

OBSERVATIONS ON EUPHAUSIID ASSEMBLAGES OF THE SOUTH COAST OF SOUTH AFRICA

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A total of 24 species of euphausiid was collected during a survey along the South African south coast during January 1992. Communities over the Agulhas Bank were of low diversity and abundance and were dominated by *Nyctiphanes capensis*. Those at the shelf-edge were of high diversity and abundance and were dominated by *Euphausia recurva* and *Thysanoessa gregaria*. Such high diversity may be maintained by vertical segregation at night. Few species displayed obvious diel vertical migration, although *N. capensis* may be able to maintain itself on the shelf by means of this behaviour. *E. recurva* appeared to feed on phytoplankton throughout the water column at night, reflecting the distribution of food.

Altesaam 24 spesies eufausiïdes is op 'n opname langs die Suid-Afrikaanse suidkus in Januarie 1992 versamel. Die diwersiteit en talrykheid van gemeenskappe bo die Agulhasbank was laag en hulle is deur *Nyctiphanes capensis* oorheers. By die plstrand was diwersiteit en talrykheid hoog en *Euphausia recurva* en *Thysanoessa gregaria* het die gemeenskappe oorheers. Sulke hoë diwersiteit word moontlik deur vertikale skeiding snags gehandhaaf. Slegs enkele spesies het vertikale migrasie oor 'n etmaal duidelik vertoon ofskoon *N. capensis* hom moontlik op die vastelandsplat deur middel van dié gedrag kan handhaaf. *E. recurva* het blykbaar snags deur die hele waterkolom gewei, en dit weerspieël die voedselverspreiding.

Euphausiid assemblages of the nearshore waters of the southern Benguela upwelling region are species-poor (Gibbons *et al.* 1995) and mostly dominated by *Euphausia lucens* (Nepgen 1957). The biology of *E. lucens* and other euphausiid species in the Benguela ecosystem is well known (Pillar *et al.* 1992), because krill constitute approximately 50% of the total zooplankton biomass of South Africa's west coast and form an important component of the diets of a number of economically valuable fish species (James 1987, Payne *et al.* 1987).

By contrast, zooplankton biomass along the south coast of South Africa is dominated by a single species of copepod, *Calanus agulhensis* (Verheye *et al.* 1994). Although *Nyctiphanes capensis* may dominate inshore communities in the vicinity of Port Elizabeth (Talbot 1974, Cornew *et al.* 1992), euphausiids are generally thought to be uncommon over most of the Agulhas Bank. The abundance, behaviour and role of *N. capensis* and other euphausiids in the South Coast system are still largely unquantified. Part of the reason for such a paucity of information is the belated understanding of the role of the Agulhas Bank in the pelagic fish production of the West Coast (Roel *et al.* 1994) and, consequently, the lack of dedicated material with which to work. These shortcomings have now been recognized (Cochrane and Krohn 1994) and addressing them has become a focus of increased attention.

This paper reports on the euphausiid collections taken during a January 1992 cruise aimed at understanding the boundary processes of the Agulhas Bank. Owing to the fragmentary nature of quantitative zooplankton sampling, however, the data are confined to patterns of cross-shelf and vertical distribution. Other reports in this series include Anon. (1992), Beckley (1994) and Probyn *et al.* (1995).

MATERIAL AND METHODS

Stations were sampled along four transects (Lines 3, 7, 12 and 20) across the south and south-east coasts of South Africa during January 1992 (Fig. 1). The lines extended across the width of the Agulhas Current to depths of 4 000 m in the east, but were mostly confined to the shelf edge west of Mossel Bay. Two additional stations at the shelf edge were also occupied (stations 6 and 10).

A variety of hydrographic and biological sampling gear was employed at each station. Near-surface and deep-water currents were determined by means of an Acoustic Doppler Current Profiler (ADCP), and measurements of temperature and salinity were made with a CTD. Fluorescence profiles were obtained with a Chelsea Instruments Aquatracker mounted

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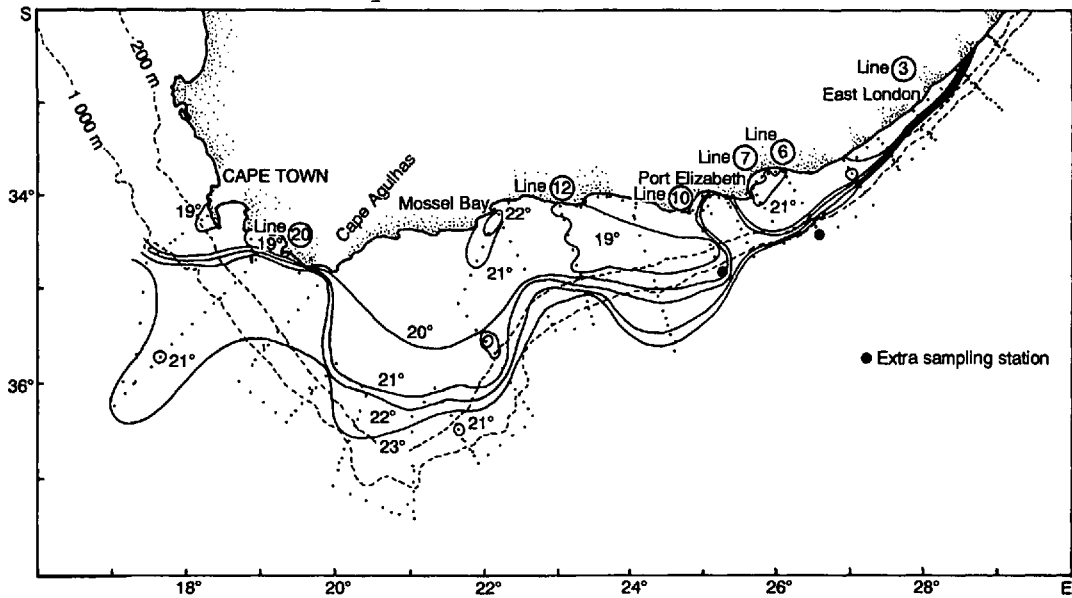


Fig. 1: Map of the survey area showing the approximate positions of sampling stations. Quantitative zooplankton samples were taken along Lines 3, 7, 12 and 20, as well as at the two stations indicated on Lines 6 and 10. The 200- and 1 000-m isobaths are illustrated, as are the approximate positions of the surface isotherms

on a magnum rosette. The vertical distribution of euphausiids was determined by means of a 1-m² multiple opening-closing rectangular midwater trawl (RMT 1 x 6) equipped with nets of 200-µm mesh. The net was towed obliquely at 2 knots over five depth strata from just above the bottom (or from a maximum depth of 200 m) to the surface. All tows were of short duration and the quantity of water filtered was estimated by means of a flowmeter mounted in the mouth of the net.

Estimates of gut pigment in euphausiids were made when they were abundant in the water column. Under such circumstances, the contents of each net were immediately immersed in seawater, and healthy adult euphausiids were removed for analysis of gut pigment within 20 minutes. Not all collections produced enough euphausiids in a suitable condition for gut analysis. The remainder were preserved in 4% buffered formalin for later counting. The total body length of each specimen used for pigment analysis was measured under a dissecting microscope, after which the euphausiid was rinsed in distilled water and homogenized in 10 ml of 90% acetone. Samples were extracted overnight at -4°C and the fluorescence read on a Turner Designs fluorometer before and after acidification. The chlorophyll and phaeo-

pigment (chlorophyll equivalents) content of each euphausiid was calculated according to the method of Dagg and Walser (1987). Carapaces of preserved individuals were examined for contamination by epizoid diatoms under a dissecting microscope (McClatchie *et al.* 1990) and found to be clean.

In determining vertical distribution and abundance, all adult euphausiids were identified (Baker *et al.* 1990) and counted from each sample. When collections were large, subsamples were taken using a Folsom splitter and at least 100 individuals were counted. Data were standardized to numbers per cubic and per square metre according to the volume of water filtered by the nets. The mean vertical position (weighted mean depth) of euphausiids in the water column was determined using the method of Pearre (1974):

$$d = \frac{\sum n_i d_i}{\sum n_i} \quad (1)$$

where n_i is the number of individuals per cubic metre at that depth range and time and d_i is the midpoint of the depth range.

To determine diel changes in euphausiid vertical position and to assess the significance of depth on gut pigment, the data were subjected to single-factor

Table 1: Euphausiids recovered from the four cross-shelf transects (Lines 3, 7, 12 and 20) and two shelf-break stations (06-01 and 10-07). Maximum abundances and longshore centres of abundance are also indicated

Species	Presence						Maximum abundance ($\cdot m^{-2}$)	Neritic (N) or shelf-break/oceanic (SB/O)
	Line 3	Station 06-01	Line 7	Station 10-07	Line 12	Line 20		
<i>Euphausia diomediae</i> Ortmann		✓		✓	–	✓	5,31	SB/O
<i>Euphausia longirostris</i> Hansen	–	–	–	✓	–	✓	6,41	SB/O
<i>Euphausia lucens</i> Hansen*	–	–	–	✓	–	✓	35,18	SB/O
<i>Euphausia mutica</i> Hansen	–	✓	–	–	–	✓	1,88	SB/O
<i>Euphausia recurva</i> Hansen*	✓	✓	✓	✓	✓	✓	180,23	SB/O
<i>Euphausia similis</i> G. O. Sars	–	–	–	–	–	✓	0,91	SB/O
<i>Euphausia similis armata</i> Hansen	–	–	–	–	–	✓	29,64	SB/O
<i>Euphausia spinifera</i> G. O. Sars	–	✓	–	✓	✓	–	8,05	SB/O
<i>Euphausia tenera</i> Hansen*	✓	✓	✓	✓	✓	✓	15,86	SB/O
<i>Nematobrachion flexipes</i> (Ortmann)	–	–	–	–	–	✓	0,62	SB/O
<i>Nematoscelis gracilis</i> Hansen*	✓	✓	–	–	✓	✓	8,40	SB/O
<i>Nematoscelis megalops</i> G. O. Sars	–	–	–	✓	–	✓	0,72	SB/O
<i>Nematoscelis microps</i> G. O. Sars*	✓	✓	–	✓	–	✓	5,81	SB/O
<i>Nematoscelis tenella</i> G. O. Sars	–	–	–	✓	–	✓	1,44	SB/O
<i>Nyctiphanes capensis</i> Hansen*	✓	–	✓	✓	✓	✓	42,99	N
<i>Stylocheiron abbreviatum</i> G. O. Sars*	✓	✓	–	–	✓	✓	5,40	SB/O
<i>Stylocheiron affine</i> Hansen*	✓	✓	–	–	✓	✓	9,41	SB/O
<i>Stylocheiron carinatum</i> G. O. Sars*	✓	✓	–	✓	✓	✓	13,14	SB/O
<i>Stylocheiron longicorne</i> G. O. Sars*	✓	✓	–	✓	✓	✓	20,25	SB/O
<i>Stylocheiron maximum</i> Hansen	✓	–	–	–	–	✓	0,90	SB/O
<i>Stylocheiron microphthalma</i> Hansen	✓	–	–	✓	✓	✓	1,10	SB/O
<i>Thysanoessa gregaria</i> G. O. Sars*	✓	✓	–	–	✓	✓	59,10	SB/O
<i>Thysanopoda acutifrons</i> Holt and Tattersall	–	✓	–	–	–	–	1,53	SB/O
<i>Thysanopoda tricuspadata</i> Milne-Edwards	–	–	–	–	✓	–	0,44	SB/O

* Species which contributed to >1% of total numbers of euphausiids

Kruskal Wallis analyses (Zar 1984).

RESULTS

Physical features

A comprehensive description of the physical oceanography of the survey area during this cruise falls outside the authority and scope of this report: the following account is summarized from Anon. (1992) and Beckley (1994). The sea surface temperature (SST) over the inner shelf was generally <21°C, although colder water (as low as 11°C) was recorded at the innermost stations along Line 20 (Fig. 1). Temperatures along the shelf edge were mostly >21°C, the core of the Agulhas Current ranging between 24 and 25°C. A sharp thermal front was evident along the shelf edge on the eastern Bank, weakening towards the western and south-western Bank. The Agulhas Current extended over the whole shelf north of East London but moved seawards of the 200-m isobath south of Port Alfred, tracking the bathymetry between

500 and 1 000 m. Near-surface current velocities were low and of variable direction over the shelf, but exceeded 300 $cm \cdot s^{-1}$ in the core of the Agulhas Current.

Species composition and distribution patterns

A total of 24 species of euphausiids was taken from the 30 RMT (1×6) hauls (Table I). The collections were dominated by three species: *Nyctiphanes capensis*, *Euphausia recurva* and *Thysanoessa gregaria*. These species accounted for more than 66% of the total number of euphausiids and, together with *E. tenera* and *Stylocheiron affine*, were the only species to contribute more than 5% of the population. A further six species contributed more than 1% of the total population (Table I).

Euphausiid species richness was lowest nearshore along the South Coast and highest at depths of about 600 m (Fig. 2a). The slight decrease in richness seawards of this depth is probably artifactual, reflecting both the paucity of krill in the open ocean and the small number of samples.

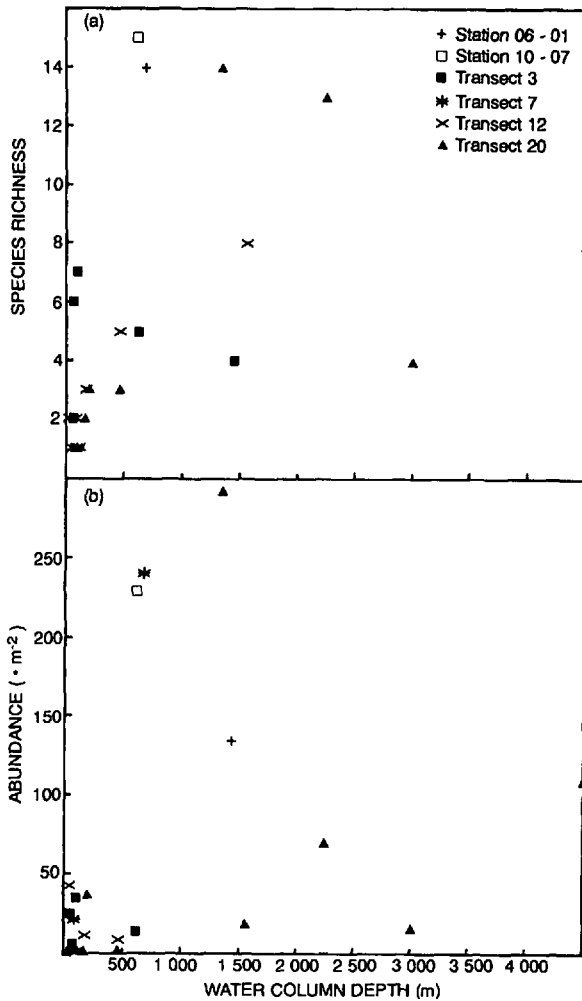


Fig. 2: Variations in euphausiid (a) species richness per haul and (b) abundance with water column depth along the South African south coast

Euphausiid abundance was generally low across the entire area, but it peaked in water depths of 600–1300 m and decreased sharply farther offshore (Fig. 2b). *Nyctiphanes capensis* was most common shallower than 200 m and tended to be restricted to the eastern parts of the survey grid, where it dominated euphausiid communities (Table I). *Euphausia recurva* and *Thysanoessa gregaria* were more abundant in the region of the shelf-break and beyond (Table I). Other species were generally widespread in deeper water.

Vertical migration patterns

Patterns of diel vertical migration were mostly ob-

scure (Fig. 3), only *Euphausia tenera* occupying significantly different ($p < 0,05$) depths by day (75,6 m) than by night (22,1 m). Although the mean depths occupied by *Nyctiphanes capensis* by day (58,9 m) and night (42,3 m) were not significantly different from each other at the 5% level, they were at a level of 10%.

The dominant euphausiids at the shelf edge along the South Coast appeared to occupy different depths at night (Table II).

Gut pigment

Euphausia recurva occurred at sufficient densities at only two night-time stations for observations on gut pigment to be made. Although the quantity of gut pigment tended to increase with increasing euphausiid size, it peaked in animals 15–17 mm long (Fig. 4). There was no significant difference in the mean gut pigment between individuals caught in the upper and those in the deeper layers of the water column at either station at night (Fig. 5), although the total quantities of pigment varied between stations.

DISCUSSION

Species composition

Although the present data represent a single snapshot of the South African south coast, the species composition of euphausiid assemblages presented is broadly similar to that of the more broad-based accounts of that region by De Decker (1973) and Talbot (1974), and any differences reflect the absence of the rarer, deep-water species of *Thysanopoda*, *Nematobranchion* and *Stylocheiron*.

Euphausiid communities during the present study were broadly divisible into those of low diversity, which were confined to the continental shelf, and those of high diversity occupying waters at and beyond the shelf-break. Similar observations have been made for euphausiids (Barange *et al.* 1992, Gibbons *et al.* 1995) and other zooplankton taxa along the south and west coasts of southern Africa (Pagès 1992, Giraudeau 1993), suggesting the existence of common differences between coastal and oceanic processes in those regions.

Distribution and abundance

Areas of high euphausiid abundance were mostly

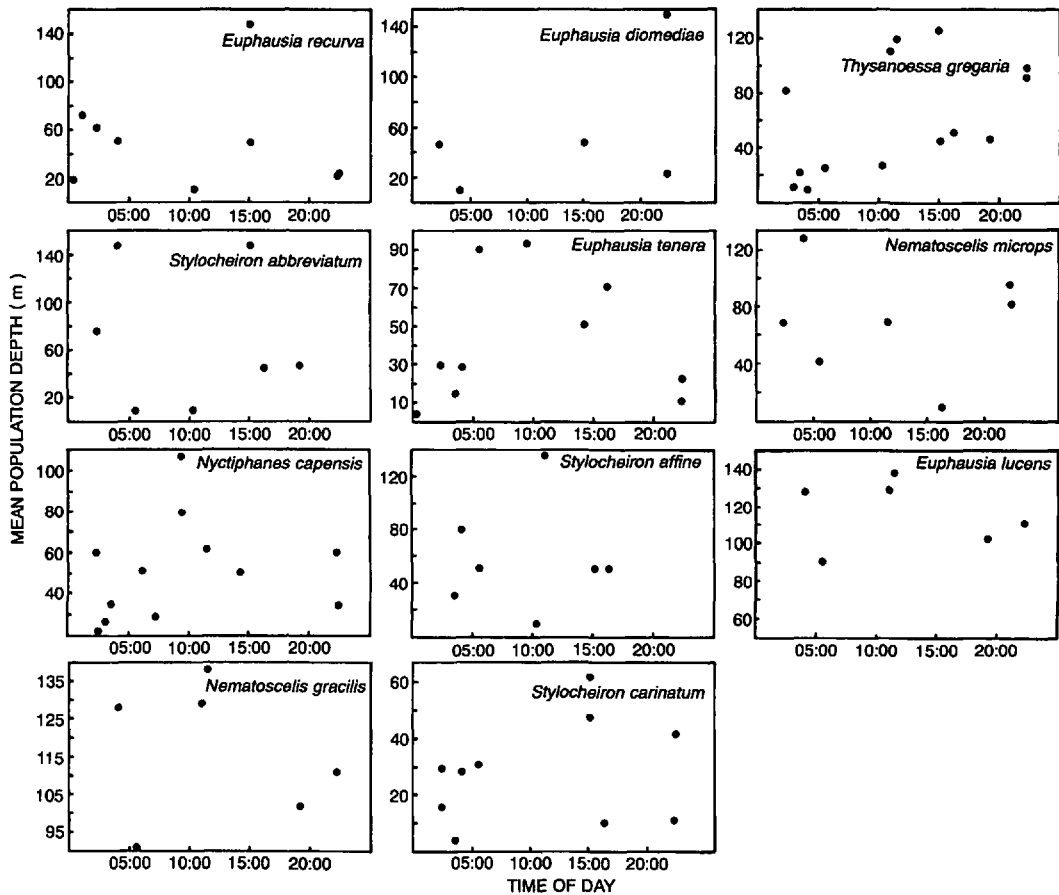


Fig. 3: Changes in weighted mean depth (see text) of the dominant euphausiids throughout 24 h

confined to the region at and beyond the shelf-break. Dense aggregations of euphausiids in similar positions with respect to the continental shelf have been made by a number of previous authors (e.g. Simard and Mackas 1989). In a recent acoustic study of the eastern Agulhas Bank, Barange (1994) noted that the intensity of zooplankton patchiness varied with the

intensity of hydrographic features. Particularly dense patches and aggregations are associated with strong frontal systems at the edge of the shelf, and Barange (1994) argues that the high densities of zooplankton there are attributable to passive accumulation (see also Sameoto 1976, Simard and Mackas 1989). Such aggregations may alternatively reflect a particular preference by euphausiids for the highly dynamic character of the region, levels of primary production often being elevated by shelf-edge upwelling (Brown *et al.* 1991, Boyd and Shillington 1994, Probyn *et al.* 1994).

Euphausia recurva and *Thysanoessa gregaria*, which dominated communities at the shelf-break during this survey, have frequently been found in large numbers at the shelf-break (Nepgen 1957, Pillar *et al.* 1991, Barange *et al.* 1992), although both species extend into oceanic regions too (Mauchline and Fisher 1969, Mauchline 1980). In the case of *E. recurva*,

Table II: Mean night-time depth (m) and standard error (SE) of the dominant species occurring at the self-edge

Species	Mean night-time depth (m)	SE
<i>Euphausia recurva</i>	41,2	18,7
<i>Euphausia tenera</i>	18,3	4,1
<i>Thysanoessa gregaria</i>	60,8	18,7
<i>Nematoscelis microps</i>	93,1	11,1
<i>Stylocheiron carinatum</i>	21,6	5,2

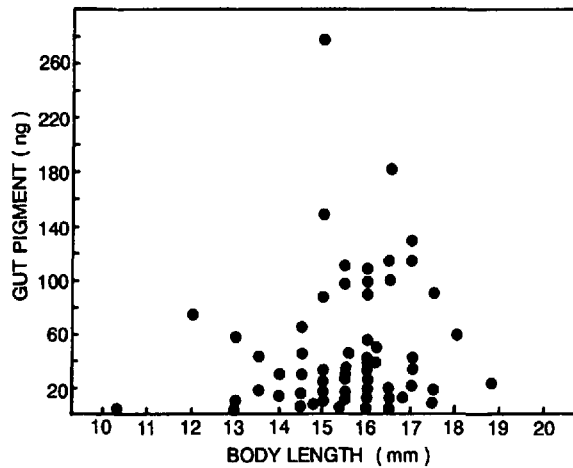


Fig. 4: Plot of gut pigment v. length of *Euphausia recurva*

there is evidence to suggest that populations can be maintained in the region of the shelf-break (Pillar *et al.* 1991), and similar behaviour may exist for most of the krill recorded persistently in such regions.

Nyctiphanes capensis, which dominated the nearshore communities in the eastern sector, is a neritic species distributed around the coast of southern Africa from Transkei (Talbot 1974) to Namibia (Barange 1990). Although its abundance peaks in northern Benguela waters (Barange *et al.* 1992), dense localized patches have been recorded in the bays around Port Elizabeth (Cornew *et al.* 1992¹). *N. capensis* can persist in the productive, inshore areas of the northern Benguela by displaying ontogenetic diurnal vertical migration, which allows it to take advantage of the various cross-shelf and alongshore water movements to stay near shore (Barange and Boyd 1992, Barange and Pillar 1992).

Diel vertical migration

Patterns of diel vertical migration were for the most part obscure (Fig 3). Indeed, few species of euphausiid appeared to undergo diurnal vertical migration. Members of the genus *Stylocheiron* generally do not (Mauchline and Fisher 1969, Mauchline 1980), and the activity itself may be obscured by asynchronous behaviour (Pearre 1973, Gibbons 1993). However,

¹ The range of densities of *N. capensis* in Algoa Bay (0–73 mg · m⁻³) presented by Cornew *et al.* (1992) reflects the total range observed from 10 samples. These data are not comparable with those of Barange and Stuart (1991), whose data for the northern Benguela (13–114 mg · m⁻³) reflect average densities taken from five surveys over a region extending from 17 to 26°S (maximum density > 1 600 mg · m⁻³).

the absence of obvious migration in the present study is probably attributable to the diverse sources of the data, a fact which makes interpretation difficult.

Clear diel vertical migration of *Euphausia tenera* has previously been observed in another western boundary current, the Florida Current (Lewis 1954, in Mauchline and Fisher 1969), although the distances over which populations moved were significantly greater than here (250 m). Given the obvious constraints with the data set, adult *N. capensis* may have been displaying diurnal vertical migration, in which case populations of the species along the South Coast may maintain themselves in the area much as they do off Namibia (Barange and Boyd 1992, Barange and Pillar 1992).

The presence of (and selection by) a number of euphausiid species in (and for) the productive waters of the shelf-break could result in competitive interactions, unless component species employ mechanisms to preclude it. Vertical segregation provides one such mechanism (Table II), and Barange (1990) has argued that it and the partitioning of trophic resources (Barange *et al.* 1991) may account for the high diversity of assemblages at the shelf edge in Namibia and elsewhere.

Gut pigment

Although gut pigment seemed to be normally distributed with respect to euphausiid size (Fig. 4), the number of data points for animals greater than the modal size-class is small. There may, therefore, be a tendency for the quantity of gut pigment to increase with increasing euphausiid size, as has been noted for other members of the genus *Euphausia* (Stuart and Pillar 1990, Gibbons 1993). Alternatively, the small quantities of gut pigment in large animals may reflect greater carnivory than herbivory (Gibbons *et al.* 1991).

The quantity of phytoplankton-derived pigment in the guts of *Euphausia recurva* at night was independent of their vertical position in the water column. Although similar observations were made for *Euphausia lucens* in the nearshore waters of the southern Benguela by Gibbons (1993), the food environment in the latter study was strongly stratified. Gibbons (1993) argued that the presence of large quantities of gut pigment in the euphausiids collected from deep water reflected asynchronous feeding in the surface layers, and a rapid return of individuals to depth. He suggested that such behaviour minimizes the time spent in the surface layers, where they are at risk from predation and advective loss. Such an argument need not be invoked to explain the results of the present

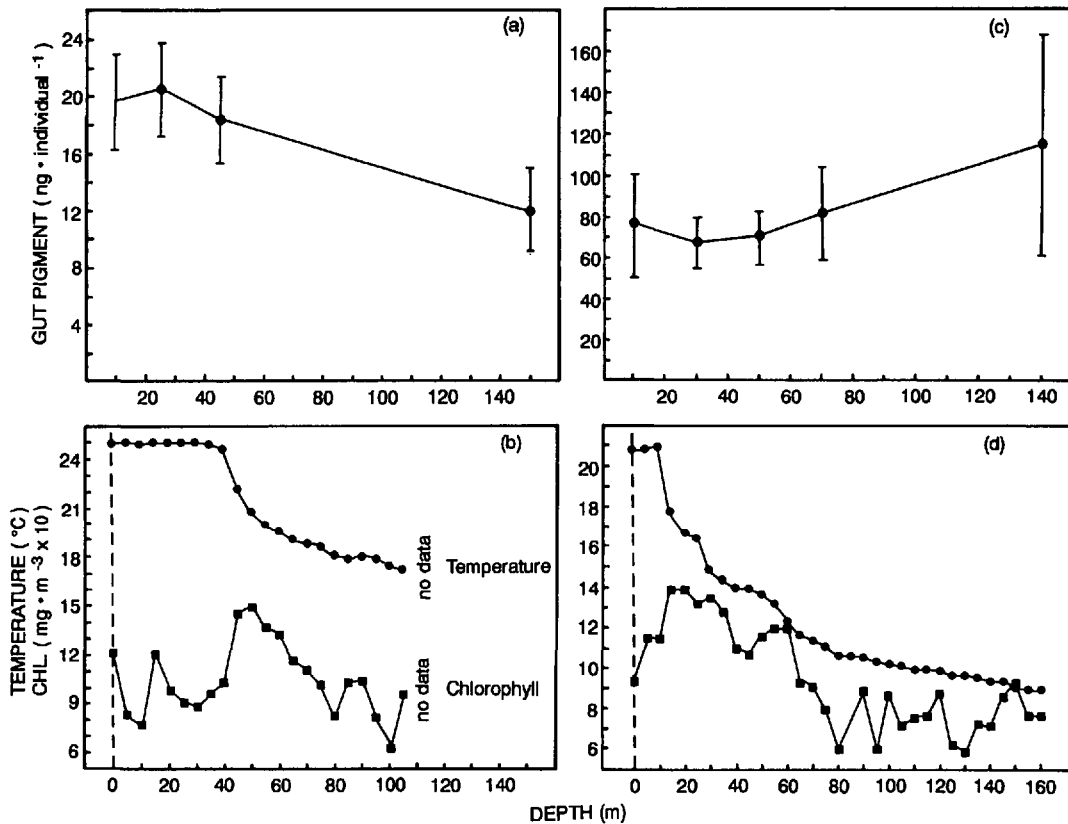


Fig. 5: Vertical distribution of mean gut pigment (\pm SE) in populations of *Euphausia recurva* at two stations sampled at night at (a) Station 06-01 and (c) Station 10-07. Vertical profiles of the thermal and chlorophyll environment at each station are given in (b) and (d) respectively

study, because the food environment of *E. recurva* was relatively unstratified. Although the gut pigment of *E. recurva* collected from deep water may have been derived from surface feeding, it is more parsimonious to suppose that individuals fed at depth. Although the risk of predation may be high in surface layers at the shelf edge as a result of elevated predator density (Barange 1994), net water movement occurs in an alongshore direction, meaning that individuals are not necessarily lost from their "preferred" environment (at the shelf edge) by remaining at the surface.

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