

DISTRIBUTION OF EUPHAUSIID CRUSTACEANS FROM THE AGULHAS CURRENT

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ABSTRACT

Twenty-nine euphausiid species were collected during the three cruises of the S.A.S. *Natal* in 1958. Of these only *Stylocheiron microphthalmum* had not previously been taken in South African waters. The commonest euphausiid represented in the collection is a larval series which is provisionally linked with *Euphausia recurva* or *E. mutica*. The vertical and horizontal distribution of each species is recorded and seasonal and latitudinal variation discussed. *Stylocheiron submii*, *S. microphthalmum* and *Thysanopoda tricuspdata* are proposed as indicators of Agulhas Current water and *Nyctiphanes capensis* and *Euphausia lucens* as indicators of water not of Agulhas Current origin. The largest number of euphausiids was found off Port Elizabeth during both summer and winter.

METHODS AND SAMPLING PROBLEMS

The material for this study consists of the euphausiids from the plankton samples collected by Mr. P. Zoutendyk on the three cruises of the S.A.S. *Natal* during the International Geophysical Year. On the I.G.Y. cruises the S.A.S. *Natal* worked at a series of stations which were arranged in lines perpendicular to the coast and across the Agulhas Current. The first cruise took place during February and March and consisted of 15 stations on four lines, between Durban and Port Elizabeth (Stations 2–16, Figure 1 a), but on the second cruise in May (Stations 17–50, Figure 1 b) and the third cruise in August (Stations 59–92, Figure 1 c) the programme was expanded to 34 stations arranged in eight lines, between Durban and Plettenberg Bay. In all 83 stations were worked during the period of the survey. At each station a 10-minute horizontal surface haul was made, as well as an oblique haul from 150 m to the surface and except at the shallow inshore stations, three vertical hauls were also included which sampled from 100–0, 200–100 and 400–200 m respectively. At shallow stations one vertical haul was made from between 30 and 50 m depth to the surface. Nets of the Nansen type were used, N 100 nets for the horizontal and oblique hauls and N 70 nets for the vertical hauls (Zoutendyk 1960).

In using the material from these cruises to assess euphausiid distribution, some limitations of the collecting method have to be taken into account. The first is that all the samples were taken during daylight hours and, since most euphausiid species perform extensive diurnal vertical migrations, it is likely that many of them would have moved down beyond the range of the nets at the time of sampling. Secondly, the only sampling below 150 m was done by the small-meshed vertical nets of relatively small diameter, which would not have been suitable for catching large agile members of the plankton, like adult euphausiids. This probably accounts for the preponderance of larvae and juveniles in the I.G.Y. material. A third factor is the time of day at which the stations were worked. The inshore stations and outer stations were done in the early morning and evening and the stations near the centre of the current were done during the middle of the day. Here again, vertical migration might lead to reduced numbers in the samples taken during the middle of the day and this could result in a misleading picture of distribution. Nevertheless,

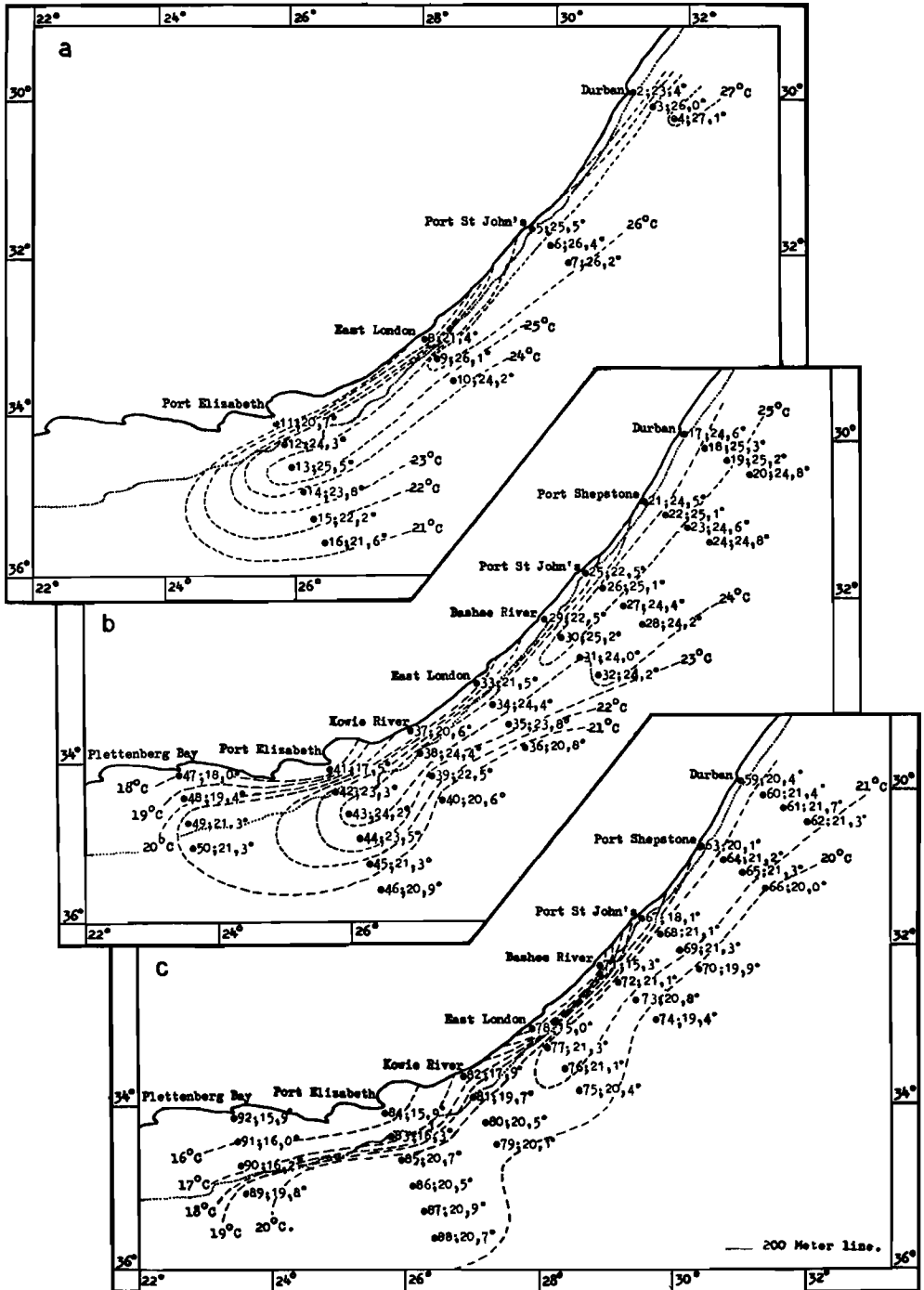


FIGURE 1
 Station numbers, surface temperatures and approximate surface isotherms on the 3 I.G.Y. cruises.
 (a) First cruise (Feb.-March), Stations 2-16.
 (b) Second cruise (May), Stations 17-50.
 (c) Third cruise (Aug.), Stations 59-92.

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the distributions obtained are of value, particularly those of larvae and juveniles and the adults of species which do not perform extensive vertical migrations.

Figures 3, 4, 5 and 9 were drawn with the aid of a camera lucida. The specimens were measured under a binocular microscope, when fully extended on a transparent grid. In the case of the young larvae in which the eyes had not yet emerged from beneath the rostral hood, length measurements were taken from the anterior margin of the carapace to the end of the telson and included the setae of both carapace and telson. The length of the later stages was measured from the anterior border of the eye to the end of the telson.

HYDROGRAPHY OF THE AREA

The survey area was in the path of the Agulhas Current which carries a stream of warm south equatorial surface water in a southwesterly direction along the east coast of South Africa. In the northern part of the area the continental shelf is narrow and the current forms a well-defined stream flowing parallel to the coast, but in the region from Port St. John southwards, the shelf widens and the current spreads out and moves away from the coast. It tends to become deflected to the southeast and eventually forms a return flow which merges with the West Wind Drift. Cooler subtropical water is found on the wide continental shelf in the southwest part of the survey area and there is a belt of cool water inshore of the Agulhas Current, where local winds may set up a northeasterly counter-current close to the coast and cause local upwelling (Clowes 1950; Darbyshire 1964).

The Agulhas Current shows considerable seasonal variation in its rate of flow (Darbyshire 1964) and this is reflected in the sea temperatures recorded from the three cruises. During the summer the current is at its strongest and on the I.G.Y. cruise during February and March, a tongue of warm water with surface temperatures of over 25°C was carried at least as far as the Port Elizabeth line (Figure 1a). Towards winter the current becomes weaker and during the second cruise in May, warm water was not carried as far down the coast and surface temperatures of over 25°C were not found further south than the Bashee River line (Figure 1b). The current is at its weakest in late winter and early spring when the southwestward penetration of warm surface water is still further reduced. During the August cruise the maximum surface temperature recorded was only 21,68°C. This was at the northern edge of the survey area on the Durban line. The lowest surface temperature was 14,99°C recorded at the inshore station of the East London line on this cruise. There appears to have been a local upwelling in the area at the time of the cruise (Figure 1c).

The surface temperatures recorded during the I.G.Y. cruises give a simplified picture of the current, but Bang's (1970) analysis of continuous thermograph records collected simultaneously in three different sectors off the South African coast has shown the complexity of the interactions of the Agulhas Current with the surrounding water masses. There is evidence of fragmentation at the boundaries, with the formation of eddies and tongues of warm water thrusting into the South Atlantic. Of particular interest with regard to the present study is Bang's suggestion that there is an asymmetrical distribution of current speed, with a zone of high current shear, very susceptible to disturbances, on the right of the velocity core. He correlates this with the sporadic occurrence of pockets of inshore upwelling on the northern boundary of the current. Another

feature he described is an intense cyclonic eddy involving the major portion of the current after it has recurved towards the east. There was evidence of upwelling at its centre and he suggests that it probably disintegrates and reforms from time to time. The eddy was in the vicinity of the southern end of the Port Elizabeth line of the I.G.Y. Survey and Zoutendyk (1970) found a patch of high zooplankton density in this area.

The surface temperatures of the three cruises showed clear differences with season and latitude, but isotherms drawn at 100, 200, 300 and 400 m respectively, indicated that these changes were less marked in the lower water masses. At these depths temperatures recorded during the summer cruise were mostly a little lower than those at equivalent positions on the autumn and winter cruises. The 100 m isotherms showed a temperature gradient from the northeast to the southwest, with the water off Durban being slightly warmer than off Port Elizabeth, but below this the isotherms were aligned parallel to the coast between Durban and Port Elizabeth, with the highest temperatures recorded offshore. At 300 and 400 m temperatures were between 11°C and 17°C, within the temperature range of the South Indian Central water mass which lies beneath the Agulhas Current (Darbyshire 1964) and it is probable that below about 200 m Agulhas Current water was replaced by South Indian Central water. On the Plettenberg Bay line, worked during the second and third cruises, temperatures recorded from 200–400 m were an average of 7,6° lower than those at equivalent positions on the Port Elizabeth line. This marked drop was probably due to the preponderance of cool subtropical shelf water off Plettenberg Bay in place of the Agulhas and South Indian Central water off Port Elizabeth. Temperatures at these depths ranged between 5,6° and 7,6° on the second cruise and 8,7° and 10,3° on the third cruise. The higher temperature recorded on the third cruise may have been due to an admixture of South Indian Central water. This is also suggested by the presence of an indicator species of Indian Ocean origin between 200 and 400 m at the same station of the Plettenberg Bay line on this cruise (see discussion of indicator species).

PREVIOUS WORK ON SOUTH AFRICAN EUPHAUSIIDS

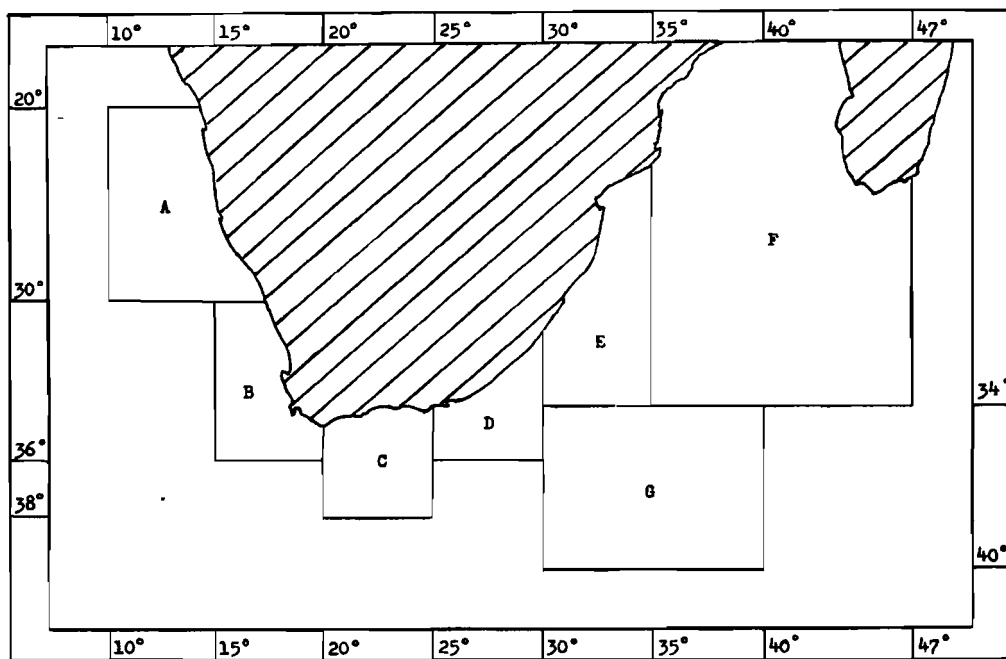
Seven authors have written on euphausiids from the waters around South Africa. Sars (1885) recorded four species collected south of the Cape of Good Hope during the voyage of H.M.S. *Challenger* in 1873. Stebbing (1905 and 1910) reported on nine species from Cape waters and Tattersall (1925) on 12 from the Cape and Natal. Illig (1930) recorded 28 species from material collected by the *Valdivia* expedition in the waters of the western Cape and 12 species from the area south of Port Elizabeth.

The only paper covering the whole South African region was published by Boden (1954). He based it mainly on material collected by the ships of the Discovery Investigation, supplemented by the collection of the Zoology department of the University of Cape Town and material in the British Museum. He described and illustrated 42 species and constructed a key to the euphausiids of the area. Subsequently he published a report on 14 species from the Benguela Current taken during the survey made by the R.R.S. *William Scoresby* off the coast of South West Africa (Boden 1955).

Nepgen (1957) reported on 18 species collected over a two-year period off the west coast of

South Africa during routine cruises of the R.S. *Africana II*. These are all included in Boden's key, but Brinton (1962b) later recorded one of the specimens as belonging to a new species, *Stylocheiron robustum*. The South African Museum conducted a marine survey between 1960 and 1963, using an Isaac-Kidd mid-water trawl to sample bathypelagic animals down to a depth of approximately 500 m. All but a few of the trawls were made at night and the stations were spread over most of the South African region. From the resulting collections Grindley & Penrith (1965) listed 18 euphausiid species. Of these, only *Thysanopoda cristata* is not included in Boden's key.

The 29 euphausiid species collected during the I.G.Y. Survey are also described and keyed by Boden, except for *Stylocheiron microphtalma* which has not previously been taken in South African waters. His key was found to be suitable for the identification of mature adults, but not



Chronological List of Authors

- | | |
|-----------------------------------|---|
| 1. Sars, G. O. 1885 (B). | 6. Boden, B. P. 1954 (A, B, C, D, E, F, G). |
| 2. Stebbing, T. R. R. 1905 (C). | 7. Boden, B. P. 1955 (A). |
| 3. Stebbing, T. R. R. 1910 (B). | 8. Neppen, C. S. de V. 1957 (B). |
| 4. Tattersall, W. M. 1925 (B, E). | 9. Grindley, J. R. & Penrith, M. J. 1965 (B, C, E, F, G). |
| 5. Illig, G. 1930 (B, D). | IGY. Records of the I.G.Y. Survey (C, D, E, F) |

FIGURE 2

The distribution of the euphausiids of the I.G.Y. Survey recorded in South African seas.

Areas investigated in South African seas with list of authors who have recorded euphausiids from these areas.

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TABLE 1
THE DISTRIBUTION OF THE EUPHAUSIIDS IN THE AREAS INVESTIGATED, AS RECORDED BY THE AUTHORS LISTED IN FIGURE 2

	A	B	C	D	E	F	G
	South West Africa	Western Cape	Southern Cape	Eastern Cape	Natal & S. Moçambique	Tropical Indian Ocean	Southern Indian Ocean
<i>Thysanopoda tricuspidata</i>			IGY	IGY	9;IGY	6	
<i>Thysanopoda acutifrons</i>		4;5;9	9	IGY	9;IGY	9	9
<i>Thysanopoda monacantha</i>		3;9	9		9;IGY	6;9	
<i>Thysanopoda aequalis</i>	?6	6	6	6;IGY	6;IGY	?6	?6
<i>Thysanopoda subaequalis</i>					IGY	6	
<i>Thysanopoda orientalis</i>		9		IGY	9	6;9	9
<i>Nyctiphanes capensis</i>	7	6;8	2;IGY	IGY			
<i>Euphausia recurva</i>	7	1;4;5;8;9	IGY	5;IGY	IGY		
<i>Euphausia mutica</i>	?6	5;6;8	6	5;6;IGY	6;IGY	?6	?6
<i>Euphausia brevis</i>		5		IGY	IGY	6	
<i>Euphausia diomediae</i>				5	IGY	6	
<i>Euphausia tenera</i>	6;7	4;5;6	6;IGY	5;6;IGY	6;IGY	6	
<i>Euphausia lucens</i>	7	1;4;6;8;9	IGY	IGY			
<i>Euphausia spinifera</i>		4;5;6	6;9;IGY		9		9
<i>Euphausia paragibba</i>		5;6	6	6	6;IGY	?6	
<i>Euphausia hemigibba</i>		?6	6	6	6;IGY	?6	
<i>Thysanoëssa gregaria</i>	7	1;5;6;8	6;IGY	6;IGY	4;6;IGY	6;9	
<i>Nematoscelis megalops</i>	7	4;6;8;9	6;9	6;IGY	6;9;IGY	6;9	9
<i>Nematoscelis microps</i>		5;6;8	6;IGY	5;6;IGY	4;6;IGY	6	
<i>Nematoscelis tenella</i>		1;5;9	?6	6;IGY	6;IGY	6	
<i>Nematobranchion flexipes</i>	6	5;8;9			IGY		
<i>Stylocheiron carinatum</i>		5;6;8	6;IGY	6;IGY	6;IGY	?6	
<i>Stylocheiron affine</i>	7	5;6;8	6;IGY	5;6;IGY	6;IGY	?6	
<i>Stylocheiron longicorne</i>	6;7	1;5;6;8	6	5;6;IGY	6;IGY	6	
<i>Stylocheiron elongatum</i>	7	5;8	IGY	5;IGY	IGY		
<i>Stylocheiron suhmii</i>		5	IGY	5;?6;IGY	6;IGY	6	
<i>Stylocheiron microphthalmum</i>				IGY	IGY		
<i>Stylocheiron abbreviatum</i>		5;6;8;9	6	5;6	6;9;IGY	6;9;IGY	
<i>Stylocheiron maximum</i>	6;7	4;6;8;9	6;9	6	6;9;IGY	6;9	6;9

for many of the sub-adults and juveniles in the collection. It does not include larval stages. The different areas covered by the above authors are shown in Figure 2 and the recorded occurrence in these areas of the I.G.Y. Survey euphausiids is given in Table 1.

Since this paper was submitted for publication, Brinton & Gopalakrishnan (1973) have produced a study of the distribution of euphausiids in the Indian Ocean which contains data on species off the east coast of South Africa. Thirteen of the I.G.Y. species are figured in their distribution maps and nine of these have tropical or tropical-subtropical distribution ranges which are extended southwards in the region of the Agulhas Current.

SPECIES LIST

		1st Cruise (Feb.-March)	2nd Cruise (May)	3rd Cruise (August)	Total
<i>Thysanopoda tricuspidata</i> Milne-Edwards	2 (1 juv. 1 larva)	32 (10 juvs. 22 larvae)	—	34	
<i>Thysanopoda acutifrons</i> Holt & Tattersall	1 larva	2 juvs.	6 larvae	9	
<i>Thysanopoda monacantha</i> Ortmann	—	1 ♀	1 ♀	2	
<i>Thysanopoda aequalis</i> Hansen ..	7 larvae	13 (6 juvs. 7 larvae)	7 larvae	27	
<i>Thysanopoda subaequalis</i> Boden	—	—	1 ♂	1	
<i>Thysanopoda orientalis</i> Hansen ..	—	—	1 ♀	1	
<i>Nyctiphanes capensis</i> Hansen ..	29 larvae	1 342 (44 ♂, 189 ♀, 103 juvs. 1 006 larvae)	1 816 (586 ♂, 598 ♀, 33 juvs. 599 larvae)	3 187	
<i>Euphausia recurva</i> Hansen ..	38 (1 ♀, 37 juvs.)	34 (14 ♂, 9 ♀, 11 juvs.)	132 (29 ♂, 35 ♀, 68 juvs.)	204	
<i>Euphausia mutica</i> Hansen ..	2 (1 ♂, 1 juv.)	44 (15 ♂, 27 ♀, 2 juvs.)	12 (5 ♂, 6 ♀, 1 juv.)	58	
<i>E. recurva</i> & <i>E. mutica</i> larvae ..	1 097	979	2 609	4 685	
<i>Euphausia brevis</i> Hansen ..	—	18 (8 ♂, 7 ♀, 3 juvs.)	5 (1 ♂, 1 ♀, 3 juvs.)	23	
<i>Euphausia diomediae</i> Ortmann ..	—	1 ♀	—	1	
<i>Euphausia tenera</i> Hansen ..	9 (2 ♂, 1 ♀, 1 juv., 5 larvae)	61 (21 ♂, 13 ♀, 8 juvs., 19 larvae)	32 (2 ♂, 2 ♀, 9 juvs., 19 larvae)	102	
<i>Euphausia lucens</i> Hansen ..	—	6 (2 ♂, 4 ♀)	62 larvae	68	
<i>Euphausia spinifera</i> G. O. Sars ..	—	—	1 larva	1	
<i>Euphausia gibba</i> group:					
<i>Euphausia paragibba</i> , ♂ Hansen	—	1	—	1	

	1st Cruise (Feb.-March)	2nd Cruise (May)	3rd Cruise (August)	Total
<i>Euphausia hemigibba</i> , ♂ Hansen	—	2	1	3
<i>E. paragibba</i> & <i>E. hemigibba</i> , ♀, juvs. & larvae	—	19	12	31
<i>Thysanoëssa gregaria</i> G. O. Sars	10 (4 ♀, 1 juv., 5 larvae)	31 (7 ♂, 9 ♀, 10 juvs., 5 larvae)	353 (9 ♂, 6 ♀, 74 juvs., 264 larvae)	394
<i>Nematoscelis megalops</i> G. O. Sars	2 larvae	9 (3 juvs., 6 larvae)	—	11
<i>Nematoscelis tenella</i> G. O. Sars	—	12 (5 ♂, 2 ♀, 3 juvs.)	9 (7 juvs., 2 larvae)	21
<i>Nematoscelis microps</i> G. O. Sars	92 (18 juvs., 74 larvae)	270 5 ♂, 21 ♀, 168 juvs., 108 larvae)	272 (3 ♂, 18 ♀, 140 juvs., 111 larvae)	634
<i>Nematobranchion flexipes</i> (Ortmann) Calman	—	—	3 ♀	3
<i>Stylocheiron carinatum</i> G. O. Sars	6 (3 ♂, 2 ♀, 1 juv.)	385 (68 ♂, 149 ♀, 112 juvs., 56 larvae)	200 (20 ♂, 59 ♀, 72 juvs., 49 larvae)	591
<i>Stylocheiron affine</i> Hansen ..	1 ♂	49 (6 ♂, 18 ♀, 23 juvs., 2 larvae)	4 (3 juvs. 1 larva)	54
<i>Stylocheiron longicorne</i> G. O. Sars	6 (2 ♂, 2 juvs., 2 larvae)	17 (4 ♂, 3 ♀, 6 juvs., 4 larvae)	17 (3 ♀, 9 juvs., 5 larvae)	40
<i>Stylocheiron elongatum</i> G. O. Sars	2 larvae	4 (2 ♀, 2 larvae)	7 (1 ♂, 2 ♀, 2 juvs., 2 larvae)	13
<i>Stylocheiron suhmii</i> G. O. Sars ..	14 (1 ♂, 2 ♀, 6 juvs., 5 larvae)	44 (7 ♂, 19 ♀, 5 juvs., 13 larvae)	12 (2 ♀, 3 juvs., 7 larvae)	70
<i>Stylocheiron microphthalma</i> Hansen	—	18 (2 ♂, 9 ♀, 4 juvs., 3 larvae)	7 (2 ♀, 3 juvs., 2 larvae)	25
<i>Stylocheiron abbreviatum</i> G. O. Sars	47 (26 juvs., 21 larvae)	111 (1 ♀, 41 juvs., 69 larvae)	84 (3 ♀, 21 juvs., 60 larvae)	242
<i>Stylocheiron maximum</i> Hansen	—	3 (2 ♀, 1 larva)	—	3

NOTES ON TAXONOMY, DEVELOPMENT AND FEEDING

Thysanopoda orientalis

The I.G.Y. material included one female of this species. It was 27 mm in length and carried a pair of small, but distinct postero-lateral denticles on the carapace margin. In *T. orientalis* the lateral denticle is a juvenile character which usually disappears when the animal reaches about

30 mm in length. The use of the presence or absence of this feature in current keys to the genus (Sheard 1942; Boden 1954; Boden, Johnson & Brinton 1955; Mauchline & Fisher 1969), can be misleading with regard to the identification of sub-adults of *T. orientalis*. During an examination of Grindley & Penrith's (1965) collection by the present author, 18 of 21 sub-adults of this species were found to have lateral denticles. These animals were between 26 and 31 mm in length.

The I.G.Y. specimen had the exceptionally small eye and large antennal scale characteristic of the species (Banner 1949). The maximum diameter of the eye is less than 0,8 the width of the first antennular segment and the antennal scale reaches almost to the end of the third antennular segment. The posterior margins of the abdominal terga are very slightly acuminate, particularly on the fourth and fifth segments (Figure 3).

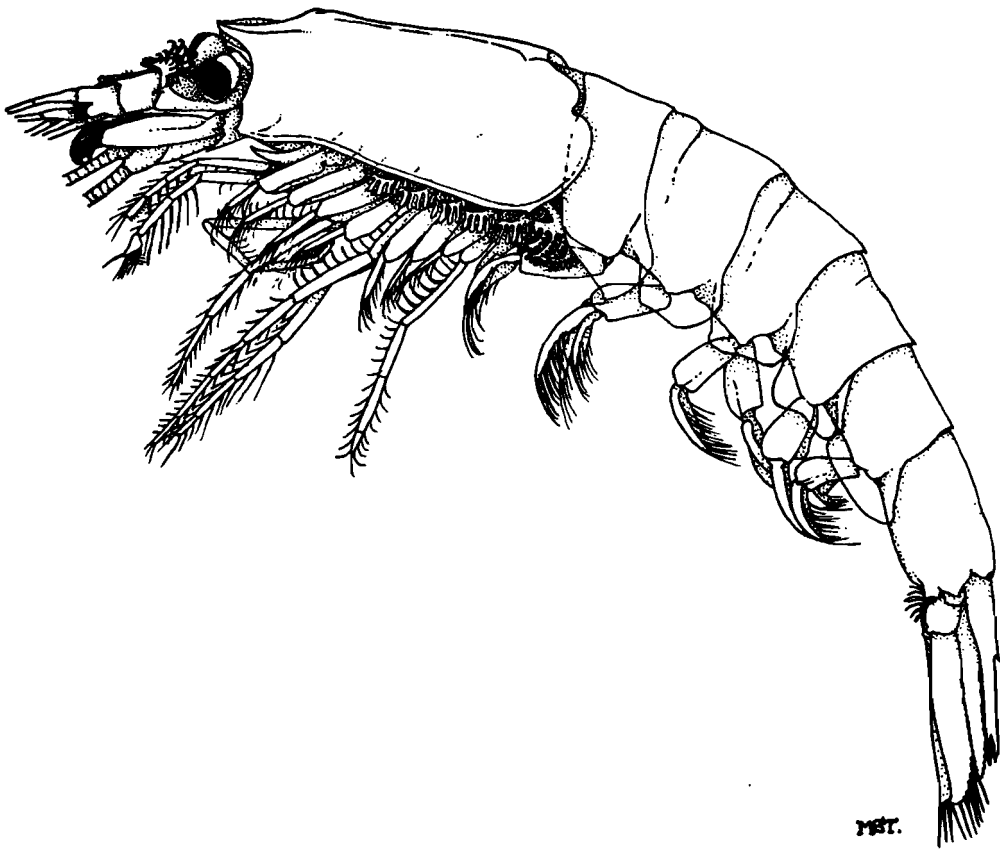


FIGURE 3

Thysanopoda orientalis ♀.

Length, anterior border of eye to end of telson, 27 mm.

Stylocheiron microphthalmalma

S. microphthalmalma has not previously been found in South African waters. It is a tropical Indo-Pacific species morphologically allied to *S. suhmii*, which also occurs in the Indo-Pacific and which is known from South Africa (Illig 1930; Boden 1954). In adult *S. microphthalmalma* there are only two crystalline cones in a transverse row in the upper part of the eye, while in adult *S. suhmii* there are three. However, juveniles of *S. suhmii* may have only two cones per row, and these can be mistaken for *S. microphthalmalma* (Boden, Johnson & Brinton 1955; Brinton 1962a). As most of the I.G.Y. specimens of *S. microphthalmalma* were adult, it was possible to distinguish them positively from *S. suhmii*. Apart from eye structure, the two species differ in that *S. suhmii* is relatively slender, while *S. microphthalmalma* has a more robust appearance, with a characteristically deep sixth abdominal segment. The height to length ratio of the segment was approximately 4:5 in the I.G.Y. *S. microphthalmalma* and 1:2 in *S. suhmii*. In males the species could be separated on the structure of the copulatory organ.

Larvae of Euphausia lucens, E. recurva and E. mutica

The commonest euphausiid captured on all three cruises was a series of larval stages (Figure 4) morphologically similar to a series described by Boden from the Benguela Current. All the late larvae in Boden's collection were accidentally destroyed before he was able to describe them in detail, but he considered he had sufficient evidence to link them with *Euphausia lucens*. Evidence will be presented below, however, which suggests that his series is more likely to belong to *E. recurva* and that the I.G.Y. larvae probably belong to *E. recurva* or *E. mutica*.

E. lucens is a southern temperate species with a distribution lying mainly between the Antarctic and Subtropical Convergences. Its distribution range is extended into unusually low latitudes in the cold waters of the Benguela Current, but it has not been found in the warm Agulhas Current. On the I.G.Y. Survey adults of *E. lucens* were found only on the autumn cruise and these were taken at only one station on the south-western edge of the area, in the cool subtropical water of the continental shelf (Figure 7). In contrast to this, the larval series referred to above was found on all three cruises throughout the area (Figure 6). In view of its extensive distribution in the stream of the Agulhas Current, it seems unlikely that it could belong to *E. lucens*.

Bary (1956) described a different series of larvae from New Zealand waters and he claimed that this series rather than Boden's belongs to *E. lucens*. Larvae of the same type as Bary's were taken on the winter cruise of the I.G.Y. Survey. Like the adults of *E. lucens*, they were found in the cool subtropical water in the southwestern corner of the survey area (Figure 7). Thus, on grounds of distribution, it appears that Bary's interpretation is correct and in this report the larvae corresponding with his description have been ascribed to *E. lucens*.

Among the larvae identified as belonging to Bary's *E. lucens* were three early furcilia stages not recorded in his series (Figure 5 b, c, d). It is possible that the moult pattern in this species is not rigidly fixed and that these represent an alternative series of moults between the third calyptopis stage larva and a furcilia larva with four pairs of setose and one pair of non-setose pleopods. In Bary's larvae the sequence is:

Third calyptopis – length: 2,5 mm.

First furcilia – four pairs non-setose pleopods – length: 3 mm.

Second furcilia – four pairs setose, one pair non-setose pleopods – length: 3,8 mm.

In the larvae of the I.G.Y. *E. lucens* series, it appears that the sequence can in some instances be:

Third calyptopis – length: 2 mm (Figure 5a).

First furcilia – no pleopods – length: 2,3 mm (Figure 5b).

Second furcilia – three pairs non-setose pleopods – length: 2,4 mm (Figure 5c).

Third furcilia – three pairs setose, one pair non-setose pleopods – length: 2,7 mm (Figure 5d).

Late furcilia – four pairs setose, one pair non-setose pleopods – length: 3,7 mm (Figure 5e and Bary's second furcilia).

Assuming that the larval series described by Boden from the Benguela Current does not belong to *E. lucens*, it is most likely that it should be linked with *E. recurva*, as this was the only other species of the genus *Euphausia* which was well represented in the Benguela Current Survey material. Adults of *E. recurva* were caught at offshore stations in both the northern and southern parts of the area and the greatest concentrations of the larvae were found at the southern offshore stations, while the greatest numbers of *E. lucens* were found at the southern inshore stations. Another euphausiid species recorded in large numbers off the west coast of South Africa is *E. similis* var. *armata* (Grindley & Penrith 1965). Its larval stages have not yet been described, but the larvae of the closely related *E. similis* are known (Sheard 1953) and do not resemble Boden's series. It is, therefore, unlikely that the series belongs to *E. similis* var. *armata*.

In the I.G.Y. material the late stages of the larval series show a morphological gradation towards the young juveniles of *E. recurva*, but they are also similar to small juveniles of *E. mutica*. *E. recurva* and *E. mutica* are considered to be closely related. The genus *Euphausia* has been divided into four morphological groups, A, B, C and D (Hansen 1911; John 1936) and *E. recurva* and *E. mutica* are both in Group A. The only members of Group A whose larval stages have been described with certainty are *E. brevis* and *E. krohnii* and their larvae have several features in common. Both, for instance, possess a posterior spine on the carapace in the early stages and both have serrations on the anterior margin of the carapace. These characters are also present in Boden's larval series and the I.G.Y. series.

Two other species, *E. spinifera* and *E. longirostris*, are known to have larvae of this type. Both these species belong to Group D of the genus *Euphausia*. Group D is morphologically closer to Group A than to Groups B and C and may be regarded as an evolutionary offshoot of Group A which has colonized the southern oceans. Groups A and D show affinity in similarities in the armature of their antennae and male copulatory organs and in the fact that they both possess two pairs of lateral processes on the carapace, while Groups B and C have only one. In Group A there is a pair of anterior and posterior lateral denticles, while Group D has posteriorly a pair of lateral denticles and anteriorly, either a pair of hepatic denticles, or a pair of low mound-like projections in the hepatic region. The hepatic processes of Group D are probably homologous to the anterior lateral denticles of Group A.

Although Boden's larvae and the I.G.Y. larval series share features with the larvae of both Group A and Group D, they are much more like the larvae of *E. brevis* than those of *E. spinifera* and *E. longirostris* and thus should probably be placed in Group A. *E. recurva* was the sole representative of Group A in the Benguela Current Survey and, as has already been suggested on other grounds, Boden's larval series appears to belong to this species. In the Agulhas Current

survey area, on the other hand, four species of Group A were found, *E. recurva*, *E. mutica*, *E. brevis* and *E. diomediae*, and it is possible that the I.G.Y. larval series could belong to any of these. *E. diomediae* is an unlikely candidate, however, as only one specimen was taken at the north-eastern edge of the area. The I.G.Y. larvae are very similar to the larvae of *E. brevis*, as described by Gurney (1942) and Lebour (1949), but *E. brevis* is a small species and this applies to the larvae as well as the adults. Lebour gives the length of the third calyptopis stage of *E. brevis* as 1,68 mm, while that of the I.G.Y. larval series was between 2,2 and 2,75 mm and Boden's third calyptopis ranged between 2,1 and 2,33 mm. Apart from the size difference, the distribution of *E. brevis* in the Agulhas Current makes it unlikely that the larval series could belong to it. It was found only in the northern part of the area and was never taken in large numbers.

It has not been possible to decide on morphological grounds whether the larvae belong to one or both of the remaining members of Group A, *E. recurva* and *E. mutica*, but it is probable that most of them should be linked with *E. recurva*. The area of the survey is in the centre of the distribution range of *E. recurva* and, like the larvae, adults of *E. recurva* were present throughout the region on all three cruises. *E. mutica*, in contrast, was probably approaching the southern end of its range in the area. It was less numerous than *E. recurva* and during the autumn and winter cruises it was not found on the southernmost lines. An analysis of the plankton samples, using McConnaughey's (1964) formula for grouping species, showed that the larvae had a positive grouping coefficient with *E. recurva* of 0,12 on the first cruise and 0,19 on the third cruise. With *E. mutica*, on the other hand, they showed a positive correlation of 0,08 on the first cruise only.

Sheard (1953) has given a brief account of some larvae which he considered to belong to *E. recurva*. In these larvae the rostrum was not serrated and there was no dorsal spine on the carapace. He did not illustrate or describe them in detail, but it seems they were not like the known larvae of Group A and should possibly rather be linked with Groups B or C.

Developmental phases of the I.G.Y. larval series

Boden described 10 stages for his larval series, one metanauplius, three calyptopis stages and six furcilia stages, followed by a juvenile phase during which the animal moults several times before reaching the adult condition. The furcilia stages were based chiefly on the emergence of the pleopods and the progressive reduction in the number of spines on the posterior border of the telson. He tabulated the six stages as follows:

<i>Stage 1</i>	<i>Stage 2</i>	<i>Stage 3</i>	<i>Stage 4</i>	<i>Stage 5</i>	<i>Stage 6</i>
Pleopods	Pleopods	Pleopods	Pleopods	Pleopods	Pleopods
non-s. 1	non-s. 4	non-s. -	non-s. -	non-s. -	non-s. -
setose -	setose 1	setose 5	setose 5	setose 5	setose 5
Telson	Telson	Telson	Telson	Telson	Telson
spines 7	spines 7	spines 7	spines 5	spines 3	spines 1
(non-s = non-setose).					

All six of these stages were found in the Agulhas Current larval series, but there are indications that the individual larvae generally go through only five of them. John (1936) has recorded a similar omission of stages in the development of five Antarctic species of the genus *Euphausia*. In the Agulhas Current series it appears that Stage 4 is usually omitted. This means that the larvae moult directly from the third furcilia stage with seven telson spines to the fifth stage with three spines. On all three cruises the total number of Stage 4 furciliars was very much smaller than Stages 3 and 5, as is shown below:

	<i>Stage 3</i>	<i>Stage 4</i>	<i>Stage 5</i>
First cruise	77	6	42
Second cruise	34	4	12
Third cruise	162	8	101
Total	273	18	155

Because a number of these larvae were in a premoult condition, it was possible to see the terminal spines of the next stage beneath the transparent integument of the telson. In 35 of the Stage 3 furciliars developing spines could be distinguished and 30 of them showed the three spines of the fifth stage (Figure 4k). Of the remaining five, two would have developed into a variant of the fifth stage with two terminal spines, while in one large third furcilia larva, 4.4 mm in length, there was a single terminal spine visible beneath the integument of the telson. This larva would, therefore, have moulted directly from the third to the sixth stage. Only two of the third furcilia larvae showed the five developing spines of the fourth stage. There were other variations in the developmental pattern of the late larvae. In four furciliars there were four terminal spines and two had six spines. Among the fourth stage furciliars, a single terminal spine was developing beneath the integument of the telson of four individuals. This indicates that these larvae were in the penultimate stage and would have omitted Stage 5 (Figure 4L). Only one fourth furcilia was found with the three spines of the fifth stage visible. Among the fifth furciliars there were a few with two terminal spines instead of the usual three.

From the above data it appears that, for the majority of larvae, the sequence of moults is: Stage 3 – Stage 5 – Stage 6, but in a few it is Stage 3 – Stage 4 – Stage 6 and on occasional larva may go directly from the third to the sixth stage. Hardly any seem to go through all six furcilia stages. It is perhaps possible that the most common moult sequence, i.e. Stage 3 – Stage 5 – Stage 6, represents the normal developmental pattern of *E. recurva* and that the sequence, Stage 3 – Stage 4 – Stage 6 is that of the less numerous *E. mutica*, but, as no other morphological differences were discernible, the two different patterns could not be traced through to the juvenile stages.

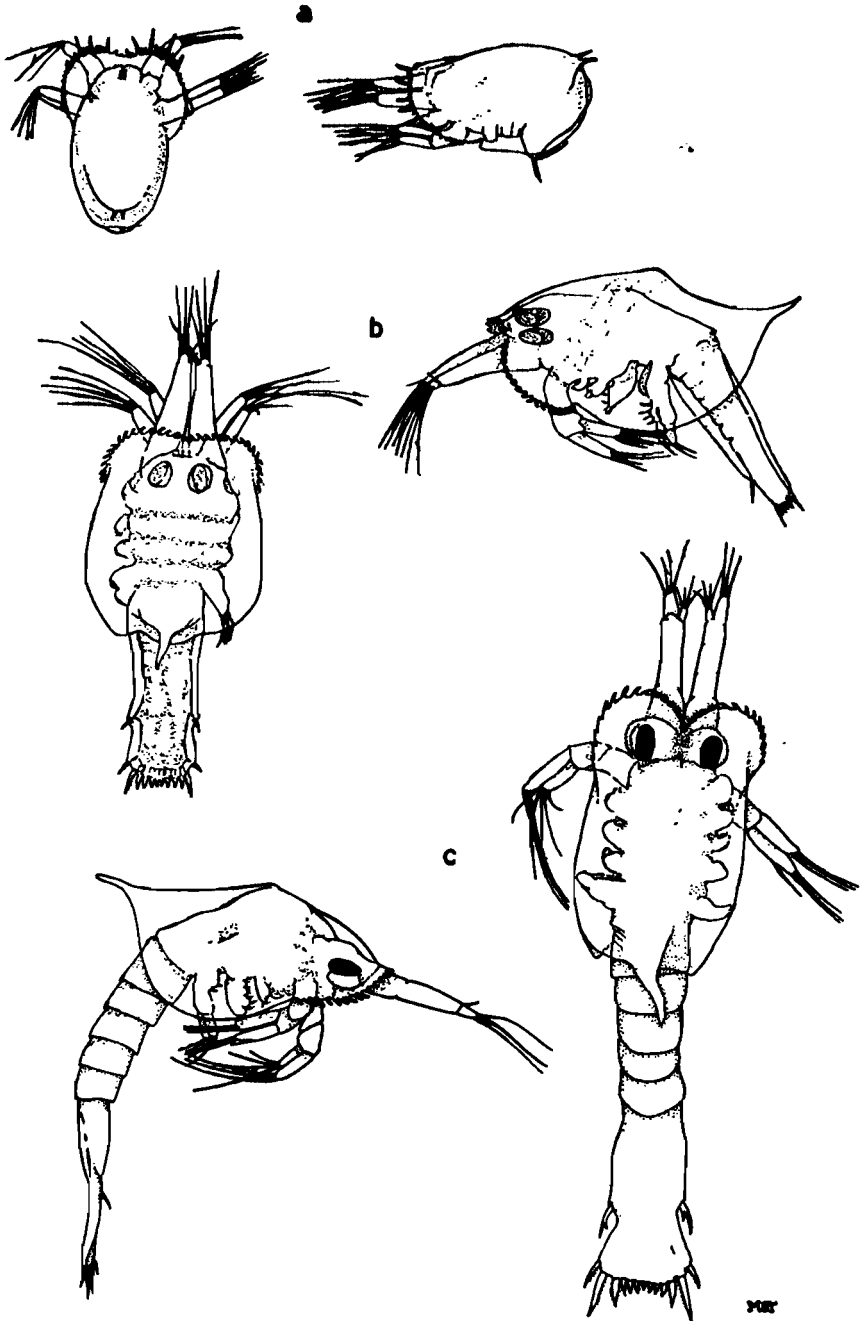


FIGURE 4
Euphausia recurva, *E. mutica* larval series.

- (a) Metanauplius. Length, 0.5 mm.
 (b) First calyptopsis stage. Length, anterior border of rostrum to end of telson, 1,1 mm.
 (c) Second calyptopsis stage. Length, anterior border of rostrum to end of telson, 1,6 mm.

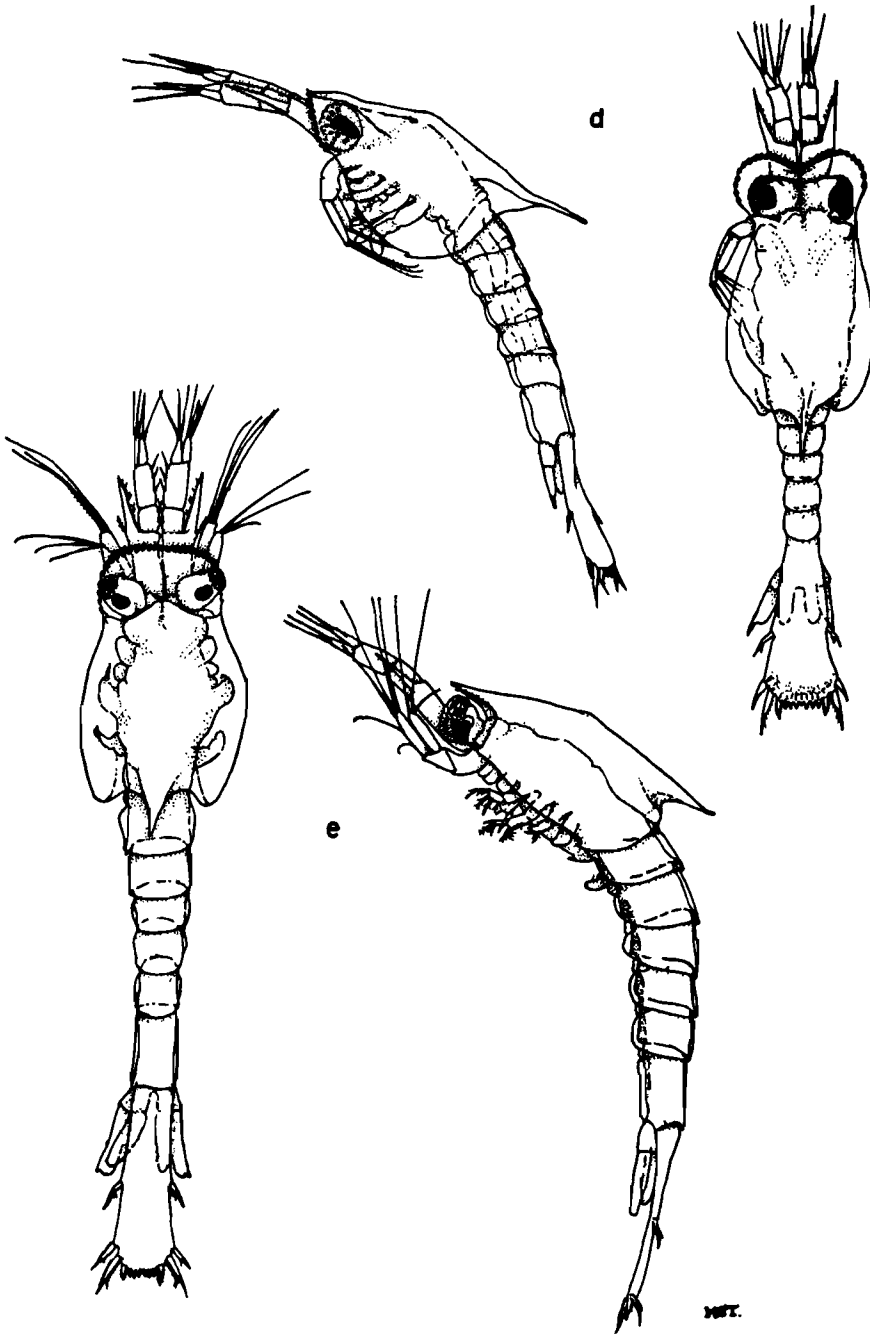


FIGURE 4 (continued)

- (d) Third calyptopis stage. Length, anterior border of rostrum to end of telson, 2,5 mm.
 (e) First furcilia stage. Length, anterior border of rostrum to end of telson, 3,0 mm.

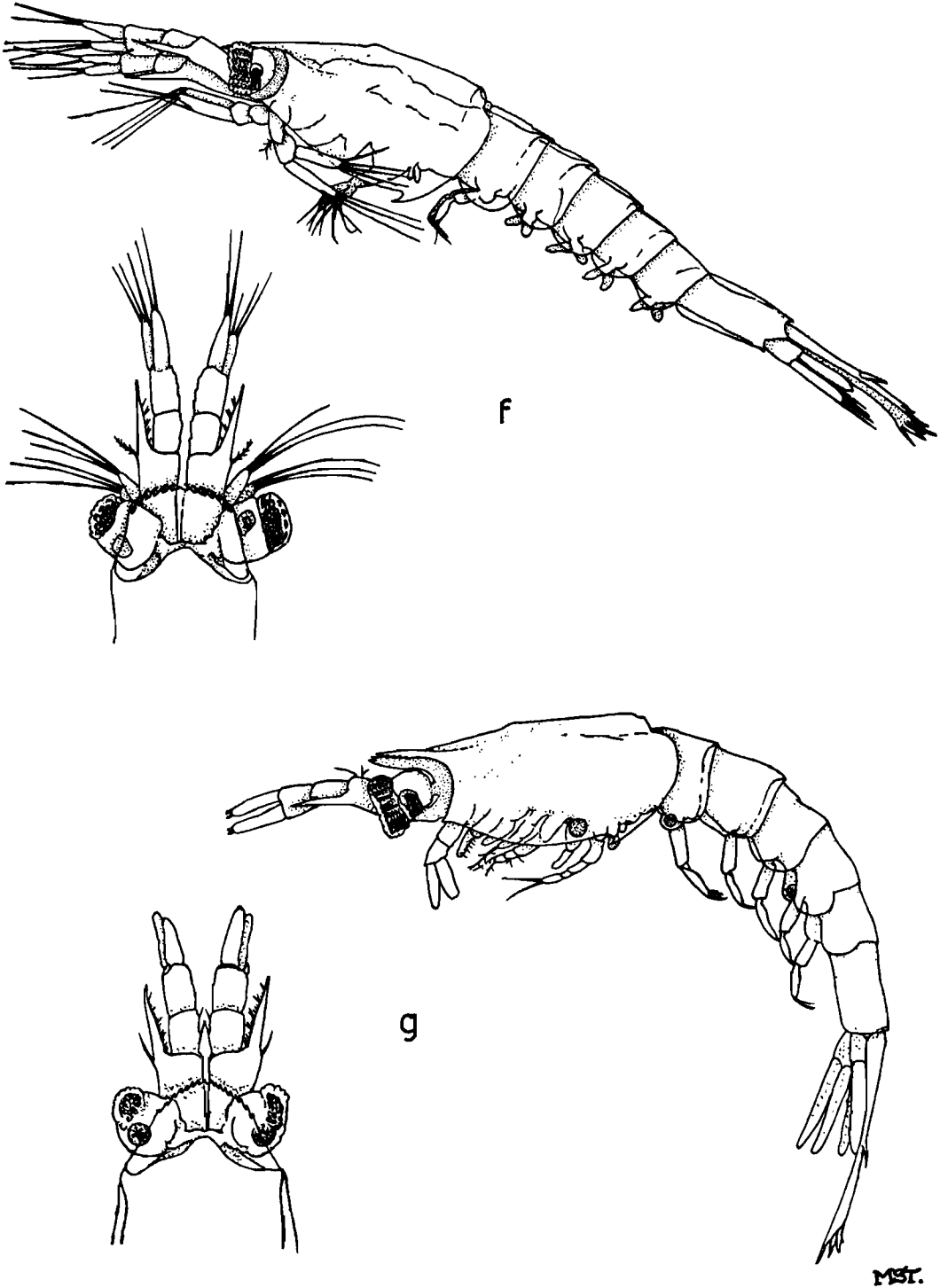
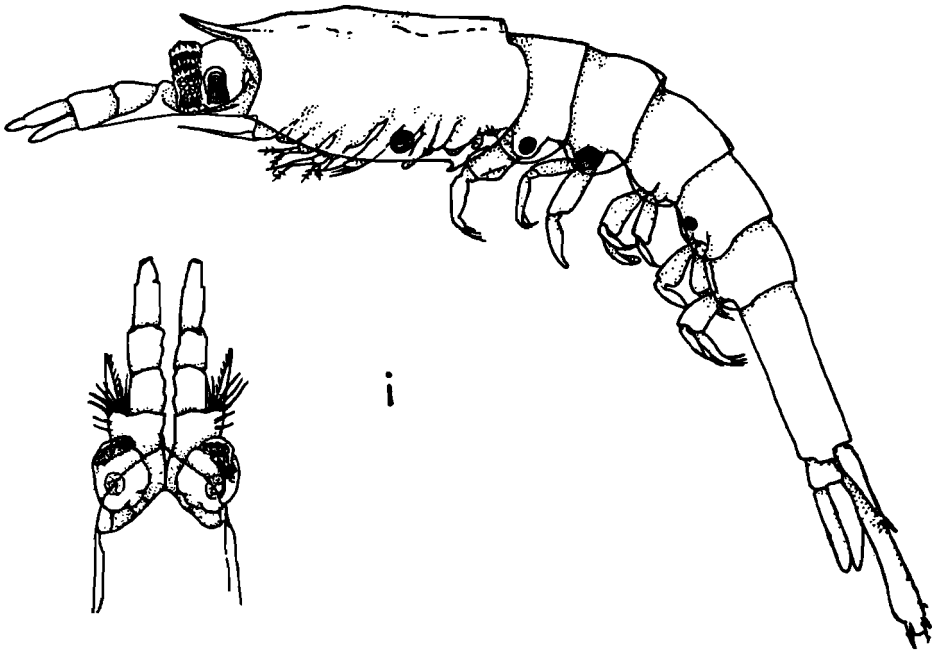
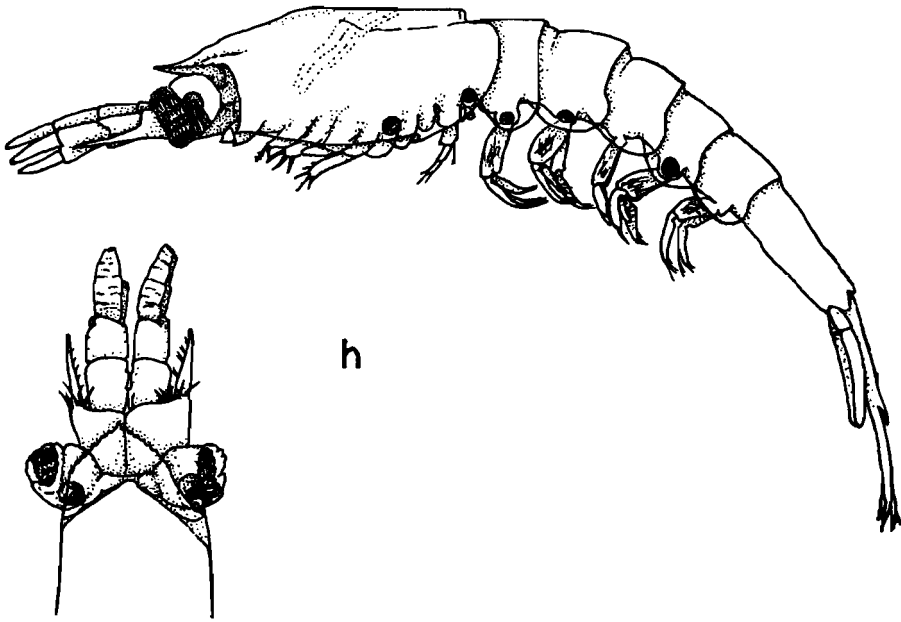


FIGURE 4 (continued)

- (f) Second furcilia stage. Length, anterior border of eye to end of telson, 3,2 mm. (Telson similar to first furcilia stage telson).
- (g) Third furcilia stage. Length, anterior border of eye to end of telson, 3,4 mm. (For telson, see figure 4 k).

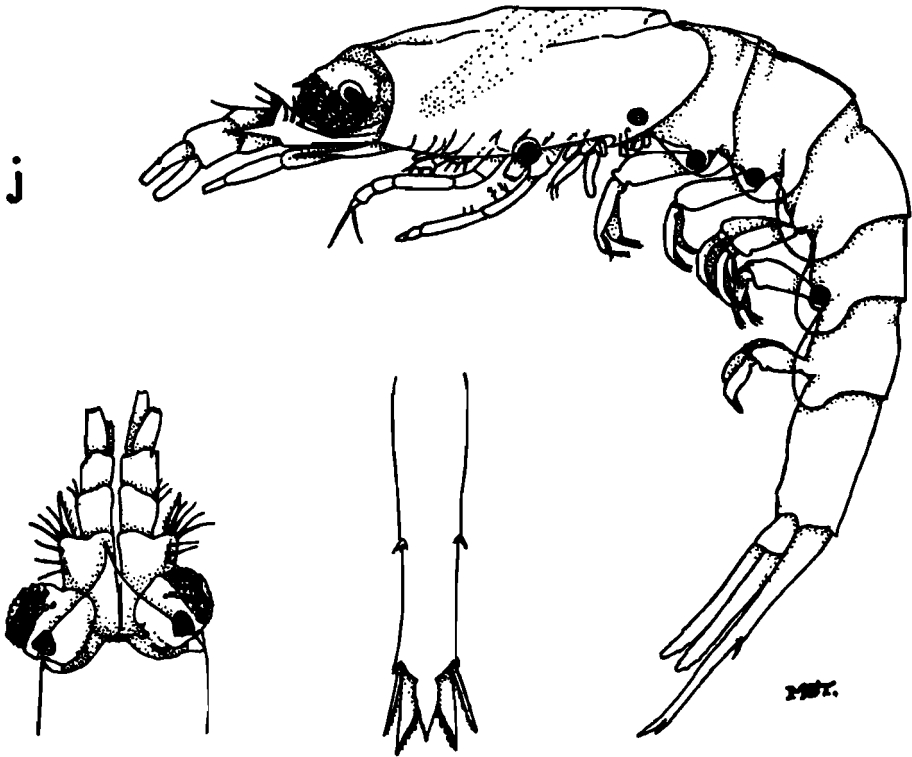
MSI.



MST.

FIGURE 4 (continued)

- (h) Fourth furcilia stage. Length, anterior border of eye to end of telson, 3,4 mm. (For telson, see figure 4 l).
- (i) Fifth furcilia stage. Length, anterior border of eye to end of telson, 3,6 mm. (For telson, see figure 4 m).



(j) Sixth furcilia stage. Length, anterior border of eye to end of telson, 4,1 mm.

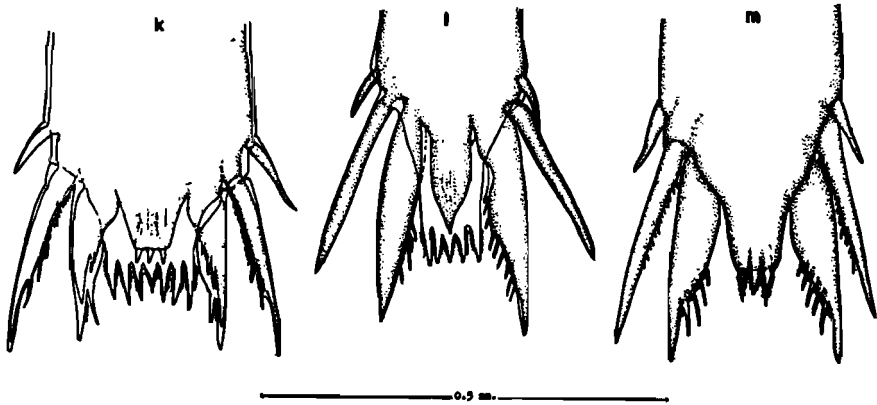


FIGURE 4 (continued)

- (k)** Third furcilia telson.
- (l)** Fourth furcilia telson.
- (m)** Fifth furcilia telson.

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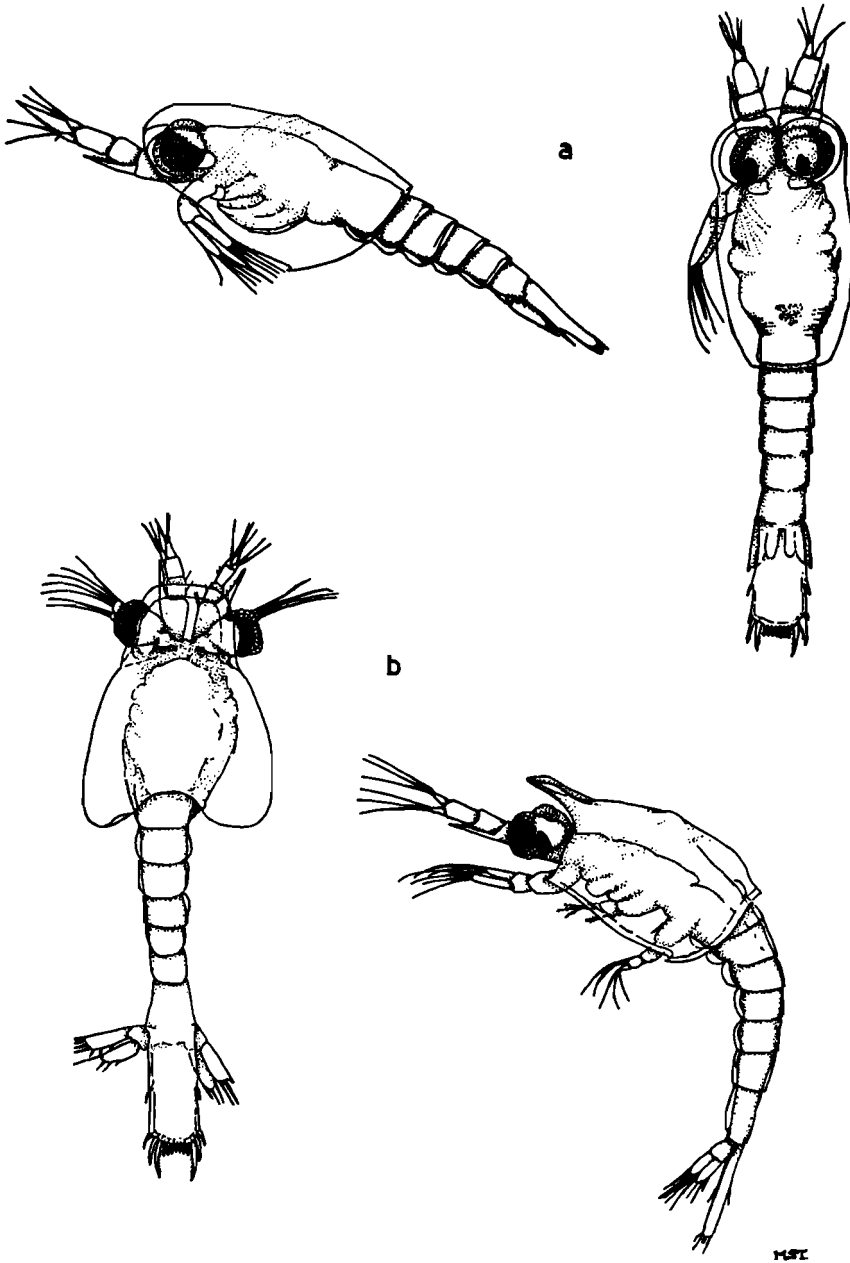


FIGURE 5
Euphausia lucens larvae.

- (a) Third calyptopis stage. Length, anterior border of rostrum to end of telson 2,0 mm.
 (b) First furcilia stage. Length, anterior border of eye to end of telson, 2,3 mm.

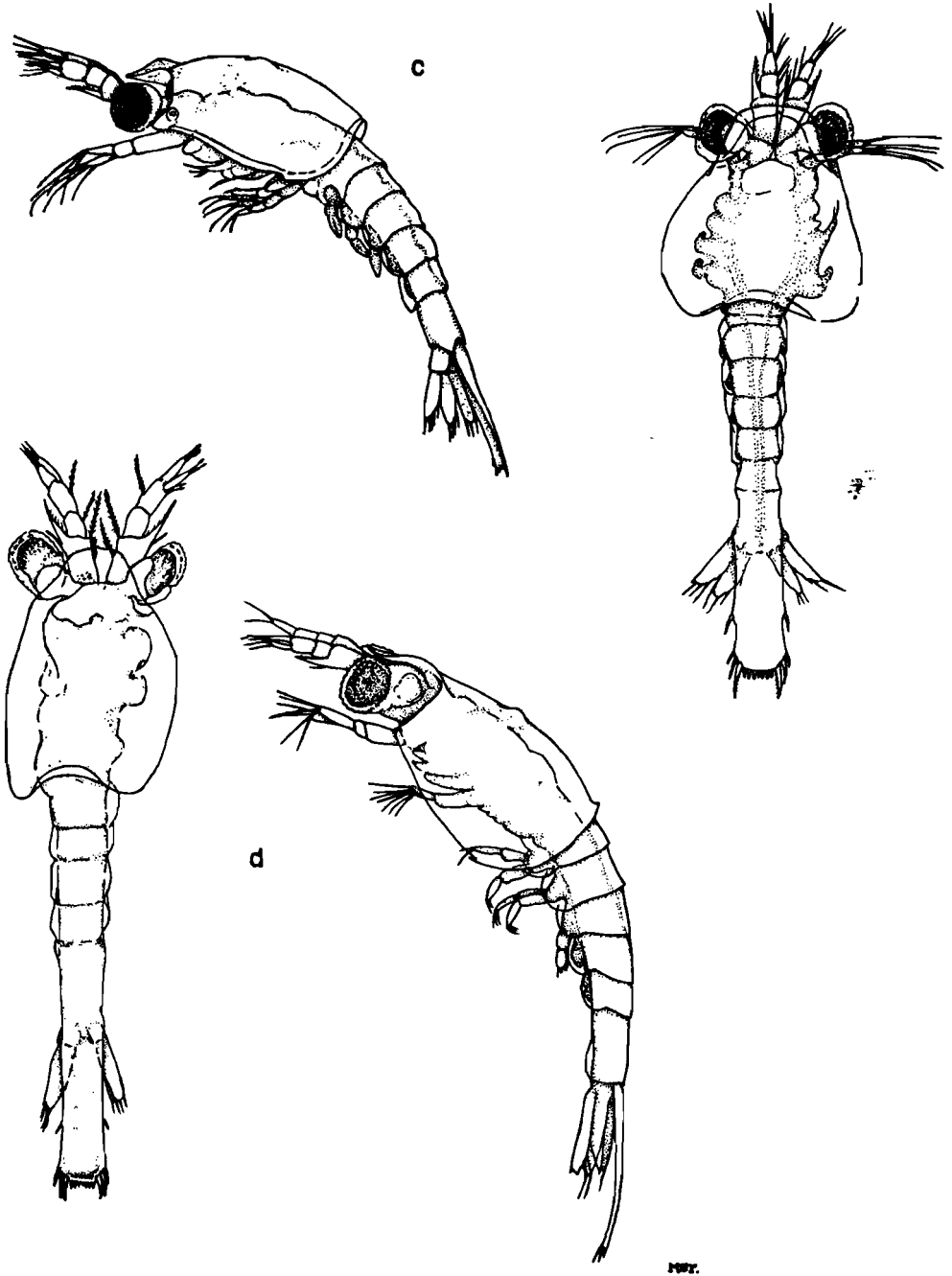


FIGURE 5 (continued)

- (c) Second furcilia stage. Length, anterior border of eye to end of telson, 2,4 mm.
 (d) Third furcilia stage. Length, anterior border of eye to end of telson, 2,7 mm.

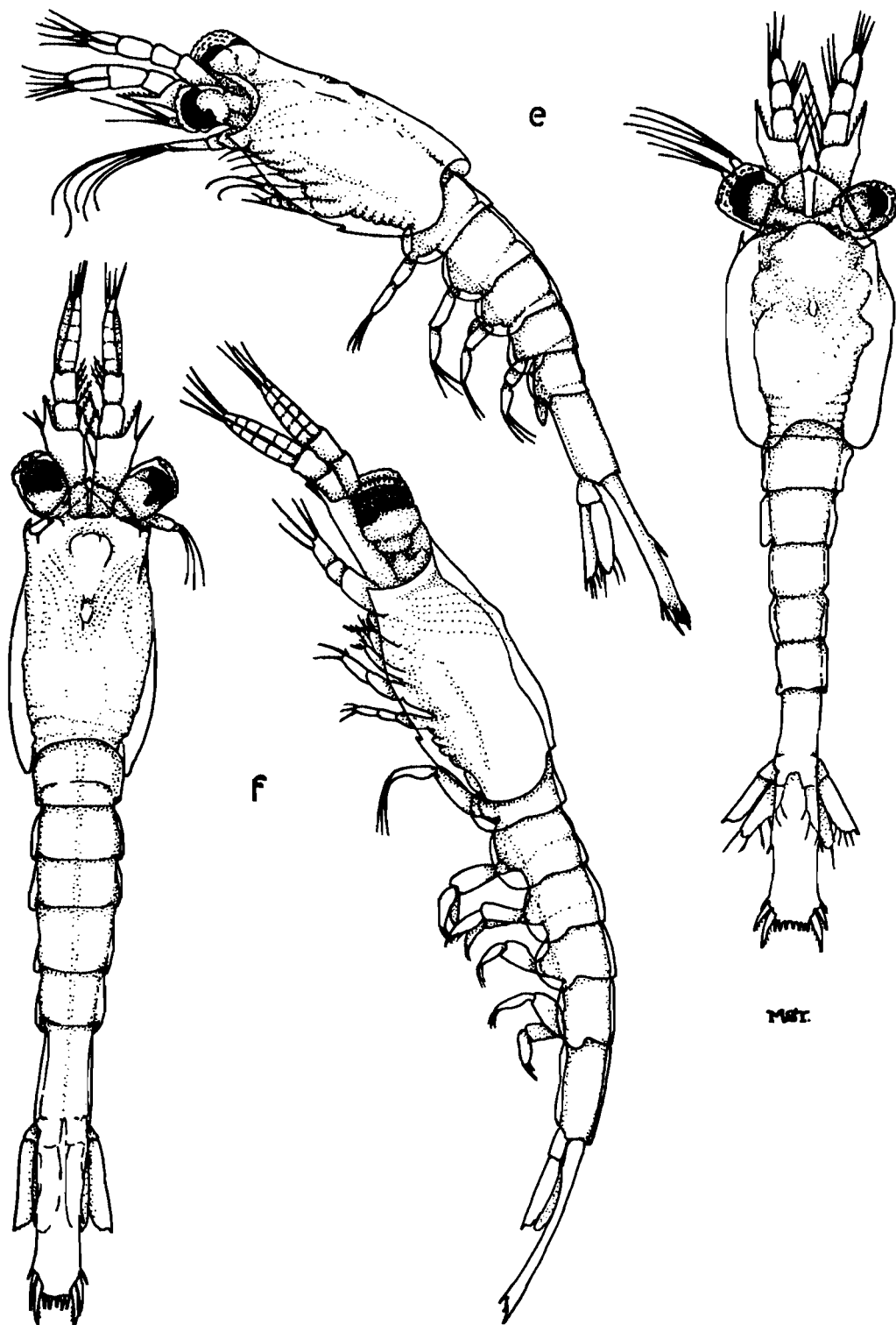


FIGURE 5 (continued)

- (e) Late furcilia stage. Length, anterior border of eye to end of telson, 3,7 mm.
- (f) Late furcilia stage. Length, anterior border of eye to end of telson, 4,3 mm.

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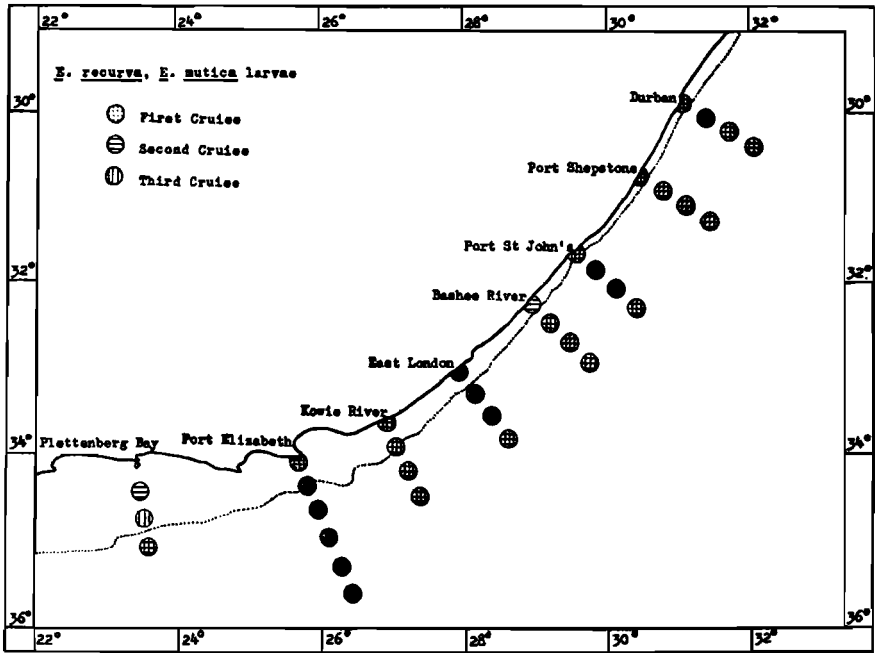


FIGURE 6
Distribution of the larval series ascribed to *Euphausia recurva* and *E. mutica* in the I.G.Y. Survey area.

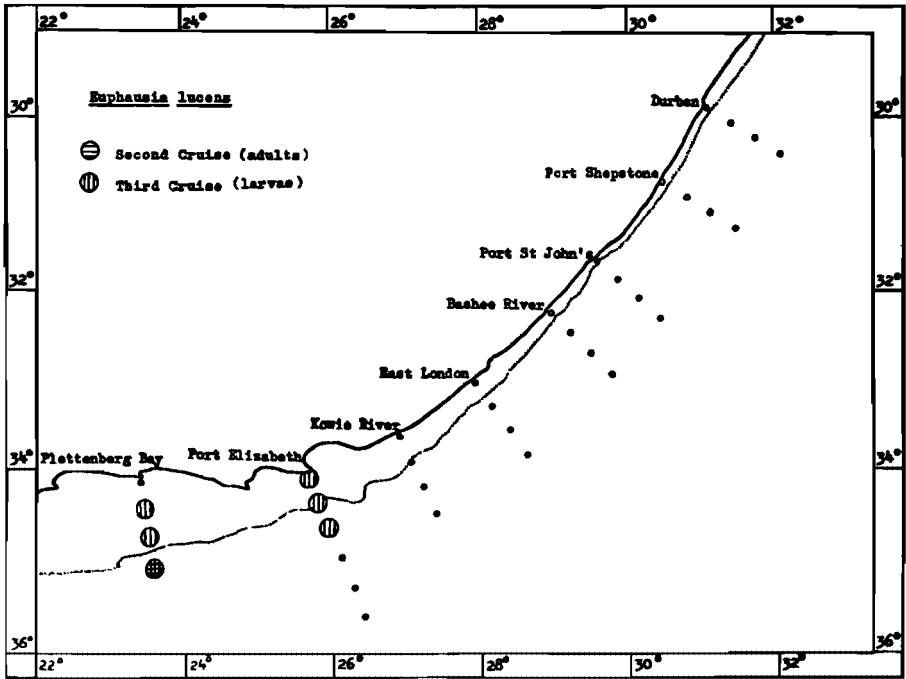


FIGURE 7
Distribution of *Euphausia lucens* in the I.G.Y. Survey area.

Gravid females in the genus Stylocheiron

In seven of the eight species of the genus *Stylocheiron* taken during the I.G.Y. Survey, a proportion of the females had the thorax conspicuously distended by a few mature eggs which filled the enlarged ovaries. They were not found on the first cruise in February and March and they were more numerous on the second cruise in May than the third in August. The maturation of the eggs in these specimens appears to coincide with the slowing down of the Agulhas Current in autumn and may be correlated with enrichment due to the increased admixture of subtropical water. The number of females in prespawning condition is listed below for each species.

		Gravid ♀s	Total ♀s
<i>S. carinatum</i> (3-7 eggs in ovary, diameter, 0,5-0,8 mm)	Second cruise	5	149
	Third cruise	3	22
<i>S. affine</i> (4-8 eggs in ovary, diameter, 0,5 mm)	Second cruise	10	18
	Third cruise	—	—
<i>S. longicorne</i> (eggs 0,5 mm in diameter)	Second cruise	—	3
	Third cruise	1	3
<i>S. elongatum</i> (3 eggs in ovary)	Second cruise	1	4
	Third cruise	—	2
<i>S. suhmii</i> (6-10 eggs in ovary, diameter, 0,5-0,7 mm)	Second cruise	6	17
	Third cruise	1	2
<i>S. microphthalma</i> (eggs 0,5-0,7 mm in diameter)	Second cruise	1	9
	Third cruise	1	2
<i>S. abbreviatum</i>	Second cruise	—	1
	Third cruise	—	3
<i>S. maximum</i>	Second cruise	1	2
	Third cruise	—	—

Feeding in Nyctiphanes capensis

In five hauls from the August cruise of the I.G.Y. Survey there were a number of euphausiids which appear to have been feeding at the time they were captured. The hauls were made in the upper water layers at Stations 78, 79, 83 and 84 and except for 17 larvae of the *Euphausia recurva*, *E. mutica* type, all the animals which had been feeding belonged to *Nyctiphanes capensis*. The *E. recurva*, *E. mutica* larvae were taken at Station 83 with 67 adults and larvae of *N. capensis* which were also feeding, but the greatest concentration of feeding *N. capensis* was found at Station 78, the innermost station on the East London line. Here, 991 adults were taken in a mid-afternoon surface haul and in nearly every specimen, the oesophagus and crop were packed with an amorphous green substance, presumably algal in origin. In most of them the hind-gut was also full. This mass of feeding *N. capensis* may be correlated with the presence of a body of cold water which appears to have been welling up along the coast in the East London area at the time of the winter cruise (Figure 1c).

Apart from the 17 *E. recurva*, *E. mutica* larvae mentioned above, *N. capensis* was the only euphausiid species from the I.G.Y. Survey in which food was apparent in the gut.

SPECIES DISTRIBUTION

Thysanopoda tricuspidata MILNE-EDWARDS

First Cruise (February–March), Stations 7, 13.

Second Cruise (May), Stations 19, 20, 23, 25, 27, 28, 32, 34, 38, 39, 40, 45, 46, 50.

This widely distributed tropical species has not been found in the waters off the west coast of southern Africa, but it has twice been taken off the east coast. Boden (1954) recorded it from the straits of Moçambique and Grindley & Penrith (1965) collected it off Durban in an Isaac-Kidd mid-water trawl. In the present survey it was found only on the first and second cruises. Thirty-four specimens were collected and all were either juveniles or larvae.

Vertical distribution: All the specimens, bar one, were found in the upper 150 m of water. The exception was a third calyptopis stage larva (the only calyptopis of this species which was found), which was caught off Durban at Station 20 between 400 and 200 m.

Horizontal distribution: The stations at which *T. tricuspidata* was taken were all in the main stream of the Agulhas Current with surface temperatures of over 20°C. On the second cruise it was taken on the most westerly line off Plettenberg Bay at Station 50. This record extends its known westward distribution in the Agulhas Current from 31° E to 23° 27' E (Table 1).

Thysanopoda acutifrons HOLT & TATTERSALL

First Cruise (February–March), Station 10.

Second Cruise (May), Stations 20, 27.

Third Cruise (August), Stations 64, 68, 74, 79.

T. acutifrons has a temperate distribution in the Pacific and Atlantic Oceans. It has been recorded from South African waters by Tattersall (1925), Illig (1930), Boden (1954) and Grindley & Penrith (1965). Seven furcilia larvae and two juveniles identified as *T. acutifrons* were taken on the I.G.Y. Survey. The larvae correspond with Frost's (1939) description of the larval stages of this species.

Vertical distribution: Five of the specimens were found between 400 and 200 m and the rest between 200 m and the surface.

Horizontal distribution: *T. acutifrons* was caught in the central and north-eastern areas of the survey. It was not found at inshore stations.

Thysanopoda monacantha ORTMANN

Second Cruise (May), Station 20.

Third Cruise (August), Station 70.

T. monacantha is known to occur in tropical and temperate waters in all three oceans. It has been recorded from South Africa by Stebbing (1910), Boden (1954) and Grindley & Penrith (1965), who took it off both east and west coasts. On the I.G.Y. Survey two immature females of this species were caught, one on the second cruise and one on the third.

Vertical distribution: The first specimen was taken between 200 and 100 m and the second between 150 m and the surface.

Horizontal distribution: Both were in the north-eastern part of the survey area, the first on the outermost station of the Durban line and the second on the outermost station of the Port St. John line.

Thysanopoda aequalis HANSEN

First Cruise (February–March), Stations 9, 12, 13.

Second Cruise (May), Stations 19, 20, 24, 26, 28, 35, 46.

Third Cruise (August), Stations 59, 60, 64, 72, 77, 80.

T. aequalis is widely distributed in the tropical and subtropical waters of the Atlantic, Indian Ocean and southern and north-eastern Pacific. Boden (1954) found it in South African waters. Twenty-seven larvae and juveniles assigned to this species were found during the I.G.Y. Survey. They occurred on all three cruises. These young forms agree with Lebour's (1926) description of *T. aequalis* larvae, but it is possible that some of them may belong to *T. subaequalis*, a closely related species, whose larvae have not been distinguished from those of *T. aequalis*. The I.G.Y. specimens were widely distributed in the survey area, however, and this makes it more likely that they belong to *T. aequalis*, as the latter is known to occur throughout most of the South African region (Boden 1954). *T. subaequalis*, on the other hand, has, as yet, been found only in the Straits of Moçambique, apart from a single male taken off Durban during the I.G.Y. Survey.

Vertical distribution: Twenty specimens were caught in the upper 150 m, four between 200 and 100 m and three between 400 and 200 m.

Horizontal distribution: They were found throughout the area of the survey on each cruise, usually at stations towards the centre of the current (Figure 10).

Thysanopoda subaequalis BODEN

Third Cruise (August), Station 62.

T. subaequalis was described by Boden (1954) from the Straits of Moçambique. It has since been found in the tropical and subtropical waters of the Indian Ocean, the Atlantic and southern and north-western Pacific. One male which can be definitely assigned to this species was found on the third cruise of the I.G.Y. Survey. It was 17.5 mm in length and sufficiently mature for the

dactylus of the third cormopod to be modified in the manner characteristic of the species (Boden & Brinton 1957).

Vertical position: between 400 and 200 m.

Horizontal position: the outermost station of the Durban line.

Thysanopoda orientalis HANSEN

Third Cruise (August), Station 79.

T. orientalis occurs in the tropical and subtropical regions of all three oceans and has been found in the waters off the western Cape coast and off Natal by Grindley & Penrith (1965) and in the Straits of Moçambique by Boden (1954).

The only specimen in the I.G.Y. material was a female, taken on the winter cruise.

Vertical position: between 400 and 200 m.

Horizontal position: the outermost station of the Kowie River line.

(See Figure 3 and note on taxonomy in previous section.)

Nyctiphanes capensis HANSEN

First Cruise (February–March), Stations 8, 11, 12, 14.

Second Cruise (May), Stations 37, 38, 41, 42, 43, 47, 48, 49, 50.

Third Cruise (August), Stations 71, 72, 73, 78, 79, 80, 81, 82, 83, 84, 85, 89, 90, 91, 92.

The genus *Nyctiphanes* consists of four species which are unusual among euphausiids in that they are all shallow-water neritic forms with limited geographical ranges. They are associated with near-shore waters in regions of transition between warm and cold currents and are also a conspicuous element of the plankton where coastal upwelling is a characteristic feature (Brinton 1962a). The centre of distribution of *N. capensis* is in the comparatively cool water of the south-west and west coastal regions of South Africa. Nepten (1957) found it in large numbers at inshore stations off the western Cape coast and Boden (1955) also found it further north along the west coast at the shelf stations of the Benguela Current Survey. It has been reported off Cape St. Blaize by Stebbing (1905) and from southern Cape coastal waters generally by Boden (1954). *N. capensis* was taken on all three cruises of the I.G.Y. Survey, although in far greater numbers on the second and third cruises in autumn and winter than on the first cruise in summer. On the summer cruise only 29 larvae were taken, while on the autumn and winter cruises, over 1 000 adults and larvae were collected per cruise.

Vertical distribution: Like the other members of the genus, *N. capensis* is found almost exclusively in the upper water layers. Of the 3 187 specimens taken on the I.G.Y. Survey, only two larvae were caught below 200 m, while 1 387 adults and larvae were captured in horizontal hauls at the surface. Five of these surface hauls were taken in the early morning between 0700 h and 0800 h and they caught an average of 30 animals per haul. The remainder were taken later in the day between 0925 h and 1550 h. and these caught an average of 159 per haul. This suggests that *N. capensis* does not tend to migrate downwards away from the surface during the middle of the day. Boden's table showing numbers of this species taken in vertical hauls during the Benguela Current Survey reveals a similar tendency for the animals to occur in the upper layers (Boden 1955).

Horizontal distribution: The species was largely confined to the cool waters of the south-western part of the survey area (Figure 8). The continental shelf is wide here and this is probably an important factor contributing to the abundance of *N. capensis* in the region. It was found at all stations on the Plettenberg Bay line and was also present at the innermost three stations of the Port Elizabeth line on all three cruises. On the first cruise it was found as far to the north-east as the inshore station of the East London line (Figure 8a). Its occurrence here may be linked with the presence of a counter current. Such currents are frequently to be found in the area, flowing inshore of the Agulhas Current in a north-easterly direction, following the line of the coast (Clowes 1950). During the August cruise when the warm Agulhas Current did not penetrate as far south as in the summer months, the distribution of *N. capensis* extended northwards to reach the Bashee River line (Figure 8c). The I.G.Y. Survey extended the known distribution of this species into the coastal waters of the eastern Cape (Table 1).

Distribution of ovigerous females: In the genus *Nyctiphanes* the eggs are carried in a sac attached to the posterior cormopods of the female. Only two samples of the I.G.Y. Survey contained *N. capensis* females carrying eggs. On the second cruise there were 26 females with ruptured egg-sacs at Station 37 (Figure 8b). Eggs and early larvae were also present in the sample. On the third cruise at Station 71 there were 34 females, most of which had ruptured egg-sacs (Figure 8c). About 100 eggs, approximately 0,5 mm in diameter were again present. It is interesting that in both cases the mature females with eggs were found at inshore stations towards the northern limit of the range of *N. capensis*. If the occurrence of ovigerous females in this type of situation is a regular phenomenon, it could be of significance in maintaining the geographical distribution of the species. In the enriched mixed waters over the continental shelf, maturing juveniles and adults would tend to be carried northwards by the inshore counter current. This would probably have been the situation at Station 84, the innermost station of the Port Elizabeth line on the third cruise, where 25 immature males and 43 small females were found. In the ovaries of 35 of the females there were developing eggs 0,2–0,3 mm in diameter. As the maturing adults are carried northwards, the warmer temperatures encountered might induce spawning and the resulting young larvae eventually released from the egg-sacs of the females would tend to be swept south again by the Agulhas Current. By means of this clockwise circulation the position of the species on the southern continental shelf would be maintained. With the limited information as yet available on *N. capensis* in the I.G.Y. Survey area, the scheme outlined above cannot be more

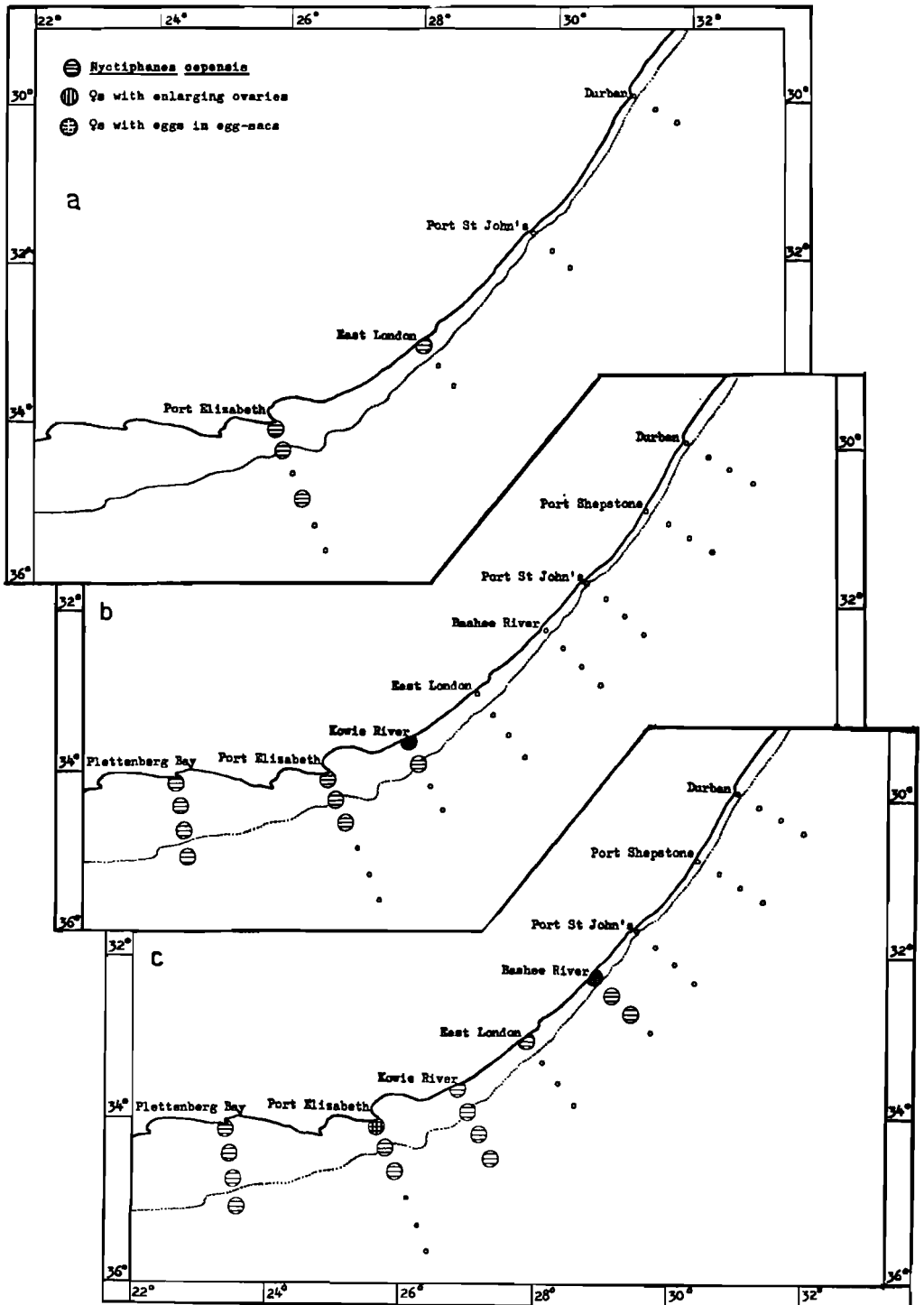


FIGURE 8
 The distribution of *Nyctiphanes capensis* on the three I.G.Y. cruises.
 (a) First cruise, February-March.
 (b) Second cruise, May.
 (c) Third cruise, August.

than a speculative suggestion. It does, however, point to the need for a more prolonged and detailed study of the biology and distribution of this interesting species in eastern Cape coastal waters.

* * *

It has not been possible to separate the larvae of *Euphausia recurva* from those of the closely related *E. mutica* (see preceding section). The distribution of the larvae of these two species will therefore be considered together, after their adults and juveniles have been discussed separately.

Euphausia recurva HANSEN

First Cruise (February–March), Stations 3, 7, 10, 12, 13, 14, 15, 16.

Second Cruise (May), Stations 18, 23, 24, 28, 32, 35, 36, 39, 40, 45, 46, 50.

Third Cruise (August), Stations 60, 61, 62, 64, 68, 69, 70, 72, 73, 75, 76, 78, 79, 80, 81, 86, 87, 89.

E. recurva has a wide distribution in the subtropical and temperate waters of the Pacific, South Atlantic and southern Indian Oceans. In the South African region it is known to occur off both the east and west coasts of the Cape. Illig (1930) caught it in large numbers off Port Elizabeth, Nepgen (1957) and Grindley & Penrith (1965) found it west of the Cape Peninsula and Boden (1955) found it off the west coast in the waters of the Benguela Current. *E. recurva* was present on all three cruises of the I.G.Y. Survey and its known eastward distribution was extended into the waters off Natal (Table 1). There was some evidence that it was breeding in the north-eastern part of the area, since most of the adult females captured between Durban and East London carried spermatophores.

Vertical distribution: It was found at all depths between 400 m and the surface. Approximately half the specimens were taken below 200 m.

Horizontal distribution: This species was fairly evenly distributed throughout the whole area. During each cruise adults and juveniles occurred in small numbers on every line of the survey, although only one of the 204 specimens taken was found at an inshore station, all the others occurring at stations further out in the stream of the current.

Euphausia mutica HANSEN

First Cruise (February–March), Stations 9, 15.

Second Cruise (May), Stations 20, 21, 22, 24, 25, 26, 28, 35.

Third Cruise (August), Stations 60, 61, 68, 72, 75, 76, 79, 80, 81.

E. mutica occurs in the tropical and subtropical zones of all three oceans. In the southern Indian Ocean its distribution overlaps with the closely related *E. recurva*, but it does not extend as far south as the latter species which is known to occur south of the subtropical convergence (Boden 1954, Figure 24). Illig (1930) found *E. mutica* off the western Cape and off Port Elizabeth,

Boden (1954) reported it as plentiful in the South African region and Neppen (1957) recorded one female in his survey of western Cape coastal waters. On the I.G.Y. Survey 58 adults and juveniles were taken. Fourteen of the females carried spermatophores, an indication of breeding in the area.

Vertical distribution: They occurred at all depths between 400 m and the surface. One third of the specimens were taken below 200 m.

Horizontal distribution: During the summer cruise *E. mutica* was caught at two southern stations, but on the autumn and winter cruises, it was not found as far south as the Port Elizabeth line.

LARVAE OF *Euphausia recurva* AND *E. mutica*

First Cruise (February–March), Stations 3, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16.

Second Cruise (May), Stations 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 42, 43, 44, 45, 46, 48, 50.

Third Cruise (August), Stations 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90.

The series of larvae (Figure 4), considered to belong to *E. recurva* and/or *E. mutica* was abundant on all three cruises of the I.G.Y. Survey.

Vertical distribution: The larvae were present throughout the water column between 400 m and the surface. The table below gives the percentages of the catch from vertical hauls at 400–200 m, 200–100 m and 100–0 m for each cruise:

	400–200 m	200–100 m	100–0 m
First cruise	27,5 %	38,5 %	34,0 %
Second cruise	25,5 %	34,4 %	40,1 %
Third cruise	29,6 %	44,8 %	25,6 %

It shows that approximately one quarter of the larvae were taken between 400 and 200 m on all three cruises. The proportions in the upper layers at 200–100 and 100–0 m also showed only a moderate amount of variation during the period of the survey.

Horizontal distribution: The numbers of larvae fluctuated along each line of the survey in a fairly consistent pattern. At the inshore stations they were usually absent, or present in very small numbers. At the next series of stations their numbers rose to a maximum, but were reduced again at the third series to a very low figure. They then usually increased to some extent at the outermost stations. Their distribution suggests that conditions are more favourable for the larvae at the periphery than at the relatively impoverished centre of the Agulhas stream. On each cruise of the I.G.Y. Survey the larvae were particularly numerous on the Port Elizabeth line.

This increase in numbers may be related to the widening of the continental shelf and the increased admixture of shelf water with Agulhas Current water in this region.

Euphausia brevis HANSEN

Second Cruise (May), Stations 20, 23, 24, 26, 27, 35.

Third Cruise (August), Stations 68, 72, 75.

E. brevis is known from the tropical and subtropical regions of all three oceans. In the Indian Ocean it has been found as far south as 34° 14' S by Illig (1930), who also recorded it off Cape Town. On the I.G.Y. Survey it was not taken south of the East London line which lies between 33° S and 34° S. Eighteen specimens were caught on the second cruise and five on the third.

Vertical distribution: Of the 23 specimens taken, 10 were found between 400 and 200 m and the remainder above 200 m.

Horizontal distribution: Twelve specimens of *E. brevis* were caught at Station 20, the outermost station of the Durban line on the second cruise. They included three females carrying spermatophores. The other 11 specimens were also found in the northern part of the survey area, but usually as single specimens from samples taken in the centre of the current.

Euphausia diomediae ORTMANN

Second Cruise (May), Station 20.

E. diomediae has a widespread distribution within the tropics in the Pacific and Indian Oceans, but it has not been taken in the Atlantic (Brinton 1962a; Baker 1965). In South African waters it was taken off Port Elizabeth by Illig (1930) and it was encountered by Boden (1954) in the north-eastern part of the region. Only one specimen, an immature female, was caught during the period of the I.G.Y. Survey.

Vertical position: between 400 and 200 m.

Horizontal position: the north-eastern edge of the survey area at the outermost station of the Durban line.

Euphausia tenera HANSEN

First Cruise (February–March), Stations 5, 7, 9, 12.

Second Cruise (May), Stations 18, 20, 21, 23, 24, 25, 26, 28, 30, 31, 34, 35, 36, 38, 40, 43, 44, 50.

Third Cruise (August), Stations 59, 60, 61, 64, 72, 74, 75, 76, 79, 80, 81, 87, 89.

This species has an extensive range in the tropical and subtropical waters of all three oceans. It has been reported off the western Cape by Tattersall (1925) and Illig (1930) who also found it off Port Elizabeth. Boden (1954) found it in all but the southernmost part of the South African region and it was present on each of the three cruises of the I.G.Y. Survey. Out of a total of 102 specimens, 33 were larvae. These were of the same order of size as the *E. tenera* larvae described by Lebour (1949) and much smaller than those which Boden (1955) linked with this species. Nine of the 16 females captured were carrying spermatophores attached to the thelycum.

Vertical distribution: *E. tenera* was taken at all depths from 400–0 m. The fraction of the total taken below 200 m was approximately 0,4 on the first and third cruises and 0,2 on the second cruise.

Horizontal distribution: It was present in small numbers throughout the area on each cruise.

Euphausia lucens HANSEN

Second Cruise (May), Station 50.

Third Cruise (August), Stations 83, 84, 85, 89, 90, 91.

The distribution of *E. lucens* is restricted to the southern oceans where it is found in temperate regions. It is a dominant species in the cold waters of the western Cape region and the Benguela Current (Boden 1955; Neppen 1957). On the I.G.Y. Survey it was taken only during the autumn and winter cruises and its known distribution was extended into the waters of the eastern Cape region on the latter cruise (Table 1).

Vertical distribution: All the specimens were taken in the upper water layers between 150 m and the surface.

Horizontal distribution: *E. lucens* was found in the southwestern part of the survey area (Figure 7). On the second cruise six adults were caught at the outermost station of the Plettenberg Bay line and on the third cruise a total of 62 larvae were taken on the Port Elizabeth and Plettenberg Bay lines. (Larval identification is discussed in the preceding section and the larvae are illustrated in Figure 5.)

Euphausia spinifera G. O. SARS

Third Cruise (August), Station 89.

This is a southern subtropical-temperate species which occurs in all three oceans and is known from the South African region (Tattersall 1925; Illig 1930; Boden 1954; Grindley & Penrith 1965). A single larva identified as *E. spinifera* was taken on the third I.G.Y. cruise (Figure 9).

Vertical position: between 100 m and the surface.

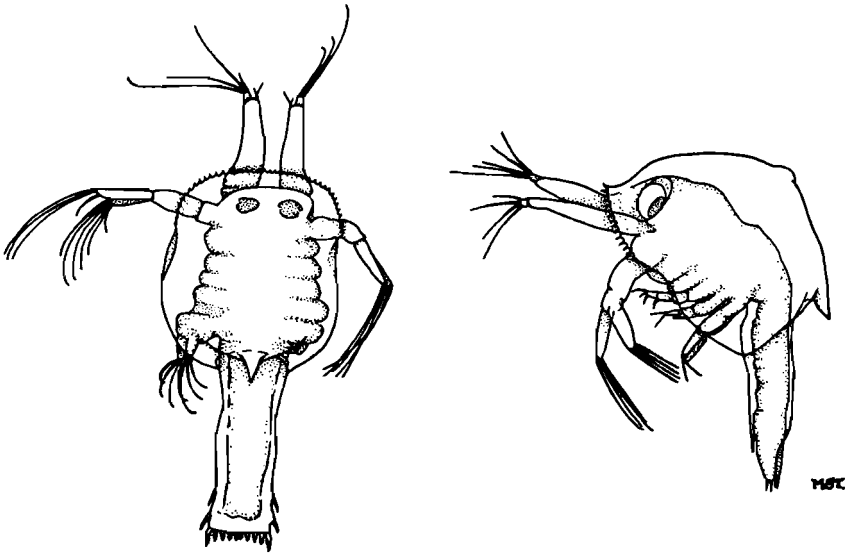


FIGURE 9
Euphausia spinifera, first calyptopsis stage larva.
 Length, anterior border of rostrum to end of telson, 1.0 mm.

Horizontal position: the outermost station of the Plettenberg Bay line which is at the southwestern edge of the survey area.

Euphausia paragibba HANSEN and *Euphausia hemigibba* HANSEN

Second Cruise (May), Stations 20, 21, 22, 24, 27, 28, 35.

Third Cruise (August), Stations 59, 60, 62, 68, 75.

E. paragibba and *E. hemigibba* belong to a group of morphologically similar species, known as the "*Euphausia gibba* group" (Brinton 1962a). The structure of the male copulatory organ is diagnostic for each of these species, but females and immature specimens have not been reliably separated. As almost all of the I.G.Y. specimens were juveniles and could not be distinguished with certainty, these two species will be considered together.

Both *E. paragibba* and *E. hemigibba* are found in all three oceans, but *E. paragibba* has a distribution which lies mostly within the tropics, while *E. hemigibba* is tropical and subtropical (Brinton 1962a; Baker 1965). Both are known to occur in the South African region (Boden 1954). During the I.G.Y. Survey a total of 35 were taken on the second and third cruises.

Vertical distribution: They were found at all depths sampled, with approximately one third of the total being captured between 400 and 200 m, and the rest between 200 m and the surface.

Horizontal distribution: They appeared to be restricted to the north-eastern part of the area, as they were not found south of the East London line. One adult male taken off Port Shepstone at station 24 could definitely be identified as *E. paragibba* and three females in the same sample probably also belong to this species. However, as the area of the survey is at the limit of *E. paragibba*'s known latitudinal range, most of the other specimens probably belong to *E. hemigibba*. It was possible to make a positive identification of three males belonging to this species, two at Station 28 off Port St. John on the second cruise and one at Station 62 off Durban during the third cruise.

Thysanoëssa gregaria G. O. SARS

First Cruise (February–March), Stations 12, 13, 14.

Second Cruise (May), Stations 20, 26, 27, 28, 30, 31, 45, 46, 50.

Third Cruise (August), Stations 59, 60, 62, 64, 65, 66, 67, 69, 70, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 83, 85, 86, 87, 88, 89.

T. gregaria has a widespread temperate distribution in the north and south Atlantic and Pacific Oceans and in the southern Indian Ocean. Sars (1885) and Illig (1930) found it in western Cape waters and Tattersall (1925) off Natal, Boden (1954) records it as occurring throughout the South African region and Grindley & Penrith (1965) report it from the south-west Indian Ocean. Off the west coast of South Africa Nepgen (1957) found *T. gregaria* regularly in small numbers during every month of the year over a two-year period. It was most abundant at offshore and southern stations and very scarce at northern inshore stations. Although *T. gregaria* was taken on all three cruises of the I.G.Y. Survey, by far the greatest number of specimens was caught on the winter cruise. On the first and second cruises adults accounted for half the number of specimens, but the great increase on the third cruise was made up of larvae and juveniles.

Vertical distribution: Of the 394 specimens taken, only 14 were between 400 and 200 m. The rest were all in the upper water layers between 200 m and the surface.

Horizontal distribution: On the first cruise only 10 individuals were found and these were all in the southern part of the area on the Port Elizabeth line. On the second cruise small numbers were caught throughout the area, usually at offshore stations, 31 specimens being taken in all. On the third cruise *T. gregaria* was found on every line, at 25 of the 34 stations and a total of 353 specimens was taken. The distribution pattern was similar to that reported by Nepgen (1957) in that specimens were found at few stations on the continental shelf, but the species was invariably present at the outer station of each line.

Nematoscelis megalops G. O. SARS

First Cruise (February–March), Station 13.

Second Cruise (May), Stations 18, 19, 23, 44, 45, 46.

This species is known from tropical and subtropical areas of the Atlantic and Indian Oceans and occurs throughout the South African region (Tattersall 1925; Boden 1954 and 1955; Nepgen 1957; Grindley & Penrith 1965). Eleven immature individuals were collected during the first and second I.G.Y. cruises.

Vertical distribution: They were all caught in the upper water layers between 200 m and the surface.

Horizontal distribution: On the first cruise two were taken at the southern end of the survey area on the Port Elizabeth line and on the second cruise a few were caught off Durban and Port Shepstone as well as off Port Elizabeth.

Nematoscelis tenella G. O. SARS

Second Cruise (May), Stations 20, 23, 27, 31.

Third Cruise (August), Stations 76, 77, 80, 85, 86, 88.

N. tenella has a tropical and subtropical distribution and is known from all three oceans. Sars (1885) and Illig (1930) found it south of Cape Town, Boden (1954) reported it from the south and east of the South African region and Grindley & Penrith (1965) collected it west of the Cape Peninsula. A few individuals belonging to this species were taken on the second and third cruises of the I.G.Y. Survey.

Vertical distribution: One female was caught between 400 and 200 m, but all the other specimens were collected in the upper water layers, from 150–0 m.

Horizontal distribution: On the second cruise 12 specimens were found in the north-eastern quarter of the survey area and on the third cruise nine were taken further south.

Adult males of *N. tenella* taken from the Pacific Ocean have been found to be morphologically distinct from those of the Atlantic. Males from the Atlantic carry a lateral denticle on the lower border of the carapace, but the denticle is missing in males from the Pacific (Boden, Johnson & Brinton 1955). The adult males from the Agulhas Current also lack the denticle. This points to a closer affinity with the Pacific than the Atlantic stock.

Nematoscelis microps G. O. SARS

First Cruise (February–March), Stations 3, 4, 5, 6, 7, 9, 10, 12, 13, 14, 15, 16.

Second Cruise (May), Stations 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 30, 31, 32, 34, 35, 36, 38, 39, 40, 43, 44, 45, 46, 49, 50.

Third Cruise (August), Stations 59, 60, 63, 64, 65, 66, 68, 69, 70, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 85, 86, 87, 88, 89.

N. microps occurs in tropical and subtropical areas of all three oceans. Tattersall (1925)

reported it off Natal, Illig (1930) off the south-west Cape and Port Elizabeth, Boden (1954) found it throughout the South African region and Nepgen (1957) recorded a few individuals off the west coast of the Cape. *N. microps* was one of the commonest species collected during the I.G.Y. Survey. Although it was never caught in large numbers, it was present at most stations on all three cruises.

Vertical distribution: Although it was caught at all depths between 400 m and the surface, *N. microps* usually occurred in the upper water layers. Only 45 of the 634 specimens were taken below 200 m.

Horizontal distribution: *N. microps* was seldom found on the continental shelf, but it was caught at every offshore station, except two. The largest concentrations of this species were always on the Port Elizabeth lines.

Nematobranchion flexipes (ORTMANN) CALMAN

Third Cruise (August), Stations 62, 64, 68.

The distribution of *N. flexipes* is mainly tropical and subtropical. It has been previously caught in South African waters, but only in the western part of the region (Illig 1930; Boden 1954; Nepgen 1957; Grindley & Penrith 1965). Three damaged immature females identified a *N. flexipes* were found on the third I.G.Y. cruise.

Vertical distribution: Two were taken at 400–200 m and the third at 200–100 m.

Horizontal distribution: One caught on each of the three northern lines.

Stylocheiron carinatum G. O. SARS

First Cruise (February–March), Stations 4, 7, 12, 13, 16.

Second Cruise (May), Stations 17, 18, 19, 20, 21, 22, 23, 24, 26, 27, 28, 29, 30, 31, 32, 34, 35, 36, 38, 39, 40, 42, 43, 44, 45, 46, 49, 50.

Third Cruise (August), Stations 60, 61, 62, 65, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 79, 80, 85, 86, 87, 88, 90.

S. carinatum has a widespread distribution mainly in tropical and subtropical areas of all three oceans. Boden (1954) reported it throughout most of the South African region and Illig (1930) and Nepgen (1957) found it in western Cape coastal waters. On the I.G.Y. Survey *S. carinatum* was one of the most frequently occurring of the euphausiid species.

Vertical distribution: In the Agulhas Current this species showed a tendency to concentrate in the upper water layers, similar to that described by Brinton (1962a) for *S. carinatum* in the Pacific. He found that most of the Pacific population was above 140 m at all times of day. On the I.G.Y.

Survey only 18 of the 591 specimens were taken in hauls which sampled below 200 m and all the others were collected between 200 and 0 m.

Horizontal distribution: Although never taken in large numbers, *S. carinatum* was present at almost all the offshore stations, particularly on the second and third cruises. It was rare at inshore stations, however, and only 11 individuals were collected on the continental shelf.

Stylocheiron affine HANSEN

First Cruise (February–March), Station 6.

Second Cruise (May), Stations 18, 19, 20, 22, 23, 26, 31, 32, 34, 36, 38, 44, 45, 46, 49, 50.

Third Cruise (August), Stations 69, 72.

S. affine has an extensive range, chiefly in tropical and subtropical parts of all three oceans. It is known to occur in most of the South African region and a few were taken off the west coast by Illig (1930), Boden (1955) and Neppen (1957). Illig also found it off Port Elizabeth. On the I.G.Y. Survey 54 specimens were collected, mostly during the autumn cruise.

Vertical distribution: This species is known to frequent the upper water layers (Brinton 1962 a) and only four of the I.G.Y. specimens were caught below 200 m.

Horizontal distribution: On the first cruise one individual was found off Port St John, but on the second, *S. affine* was taken in small numbers throughout the region. It was picked up on every line of this cruise, although it was never found at inner stations on the continental shelf. On the third cruise only four specimens were taken, two off Port St. John and two on the Bashee River line.

Stylocheiron longicorne G. O. SARS

First Cruise (February–March), Stations 4, 10, 14.

Second Cruise (May), Stations 19, 27, 28, 35, 39, 43, 44, 46.

Third Cruise (August), Stations 64, 65, 66, 68, 76, 78, 80, 82, 86.

This species has a wide geographical range in tropical, subtropical and temperate areas in all three oceans. Boden (1954) states that it occurs over the whole South African region, Sars (1885), Illig (1930) and Neppen (1957) collected it off the western Cape coast and Illig found it off Port Elizabeth. On each of the I.G.Y. cruises *S. longicorne* was taken in small numbers.

Vertical distribution: In the Pacific the greater part of the *S. longicorne* population is known to occur below 140 m during both day and night (Brinton 1962a). Although most of the I.G.Y. sampling was done in the upper water layers, nearly half (17 out of a total of 40) of the *S. longicorne* specimens was collected below 200 m.

Horizontal distribution: The species was found throughout the area, except in the extreme west on the Plettenberg Bay line.

Stylocheiron elongatum G. O. SARS

First Cruise (February–March), Station 7.

Second Cruise (May), Stations 20, 24, 35, 36.

Third Cruise (August), Stations 60, 61, 70, 74, 80, 89.

S. elongatum has an extensive scattered distribution in the Pacific and is also widespread in the Atlantic and Indian Oceans (Brinton 1962a). Illig (1930) reported it from the South African region and both Boden (1955) and Neppen (1957) found a small number of larvae off the west coast. On each of the I.G.Y. cruises a few individuals of this species were caught and its known distribution has been extended into the region off Natal (Table 1).

Vertical distribution: Boden, Johnson & Brinton (1955) report *S. elongatum* as occurring below 300 m in the North Pacific and the I.G.Y. specimens show a similar depth distribution, in that all but two of the 13 collected were from deep hauls between 200 and 400 m.

Horizontal distribution: *S. elongatum* was taken throughout the survey area, usually at outer stations.

Stylocheiron suhmii G. O. SARS

First Cruise (February–March), Stations 4, 7, 10.

Second Cruise (May), Stations 18, 19, 20, 22, 23, 26, 28, 30, 31, 32, 35, 38, 40, 44, 45, 46.

Third Cruise (August), Stations 59, 62, 68, 69, 72, 85, 86, 88, 89.

This species has a tropical and subtropical distribution in all three oceans. Illig (1930) found three females in the western part of the South African region and one off Port Elizabeth and Boden (1954) reported it as occurring only sparsely in the eastern part. During the I.G.Y. Survey, however, *S. suhmii* was found on every cruise, although it was always taken either singly, or in very small numbers.

Vertical distribution: It was almost always in the upper water layers. Out of a total of 70 specimens, only two were collected below 200 m.

Horizontal distribution: It occurred in both the northern and southern parts of the survey area, but was almost invariably missing from inshore stations. Only one larva, taken off Durban on the third cruise, was found at a station on the continental shelf. The other specimens were all caught offshore.

Stylocheiron microphthalma HANSEN

Second Cruise (May), Stations 18, 19, 20, 22, 23, 26, 28, 31, 35.

Third Cruise (August), Stations 70, 72, 76, 77, 88.

S. microphthalma is a tropical Indo-Pacific species which has not previously been found in South African waters. A total of 25 specimens was taken on the second and third I.G.Y. cruises. (The identification of *S. microphthalma* is discussed in the preceding section.)

Vertical distribution: All the specimens were in the upper water layers above 200 m.

Horizontal distribution: They were all at offshore stations. The majority were caught in the north-eastern half of the survey area, between the Durban and East London lines, but on the third cruise two larvae probably belonging to this species were found in the southern part at the outermost station of the Port Elizabeth line.

Stylocheiron abbreviatum G. O. SARS

First Cruise (February–March), Stations 8, 9, 10, 13, 14, 15, 16.

Second Cruise (May), Stations 18, 19, 20, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 34, 35, 36, 40, 43, 44, 45, 46.

Third Cruise (August), Stations 59, 61, 62, 64, 65, 68, 69, 70, 72, 73, 74, 75, 76, 79, 80, 81, 85, 87, 88.

S. abbreviatum occurs in all three oceans and has been found in most parts of the South African region. Illig (1930), Neppen (1957) and Grindley & Penrith (1965) collected it west of the Cape Peninsula, Illig found it off Port Elizabeth and Grindley & Penrith took it in the waters off Natal. On the I.G.Y. cruises 238 larvae and juveniles and four adults belonging to *S. abbreviatum* were taken.

Vertical distribution: *S. abbreviatum* did not appear to have a restricted vertical distribution, as specimens were regularly found in both the lower water layers between 400 and 200 m and the upper layers above 200 m.

Horizontal distribution: On the first cruise this species was found in the southern part of the area at each station of the East London line and at all but the two inner stations of the Port Elizabeth line. On the second and third cruises it was collected on every line of the survey except the Plettenberg Bay line at the western edge of the area.

Stylocheiron maximum HANSEN

Second Cruise (May), Station 46.

S. maximum is a mesopelagic species which is rarely found above a depth of 140 m (Brinton 1962a). It has a widespread distribution in all three oceans and occurs throughout the South African region (Tattersall 1925; Boden 1954 and 1955; Neppen 1957; Grindley & Penrith 1965). Three specimens of *S. maximum* were caught on the second I.G.Y. cruise.

Vertical distribution: One individual was taken at 200–100 m and the other two were caught at 400–200 m.

Horizontal distribution: All three were at the outermost station of the Port Elizabeth line.

DISCUSSION ON DISTRIBUTION PATTERNS

Seasonal and latitudinal variation in species distribution

In considering seasonal variations in the distribution of the species of euphausiids in the area of the survey, it must be taken into account that the first cruise in February and March consisted of only 15 stations on four lines, while the second and third cruises in May and August respectively, sampled the area much more intensively. They each consisted of 34 stations arranged in eight lines. The fact that the first cruise yielded only 16 species, as opposed to the 25 species recorded from each of the later cruises, is probably an indication of less adequate sampling on this cruise and it cannot be assumed that the 13 species not found during February and March were in fact missing from the area in summer. The species were *Thysanopoda monacantha*, *T. subaequalis*, *T. orientalis*, *Euphausia brevis*, *E. diomediae*, *E. lucens*, *E. spinifera*, *E. paragibba*, *E. hemigibba*, *Nematoscelis tenella*, *Nematobranchion flexipes*, *Stylocheiron microphthalmum* and *S. maximum*. None of them were abundant on the second and third cruises, most occurring singly, or in very small numbers. Six of these species, *Thysanopoda monacantha*, *T. subaequalis*, *T. orientalis*, *Euphausia diomediae*, *E. spinifera* and *Stylocheiron maximum*, were caught only at the outermost stations of the lines on the second and third cruises. These stations were not worked on the first cruise.

In the case of one species, *Euphausia lucens*, however, it is likely that its absence from the first cruise samples is a valid reflection of a seasonal change in distribution. This southern temperate species is common in the cold waters of the western part of the South African region (Table 1) and it was found only in the south-western section of the I.G.Y. Survey area (Figure 7). On the second cruise it was caught on the Plettenberg Bay line and on the third cruise, in winter, when the Agulhas Current was at its weakest and temperatures were at their lowest (Figure 1c), it reached as far as the Port Elizabeth line. During the summer cruise the strongly flowing current brought a stream of warm tropical water to the southern part of the area (Figure 1a) and this probably shifted the limit of the summer range of *E. lucens* in a westerly direction beyond the region of the survey.

Nyctiphanes capensis is another cold water form restricted to the south-western part of the survey area and its distribution was similarly curtailed during the summer and extended in a north-easterly direction during the winter (Figure 8). *Thysanoëssa gregaria* is a third species which showed an increase on the winter cruise. Its distribution is mainly temperate and it was

found only on the Port Elizabeth line on the first cruise. On the second cruise a few specimens were found as far north as Durban, but on the third cruise it showed a great increase in numbers, mainly in the form of larvae and juveniles, and was caught on every line of the survey.

Of the total of 29 species recorded from the three cruises, four were missing from the second cruise in autumn. These were *Thysanopoda orientalis*, *T. subaequalis*, *Euphausia spinifera* and *Nematobranchion flexipes*. They were all rare species which were caught singly, or in very small numbers on the third cruise only.

Four species were missing from the third cruise, in winter; *Thysanopoda tricuspidata*, *Euphausia diomediae*, *Nematoscelis megalops* and *Stylocheiron maximum*. Of these, *S. maximum* was taken at one station on the second cruise only and *N. megalops* was found in small numbers on both the first and second cruises. The remaining two, *E. diomediae* and *T. tricuspidata* are tropical species which were carried into the area when the Agulhas Current was flowing strongly and were apparently not present as far south in winter when the current was weak.

Several species appeared to have a southern, or southwestern limit to their distribution within the survey area. *Thysanopoda monacantha* was not found south of the Port St. John line, *Euphausia brevis*, *E. paragibba* and *E. hemigibba* were not found south of the East London line and *Thysanopoda aequalis*, *Euphausia mutica*, *Stylocheiron abbreviatum*, *S. longicorne* and *S. microphthalma* were not found in the extreme southwest on the Plettenberg Bay line. However, since all these species, except *S. microphthalma*, have been recorded from both sides of the continent, the fact that they were not taken in the southwest part of the survey area is probably not significant in the picture of their overall distribution in the South African region. *S. microphthalma*, on the other hand, is usually found within the tropics and has not previously been recorded south of 10°S in the Indian Ocean (Mauchline & Fisher 1969). It may have been reaching the southern limit of its range in the waters off the eastern Cape coast.

Seven species, *Euphausia recurva*, *E. tenera*, *Nematoscelis microps*, *Stylocheiron carinatum*, *S. affine*, *S. elongatum* and *S. suhmii* had distributions which extended over all the lines of the survey. These species were found on all three cruises and four of them, *E. tenera*, *N. microps*, *S. carinatum* and *S. affine* are known to occur throughout the South African region. Of the remaining three, *S. suhmii* has previously been taken only from the eastern part of the region, except for three specimens recorded by Illig (1930) from western Cape coastal waters. *E. recurva* has been found in the waters off South West Africa and the Cape, but has not been collected off Natal, except from the stomachs of fin and sei whales taken off Durban (Baker 1965). *S. elongatum* has also not previously been recorded from Natal. The latter species is known to occur within the tropics in the Indian Ocean (Mauchline & Fisher 1969), but *E. recurva* has been most often found from south of 30°S to the Subtropical Convergence. It is thus possible that *E. recurva* is approaching the north-eastern limit of its range in South African seas in the area off Durban (Table 1).

Horizontal distribution of the euphausiid species across the current

As a means of assessing the horizontal spread of the various euphausiid species, into the nearshore part of the survey area, across the centre of the current and in the outer part of the area, towards the current's offshore edge, the stations were divided into the following three groups:

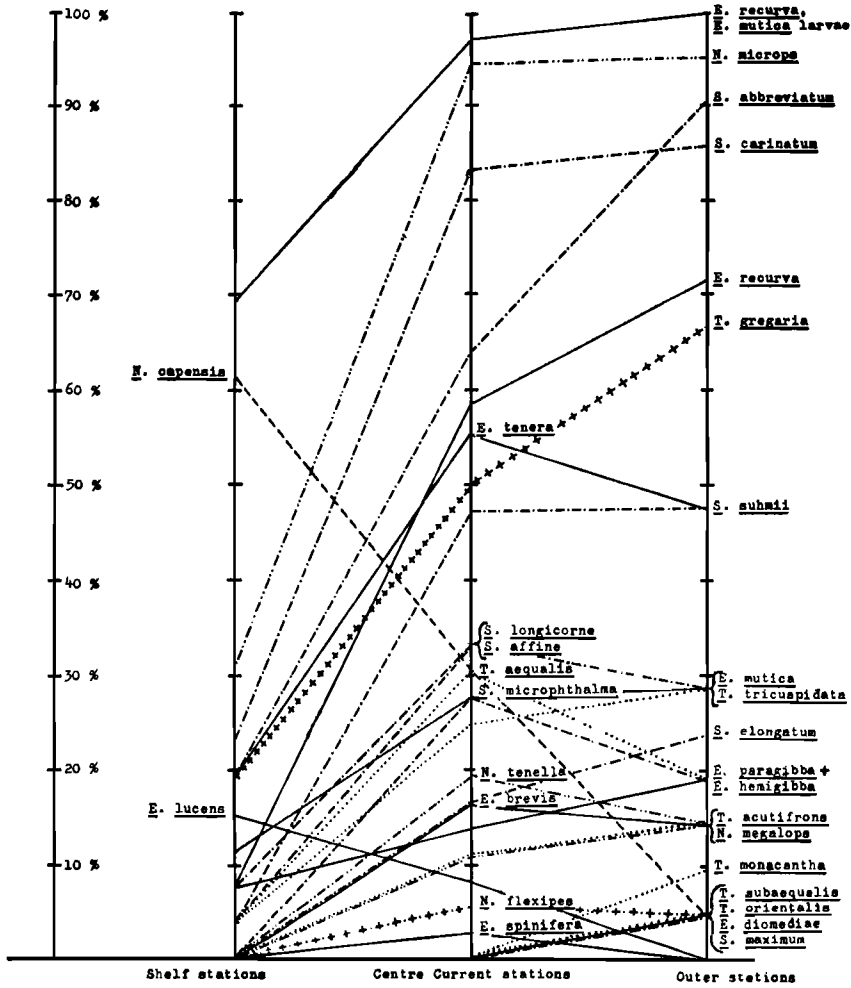
- 26 inshore stations which were all on the continental shelf,
- 36 stations in the centre of the current,
- 21 outer stations.

The outer group consists of the outermost three stations on the Port Elizabeth line on all three cruises and the outer station on each line between Durban and the Kowie River on the second and third cruises. (These lines were not extended as far on the first cruise.) Figure 10 shows the distribution of the species in the three zones outlined above. The number of stations at which each species was caught in a particular zone is expressed as a percentage of the total number of stations in that zone. Species associated with the shelf are shown on the left of the figure, those predominantly linked with the centre of the current are listed in the middle and those associated with the outer part on the right.

The larval series ascribed to *Euphausia recurva* and *E. mutica* was almost ubiquitous. In all three provinces it was present at a greater proportion of the stations than any other group. It occurred at nearly 70% of the shelf stations, at all but one of the centre current stations and at all of the outer stations. *Nematoscelis microps* was almost as well represented at central and outer stations, but it showed a much greater reduction in coastal waters. Only two species had the greater proportion of their populations on the continental shelf. These were *Nyctiphanes capensis*, the neritic species, and *Euphausia lucens*, the southern temperate species, which was found only at the western edge of the survey area where the shelf was wide. These two species are also found in coastal waters off the western Cape and South West Africa (Boden 1955; Neppen 1957). Of the other 27 species, 14 had a markedly lower proportion on the shelf than in the other two provinces and 13 were not represented at all in shelf samples. In the central and outer parts of the current most euphausiid species do not show large variations between the two regions. Nine species were found predominantly in the centre and 18 were more often linked with outer stations, but in many of these the differences were small. Of those associated with the current centre, *Thysanopoda aequalis* had the greatest reduction at outer stations, and of those belonging to the outer group, *Stylocheiron abbreviatum* and *Thysanoëssa gregaria* showed the greatest increase from central to outer stations. One species was found only in the centre of the current and five were found only at outer stations. These were all rare species, represented in the collection by single specimens or a few individuals.

Vertical distribution of the euphausiid species

In order to examine the distribution of the species between the five types of zooplankton sample employed during the survey, the number of times each species was caught in each kind of haul was assessed as a percentage of the total number of hauls of each type. Since adult specimens were not well represented in the collection (except for species such as *Nyctiphanes capensis*, in which all stages usually remain in the upper water layers) it was not considered worthwhile to treat the vertical distribution of adult and young forms separately. The sampling described below relates mainly to larvae and juveniles, rather than the fully mature adults of most of the species concerned. None of the euphausiid species was predominantly linked with the horizontal surface hauls, but eight were found in a greater percentage of the oblique hauls from 150 m to the surface than in the other types of haul. These were: *Thysanopoda tricuspadata*, *Nematoscelis*



The number of stations at which a species was taken in a particular province is expressed as a % of the total number of stations in that province.

- Thysanopoda spp.
- Nyctiphanes spp. ----
- Euphausia spp. ——
- Thysanoessa spp. ++++
- Nematocalia spp. - - - -
- Nematobranchion spp. + + +
- Stylocbeiron spp. - - - -

FIGURE 10

Variations in the distribution of the euphausiid species between the shelf stations, centre current stations and outer stations of the I.G.Y. Survey.

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tenella, *N. microps*, *Stylocheiron carinatum*, *S. abbreviatum*, *S. affine*, *S. suhmii* and *S. microphthalmum*. The following six species were most often found in vertical hauls between 100 m and the surface: *Thysanopoda aequalis*, *Nyctiphanes capensis*, *Euphausia lucens*, *E. spinifera*, *Thysanoëssa gregaria* and *Nematoscelis megalops*, and only one rare species, *Thysanopoda monacantha*, was chiefly associated with the 200–100 m vertical hauls. The *Euphausia recurva*, *E. mutica* larval series together with the remaining 14 species: *Thysanopoda acutifrons*, *T. subaequalis*, *T. orientalis*, *E. recurva*, *E. mutica*, *E. brevis*, *E. diomediae*, *E. tenera*, *E. paragibba*, *E. hemigibba*, *Nemato-brachion flexipes*, *Stylocheiron longicorne*, *S. elongatum* and *S. maximum* were all found in a greater percentage of the deep vertical hauls between 200 and 400 m than in any other type of haul. These results show that approximately half of the euphausiid species appeared to be most closely associated with the deepest water layers sampled. Three of the rare species were caught only at these depths. This emphasizes the importance of deep sampling in the assessment of euphausiid populations, especially if the samples are taken only during daylight hours.

Analysis of species groups

A method proposed by McConnaughey (1964) was employed for the purpose of discovering whether any of the euphausiids were associated in recognizable species groups. The species were assessed for presence or absence in individual samples, and grouping coefficients for each species and for the *Euphausia recurva*, *E. mutica* larval series were calculated using McConnaughey's formula. By means of these coefficients, species groups were selected in accordance with the scheme described by him. It was found, however, that almost every species was associated with a different group on each cruise. The main group contained the most frequently occurring species and is given below, for each cruise:

First cruise: *Euphausia recurva*, *E. mutica* larval series

Nematoscelis microps

Stylocheiron abbreviatum

Nematoscelis megalops

Second cruise: *Nematoscelis microps*

Stylocheiron abbreviatum

Stylocheiron carinatum

Third cruise: *Euphausia recurva*, *E. mutica* larval series

Thysanoëssa gregaria

Nematoscelis microps

Thysanopoda aequalis

Only one species, *Nematoscelis microps*, appeared in all three main groups. The *Euphausia recurva*, *E. mutica* larval series was in that of the first and third cruise and *Stylocheiron abbreviatum* in the first and second. But, although they did not all occur together in every main group, *N. microps*, *S. abbreviatum* and the larval series did have positive grouping coefficients with each other on each cruise and their common occurrence appeared to coincide fairly well with the

centre of the stream of the Agulhas Current. Further sampling may prove this group to be a characteristic feature of Agulhas water in the region of the survey. Apart from these, *Nyctiphanes capensis* and *Euphausia lucens* were the only species which were grouped together on more than one cruise. They occurred together on both the second and third cruises in the south-western part of the survey area.

Indicator species

Four of the I.G.Y. euphausiid species, *Thysanopoda tricuspidata*, *Euphausia diomediae*, *Stylocheiron suhmii* and *S. microphthalma*, could be regarded as potential indicators of Agulhas Current water, and two, *Nyctiphanes capensis* and *Euphausia lucens*, would be indicative of water of a different origin. All the other species have extensive distributions in all three oceans and are known to occur in both the Atlantic and Indian Ocean provinces off South Africa.

Two of the four possible indicators of Agulhas water, *E. diomediae* and *S. microphthalma*, are Indo-Pacific species, not known from the Atlantic (Mauchline & Fisher 1969). *E. diomediae* has a tropical distribution and appears to reach its southern limit in the eastern part of the South African region. As only one individual was recorded from the I.G.Y. material, the species is probably too rare to be useful as an Agulhas Current indicator. *S. microphthalma* is also a tropical species, but, although not previously reported from South Africa, it was found in the centre of the current, as far south as the Port Elizabeth line on the I.G.Y. winter cruise (Figure 11h). Another feature which makes it a potentially useful indicator is its shallow vertical range. It was found only in the upper 200 m. *S. suhmii* was also usually taken in the upper water layers above 200 m. It is known to occur in all three oceans, but only three specimens have been recorded from the western part of the South African region (Illig 1930). It was well-represented at stations in the centre of the current on all the I.G.Y. cruises and it penetrated as far to the south-west as the outermost station of the Plettenberg Bay line on the winter cruise (Figure 11 f, g, h). Because of the characteristic structure of their eyes, *S. suhmii* and *S. microphthalma* can readily be distinguished from other species in the plankton. This is another worthwhile feature in indicator species (Figure 11 b, c). The fourth potential indicator of Agulhas Current water, *T. tricuspidata*, is known from the Atlantic and Indo-Pacific, but has not been found off the west coast of South Africa. Only juveniles and larvae were present in the I.G.Y. material. The young stages have a strikingly distinctive appearance (Figure 11a) and occur in the upper water layers, but the species would probably be less useful as an indicator than *S. suhmii*, since it was not as abundant on the first two cruises and was not taken at all on the third cruise.

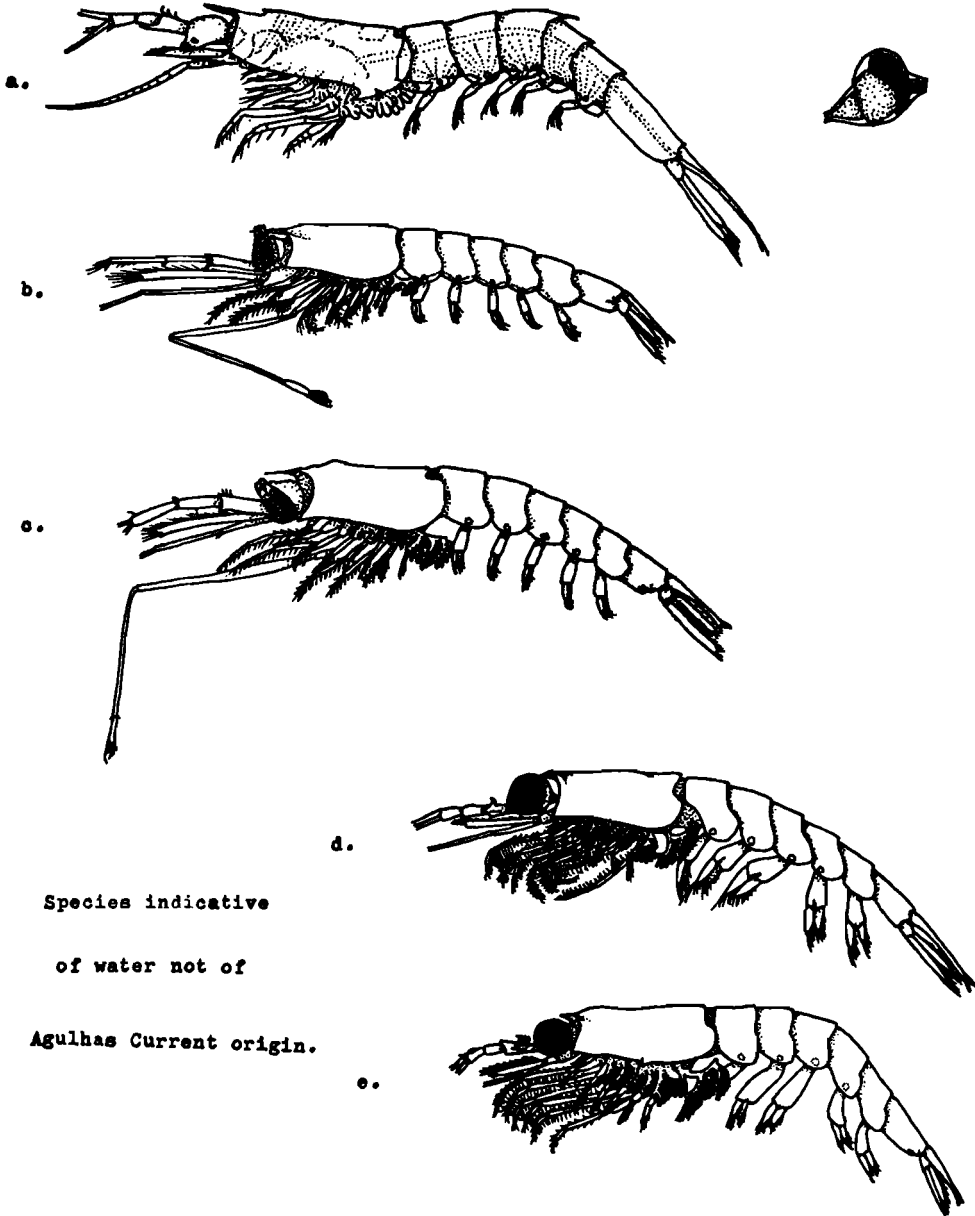
Of the two indicators of non-Agulhas water, *N. capensis* is the more abundant in the I.G.Y. Survey area. Its centre of distribution is the neritic province which extends from South West Africa, around the Cape coast and towards East London. In the survey area its range may be extended by the counter current which sometimes flows northwards between the Agulhas Current and the coast. This species is caught mostly in the upper water layers and its occurrence in plankton samples would be indicative of water from the continental shelf. *E. lucens* is a southern temperate species with a circumpolar distribution, usually between about 38° and 45°S. It is carried northwards into the western part of the South African region by the Benguela Current. It was found at the southwestern edge of the survey area on the second and third cruises and may indicate the presence of temperate water, or at least some admixture of water

which had originally come from temperate latitudes.

Figure 11 f, g, h gives the stations at which the species discussed above were caught on the three cruises. On the first cruise only *S. suhmii*, *T. tricuspidata* and *N. capensis* were found, the Agulhas Current indicators, *S. suhmii* and *T. tricuspidata* did not occur at the same stations as the southern neritic species, *N. capensis* (Figure 11f). As the first cruise was made during summer when the current was flowing strongly, there was probably less mixing of Agulhas water with shelf water in the survey area than on the two later cruises. During the second cruise, the distributions of *S. suhmii* and *T. tricuspidata* overlapped with that of *N. capensis* at Station 38, the second station on the Kowie River line, and *T. tricuspidata* overlapped with *N. capensis* and *E. lucens* at Station 50, the outermost station of the Plettenberg Bay line (Figure 11g). At Station 38 all three species occurred together in the sample taken between 100 m and the surface, and at Station 50 *T. tricuspidata* and *N. capensis* were both in the surface sample (0–5 m). The second cruise took place in autumn when the current would have been slower than during the summer cruise and it appears that there could have been some mixing of shelf water with the upper layers of the Agulhas Current at Stations 38 and 50, both of which are near the edge of the continental shelf. On the third cruise in winter, *S. suhmii* and *S. microphthalmalma* overlapped with *N. capensis* at Station 72 on the Bashee River line and *S. suhmii* overlapped with *N. capensis* and *E. lucens* at Station 85 on the Port Elizabeth line and at Station 89 on the Plettenberg Bay line (Figure 11h). At Station 72 *N. capensis* was the only euphausiid species in the surface haul and it did not occur in either of the hauls in which the two Agulhas Current species were taken. Station 72 was off the edge of the continental shelf near a region where there appeared to be an upwelling of cold water and euphausiid distribution suggests that in this area there was shelf water or upwelled water at the surface with Agulhas and South Indian Central water beneath. Station 85 was the first station beyond the edge of the shelf on the Port Elizabeth line and here *N. capensis* and *E. lucens* were present in the upper 100 m, while the Agulhas Current species, *S. suhmii*, was caught at a lower level between 200 and 100 m. Station 89 was again off the edge of the continental shelf on the Plettenberg Bay line and at this station *N. capensis* and *E. lucens* were found in three of the four samples down to 200 m, while *S. suhmii* was taken at depths between 200 and 400 m. *N. capensis* larvae were also in this deep sample. Progressive changes can be seen in the depth distributions of the indicator species at the above three stations. *N. capensis* was found only in the surface layers in the northeast, down to 100 m further south off Port Elizabeth and throughout the entire water column sampled, in the southwest off Plettenberg Bay. The depth distribution of the Agulhas Current indicators was the inverse of that of *N. capensis*. They occurred at both upper and lower levels in the northeast, but only at depth in the southwest. From the above distributions it can be postulated that during the winter cruise, when the Agulhas Current was at its slowest, non-Agulhas water was probably present in the surface layers as far north as the Bashee River line and that it occurred at progressively greater depths towards the southwest. At the southwest edge of the survey area off Plettenberg Bay, there was evidence of water from the north-east in the deep sample only, while non-Agulhas water appeared to be present at all levels sampled.

The fact that the temperatures recorded at depth off Plettenberg Bay were approximately 3° higher on the third cruise than on the second also suggests that there could have been an admixture of warm Indian Ocean water at this level during the third cruise.

Agulhas Current Indicator Species.



Species indicative
of water not of
Agulhas Current origin.

FIGURE 11
Indicator species in the I.G.Y. Survey area.

- (a) *Thysanopoda tricuspidata* juvenile and eye of late juvenile (after Sars 1885) – Agulhas Current indicator.
- (b) *Stylocheiron suhmii* ♀ (after Boden 1954) – Agulhas Current indicator.
- (c) *Stylocheiron microphthalmum* ♀ (after Boden, Johnson & Brinton 1955) – Agulhas Current indicator.
- (d) *Nyctiphanes capensis* ♂ (after Boden 1954) – indicator of water not of Agulhas Current origin.
- (e) *Euphausia lucens* ♀ (after Boden 1954) – indicator of water not of Agulhas Current origin.

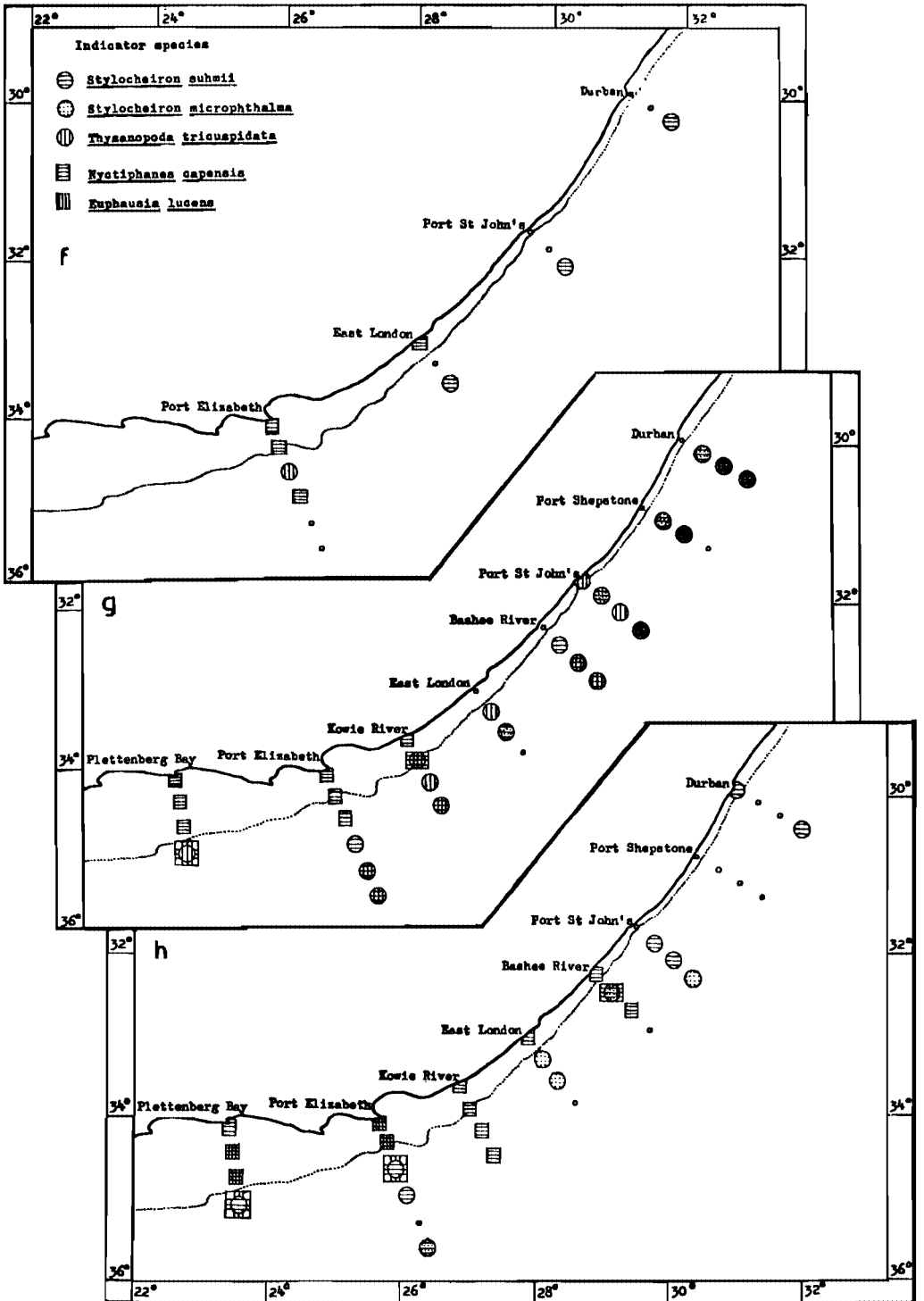


FIGURE 11 (continued)

(f) Distribution of the euphausiid indicator species on the first I.G.Y. cruise (February–March).

(g) Distribution of the euphausiid indicator species on the second I.G.Y. cruise (May).

(h) Distribution of the euphausiid indicator species on the third I.G.Y. cruise (August).

TOTAL EUPHAUSIID NUMBERS

Variation in numbers with distance offshore

The distribution of euphausiid numbers followed a fairly consistent pattern across the current (Figure 12). Usually few were caught at inshore stations on the continental shelf. Exceptions, such as the Kowie River line on the second cruise and the East London line on the third cruise were due to the presence of the neritic species, *Nyctiphanes capensis*, at the inshore station. At the second station on each line numbers usually increased. This might have been an "edge effect" at the border of the Agulhas Current and the coastal water on the shelf. Further out to sea in the more impoverished core of the current, there was usually a fall in numbers, while at the outer edge of the current they often increased again. The pattern can be seen most clearly on the Port Elizabeth line of each cruise. Here numbers first reached a peak at the second or third inshore station, then fell away at the station with the highest surface temperature in the centre of the current and subsequently rose again at the outer stations beyond the middle of the Agulhas Stream.

Because the stations in the centre of the current were sampled during the middle of the day, the reduction in numbers at these stations could have been due to the vertical migration of the majority of euphausiids beyond the range of the nets at the time of sampling. However, since most of the specimens caught were juveniles and larvae which did not show evidence of extensive vertical movements, the pattern which emerged probably reflected their distribution across the current with some validity.

Changes with season and latitude

The range in variation in euphausiid numbers between the three I.G.Y. cruises is indicated below. All the lines of the first cruise are included and the corresponding lines of the second and third cruises. On the second and third cruises the lines were extended beyond those of the first cruise and, in order to keep their numbers comparable, the outermost stations of the two later cruises have been omitted. Similarly, only the inner three stations on the Port Elizabeth line of each cruise have been totalled.

First Cruise (February–March)

Durban line, Stations 2, 3, 4	94 euphausiids
Port St. John line, Stations 5, 6, 7	161 euphausiids
East London line, Stations 8, 9, 10	394 euphausiids
Port Elizabeth line, Stations 11, 12, 13	519 euphausiids

Second Cruise (May)

Durban line, Stations 17, 18, 19	320 euphausiids
Port St. John line, Stations 25, 26, 27	288 euphausiids
East London line, Stations 33, 34, 35	105 euphausiids
Port Elizabeth line, Stations 41, 42, 43	849 euphausiids

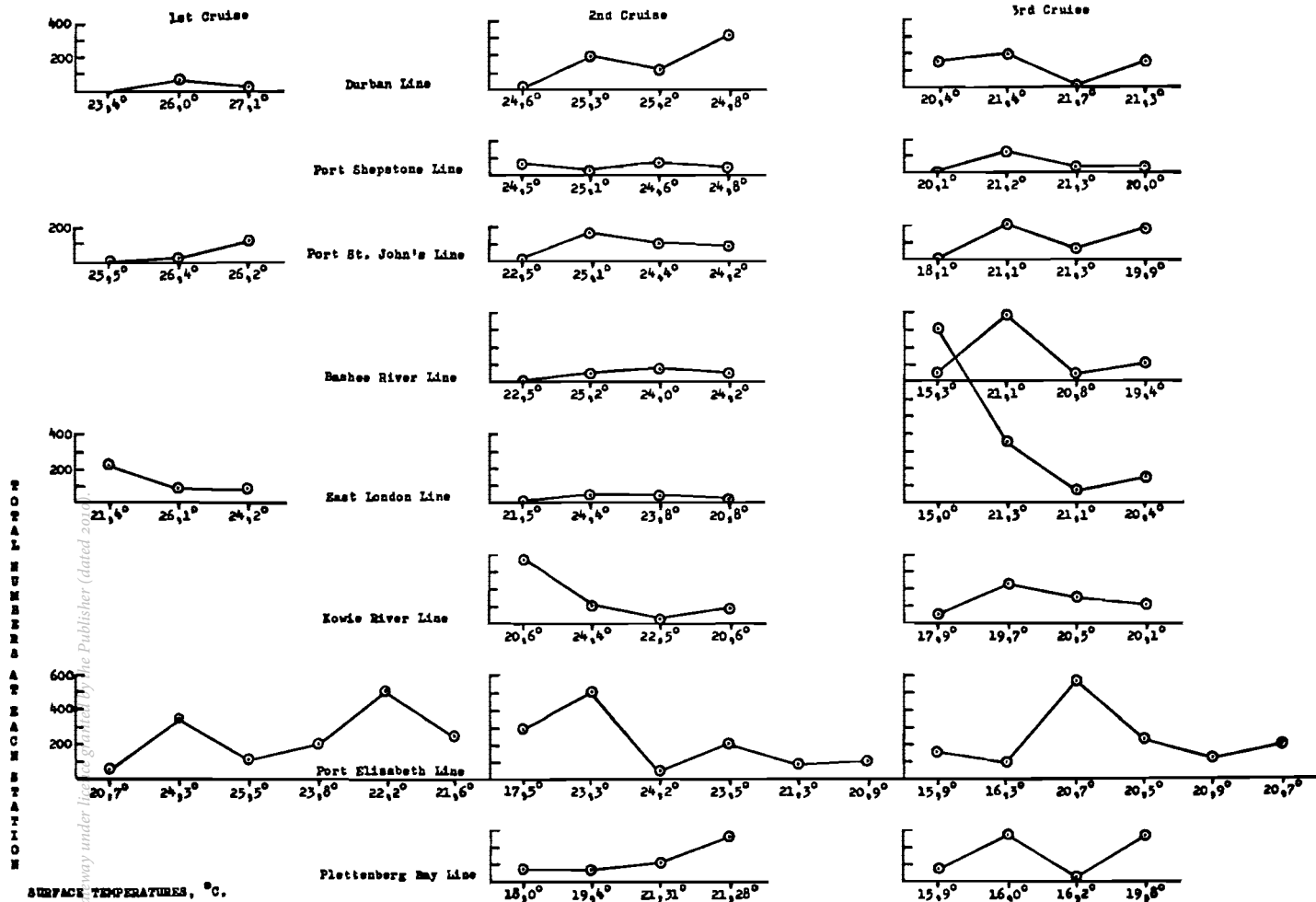


FIGURE 12
Total numbers of euphausiids at each of the I.G.Y. stations.

Third Cruise (August)

Durban line, Stations 59, 60, 61	368 euphausiids
Port St. John line, Stations 67, 68, 69	294 euphausiids
East London line, Stations 76, 77, 78	1 415 euphausiids
Port Elizabeth line, Stations 83, 84, 85	858 euphausiids

On the first cruise the number of euphausiids taken on each line increased progressively from Durban to Port Elizabeth. At this time the Agulhas Current formed a strongly-flowing stream, bringing warm, relatively impoverished South Equatorial water down the east coast. The small number of euphausiids taken on the two northern lines suggests that during the summer the current supported sparse plankton populations in the area off Durban and Port St. John. The relatively large numbers of euphausiids taken further south, off East London and particularly off Port Elizabeth, can probably be correlated with the widening of the continental shelf and the tendency for the current to be deflected away from the coastline in this region. This would lead to an enrichment of the area by the subtropical water on the shelf and a corresponding increase in plankton numbers.

During the second cruise, when the current was weaker and south equatorial surface water was not carried as far down the coast, there was an increase in euphausiid numbers on the northern lines, which suggests that this region was less impoverished in autumn than in summer, although the area off Port Elizabeth still supported the largest euphausiid populations. During the third cruise, when the current was at its weakest and there were indications of upwelling off East London, euphausiid numbers were at their highest, with a great increase on the East London line, due to a large swarm of the neritic species, *Nyctiphanes capensis*, at the inshore station. The consistently high numbers on the Port Elizabeth line on all three cruises point to this as an area of enrichment during both summer and winter. These findings may be correlated with Bang's (1970) discovery of an area of intermittent upwelling off Port Elizabeth and with the high zooplankton density found by Zoutendyk (1970) in this region.

An interesting feature of the survey is that, when it was extended beyond Port Elizabeth to Plettenberg Bay on the second and third cruises, far fewer euphausiids were caught off Plettenberg Bay than at comparable stations off Port Elizabeth on both occasions.

Second Cruise

Port Elizabeth line, Stations 41, 42, 43	849 euphausiids
Plettenberg Bay line, Stations 47, 48, 49	244 euphausiids

Third Cruise

Port Elizabeth line, Stations 83, 84, 85	858 euphausiids
Plettenberg Bay line, Stations 90, 91, 92	382 euphausiids

This may be due partly to the fact that the continental shelf is even wider off Plettenberg Bay than off Port Elizabeth and the neritic euphausiid, *Nyctiphanes capensis*, was the only species regularly represented in the hauls from the three inner stations there. It may also be important that the maximum surface temperature on the Plettenberg Bay line was approximately

3° below that of the Port Elizabeth line on both cruises. The raising of the temperature of the comparatively rich shelf water, as it moves towards the north-east inshore of the warm Agulhas Current, could accelerate the growth of phytoplankton and thereby contribute to the increase in euphausiid numbers observed off Port Elizabeth.

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