

Euphausiid life cycles and distribution around South Georgia

PETER WARD, ANGUS ATKINSON, JULIE M. PECK and ANDREW G. WOOD

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Abstract: Euphausiid life histories and distribution in the vicinity of South Georgia were studied from a series of samples taken in April 1980, November–December 1981, and July–August 1983. Size frequency data indicated a two-year life cycle for *Euphausia frigida* and the possibility of a three-year cycle for *E. triacantha*. The genus *Thysanoessa* was represented by a mixture of *T. macrura* and the dominant *T. vicina*. A one-year life cycle is proposed for the latter but that of the former is unknown. Spawning in *E. frigida* and to a lesser extent *Thysanoessa* spp. commenced as early as July and euphausiid calyptopes were a feature of the plankton for much of the year. *E. superba* eggs were found in low abundance over the shelf to the north of the island, but no hatched larvae were found. Behaviour patterns such as diurnal and seasonal migration partially confounded attempts to relate euphausiid distribution to environmental features. However calyptopes of most species, were generally more abundant in oceanic water deeper than 500 m and there was limited evidence that in August, *E. frigida* had commenced spawning in the colder part of the survey area.

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Key words: oceanic, population structure, regional variation, shelf, spawning periodicity.

Introduction

South Georgia lies in the path of the Antarctic Circumpolar Current (ACC) outside the zone influenced by seasonal pack ice. It is an area where the biogeographical ranges of six species of euphausiid overlap (John 1936), the most conspicuous of these being *Euphausia superba* Dana. Other species are *Euphausia frigida* Hansen, *Euphausia triacantha* (Holt & Tattersall) and two species of the genus *Thysanoessa*, *Thysanoessa macrura* G.O. Sars and *Thysanoessa vicina* Hansen. Around South Georgia, the sixth species, *Euphausia vallentini* Stebbing is at the extreme southern edge of its range and is more properly considered a member of the subantarctic fauna.

Production in the marine environment around South Georgia is highly seasonal (Hart 1942, Clarke 1988). In general the production cycles in the northern part of the Atlantic sector of the Southern Ocean start earlier and finish later than further south (Hart 1942, Foxton 1956). However, because South Georgia lies in the easterly flowing ACC the composition and development of zooplankton populations will be determined not only by local conditions but also by those occurring upstream of the island, to the south and west. The ACC encompasses both the Polar Frontal Zone to the north and the Weddell Scotia Confluence to the south (Amos 1984). Movement and change in the strength of flow of either of these frontal zones can influence the relative abundance and distribution of zooplankton in the region of South Georgia (Priddle *et al.* 1988, Atkinson & Peck 1988).

In this paper we report on the population biology and distribution patterns of the five commonly occurring euphausiid species during three surveys undertaken around South Georgia and attempt to relate these to physical and environmental parameters.

Materials and methods

Three biological surveys were undertaken around South Georgia during March–April 1980, late November–December 1981 and late July–August 1983. In April 1980 24 stations were worked along a series of transects covering shelf (water depth <500 m) shelf break and open ocean (water depth >500 m) (Fig. 1). In December 1981 the survey area comprised a series of nine transects each 30 nautical miles apart oriented in a NE–SW direction. Each transect was 180 nautical miles long with seven stations positioned at intervals of approximately 30 nautical miles along each (Fig. 1). A total of 63 stations were worked although samples were only available from 59 of them. In August 1983 the same survey grid was used but the stations had been repositioned by a few nautical miles, generally to the south and west, to allow a greater proportion of the hauls to be carried out without hindrance from foul ground. Unfortunately during this survey it was only possible to sample 42 of the 63 stations.

Zooplankton was sampled at each station using a Rectangular Midwater Trawl (RMT1+8) which was fished obliquely downwards from the surface to 250 m at a ship's speed of approximately 1 m s⁻¹. At some of the shelf stations, where water depth was less than 250 m, the net was fished to within 20 m of the bottom. In August 1983 additional hauls were carried out at shelf stations using a multiple RMT, so that at some stations the downward oblique haul was followed by an upward oblique; thus a total of 21 samples were taken from 13 shelf stations. The distance travelled by the net was calculated from a flowmeter mounted on the net monitor and volume filtered then calculated from the equations of Pommeranz *et al.* (1983). Haul duration was approximately 30 min, during which between 1000–1500 m³ of water were swept. Filtration was assumed 100% efficient. During the

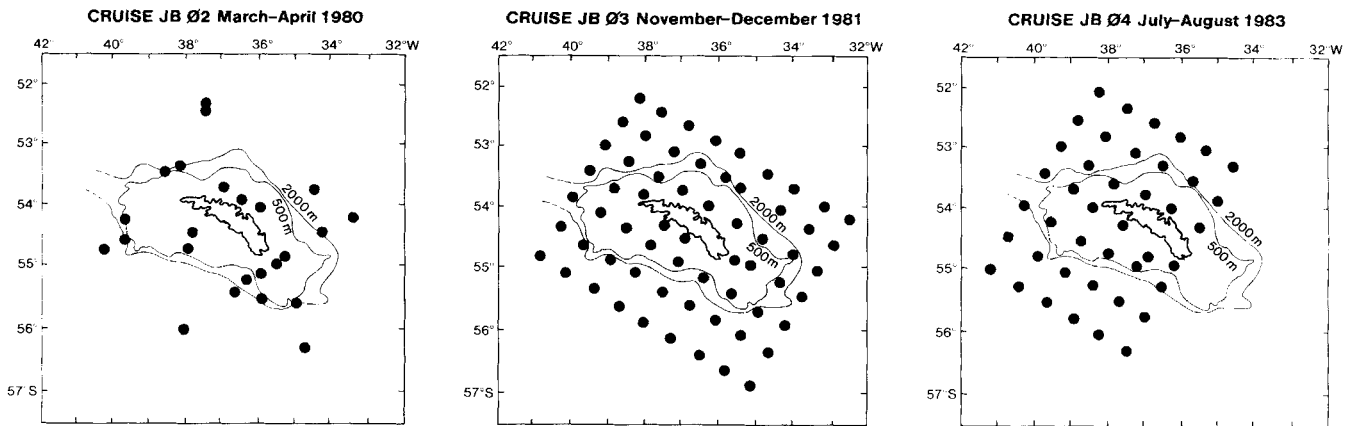


Fig. 1. Position of sampling stations worked during April 1980, December 1981 and August 1983.

August and December surveys salinity and temperature profiles were taken at every station with a CTD carrying Niskin bottles to provide water samples for nutrient chemistry and phytoplankton analysis. Zooplankton samples from the RMT1 (1 m² nominal mouth area, mesh size 330 µm) were preserved in 4% neutralized sea-water formalin and shipped to the UK for routine analysis (see Atkinson & Peck 1988 for details).

Counts of each euphausiid species by stage are expressed as values per 1000 m³ of water filtered. The term krill used herein refers to *E. superba*.

Results

Population structure

Euphausia frigida. The presence of males and females with spermatophores (Fig. 2) and the relatively high numbers of calyptopes (Fig. 3) indicates that spawning at South Georgia starts as early as August. Although the juvenile class (0 group) was not apparent until April, the larger members of this group, could, by then, already be distinguished as male and female. In addition, in April, a maturing class of animals (1+) was present. In this group very few males with spermatophores present in the ejaculatory ducts were found, but through August to December increasing proportions of males and females with spermatophores were present. The high proportion of females with spermatophores in December and their absence in April indicates that spawning at South Georgia had finished by April, although Fig. 3, illustrating the relative abundance of larval and postlarval euphausiids in shelf and oceanic waters during the three surveys (see below), shows that calyptopes were still present in April.

The size frequency histograms (Fig. 2) confirm the interpretation of a two-year life span proposed by Brinton (1985) and Siegel (1987). Overall *E. frigida* was one of the most abundant euphausiids found during the surveys (Fig. 3).

Thysanoessa spp. In the region of South Georgia the

distribution of two species of this genus, *Thysanoessa macrura* and the smaller, more northerly distributed *T. vicina*, overlap. It was not possible to separate either the larvae, immatures, or females to species level because the younger stages are virtually indistinguishable (Hempel & Marschoff 1980) and net damage to the older stages often precluded identification. However males were separated on the form of the petasma and the proportion of each species derived. In December *T. vicina* comprised c. 70% and in August 91% of the male population. Both species occurred at many of the stations sampled with no tendency for them to be geographically separated. No data are available for April, although Hardy & Gunther (1935) indicate that *T. vicina* was the most abundant species of the genus in surveys carried out during March/April 1926.

With a mixture of two species, interpretation of size frequency distributions (Fig. 2) is difficult, although we may suppose that those animals larger than 15–16 mm are *T. macrura* (Mauchline 1980). In August the majority of males were carrying spermatophores in their ejaculatory ducts, and appeared in a unimodal class with juveniles and immature and mature females, including those with spermatophores attached. In December the picture is rather similar. In April a unimodal size class was found consisting primarily of juveniles and immature males and females (0 group). This confusion undoubtedly arises because of the mixing of the two species. Given the unimodal group and the absence of either mature males or females with spermatophores in April we suggest that a one-year life cycle for *T. vicina* around South Georgia is possible, although that of *T. macrura* is unknown.

Spawning had started by August although the mean abundance of calyptopes was low and the furcilia present probably represent larval forms from the previous season's spawning (Fig. 3). By December numbers of all larval stages had increased dramatically but by April had decreased, with early and late furcilia dominating the larval forms. *Thysanoessa* spp. along with *E. frigida* clearly dominated the euphausiid fauna (Fig. 3).

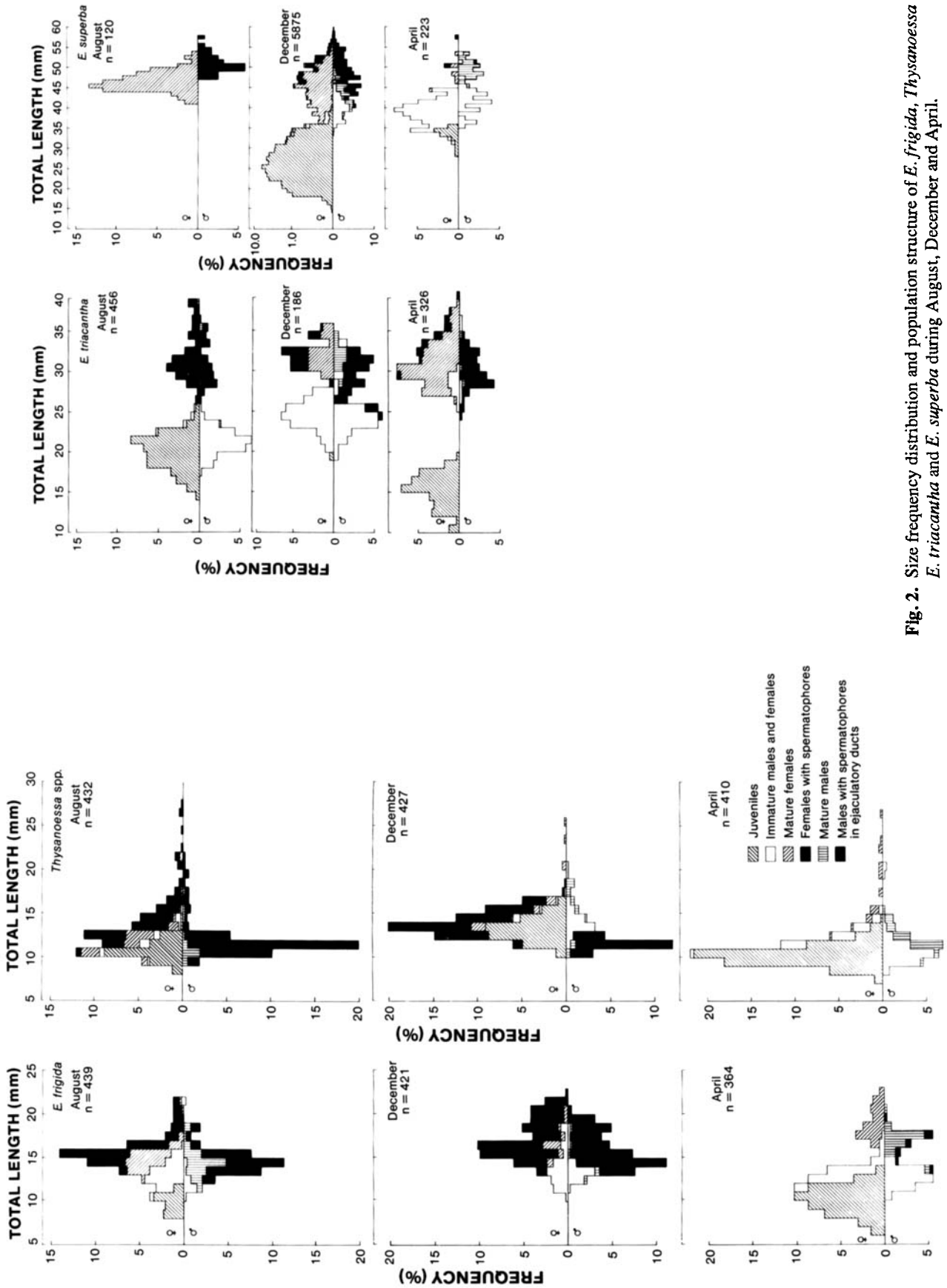


Fig. 2. Size frequency distribution and population structure of *E. frigida*, *Thysanoessa* spp., *E. triacantha* and *E. superba* during August, December and April.

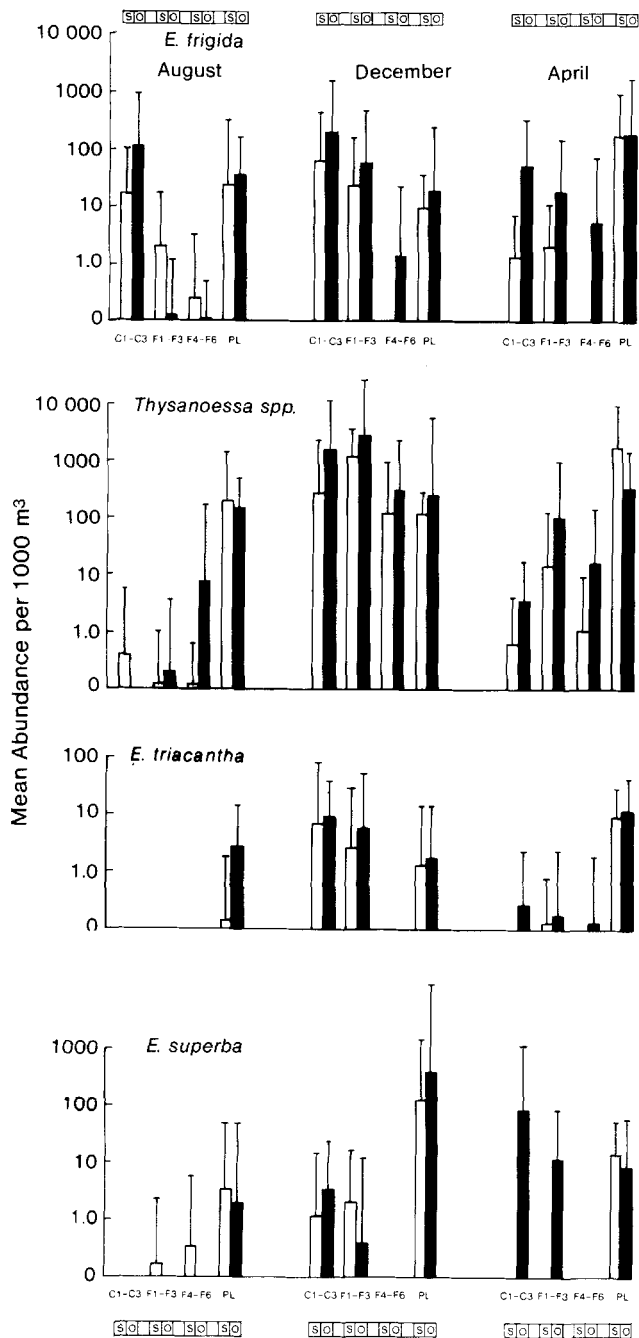


Fig. 3. Mean abundance per 1000 m³ at shelf (S) and oceanic (O) stations of calyptopes (C1–C3), early furcilia (F1–F3), late furcilia (F4–F6) and post-larval stages (PL) of *E. frigida*, *Thysanoessa* spp., *E. triacantha* and *E. superba*. Lines extending from each bar indicate maximum values. All minimum values were zero. Note log scale.

Euphausia triacantha. For this species at least two year classes were present in all three of the months sampled (Fig. 2). They comprised 0 and 1+ in August, 1+ and 2+ in December and in April 0 and an older class which is probably a mixture of 1+ and 2+ animals. The larger animals (>35 mm)

present in April and August may represent a proportion of the population surviving to 3+ (Baker 1959, Siegel 1987).

The 0 class in August has differentiated by December into males and females (1+ group) which by April is mixed with the 2+ group and consists of maturing females (some with spermatophores attached) and males with spermatophores present in the ejaculatory ducts. By August all mature females were carrying spermatophores, although there was no evidence that spawning had commenced (Fig. 3). In December calyptopes and early furcilia dominated the population which by April was predominantly postlarval (Fig. 3). Overall *E. triacantha* was the least abundant species found.

Euphausia superba. The problems of interpreting size frequency data for this species in respect of overlapping age classes and skewed length frequency distributions are well documented (see for instance Mackintosh 1972, Siegel 1987). Our data shed little light on this problem.

Abundance in August 1983 was very low, (see Heywood *et al.* 1985, Priddle *et al.* 1988). Of those captured, all males had spermatophores present in the ejaculatory ducts whilst females, although apparently mature, had none attached. In December both immature males and those carrying spermatophores were present although by April the latter individuals had virtually vanished from the sampled population. In August only furcilia representative of the previous season's spawning were present (Fig. 3) although by December calyptopes appeared in low abundance. By April calyptopes dominated the larval forms and no later furcilia were found indicating that most spawning takes place in this region from December onwards.

Spawning periods

Throughout the three sampling periods no euphausiid eggs, nauplii or metanauplii were found in either shelf or oceanic waters. This is perhaps not surprising as hauls reported on here were carried out in the surface waters (down to 250 m) and not fished to the depths in excess of 1000 m where hatching in oceanic water is thought to take place (Marr 1962, Makarov 1975). However during the August and December surveys, deep hauls to 1000 m and 2000 m respectively were made at the outer stations on each north-south transect. These also failed to disclose any euphausiid eggs or naupliar stages. The only direct evidence of spawning comes from a series of 26 hauls over the northern South Georgia shelf in the week subsequent to the completion of the April survey. Here 21 of 26 hauls aimed at *E. superba* swarms sampled eggs, although no newly hatched larvae were found. Krill eggs were taken in a water depth of 265 m and increased in abundance with depth (Table I). These could not have been spawned in the net as they corresponded to all four developmental stages recognized by Hempel *et al.* (1979).

Table I. Mean abundance per 1000 m³ of *E. superba* eggs in a series of hauls taken over the north-eastern shelf of South Georgia. SD = standard deviation.

| Depth horizon (m) | Eggs/1000 m ³ | SD | No. hauls |
|-------------------|--------------------------|--------|-----------|
| 5–25 | 17.33 | 14.17 | 3 |
| 25–50 | 27.10 | 33.20 | 7 |
| 50–100 | 34.70 | 26.00 | 6 |
| 100–150 | 143.60 | 120.90 | 5 |

Overall mean abundance = 55.7/1000 m³ SD = 59.0

Euphausiid distribution

We have attempted to interpret euphausiid distribution patterns in relation to environmental conditions within the survey area. Because of low and variable occurrence of some species and stages, especially during winter, relationships with environmental features are unclear in many cases. Additionally, the extent to which these species undergo diurnal and seasonal migrations will influence abundance in the surface 250 m. The only evidence we have for diurnal migration is for August when both *Thysanoessa* spp. and *E. triacantha* were significantly more abundant in the top 250 m at night (t-test $P < 0.05$). Atkinson & Peck (1988)

provide evidence that *Thysanoessa* spp. may migrate seasonally, whilst *E. superba* and *E. frigida* do not. *E. triacantha* was classified as a mesopelagic species.

On-shelf/off-shelf distribution and abundance. The on-shelf/off-shelf distribution (defined by the 500 m isobath) in the surface 250 m for all three sampling periods was compared. Contingency table analysis (Chi-square Table II) indicates that in the majority of cases there was no significant difference in the proportion of stations at which euphausiids occurred on the shelf or in oceanic waters. Only *E. superba* calyptopes and early furcilia during April and postlarval *E. triacantha* during August were found at significantly more oceanic stations than expected ($P < 0.05$). Fitting a generalized linear model (with log link and poisson error) (McCullagh & Nelder 1983) shows that the mean abundance of calyptopes of all species tended to be greater in oceanic waters (GLM Table II), whilst with a few exceptions, notably *E. triacantha* in April, there were no significant differences in abundance of the post-larval stages. From these data we conclude that in most species spawning takes place in oceanic waters and, that as development proceeds, there is an increasing likelihood that larval and immature stages will be found over the shelf as well as in oceanic waters.

Table II. A comparison of on-shelf and off-shelf distributions. Total numbers of on-shelf (SH) and off-shelf (OC) stations worked during each month and the number of those stations at which larval and post-larval stages were present. Significant Chi squared values indicate unequal frequency of presence/absence between shelf and ocean.

The mean deviance ratio (approximately an F ratio) derived from the Generalized Linear Model (GLM) indicates whether mean abundance of any stage is significantly greater in shelf or oceanic waters. Unless otherwise indicated (sh), significant values indicate higher mean abundance in oceanic water. *** = $P < 0.01$, ** = $P < 0.05$, (*) = $P > 0.05 < 0.01$.

| | August | | | | December | | | | April | | | |
|-------------------------|--------|----|---------|---------------------------|----------|----|---------|---------------------------|-------|----|-----------------|---------------------------|
| | SH | OC | Chi Sq. | GLM (Mean deviance ratio) | SH | OC | Chi Sq. | GLM (Mean deviance ratio) | SH | OC | Chi Sq. | GLM (Mean deviance ratio) |
| Total stations | 21 | 29 | | | 15 | 44 | | | 8 | 16 | | |
| <i>E. frigida</i> | | | | | | | | | | | | |
| Cal. | 10 | 17 | 0.27 | 11.47*** | 10 | 37 | 0.42 | 5.73** | 2 | 13 | 2.70 | 8.50*** |
| Fur. 1–3 | 4 | 3 | 0.66 | 4.47**(sh) | 9 | 32 | 0.26 | 2.77 | 3 | 13 | 1.53 | 5.27*** |
| Fur. 4–6 | 1 | 3 | 0.47 | 1.14**(sh) | 0 | 3 | 1.02 | 6.06** | 0 | 5 | 2.5 | 4.71** |
| PL | 15 | 27 | 0.68 | 0.0 | 6 | 32 | 1.86 | 4.08** | 7 | 11 | 0.25 | 0.05 |
| <i>Thysanoessa</i> spp. | | | | | | | | | | | | |
| Cal. | 2 | 1 | 0.75 | 0.0 | 11 | 41 | 0.50 | 13.73*** | 1 | 10 | 2.90(*) | 5.29** |
| Fur. 1–3 | 1 | 2 | 0.92 | 1.08 | 11 | 41 | 0.50 | 5.08** | 2 | 12 | 2.28 | 3.38 |
| Fur. 4–6 | 1 | 2 | 0.92 | 7.67** | 9 | 31 | 0.18 | 5.13** | 1 | 8 | 2.00 | 5.30** |
| PL | 20 | 28 | 0.002 | 4.47**(sh) | 14 | 42 | 0.005 | 3.34 | 6 | 16 | 0.36 | 6.66**(sh) |
| <i>E. triacantha</i> | | | | | | | | | | | | |
| Cal. | 0 | 0 | — | — | 2 | 11 | 0.50 | 0.01 | 0 | 2 | 1.00 | 4.27** |
| Fur. 1–3 | 0 | 0 | — | — | 2 | 10 | 0.33 | 0.81 | 1 | 2 | 10 ⁶ | 0.75 |
| Fur. 4–6 | 0 | 0 | — | — | 0 | 0 | — | — | 0 | 1 | 0.5 | 3.21 |
| PL | 3 | 24 | 10.58** | 35.0*** | 1 | 18 | 3.5(*) | 0.86 | 6 | 7 | 0.96 | 0.38 |
| <i>E. superba</i> | | | | | | | | | | | | |
| Cal. | 0 | 0 | — | — | 3 | 9 | 0.001 | 1.83 | 0 | 10 | 5.0** | 4.17 |
| Fur. 1–3 | 2 | 0 | 2.76(*) | 16.05*** (sh) | 2 | 2 | 1.27 | 5.58** (sh) | 0 | 10 | 5.0** | 7.27** |
| Fur. 4–6 | 2 | 0 | 2.76(*) | 17.47*** (sh) | 0 | 0 | — | — | 0 | 0 | — | — |
| PL | 8 | 7 | 0.79 | 1.39 | 10 | 22 | 0.57 | 2.59 | 7 | 8 | 1.20 | 1.06 |

Regional distribution. Regional changes in abundance in response to other environmental factors were harder to detect. Hydrographic information was available only for August and December and has been summarized by Heywood *et al.* (1985) and Priddle *et al.* (1986). Briefly, during December South Georgia was not an area influenced by major water mass boundaries; the water types invoked by Priddle *et al.* (1986) were all essentially variants of the Antarctic Surface Water. Temperature and salinity characteristics of the surface layer as well as the low silica concentration indicated that Weddell Sea water was absent

from the survey area. At several stations in the north-west of the survey grid slightly elevated near surface salinities were taken as possible evidence for mixing with small quantities of Subantarctic surface water.

All of the five species of euphausiid considered in this paper have distributions that span the Antarctic Circumpolar Current and in the main, apart from on-shelf/off-shelf differences noted, local features within the survey's ambit (meanders, eddies etc.) seem to have had little effect, at least in summer. Indeed Priddle *et al.* (1986) found that during December there was no congruence of acoustically estimated

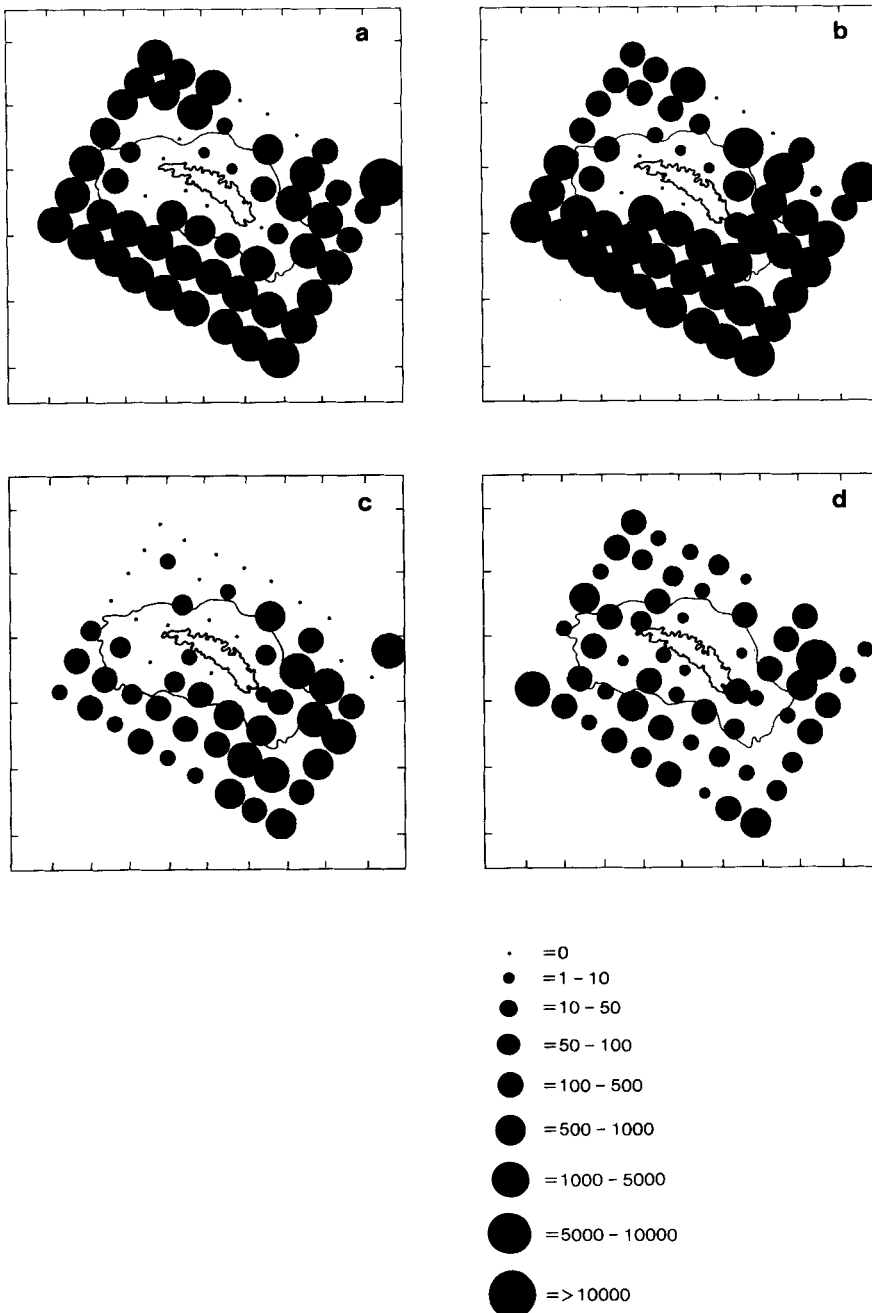


Fig. 4. Abundance per 1000 m³ of *Thysanoessa* spp. stages during December. **a.** = calyptopes, **b.** = early furcilia (1-3), **c.** = late furcilia (4-6), **d.** = post-larval stages.

zooplankton abundance (principally krill) with the pattern of the water masses or with phytoplankton distribution.

Where patterns are discernible they probably represent a complex mixture of temporal and spatial effects. For example the distribution of larval and post larval stages of *Thysanoessa* spp. in December are illustrated in Fig. 4. Calyptopes appear around the island, although mean abundance is far greater offshore than on. Progression through early and late furcilia stages indicates an increasing tendency for their distribution to be restricted to the south-east portion of the survey grid and an increasing tendency for them to spread onto the shelf. Post-larvae however show no regional differences in distribution and on-shelf/off-shelf differences are no longer significant.

During August the influence of subantarctic water was greater and South Georgia lay within the Polar Front which was broad and diffuse in the eastern Scotia Sea. There was a greater influence of Subantarctic surface water and a rise in temperature towards the north-west of the survey grid. Plots of geopotential topography and the orientation of surface isotherms indicate that during both December and August there was an anticlockwise circulation pattern around the island (Heywood *et al.* 1985, Priddle *et al.* 1986).

During August all euphausiid larval stages except those of *E. frigida* were too scarce for us to be able to sensibly relate their distribution to these environmental features. *E. frigida* calyptopes during August were largely restricted to the north-east and south-east of the survey grid in colder water (Fig. 5). Although the chi-squared test indicates no significant difference between observed and expected presence of larvae over the shelf, the oceanic mean abundance was significantly greater. Thus only oceanic mean abundance was used to test whether differences occurred on either side of the 0.5°C isotherm. While no significant difference was found (t-test, $t = 1.38$, $P < 0.18$, $Df = 19$), it seems that spawning had commenced mainly in the colder portion of the survey area with calyptopes being present at 90% of the oceanic stations in the colder part of the grid and only 36% in the warmer part.

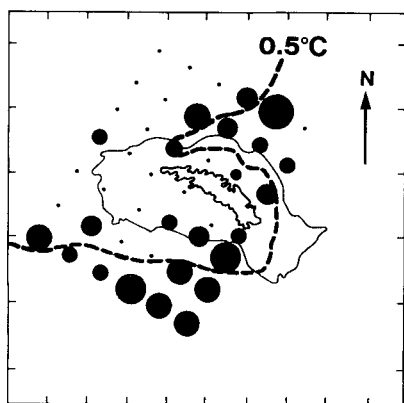


Fig. 5. Mean abundance per 1000 m³ of *E. frigida* calyptopes during August in relation to the 0.5°C surface isotherm. Water is colder to the east of the isotherm. Abundance symbols are the same as Fig. 4.

Discussion

Population structure and spawning periodicity

The size frequency and maturity stage information broadly confirms much of what is currently known about these species, *viz.* a two-year life cycle for *E. frigida* (Brinton 1985, Siegel 1987) up to three years for *E. triacantha* (Baker 1959, Siegel 1987) as well as providing comprehensive data on the changes in maturity stage over the year. Although samples were not taken within the same year, data have been interpreted as being representative of the course of events during a 'normal' year. Inter-annual variations in the physical environment undoubtedly occur (e.g. in winter 1983 the polar front, perhaps untypically, extended south around South Georgia) but data are insufficient to resolve their effects on euphausiid life histories.

Our data on spawning dates agree closely with those of Makarov (1980) who indicated that Antarctic euphausiids could be broadly categorized as either spring spawners (*E. frigida*, *E. triacantha*, *T. macrura* and presumably *T. vicina*) or summer spawners (*E. superba*). Our results further support his suggestion that cold water species (with the exception of *E. superba*) tend to spawn earlier than warm water species when they occur in the same water body. The occurrence of *E. frigida* calyptopes in late July indicates that spawning must have taken place some time previously that month. The early and late furcilia which were also present probably represent overwintering stages, because calyptopes were still present in the larval population in April. Apart from a few calyptopes of *Thysanoessa* spp. there was no evidence that other species had started spawning in August.

In July and August biological productivity in the seas surrounding South Georgia is usually low (Hart 1942). Despite this, spawning and larval development, notably in *E. frigida*, was occurring at a time when the amount of phytoplankton was low and uniformly dispersed throughout the top 100–160 m of the water column. Although values fell within the lower range found in summer (15.8–41.1 mg chlorophyll *a* m⁻² to 100 m), it was not until late September that a near surface biomass maximum developed, suggesting the initiation of spring population growth (Heywood *et al.* 1985). What energy source *E. frigida* in particular uses for vitellogenesis and what resources are available for the larvae to survive is not clear. Zooplankton biomass in the surface 250 m is much reduced in winter (Foxton 1956, Hopkins 1971, Atkinson & Ward 1988). Whether this means that more of the relatively scarce resources in the top 250 m are available to adult and larval euphausiids at this time of year, or that the spring spawning euphausiids store lipid over winter is unknown. Certainly some species of Antarctic copepods in the Weddell Sea seem able to reproduce in advance of the spring phytoplankton increase (Fransz 1988) and the possession of stored internal reserves or carnivory have been implicated as means of achieving this. In contrast, the summer spawning *E. superba*, unlike the neritic *E.*

crystallorophias, does not appear to synthesize an overwintering lipid store with which to fuel egg production (Clarke 1984).

South Georgia is noted for the presence of large concentrations of *E. superba* (Marr 1962). Despite this, intensive sampling has failed to disclose spawning areas close to the island. Marr (1962) showed that *Discovery* Expeditions repeatedly failed to find evidence of successful spawning. During operations in November–March, 196 closely spaced stations were worked but only 11 eggs and 2 metanauplii were found. Collections of older larvae were also consistently small. A catch of 707 calyptopes, accounting for 60% of the total calyptopes and furcilia caught were thought to have arisen from hatching in the Weddell stream to the south of the island. In fact the largest catches of early calyptopes made during our April survey were also found well to the south-east of South Georgia. More recently Witek *et al.* (1980) found krill eggs in January (10–430/m²) and March (up to 1000/m²) around the northern shelf break of South Georgia although again naupliar and metanaupliar stages were not found.

Whether the eggs of *E. superba* can hatch successfully in this northern part of their range is still questionable. Their contribution to local production is in any case unlikely to be great as firstly they appear in relatively low abundance and secondly, as is discussed below, there appears to be no mechanism by which larvae can become entrained around the island.

Distribution

The distribution of euphausiids in relation to the shelf seems to indicate that for most species the mean abundance of larval stages is higher in oceanic waters (Fig. 3, Table II) and it is here that we assume that most spawning takes place. Interestingly, of the eight significant results in August, five indicated a higher abundance over the shelf (compared with December and April where only one in each month was significantly greater over the shelf). Atkinson & Peck (in press) also found that on-shelf/off-shelf differences in zooplankton abundance were more marked during the August survey than in December. Seasonal migrants were relatively more abundant over the shelf than non-seasonal or mesopelagic species. They hypothesized that this was due to two factors. First the shelf prevented the seasonal descent of some species. Second, and more importantly with respect to euphausiids, a limited exchange of shelf and oceanic water may have enabled several cold water species to maintain their distribution over the shelf throughout the winter even though a southerly movement of the Polar Front displaced many elements of the Antarctic fauna, e.g. *E. superba*, almost certainly well to the south.

During December the temperature range across the survey area was not great and the overall distribution of chlorophyll *a* was markedly heterogenous (Priddle *et al.* 1986). Areas of

local turbulence were apparent and eddies and meanders were found on the eastern side of the island due to separation of the ACC flowing north and south of the Scotia ridge. This in itself did not seem to promote pronounced aggregation of either larvae or post-larvae of any species. In August the circulation pattern was broadly the same, the temperature range was relatively small and the only obvious effect of the temperature gradient appeared to be the commencement of spawning by *E. frigida* in the colder part of the survey grid.

The general lack of coherence between euphausiid distribution and other measured environmental parameters appears to arise for a number of reasons. Conditions in the surface 250 m may not adequately reflect the regional preferences of species such as *E. triacantha* where there is a significant diurnal migration and a substantial proportion of the population lives below 250 m (Baker 1959). Similarly *Thysanoessa* spp. was also shown to be a diurnal migrant, at least during winter and, although there was no evidence from our data that *E. frigida* migrates, Hardy & Gunther (1935) and Loeb & Shulenberger (1987) indicate that it does. Thus postlarval euphausiid behavioural patterns may be partially obscuring simple relationships to mesoscale variation in the environment. These results contrast with those of Atkinson (in press) who found that copepod distribution around South Georgia was closely related to water temperature.

The temporal nature of the surveys and the chronology of sampling may also have influenced our perception of larval distribution. Atkinson (1989) observed that during the December survey two species of copepods (*Calanoides acutus* and *Rhincalanus gigas*) showed distinct differences in stage distribution between the north-west and south-east corners of the grid. An older prespawning generation was generally more abundant over the shelf to the north-west and a younger summer generation in the south-east. These differences were attributed partly to the chronology of sampling, as stations in the north-west were sampled up to 3.5 weeks before those in the south-east. Copepod development rates were suggested to be sufficiently rapid to largely account for these differences. The distribution of *Thysanoessa* spp. is superficially similar, with older larval stages becoming increasingly abundant towards the south-east. Makarov (1983) estimates that each furciliar stage of *T. macrura* lasts 7–8 days and so it is feasible that larval development rates could have accounted for these regional differences; that is, they may have been due principally to the order in which the stations were sampled.

Another important reason for this lack of coherence is the presence of advected adults and larvae. South Georgia lies across the stream of the ACC and although the shelf is wide with an established neritic community (Atkinson & Peck, in press) there appears to be little evidence that the predominantly oceanic plankton is entrained around the island to any great extent. Thus, although the presence of early larvae may indicate spawning close to the island, that of later stages represents the product of spawning some way upstream. The

presence of cohorts around South Georgia most likely reflects not local conditions for growth and development but those pertaining further south and west. Post-larval *E. superba* may be an exception to this in areas such as the shelf edge of South Georgia where they congregate in local frontal zones, eddies and meanders (Witek *et al.* 1988). Such aggregations may be maintained by behavioural factors, in particular swarming, and may persist for some time (Witek *et al.* 1988).

Indeed most Antarctic euphausiids have been found in greater abundance where sharp temperature discontinuities arise, primarily at the frontal zones of major water mass boundaries. Thus *E. frigida* and *T. macrura* (Makarov 1980, Brinton 1985) and *E. superba* (Marr 1962) have all been recorded as being more abundant at the frontal zone of the Weddell Scotia Confluence, and *E. triacantha* (Baker 1959) in the region of the Polar Front, than further north or south. Such areas are of great significance for euphausiid recruitment, where local circulation and turbulence are often coincident with higher chlorophyll values (Brinton 1985).

Conclusions

Data presented here confirm the findings of Makarov (1980) indicating a winter start to spawning of some species around South Georgia and the presence of early larval stages in the plankton for much of the year. Further work could profitably investigate the means of egg production in *E. frigida* and *Thysanoessa* spp. and the factors affecting survival and development of their larvae.

Interpretation of the distribution patterns of the post-larval stages of all species appears to be confounded to an extent by behavioural patterns, (e.g. swarming and diurnal migration) operating at a fine scale. Because of this, they are in general, poor tracers of watermasses at the mesoscale level. In contrast their larvae show greater evidence of regional variation and factors such as limited water depth for spawning may restrict the distribution of larvae, at least in the early stages, mainly to oceanic water.

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