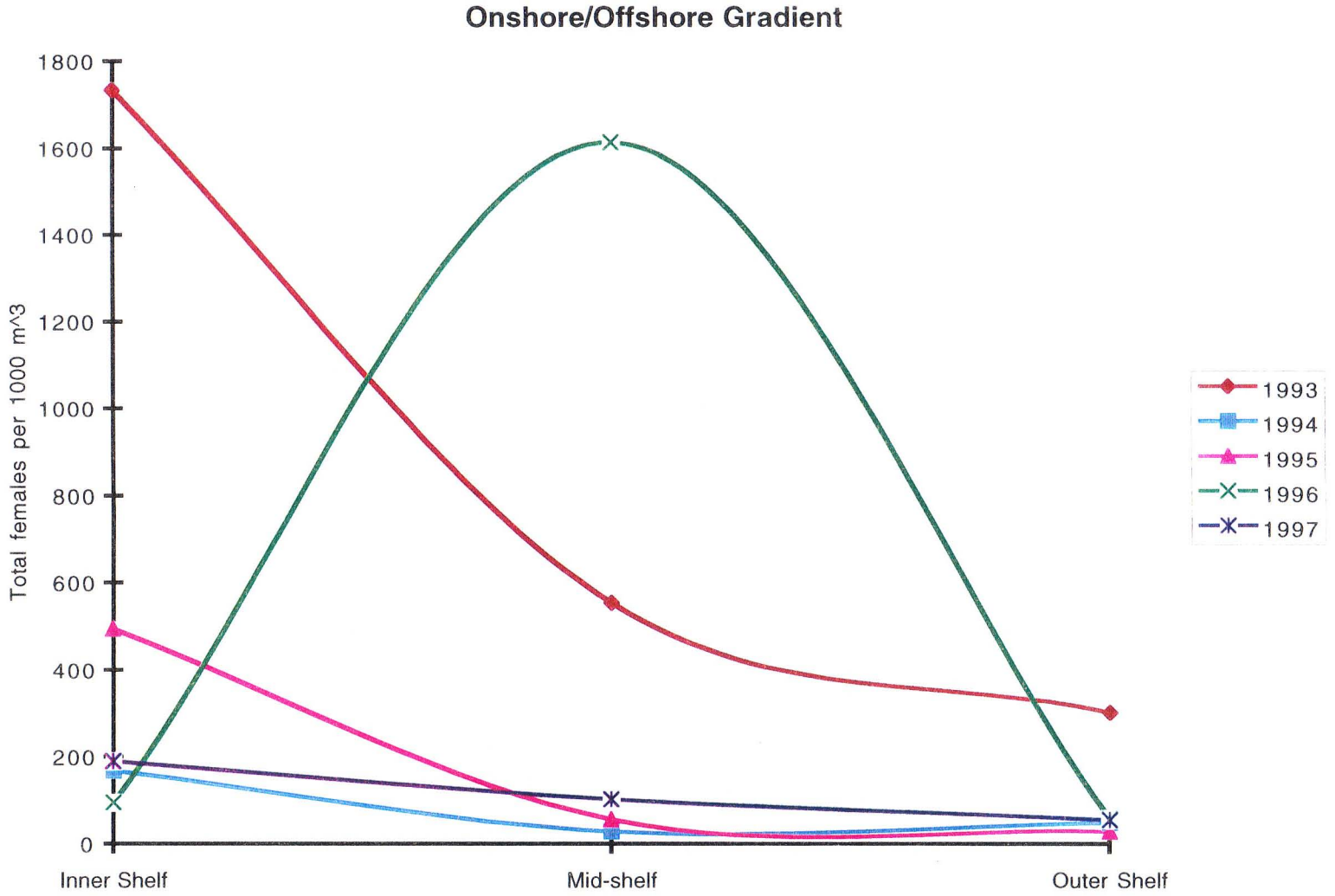

Onshore/Offshore Gradient
Total females per 1000 m^3
1800
1600
1400
1200
1000
800
600
400
200
0
Inner Shelf
Mid-shelf
Outer Shelf
1993
1994
1995
1996
1997

Figure 18: *Euphausia superba*. Alongshore gradient in total number of females per 1000 $m^3$ found on each transect line during the austral summer research cruise for each year of this study.

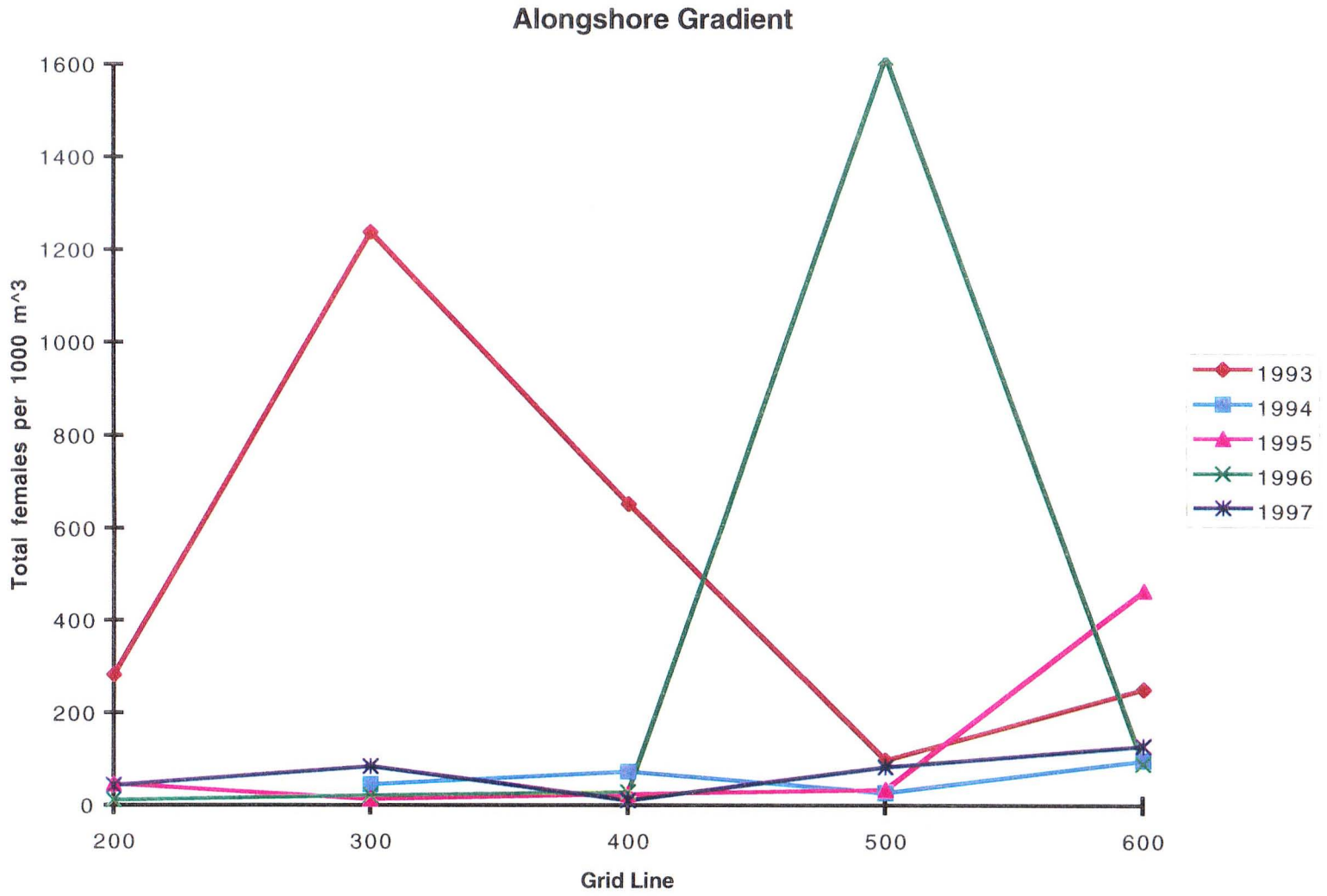

Alongshore Gradient
Total females per 1000 m^3
1600
1400
1200
1000
800
600
400
200
0
200
300
400
500
600
Grid Line
1993
1994
1995
1996
1997

Figure 19: *Euphausia superba.* Length frequency distributions for Stage 2 females during each year of this study. Length interval (bin) is 1mm.

Figure 20: *Euphausia superba.* Length frequency distributions for Stage 3 females during each year of this study. Length interval (bin) is 1mm.

Fig. 19
**Stage 2**

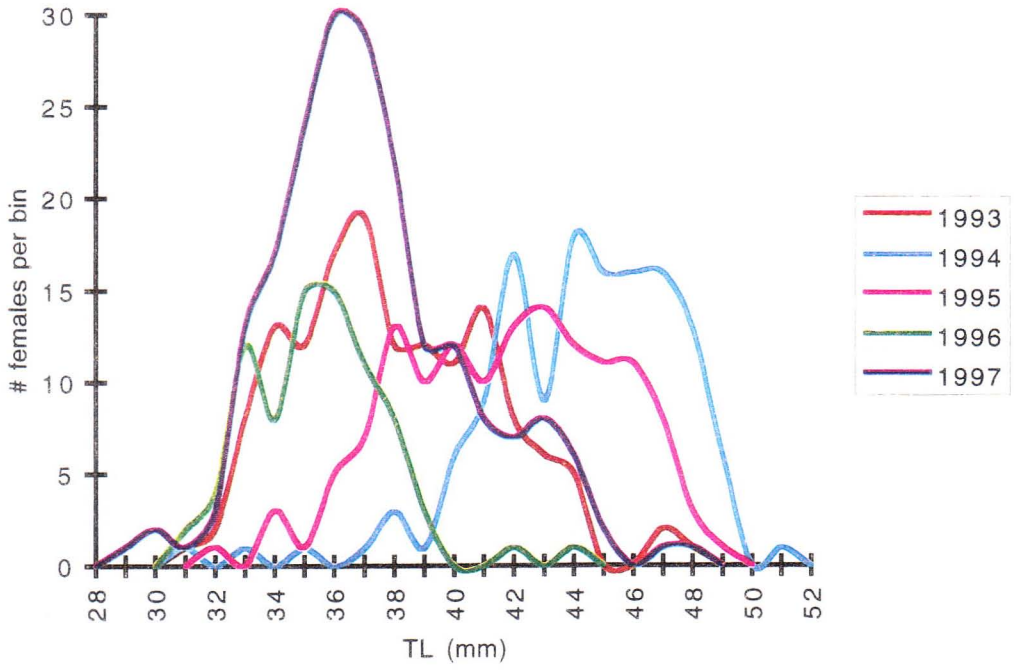



Fig. 20
**Stage 3**

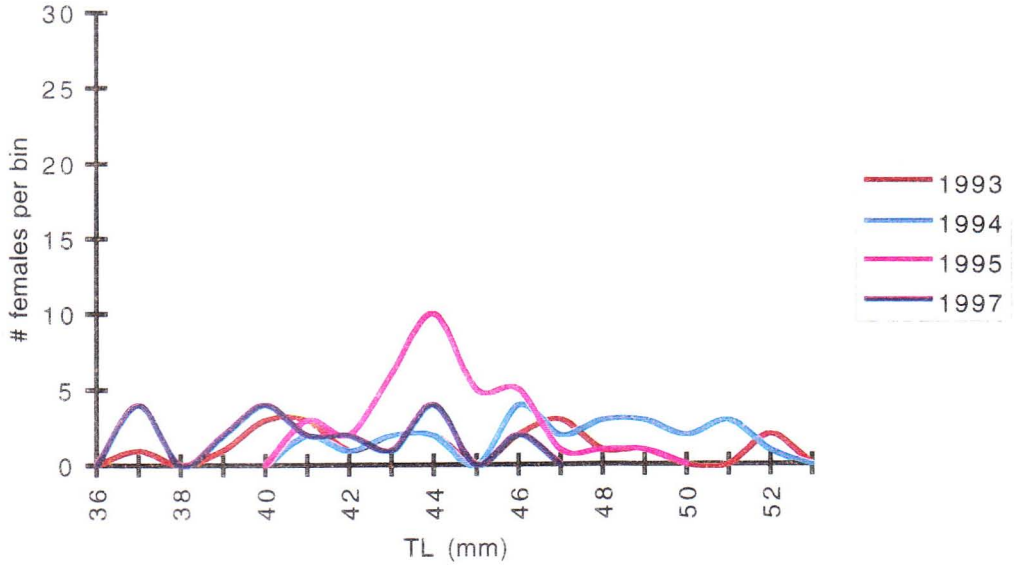


Figure 21: *Euphausia superba.* Length frequency distributions for Stage 4 females during each year of this study. Length interval (bin) is 1mm.

Figure 22: *Euphausia superba.* Length frequency distributions for Stage 5 females during each year of this study. Length interval (bin) is 1mm.

Fig. 21
**Stage 4**

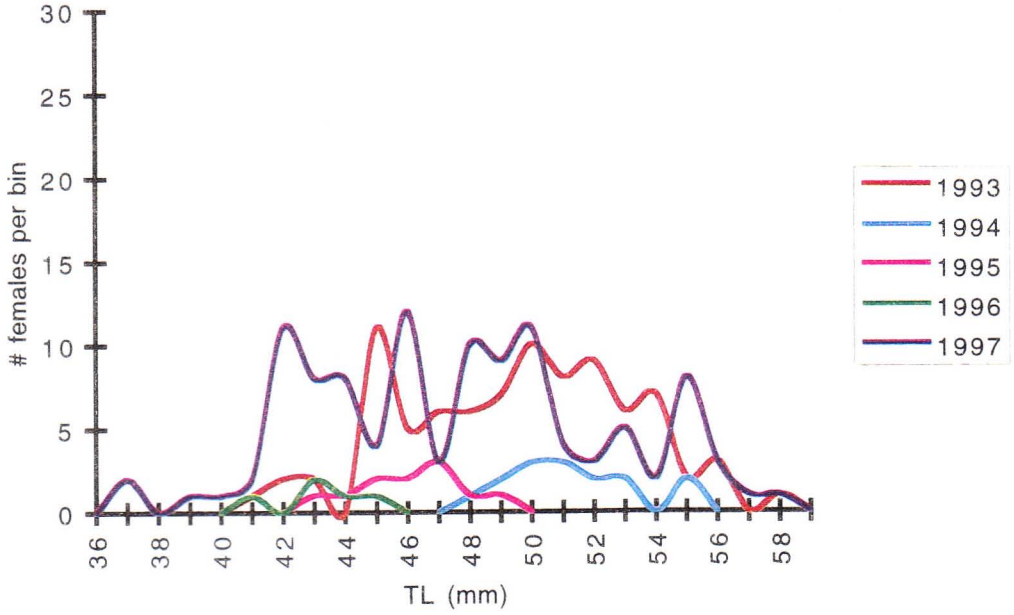



Fig. 22
**Stage 5**

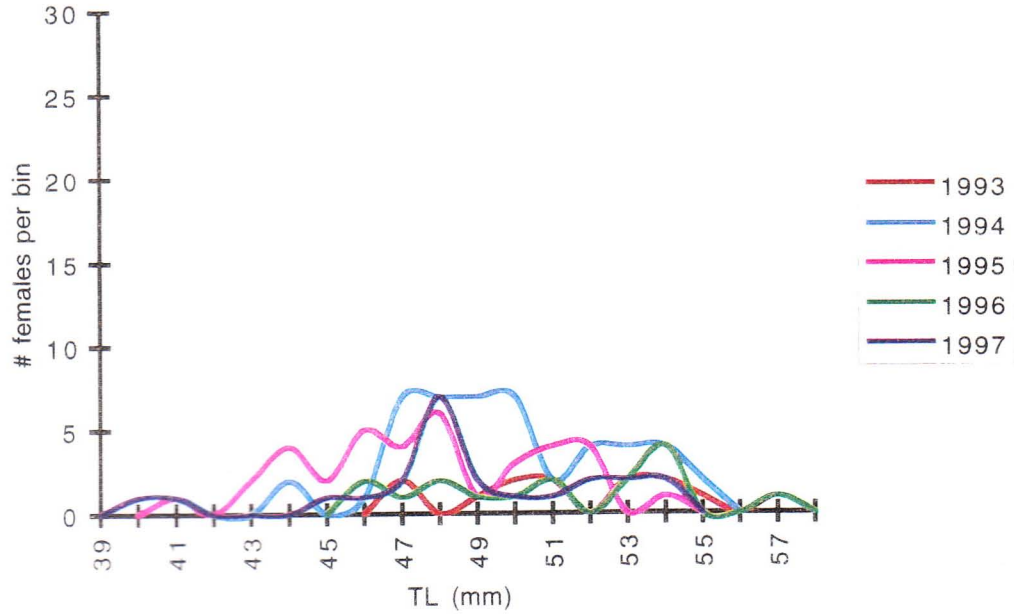


Figure 23: *Euphausia superba.* Schematic representation of post-spawning season reorganization in female krill. Numbers are by physiological maturity stage.

Figure 24: *Euphausia superba.* Migration pattern of female krill during the process of maturation of the ovary, spawning, and reorganizing. Numbers are physiological maturity stage.

Fig. 23

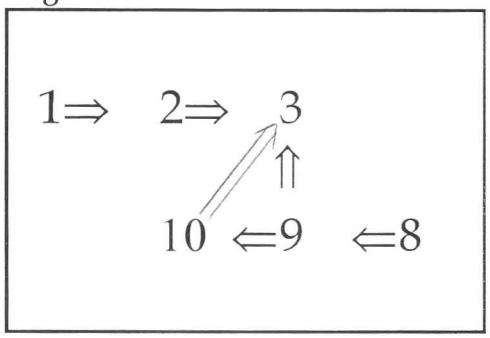



Fig. 24

| Area | Progression of Stages |
|---|---|
| inner shelf (high chl a) | 10<br>2⇒ 3⇒ 4<br>⇓<br>5⇐ 4 9<br>⇓ ⇑<br>6⇒ 7⇒ 8⇒ 8f |
| mid-shelf | |
| outer shelf/break (CDW and depth) | |

Figure 25: *Euphausia superba*. Percentage of female krill in active reproduction (Stages 4-9 of total females) for the five years of this study.

Figure 26: *Euphausia superba*. Ratio of numbers of Stage 5 females to total females in Stages 4 and 5 as an index of whether the overall population is in an earlier or later phase of the reproductive cycle during the five years of this study.

Fig. 25

**% of Population Reproducing**

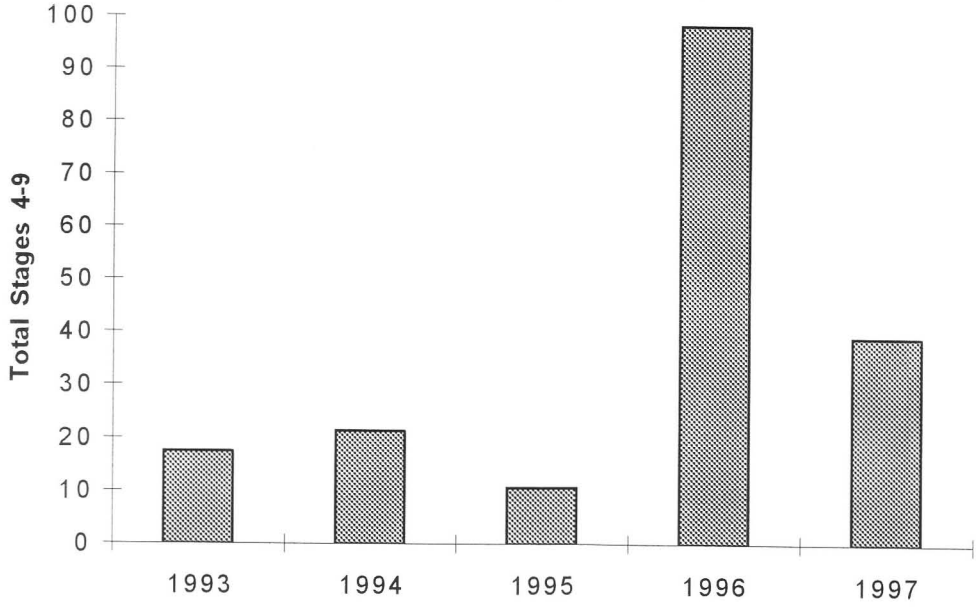



Fig. 26

**Population Reproductive Index**

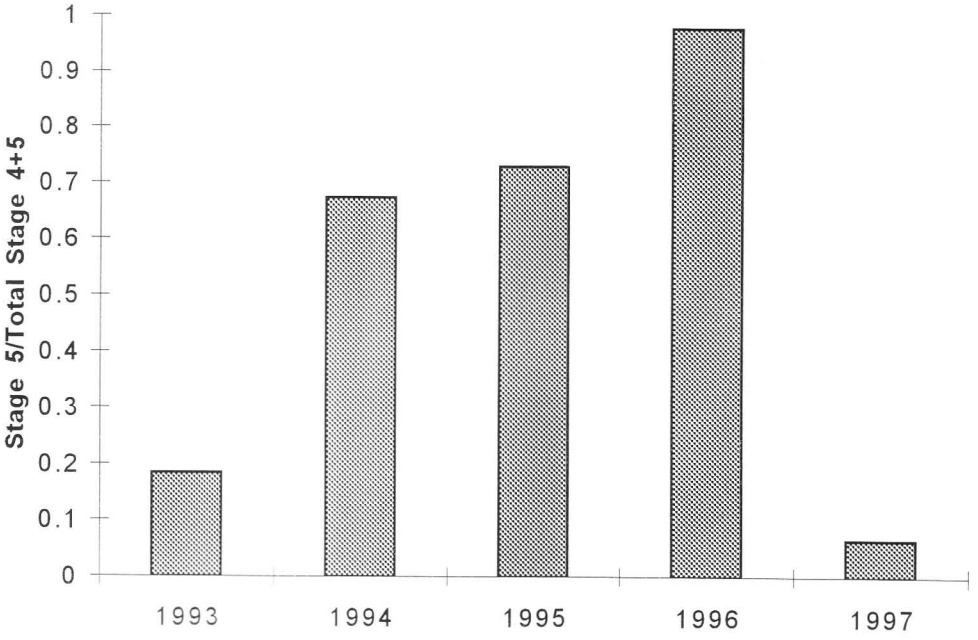
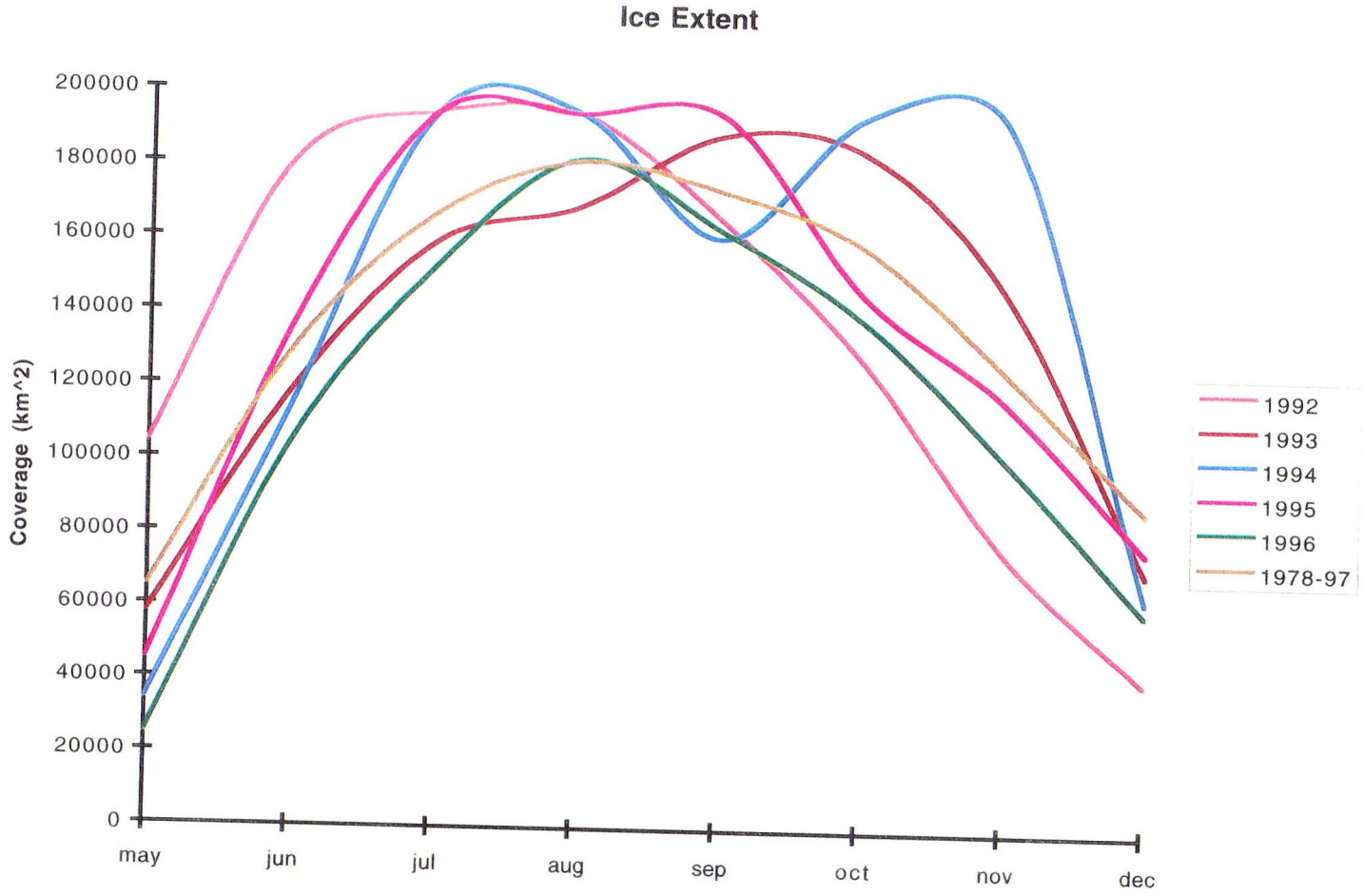


Figure 27: Ice extent in $km^2$ for each year of this study (after Smith et al., in press). Average ice extent from 17 years of data is also shown.


Ice Extent
Coverage (km^2)
200000
180000
160000
140000
120000
100000
80000
60000
40000
20000
0
may
jun
jul
aug
sep
oct
nov
dec
1992
1993
1994
1995
1996
1978-97