

## Population structure, biomass and distribution of *Nyctiphanes capensis* (Euphausiacea) in the vicinity of Algoa Bay, South Africa

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Samples taken on three research cruises along the east coast of South Africa in 1989 contained large numbers of *Nyctiphanes capensis* (Hansen), a euphausiid species commonly found in the cold waters of the west coast. Size-frequency distributions were determined for euphausiid populations at each station, and density and biomass calculated. Densities were found to be low close inshore and offshore in the warm Agulhas current and highest on the shelf and shelf-edge. A dense aggregation of *N. capensis* was analysed in greater detail to ascertain the reasons for the accumulation of euphausiids in this shelf area. This sample was dominated by females (many with brood pouches containing nauplii) with Stage 2 ovarian development. Stomach analyses showed that the majority of specimens had stomachs full of phytoplankton-derived material. It is possible that aggregations of euphausiids form to feed on high primary production associated with upwelling on the shoreward edge of the Agulhas current.

Gedurende 1989 is groot getalle van die weskus eufousied *Nyctiphanes capensis* in monsters van drie navorsingsvaarte langs die ooskus gevind. Lengte-frekwensieverspreidings, konsentrasies en biomassa van die eufousiede is by elke stasie bepaal. Konsentrasies was hoog op die kontinentale plat, maar langs die kus en in die Agulhas-seestroom was hulle laag. 'n Digte versameling van *Nyctiphanes capensis* is ontleed om die rede vir die hoë konsentrasie te bepaal. Die monster is deur wyfies met broeisakke en Stadium 2-ovaria oorheers. Maaginhoud-ontleding het getoon dat hulle fitoplankton gevreet het. Dit is moontlik dat die eufousied-versamelings op die hoë primêre produksie, geassosieer met die landwaartse grens van die Agulhas-seestroom, wei.

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The genus *Nyctiphanes* is peculiar among the Euphausiacea in that all four known species are neritic and are widely separated from one another geographically: *N. couchi* occurs around the British and European coasts, *N. simplex* in the California and Peru currents, *N. australis* off the east coasts of Australia and New Zealand and *N. capensis* off the southern African coast, in the upwelling area off N.W. Africa (Baker, Boden & Brinton 1990) and off the Cape Verde Islands (Meira 1970). The centre of distribution for the southern African population of *N. capensis* is off the coast of Namibia from 20 – 24°S (Olivar & Barange 1990; Barange & Stuart 1991), though it ranges from northern Namibia, around the Cape coast to East London (Boden 1954; Talbot 1974).

Various studies on the general biology of *Nyctiphanes capensis* including reproductive potential, larval growth and development as well as population dynamics, abundance and distribution patterns have been conducted (Pillar 1985; Stuart & Nicol 1986; Barange & Stuart 1991). These studies were carried out on specimens from the west coast of South Africa and little is known about *N. capensis* on the east coast.

The Agulhas Current carries warm tropical and subtropical surface water southwards along the east coast of South Africa before diverging from the coast and retroflecting south of Cape Agulhas (Grundlingh 1983). Talbot (1974) found that the euphausiid species *Thysanopoda tricuspdata*, *Stylocheiron suhmi* and *S. microphthalma* could be classified as indicators of Agulhas Current water, but that *N. capensis* and *Euphausia lucens* were indicative of water of a different origin.

*N. capensis* is known to be an important constituent of the diet of many commercially important fish species off the coast of Namibia (Macpherson & Roel 1987). It has also recently been found in the guts of several demersal teleosts from the Cape south and west coasts (Meyer & Smale 1991) as well as in the guts of juvenile hake (*Merluccius capensis*) from the Cape south coast (Smale 1984).

The present study was undertaken to obtain estimates of density, biomass and distribution of *N. capensis* in the Algoa Bay region. Ovarian condition and brood size of selected samples were also examined in order to provide some insight into the poorly understood reproductive biology of this species.

### Material and Methods

#### Sample collection

Samples were collected during exploratory ichthyoplankton research cruises on the R.V. *Meiring Naude* along the east coast of South Africa during 1989. Ten samples from the Algoa Bay area, collected during hours of darkness on 31 January (Station 1), 20–25 February (Stations 2–7), and 4–8 December 1989 (Stations 8–10), were examined (Figure 1). A further 14 daytime samples were also taken during the February and December cruises, but these were not examined quantitatively since euphausiids are known to undergo strong diel vertical migrations (Pillar, Armstrong & Hutchings 1989). Very low numbers of euphausiids are generally caught during the day owing to migration below the depth fished by the net, as well as visual net avoidance.

At Station 1, a dense surface swarm of *N. capensis* was sampled using a 950 µm Neuston net. At all other stations

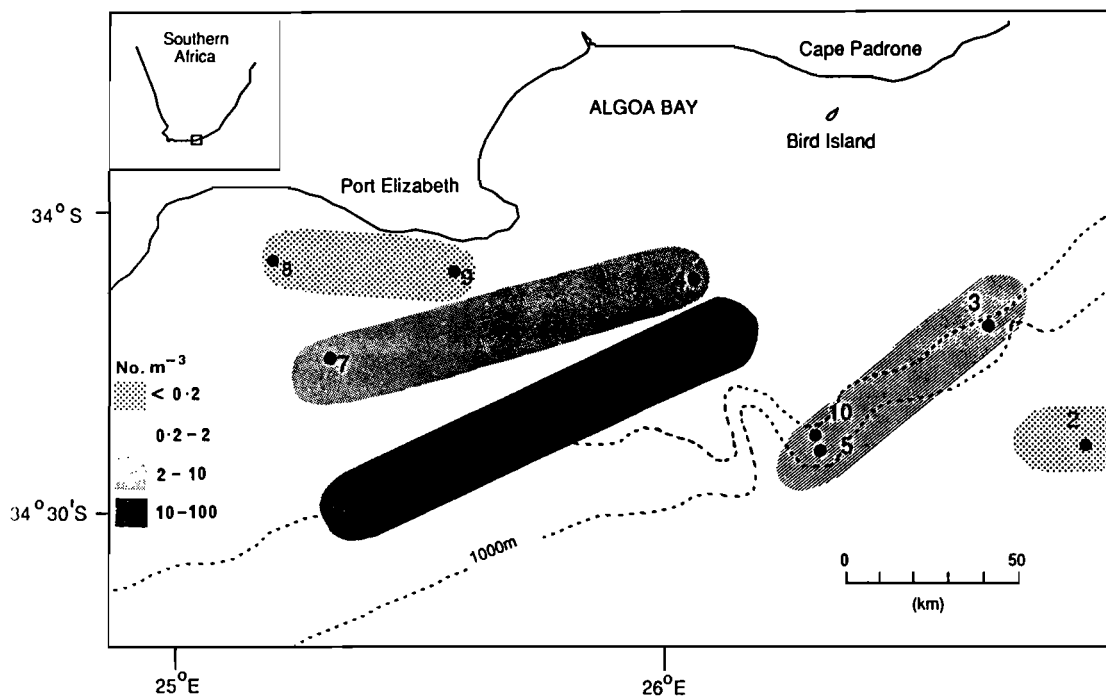


Figure 1 Map of the study area showing the location of Stations 1–10 and the density of adult and juvenile *Nyctiphanes capensis* in this area.

zooplankton samples were collected by means of oblique hauls using standard SFRI (Sea Fisheries Research Institute) Bongo nets, 57 cm in diameter, fitted with 500  $\mu\text{m}$  and 950  $\mu\text{m}$  meshed nets. Tows were of 10-min duration and ship's speed was regulated at approximately  $1 \text{ m}\cdot\text{s}^{-1}$  (2 knots). Nets were fitted with calibrated General Oceanics mechanical flowmeters (Model 2030) to obtain the volume of water filtered. At offshore stations (depths > 200 m) tows were made from about 150 m to the surface and at inshore stations tows were made from about 20 m above the sea bottom to the surface. Samples were preserved in 5% v/v formaldehyde in sea water. Oceanographic measurements were made to a maximum depth of 200 m using a NRIO hydrosonde CTD (see Goschen 1991).

#### Sample analysis

Samples from the 500- $\mu\text{m}$  net were examined for the presence of *N. capensis* adults and juveniles. Calyptopis and furcilia stages were not enumerated as they are not representatively sampled by a 500- $\mu\text{m}$  net (Pillar 1986).

In the laboratory, dense samples were split using a Folsom plankton splitter until about 100 individuals were present. All adult and juvenile *N. capensis* (> 5 mm total length) were counted, sexed and the carapace length (tip of rostrum to mid-dorsal posterior edge of carapace) measured. To establish the relationship between carapace length and total body length (tip of rostrum to distal end of telson) these parameters were measured in a subsample of 136 individuals using a dissecting microscope with a calibrated micrometer. Separate regressions for males, females and juveniles were calculated.

Females were examined for the presence of brood pouches or spermatophores in the thelycum. The number of eggs or nauplii in the brood pouch was recorded and their size measured. The presence of spermatophores in males was

also recorded.

Length/weight regressions were constructed using 20 specimens each of males, females and juveniles. Individuals were measured, rinsed briefly in distilled water and placed in pre-weighed aluminium dishes in a drying oven for 24 h at  $60^\circ\text{C}$ . Samples were transferred to a desiccator for 1 h before being weighed on a Sartorius electronic balance (Model 4503 MPG) to the nearest  $\mu\text{g}$  for dry weight determination. Weights were corrected for weight loss owing to preservation in formaldehyde (Giguère, St-Pierre, Bernier, Vézina & Rondeau 1989) (15–23 % depending on length).

Specimens from the surface swarm at Station 1 were examined in more detail in an attempt to ascertain the reason for the high density of euphausiids in this area. The ovarian development of 50 adult females was investigated by dissecting out the ovary and examining the eggs under a compound microscope (100 $\times$  mag.).

Four ovarian stages were assigned according to the scheme proposed by Mauchline (1968): Stage 1 eggs are small with a very large nucleus relative to egg size; Stage 2 eggs have a nucleus representing about 50% of the egg diameter; Stage 3 eggs have yolk globules present in the cytoplasm and Stage 4 eggs are large, opaque, and filled with globules of yolk.

The stomachs of specimens from Station 1 were dissected out and the degree of fullness estimated on a scale of 1–4 as follows: 1 = 0 to 25% full, 2 = 26 to 50% full, 3 = 51 to 75% full and 4 = 76 to 100% full (Nicol, James & Pitcher 1987). Of these stomachs, 50 were examined under a compound microscope to determine food composition.

## Results

### Oceanographic features

A representative temperature/depth section taken on 22 February, 1991 along a transect of 10 hydrosonde stations

(including Stations 2 and 3), is given in Figure 2. In general a tongue of cold, upwelled water (10–13°C) was present on the shelf (Area A) with a strong thermocline in the upper 50 m of water (Area B). On the edge of the continental shelf upward tilting isotherms (Area C) denote the edge of the Agulhas Current whilst off the shelf (Area D) warm Agulhas Current water (> 20°C) was evident. Full oceanographic details from this transect, as well as from other transects in the area, can be found in Goschen (1991).

#### Euphausiid distribution patterns and population structure

Regression analysis of carapace length (mm) and total length (mm) of male, female and juvenile *N. capensis* yielded the following equations:

$$TL = 4,12 + 2,01 CL \quad (n = 58; r^2 = 0,660) \text{ females} \quad (1)$$

$$TL = 2,29 + 2,72 CL \quad (n = 31; r^2 = 0,772) \text{ males} \quad (2)$$

$$TL = 0,44 + 3,32 CL \quad (n = 47; r^2 = 0,801) \text{ juveniles} \quad (3)$$

These were used to convert carapace length measurements to total length measurements for use in frequency distributions.

The relationship between total length (mm) and dry

weight in mg (corrected for weight loss owing to chemical preservation, Giguère *et al.* 1989) for adult and juvenile *N. capensis* resulted in the following equation:

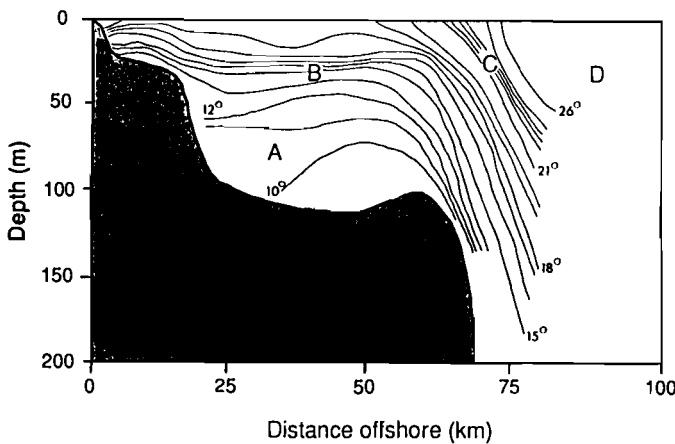
$$DW = 0,0017 \times TL^{2,92} \quad (n = 60; r^2 = 0,973) \quad (4)$$

Size frequency distributions of *N. capensis* juveniles and adults from Stations 2–10 are presented in Figure 3. The biomass of each size class was estimated from the length–dry weight regression (Eqn 4) and is also indicated on Figure 3. Total numbers and biomass per m<sup>3</sup> were calculated for each sample and are presented in Table 1. Station 2, with a depth of 2500 m, was the only true Agulhas Current station. The temperature was greater than 20°C down to a depth of 100 m. The sample contained very low numbers of *N. capensis* (Table 1), all of which were juveniles (Figure 3).

The inshore stations (4,7,8 and 9) were characterized by a seabed depth of between 70–110 m. Sea surface temperature was around 18°C at all four stations and a marked thermocline was present in the upper 50 m of water with the temperature dropping to between 10 and 11°C near the seabed indicating the presence of cold, upwelled water. It is noteworthy that Station 4 contained many calyptopis and furcilia larvae while Station 9 contained many furcilia larvae (these were not enumerated as they were not sampled quantitatively with the 500-µm mesh net). Station 8 had well mixed surface water and contained many chaetognaths, but no *N. capensis*. Densities for Stations 4, 7 and 9 varied between 0,13–6,28 m<sup>-3</sup> and biomasses between 0,28–1,87 mg DW m<sup>-3</sup> (Table 1). Juveniles dominated most of these inshore stations with specimens in the 6 mm size class being particularly numerous.

Stations along the shelf break (3, 5, 6 and 10) were characterized by depths of between 350–1200 m and warmer surface water (20–25°C) showing the influence of the Agulhas Current in the region. Deeper water (> 100 m) was < 14°C. An important feature of these samples was the increased abundance of adult *N. capensis* which were scarce in the inshore stations. This has the effect of increasing the relative biomass values on the shelf-break to between 1,77–29,56 mg DW m<sup>-3</sup>. Despite the location of Station 6 on the shelf edge, a strong thermocline was evident between 10 and 20 m (temperatures dropped from 19,8°C to 14,7°C). At this station *N. capensis* showed a bimodal distribution and, excluding Station 1, had the highest density and biomass values (68,03 m<sup>-3</sup> and 29,56 mg DW m<sup>-3</sup>).

The aggregation of *N. capensis* in the surface water at Station 1 represented the highest density and biomass recorded in the study area (Table 1). No juveniles were present, although most would have been lost through the relatively large mesh (950 µm) of the Neuston net. The sex ratio of the adults was skewed towards females (67%). Figure 4 shows the reproductive condition of these specimens. It is evident that female *N. capensis* develop immature ovaries around 9 mm total length and that the proportion of ripe females (those carrying brood pouches) increases with body size. Females carrying brood pouches were generally greater than 11 mm total length and more abundant than non-ripe females in the larger size classes. The largest ripe female was 14,2 mm total length. Males became sexually mature in the 10 mm size class, and ripe males (those with ripe spermatophores) dominated the largest two size classes. The



**Figure 2** A representative cross-shelf temperature section through Stations 2 and 3 on 22 February 1989 (adapted from Goschen 1991). See text for explanation.

**Table 1** Density (no. m<sup>-3</sup>) and biomass (mg DW m<sup>-3</sup>) of *Nyctiphanes capensis* at Stations 1–10 in relation to sea surface temperature

Station	Density no. m <sup>-3</sup>	Biomass mg DW m <sup>-3</sup>	Temperature °C
1	88,8	72,64	19,1
2	0,11	0,04	26,3
3	2,66	5,12	25,1
4	3,91	1,87	18,5
5	1,94	2,03	20,5
6	68,03	29,56	20,5
7	6,28	0,55	18,2
8	0,00	0,00	18,8
9	0,13	0,28	17,5
10	2,31	1,77	24,2

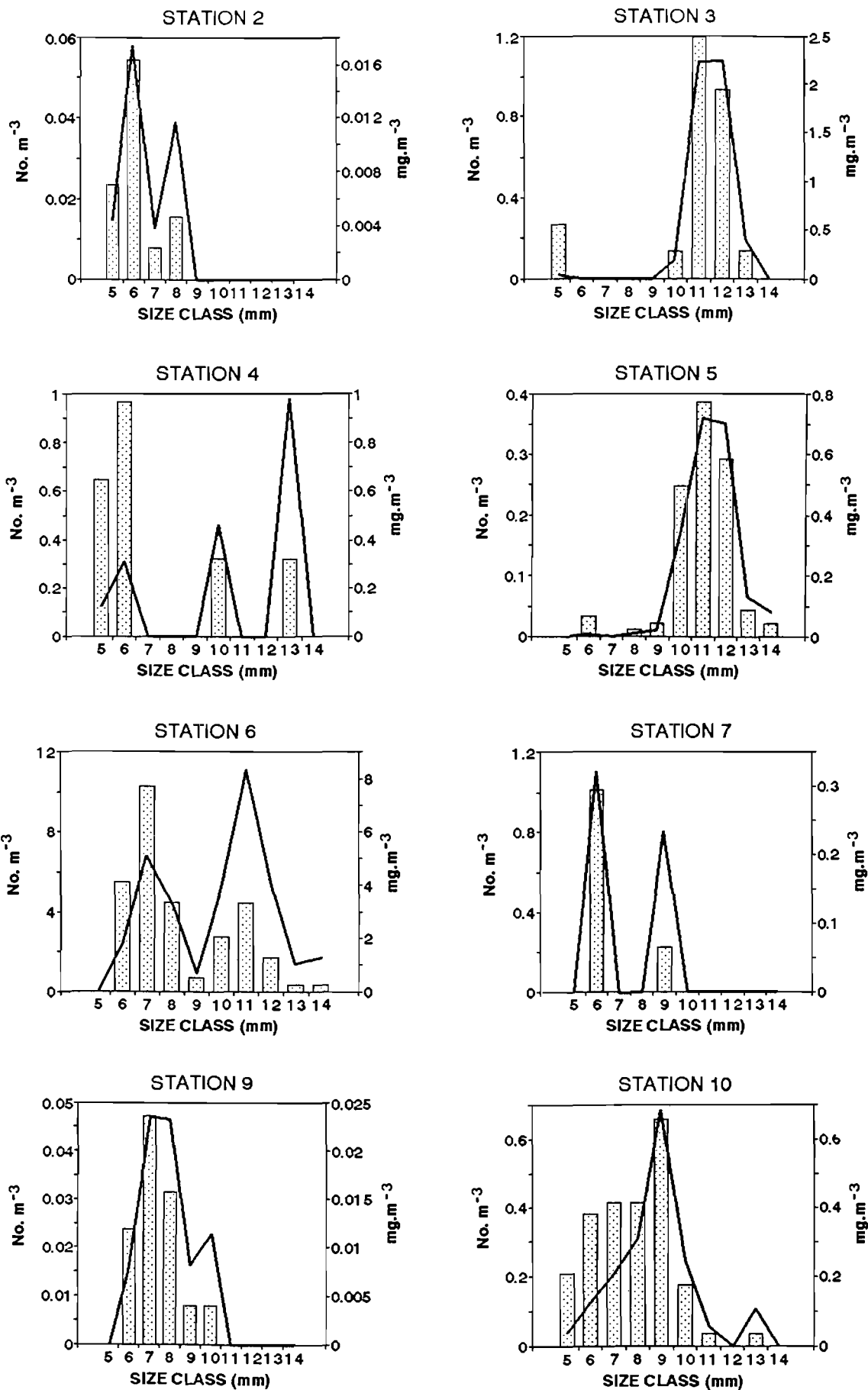
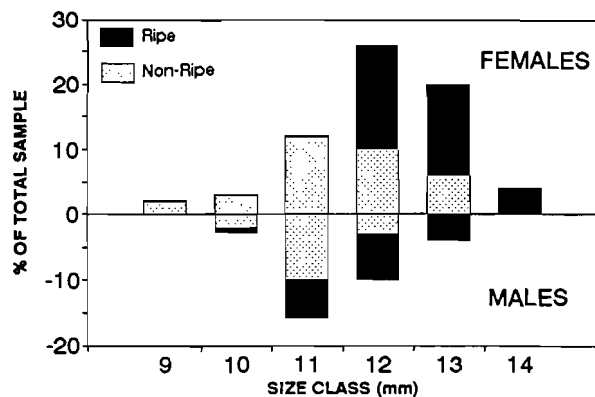
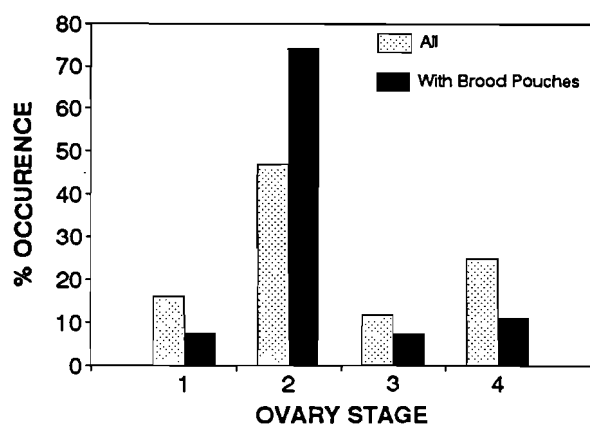


Figure 3 Size-frequency distribution (bar graphs) and biomass (line graphs) of juvenile and adult *Nyctiphanes capensis* from Stations 2–10 (excluding Station 8, which contained no *N. capensis*).



**Figure 4** Length-frequency histogram of adult *Nyctiphanes capensis* from Station 1 showing the proportion of ripe and non-ripe males and females.



**Figure 5** Stage of ovary development of adult female *Nyctiphanes capensis* (all females and those with brood pouches) from Station 1.

largest ripe male was 13,5 mm total length.

Stuart & Nicol (1986) recorded a significant positive relationship between the number of eggs in the brood pouch of female *N. capensis* and body size. No such significant relationship was found in the present study using the number of nauplii per pouch, probably owing to the low number of data points (9 specimens), since many of the brood pouches were damaged. Approximately 40–50 nauplii were found in each intact brood pouch, while one female carried 104. The mean diameter of eggs found in the brood pouches was  $401 \pm 13,6 \mu\text{m}$  ( $n = 15$ ) while the average nauplius total length was  $458 \pm 26,6 \mu\text{m}$  ( $n = 30$ ).

The ovary stages of females from this dense aggregation of euphausiids (Station 1) are shown in Figure 5. The majority of females examined (47%) were in an early stage of ovarian development (Stage 2). Of those animals carrying brood pouches, more than 70% were at the second stage of ovarian development, indicating the possibility of multiple broods.

All individuals examined contained food remains in their stomachs with varying degrees of stomach fullness. The majority of stomachs were between 25–75% full indicating that recent feeding had occurred. The stomach contents consisted mostly of green, amorphous material with a few

intact diatom and dinoflagellate cells, suggesting that it was of phytoplanktonic origin. No copepod remains were found.

## Discussion

### Distribution

Like other members of the genus, *N. capensis* is characteristically an inhabitant of shelf waters and in South African waters it occupies the same niche as *N. simplex* in Californian waters (Boden 1955). This is in contrast to its preferred habitat close inshore off Namibia, which may be a result of *Euphausia hansenii* dominating the shelf region in this area (Barange & Stuart 1991). Station 8 was the only night-time station where no *N. capensis* were recorded. This may be due to its proximity to the shore, although patchiness is a common phenomenon amongst pelagic organisms. Apart from Station 8, Station 2 had the lowest density of *N. capensis* and was situated within the path of the Agulhas Current, which supports Talbot's (1974) hypothesis that *N. capensis* is an indicator species of water of different origin to the Agulhas Current.

The biomass of both euphausiids and copepods has been found to be higher on the west coast of South Africa than over the Agulhas Bank (Pillar 1986). However, in the present study the biomass of *N. capensis* from the east coast ranged from 0,04–72,64 mg DW m<sup>-3</sup>, whereas that of adult *N. capensis* off Namibia ranged from 13,5–114,1 mg DW m<sup>-3</sup> (Barange & Stuart 1991). Similarly, densities of adult *N. capensis* in the upper 100 m of the water column along the Namibian coast ranged from around 11–21 m<sup>-3</sup> (Barange & Stuart 1991), in comparison to 0,11–88,8 m<sup>-3</sup> for *N. capensis* in the present study. It is therefore apparent that extremely high densities of euphausiids do occur along the east coast, albeit in patches, providing a substantial food resource for the many species of birds and fish in the area (see Smale 1984; Meyer & Smale 1991).

*N. capensis* off Namibia matured at 12 mm total length and reached a maximum length of 21 mm (Barange & Stuart 1991). This is substantially larger than female specimens from the southern Benguela region which matured at 7,5 mm and reached 12,5 mm total length (Stuart & Nicol 1986) and to those in the present study, which matured at 9 mm total length and reached a maximum of 14,2 mm. Barange & Boyd (in press) suggest that seasonal intrusions of warm water, together with a productive and stable environment, are responsible for the high concentrations of very large *N. capensis* in the Walvis Bay area. Differences in size have also been observed for two populations of *Thysanoessa inermis* near Japan (Hanamura, Kotori & Hamaoka 1989). These authors concluded that the two euphausiid populations originated from different stocks.

In the southern Benguela region, *Euphausia lucens* has been found to migrate offshore across the shelf for spawning purposes (Pillar & Stuart 1988; Pillar *et al.* 1989). Similarly, in the present study, juveniles and larval stages of *N. capensis* were found to occur predominantly at the inshore stations (Stations 4, 7 and 9), whereas mature females were found at the shelf edge (Stations 1 and 6) and over the shelf break (Stations 3, 5 and 10). This may indicate that ripe adult *N. capensis* also use the warmer offshore waters for

spawning purposes, but that the strong Agulhas Current imposes a limit on the extent of their offshore transportation.

### Reproductive biology

Euphausiids can be divided into those genera that retain their eggs, once laid, in a brood pouch (*Nyctiphanes*, *Pseudeuphausia*, *Nematoscelis*, and *Stylocheiron*) and those that lay their eggs freely into the sea (*Euphausia*, *Thysanopoda*, *Meganyciphanes*, *Nematobrachion*, and *Thysanöessa*) (Stuart & Nicol 1986). *N. capensis* eggs are carried in two pear-shaped sacs attached to the thoracic legs of the female (Boden 1955). Sizes of *N. capensis* eggs in the Benguela region reported by Boden (1955) ranged from 340–380  $\mu\text{m}$ . In the present study *N. capensis* eggs were found to be somewhat larger, between 387–414  $\mu\text{m}$  and nauplii between 431–485  $\mu\text{m}$ . Barange & Stuart (1991) measured *N. capensis* egg diameters to be between 350–375  $\mu\text{m}$  and nauplii lengths to range from 550–600  $\mu\text{m}$ .

The number of nauplii carried in the brood pouches of *N. capensis* in Algoa Bay is similar to that of *N. capensis* of a comparable size along the west coast (Barange & Stuart 1991). Mauchline & Fisher (1969) derived a relationship between body volume and length. Using this relationship, and the measured egg diameters, the brood volume of a 13-mm *N. capensis* was calculated to represent 6,86% of its body volume, which falls well within the range of 5–10% for crustaceans in general (Mauchline & Fisher 1969). Barange & Stuart (1991) suggested that *N. capensis* increases fecundity through decreasing egg size and producing large numbers of relatively small eggs protected by a brood pouch, as compared to species such as *E. hanseni* which release lower numbers of relatively large eggs directly into the water column.

### Aggregating behaviour

Densities of euphausiids at Stations 1 and 6 were similar, but owing to higher proportions of juveniles at Station 6, the biomass of this sample was somewhat lower (Table 1). Station 6 is on the edge of the continental shelf and the presence of large numbers of *N. capensis* may be due to dynamic upwelling in the area (Shannon, Hutchings, Bailey & Shelton 1984). Similarly, Simard, de Laurantayne & Therriault (1986) found a dense aggregation of euphausiids along one edge of the St Lawrence estuary, which they attributed to interactions between upwelling and residual circulation and the negative phototaxis behaviour of euphausiids.

A variety of euphausiid species have been observed to form day-time surface swarms (Mauchline & Fisher 1969; Nicol 1984; Nicol, James & Pitcher 1987; Miller & Hampton 1989). Many of these swarms are characterized by adults engaged in reproductive behaviour with a dominance of females (Nicol 1984) and are usually composed of individuals of a certain spawning condition and size range (Hanamura *et al.* 1989). Euphausiid densities in these day-time surface swarms are often extremely high, with reports of up to 1 550 000  $\text{m}^{-3}$  being recorded for *E. lucens* at Sandy Point harbour, off the west coast of South Africa (Nicol *et al.* 1987). However, this may not have been an entirely natural occurrence, but rather owing to passive

accumulation of euphausiids on the side of the harbour wall, caused by the prevailing winds.

Densities in swarms vary considerably with the method of estimation (nets, acoustics, buckets, photography etc.) and are generally lowest for net samples (Miller & Hampton 1989). Visual observation of the day-time samples from the ichthyoplankton survey showed no evidence of day-time surface swarms of *N. capensis*, but the night-time sample at Station 1 nevertheless represents a fairly dense aggregation (88,8  $\text{m}^{-3}$ ) of euphausiids in this area. Furthermore, it is likely that densities of the smaller individuals were underestimated owing to the use of the relatively large (950  $\mu\text{m}$ ) meshed Neuston net.

One of the features of the aggregation at Station 1 was the high percentage, (50%), of females with brood pouches. All of the pouches contained nauplii larvae, whereas only a few contained eggs. This indicated that the females had previously been fertilized and the aggregation was not for reproductive reasons. An examination of the ovarian condition of the females within the aggregation showed that most were at an early stage of development (Figure 5). The majority of females with pouches had Stage 2 ovaries, which implies the ability to produce multiple broods, as has been observed for *N. capensis* in the southern Benguela region (Stuart & Nicol 1986). *N. australis* from south-eastern Tasmania (Hosie & Ritz 1983) is also capable of producing multiple broods.

In a swarm of *E. lucens* from the west coast of South Africa, Nicol *et al.* (1987) observed that most specimens had food in their stomachs indicating recent feeding, although the reason for the swarm was not apparent. Hanamura *et al.* (1989) observed low feeding activity in a swarm of *T. inermis*, thus excluding feeding as a primary reason for swarming. In the present study, the majority of animals had stomachs more than 50% full of detrital and phytoplankton material indicating that active feeding was in progress. Juvenile and adult *N. capensis*, like other local euphausiid species, are known to be omnivorous (Pillar 1985; Shannon & Pillar 1986; Stuart 1986; Stuart & Pillar 1990). The absence of animal remains in their guts may be due to the fact that euphausiids, e.g. *E. lucens*, may exhibit diel feeding patterns, with carnivory occurring predominantly during the day and consumption of phytoplankton cells at night (Stuart & Pillar 1990). In the present study all specimens were obtained from night-time samples.

Shannon *et al.* (1984) suggested that dynamic upwelling of cold nutrient rich water on the shoreward edge of the Agulhas Current (see Figure 2) could be responsible for maintaining the high levels of chlorophyll observed by satellite imagery in the Algoa Bay area. We suggest that this enhanced primary production provides a source of food for the dense aggregations of *N. capensis* along the shelf edge in the vicinity of Algoa Bay.

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