

Vertical migration and habitat partitioning of six euphausiid species in the northern Benguela upwelling system

Manuel Barange

Instituto de Ciencias del Mar, Paseo Nacional s/n, 08039 Barcelona, Spain

Abstract. The vertical distribution of the adults of six species of euphausiids, *Thysanoëssa gregaria*, *Nematoscelis megalops*, *Euphausia americana*, *E. gibboides*, *E. hanseni*, *Stylocheiron longicorne*, as well as the larval stages of *E. hanseni*, were studied during a 48 h cycle at a fixed station in the northern Benguela upwelling system. All the species, except *T. gregaria* and *S. longicorne*, proved to perform diel vertical migration, but both migratory and non-migratory species appeared to be segregated in space during night-time hours, regardless of potential prey (phytoplankton and copepods). It is suggested that water column structure and hydrographic discontinuities caused by a warm, depth-localized intrusion, as well as the reproductive strategies of particular species, are responsible for this pattern. Eggs and larval stages of *E. hanseni* were concentrated near the surface, and the effect of the short-term pulses of the intrusion on their abundance is discussed.

Introduction

Euphausiids are generally regarded as being vertical migrators (Mauchline, 1980). The hypotheses advanced to explain this behavior, e.g. reaction to light intensities, predator avoidance, low-cost feeding and exploitation of the metabolic advantage of living at lower temperatures during the day, are similar to those for other zooplanktonic groups (see reviews in Longhurst, 1976; Pearre, 1979; Huntley, 1985; Bayly, 1986; Forward, 1988). In areas of coastal upwelling (Wroblewski, 1982; Pillar *et al.*, 1989) or strong horizontal currents (Alldredge and Hamner, 1980; Phillips, 1981; Shanks, 1986; Kimmerer and McKinnon, 1987) vertical migration has been considered as a useful strategy to avoid offshore transport, thus permitting the adult stages to remain inshore, where the food is generally more abundant.

Warm water intrusions are common off northern Namibia in late summer and early autumn (Boyd *et al.*, 1987). Major intrusions were observed in 1963 and 1984, and were likened to the El Niño phenomenon off Peru (Shannon *et al.*, 1986). During the first quarter of 1986 an extensive intrusion occurred, with a maximum southward penetration observed in April at an estimated rate of 8 km day⁻¹ (Boyd *et al.*, 1987). Although the intrusion was mainly very shallow, the authors concluded that a secondary, independent subsurface intrusion also occurred.

The study of the vertical distribution and dynamics of zooplanktonic species under such environmental conditions will provide a better understanding of the relationship between environmental fluctuations and zooplankton behavior. Migratory species often dampen the effect of advective processes in the near-surface waters by moving to more constant, deeper environments, passing through waters with very different characteristics while migrating towards the surface or to depth. Non-migratory early stages or species will be continually transported southwards during intrusions if they remain in the upper layers, and

will become spatially separated from species living elsewhere in the water column.

The present study is the first attempt to describe the diel vertical migration of the euphausiids of the northern Benguela system (Namibia). The vertical distribution of the adults of six euphausiid species including the larval stages of the dominant *Euphausia hanseni* are described, with the aim of showing the effect of a unidirectional, depth-localized current on their abundance and vertical distribution. By analyzing the vertical distribution differences, at night-time, between species and sexes, insight will be provided into habitat-partitioning between species of euphausiids in Namibian waters. Finally, vertical distribution of potential prey items will be presented, thus permitting assessment of some of the major driving forces of regulating vertical distributions.

Materials and methods

Sampling strategy

During the second SNEC (Spanish–Namibian Environmental Cruise) survey a 48 h study was conducted at 18°S, 10°30'E (northern Namibia) in a depth of 3550 m (Figure 1). Samples were taken around a fixed position during the 48 h study by relocating the ship when necessary. A strong warm water intrusion crossed the station from north to south-south-east (Figure 1), and remained constant, although with differing intensity, during the whole study.

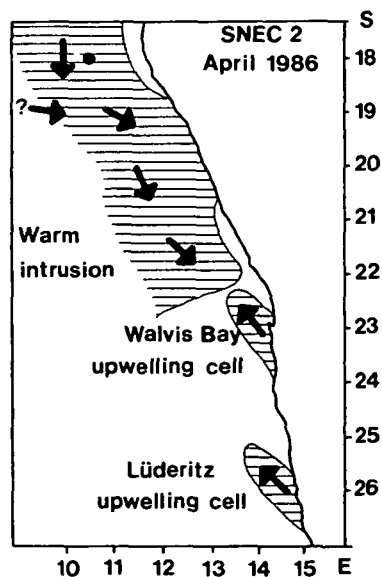


Fig. 1. Schematic representation of the major hydrographic features observed during the SNEC 2 cruise, as inferred from Boyd *et al.* (1987) and Maso (1987), showing the approximate extension and direction of the warm water intrusion and the centers of upwelling. Dot denotes position of the 48 h station.

Zooplankton samples were taken every 2–3 h using a 1 m² multiple opening and closing rectangular midwater trawl fitted with six 200 µm mesh nets (RMT 1 × 6). The net was towed at 2–3 knots (depending on net angle) and fished at five different levels in the upper 200 m of the water column: 200–100, 100–60, 60–40, 40–20 and 20 m to surface. Samples were preserved in 5% buffered formalin water for further analyses.

Salinity and temperature profiles were measured every 2–4 h using a Neils Brown Mark III CTD. A rosette of Niskin bottles attached to the CTD was used to collect water samples for the determination of nutrients, chlorophyll *a* (fluorometric method, Strickland and Parsons, 1972) and oxygen concentration at selected depths. Nutrients were analyzed on board according to standard methods (Strickland and Parsons, 1972; Mostert, 1983).

Sample processing

In the laboratory all adult euphausiids were counted, sexed and classified to species level. Eggs and larval stages (nauplius, calyptopis 1, 2 and 3, furcilia 1+2, 3+4 and 5+6 and juveniles) of the most abundant species in the area, *E. hansenii*, were also counted. When necessary, subsamples were taken (generally only for the surface samples) until total counts of at least 30 individuals of each larval stage had been made for each sample. Density estimates were standardized to individuals m⁻³ and individuals m⁻² from knowledge of the volume filtered in each depth stratum.

Results

Hydrographical description of the station

A detailed description of the hydrographic features during the survey is given by Maso (1987) and Boyd *et al.* (1987). A schematic representation of the major features as well as the position of the fixed station are shown in Figure 1. Upwelling was recorded off Lüderitz and Walvis Bay, while the warm intrusion extended as far south as Walvis Bay.

In Figure 2 profiles of average temperature, salinity, nitrate and chlorophyll *a* (Chl*a*) during the 48 h cycle are presented for the upper 80 m of the water column. A thermocline of 4°C was observed between 20 and 40 m, and Chl*a* was concentrated above the thermocline. Profiles of oxygen, salinity and Chl*a* for the upper 200 m of the water column at the beginning of the cycle (9 h 30', April 24) are shown in Figure 3. Comparison between Figures 2 and 3 reveals the decrease in the concentration of Chl*a* during the cycle, as a result of the intrusion of relatively chlorophyll-poor waters. Low oxygen water (<1 ml l⁻¹) occurred below 80 m.

During the 48 h cycle 15 species of euphausiids were recorded: *Euphausia americana* Hansen, *E. hansenii* Zimmer, *E. gibboides* Ortmann, *Thysanoessa gregaria* G.O.Sars, *Nematoscelis megalops* G.O.Sars, *Stylocheiron longicorne* G.O.Sars, *Thysanopoda orientalis* Hansen, *Nyctiphanes capensis* Hansen, *E. mutica* Hansen, *E. similis* var. *armata* Hansen, *E. recurva* Hansen, *E. lucens*

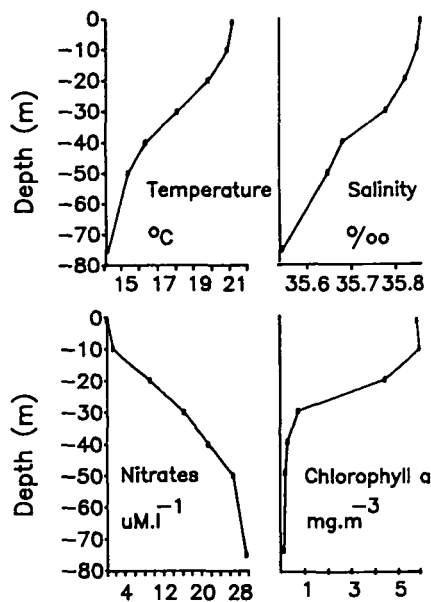


Fig. 2. Profiles of average temperature, salinity, nitrate and Chl*a* during the 48 h cycle (*n* = 14), from surface to 80 m depth.

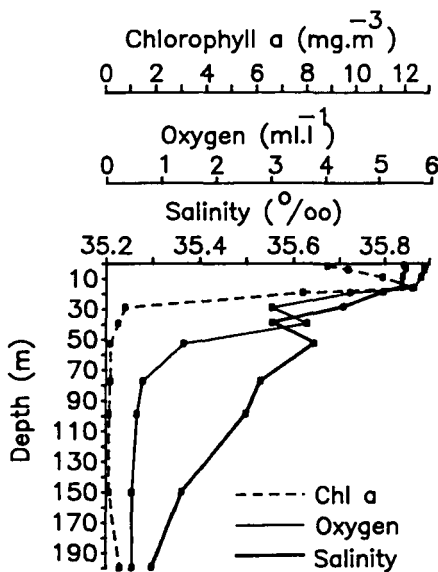


Fig. 3. Salinity, Chl*a* and oxygen profiles from surface to 200 m at the beginning of the experiment (09.30, April 24, 1986).

Hansen, *Nematoscelis microps* G.O.Sars, *Nematobrachion flexipes* (Ortmann) and *Stylocheiron abbreviatum* G.O.Sars. Only the first six species were abundant enough in the samples to allow description of their vertical distribution and dynamics.

Day and night abundances of selected euphausiid species

It should be noted that sampling was carried out in the upper 200 m of a water column of 3550 m depth. The data, therefore, do not permit analyses of vertical distribution during daylight hours since most of the adults of the migratory species remained below the sampled range during this period. The average number of individuals per square meter (0–200 m) during day and night are presented in Table I. Only *E.gibboides* and *S.longicorne* showed no significant differences between the average day and night total catches, providing evidence that these species do not migrate or migrate within the upper 200 m. Although the significant differences recorded for the rest of species provide evidence of vertical migration, the differences for *T.gregaria* and *N.megalops* might be due to net avoidance rather than migration itself (Brinton, 1967; Baker, 1970; Wiebe *et al.*, 1982), as will be discussed later.

Vertical distribution and space partitioning between species

Vertical distribution of the species considered during daytime and night-time hours (in percentage of abundance) is presented in Figure 4. Among the migratory species, *E.americana* remained above the thermocline during the night, *E.hanseni* remained above and in the thermocline, *E.gibboides* occurred mainly in the thermocline and *N.megalops* was concentrated below it. *T.gregaria* seemed to move from below, to within the thermocline, while *S.longicorne* showed no migratory pattern.

Figure 4 suggests that during the night the species partition themselves in space. In order to assess this vertical partitioning, the weighted mean depth (WMD) of each species was calculated according to the equation:

WMD = $\sum (ni * di)/N$ (1)

Table I. Average number of individuals per square meter (from 200 m to surface), recorded at day and night samples, for adults

	Day (n = 9)		Night (n = 9)		Significance
	X	SD	X	SD	
<i>Euphausia americana</i>	2.9	4.4	7.4	5.0	*
<i>E.gibboides</i>	2.2	2.6	2.7	1.3	n.s.
<i>E.hanseni</i>	22.2	28.4	78.7	42.4	*
<i>Thysanoessa gregaria</i>	4.4	3.2	25.3	27.8	*
<i>Nematoscelis megalops</i>	1.9	1.0	47.0	28.7	*
<i>Stylocheiron longicorne</i>	2.6	1.2	3.8	1.4	n.s.

Significance of the t-test: *, different at a 0.05 level; n.s., no differences at a 0.05 level.

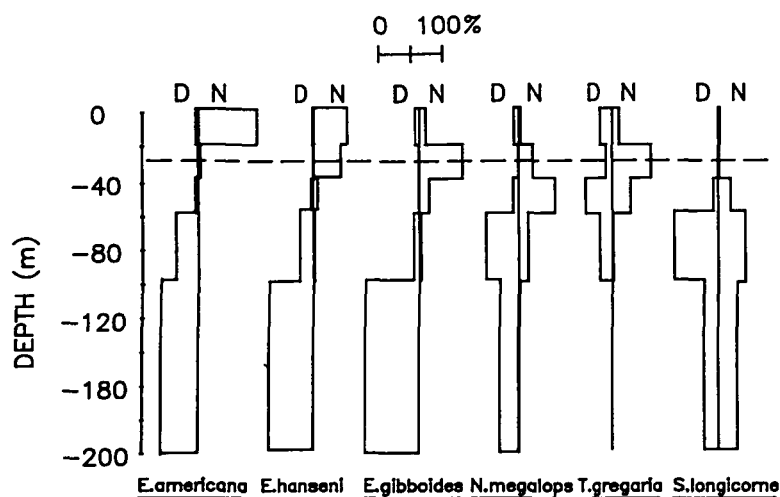


Fig. 4. Percentage of the number of euphausiids in each sampled layer for the night (N) and day (D) samples ($n = 9$ each), by species. Broken line indicates approximate thermocline position.

where di = depth of a sample i , ni = number of individuals at that depth and N = sum of the number of individuals over all sampling depths (Roe *et al.*, 1984a). The use of WMD for 'strata' sampling requires the use of the average depth of the samples for its calculation (e.g. a sample from 60–40 m results in a di of 50 m). The major shortcoming of this approach, however, is that a different WMD between two species does not necessarily mean that the species are totally partitioned, but rather that the centers of their distribution are different. The results of these computations are summarized in Table II. Significant differences were recorded between the WMD of the different species (ANOVA, Tukey test, $P < 0.001$). Multiple range tests (95% Tukey HSD intervals method) revealed no homogeneous groups, providing evidence that the center of abundance occupied by each species at night is significantly different from each other, thus supporting the hypothesis of vertical habitat-partitioning between the species. The t -test performed between day and night WMD (Table II) provides evidence that *S.longicorne* does not migrate. The nonsignificant differences for *T.gregaria* suggest that the differences recorded between day and night catches (Table I) are related to net avoidance and/or patchiness rather than vertical migration itself, as already pointed out by Brinton (1967) and Baker (1970).

Night-time distribution of euphausiid species, as well as copepod abundance (Figure 5), reveals that the strong pattern of space segregation is independent of the major potential prey (phytoplankton and copepod) distribution. Both copepods (Figure 5) and Chla (Figures 2 and 3) were largely concentrated in the upper 20 m of the water column. Segregation was obvious not only among the non-migratory species, but also among the migratory ones.

Table II. Average weighted mean depths at night for the studied species (day WMD only shown for the non-migratory species)

	WMD (night)	WMD (day)
<i>Euphausia americana</i>	12.47 ± 4.60	–
<i>E.gibboides</i>	31.70 ± 6.78	–
<i>E.hanseni</i>	23.02 ± 4.74	–
<i>Thysanöessa gregaria</i>	39.22 ± 20.11	45.56 ± 18.47
<i>Nematoscelis megalops</i>	50.90 ± 4.74	–
<i>Stylocheiron longicorne</i>	97.20 ± 20.11	98.41 ± 22.68

Day–night differences (*t*-test) not significant at a 0.05 level.

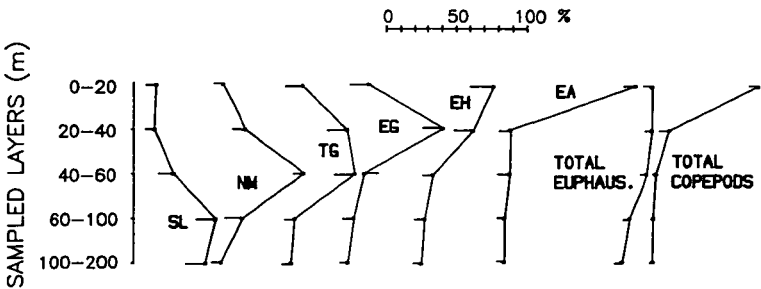


Fig. 5. Average night-time vertical distribution, in percentage of abundance by layers ($n = 9$ samples), for the euphausiid species studied. SL, *S.longicorne*; NM, *N.megalops*; TG, *T.gregaria*; EG, *E.gibboides*; EH, *E.hanseni*; EA, *E.americana*. Vertical night-time distribution is also shown for the total numbers of euphausiids and copepods. Horizontal bars denote standard deviation.

Vertical distribution and space partitioning between sexes

Among the migratory species, *E.americana*, *E.gibboides* and *N.megalops* showed no differences between male and female WMD at night (*t*-test, $P > 0.05$) (Figure 6). The difference, however, was significant for *E.hanseni* (*t*-test, $P < 0.05$), with males centered within the thermocline region (WMD = 27.8 ± 7.6 m) and females above it (WMD = 19.1 ± 6.04). The different migratory pattern between males and females of *E.hanseni* is clearer in Table III, where the night abundances of both sexes are presented for the layers 0–20 and 40–60 m. With the exception of the sample taken at the beginning of the first night (April 24), the percentages of males were always $< 50\%$ in the 0–20 m layer (average 34.4%) while always being $> 50\%$ in the 40–60 m layer (average 89.4%). This consistent pattern provides evidence that the differences observed are not due to isolated cases caused by patchiness, but rather it gives a true reflection of habitat partitioning. The difference between males and females of *E.hanseni* residing above and below the thermocline (normalized by using a logarithmic transformation to avoid patchiness effects) can be observed in Figure 7. At night a male-dominated area can be observed between 40 and 60 m depth, while the area between 0 and 20 m is dominated by females. These data support the contention that, although both sexes migrate upwards during the

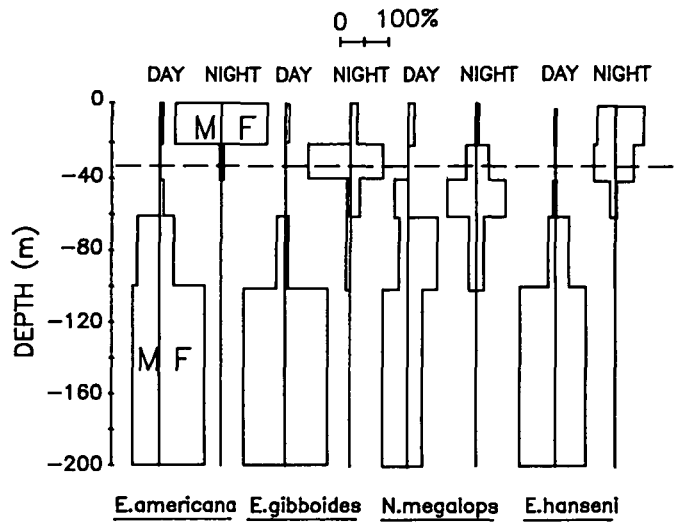


Fig. 6. Comparison of the male and female depth distribution, per layers, at day and night, for the species performing vertical migration ($n = 9$ each), in percentage of abundance. Broken line indicates thermocline position. See text for explanation.

Table III. Abundances (no. 1000 m^{-3}) of *E.hanseni* males and females in the layers 0–20 and 40–60 m in the 10 night samples taken during the cycle and percentage of males in each trawl

Night abundance (no. 1000 m^{-3})										
0–20 m	April 24					April 25				
Females	111	1103	143	3871	1966	1612	430 ^a	1082	125	2092
Males	1680	583	90	1135	894	475	125 ^a	69	119	619
% Males	93.8	34.6	38.6	22.7	31.2	22.7	22.5	6.0	48.7	22.8
40–60 m	April 24					April 25				
Females	10	10	0	124	11	0	169	17	13	0
Males	154	282	44	427	65	10	205	209	178	131
% Males	93.9	96.6	100	77.5	85.5	100	54.8	92.5	93.2	100

^aIntegrated 0–40 m.

night, the males of *E.hanseni* tend to stop their vertical migration before the females.

Vertical distribution of *E.hanseni* larval stages

The abundance of each larval stage in the upper 200 m, including the WMD of day and night samples is presented in Table IV. No significant differences were recorded between night and day densities of the larval stages, suggesting that they remained within the upper 200 m of the water column during the sampling period. Only furcilia stages 3 + 4 and 5 + 6 as well as juveniles showed

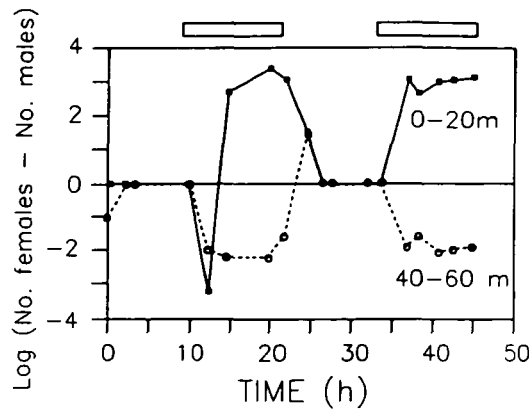


Fig. 7. Differences (log scale) between the abundance of *E. hanseni* males and females in the layers 0–20 and 40–60 m along the 48 h cycle. Night samples are indicated by the bars at the top. Positive values reflect dominance of females, negative values dominance of males.

significant differences between day and night WMD, suggesting a migratory behavior of the older larvae, while calyptopis stages and early furcilia do not migrate. All the larval stages remained close to the surface at night, while occupying deeper layers during the day according to its ontogenic stage. Figure 8 provides more evidence for this increased migration according to developmental stage.

Eggs and nauplii remained between 20 m and the surface (Figure 8), suggesting that *E. hanseni* shows a developmental strategy similar to an inshore species rather than to an oceanic species.

Boyd *et al.* (1987) described the extension of the saline, warm intrusion that affected the study area in the first quarter of 1986 (Figure 1). Analysis of the short-term effects of the intrusion on the particulate organic carbon stocks (unpublished data) revealed that the intrusion was not a continuous process but a succession of pulses, the major pulse recorded 26 h after the beginning of the experiment. This was confirmed by performing a principal components analysis (PCA) with the hydrographical parameters (temperature, salinity and nutrients), the first component being associated with the intensity of the intrusion. In Figure 9 it can be observed that this major intrusion coincided with an extreme increase in calytopes larvae, specially stages 2 and 3, but does not explain the variability observed for eggs, nauplii and furcilia stages.

Discussion

Although no comparison between the present study and previous studies in the area can be accomplished, several papers have described the migratory pattern and extension of the studied species in other areas. Thus, the migratory behavior of *E. americana* and *E. gibboides*, and the lack of migration in *S. longicorne* and *T. gregaria* are well documented and in agreement with the results presented here (Brinton, 1967, 1979; Baker, 1970; Youngbluth, 1975, 1976; Mauchline,

Table IV. Abundances (no. m⁻²) and WMD of the different larval stages of *E.hanseni*, and significance of the day-night differences (t-test)

	Day	Night	Significance
<i>E.hanseni</i> larval stages (no. m ⁻² ; 0–200 m; n = 9)			
Calyptopis 1	38.2 ± 43.6	93.9 ± 166.0	n.s.
Calyptopis 2	103.0 ± 72.9	314.6 ± 638.1	n.s.
Calyptopis 3	45.2 ± 38.6	183.7 ± 310.6	n.s.
Furcilia 1 + 2	38.1 ± 18.9	40.4 ± 25.5	n.s.
Furcilia 3 + 4	12.9 ± 8.0	11.5 ± 10.1	n.s.
Furcilia 5 + 6	10.6 ± 6.5	11.0 ± 8.1	n.s.
Juveniles	10.8 ± 15.6	12.2 ± 16.7	n.s.
Total calyptopis	186.4 ± 129.9	592.3 ± 1110.1	n.s.
Total furcilia	61.6 ± 25.6	62.9 ± 42.3	n.s.
<i>E.hanseni</i> larval stages: WMD (n = 9)			
Calyptopis 1	12.9 ± 5.6	11.6 ± 1.9	n.s.
Calyptopis 2	11.5 ± 3.9	12.3 ± 3.6	n.s.
Calyptopis 3	19.0 ± 17.3	12.8 ± 3.9	n.s.
Furcilia 1 + 2	13.8 ± 4.4	11.8 ± 2.4	n.s.
Furcilia 3 + 4	17.6 ± 7.2	10.3 ± 0.7	*
Furcilia 5 + 6	29.9 ± 14.1	10.4 ± 0.5	*
Juveniles	49.3 ± 8.2	22.4 ± 25.8	*
Total calyptopis	12.1 ± 4.9	12.3 ± 3.1	n.s.
Total furcilia	11.7 ± 6.1	11.2 ± 1.4	*

n.s., No differences at a 0.05 level; *, significant differences at a 0.05 level.

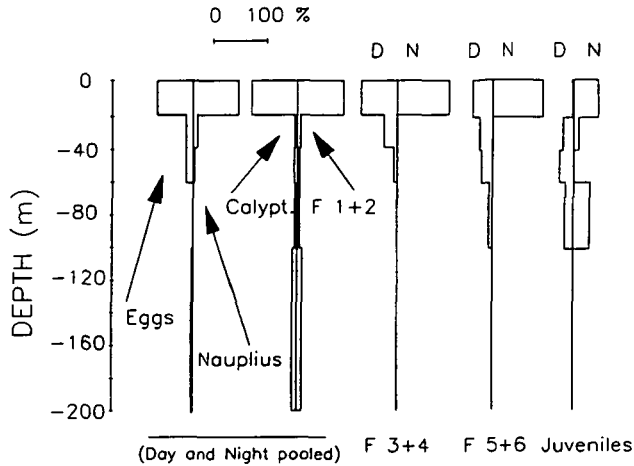


Fig. 8. Depth distribution of *E.hanseni* larval stages along the 48 h cycle (in percentage of abundance per layers). Day and night samples are shown separately for the stages performing vertical migration (see Table IV). Calypt. means the three calyptopes stages together.

1980; Roe *et al.*, 1984b). Although net avoidance of *N.megalops* has been demonstrated (Wiebe *et al.*, 1982), the authors concluded that the vertical distribution pattern does not change, leading to the conclusion that, in the present study, the species migrated, its upper limit being in relation with the

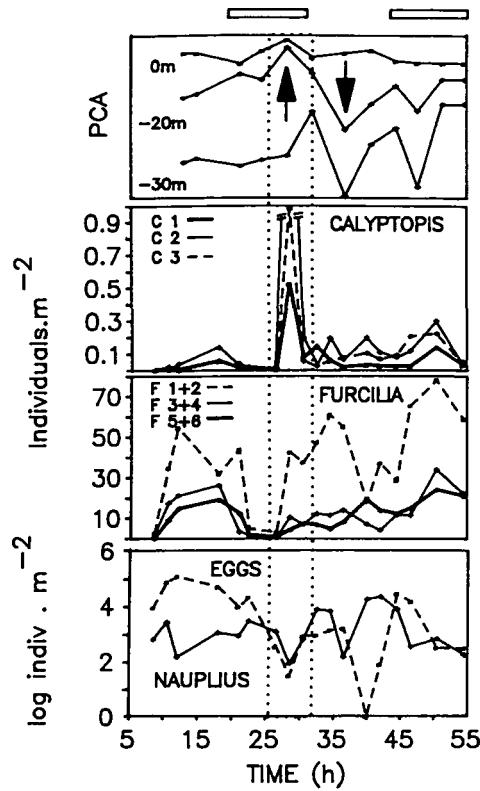


Fig. 9. Number of individuals per square meter (0–200 m) for *E. hanseni* larval stages along the 48 h cycle. PCA means values of the first component of the principal component analysis performed with the hydrographical parameters at 0, 20 and 30 m depth (see text for explanation). The arrow pointing up indicates the time when the major pulse of warm water intrusion took place. The arrow pointing down shows relaxation of the intrusion process. Bars at the top indicate night samples.

thermocline position, as previously stated (Baker, 1970; Mauchline, 1980; Roe *et al.*, 1984b).

The findings of this study show that *E. hanseni* migrates extensively, living below 200 m during the day and above and in the thermocline during the night. Differential night-time vertical distribution between males and females was observed. Although sex ratios >1 have been observed several times for other species, only Roe *et al.* (1984b) provided evidence of differential ratios in relation to depth. The authors recorded 5% of males of *S. longicorne* at 100 m depth as compared to 14% at 250 m depth, but no explanation for this observation was provided. Although females are slightly larger than males (M. Barange and V. Stuart, submitted), differential migration of *E. hanseni* cannot be explained by any clear morphological distinction between sexes. Since

the species was spawning during the study, upward migration could be advantageous in that the eggs can be laid in the warmer surface waters ($>20^{\circ}\text{C}$), as opposed to the cooler subsurface waters where the majority of the males were observed ($14\text{--}16^{\circ}\text{C}$), thus increasing the development rate of the eggs.

Euphausia hansenii in the Namibian system displays higher densities over depths between 200 and 100 m (M.Barange and V.Stuart, submitted). The low sinking rates of their eggs and nauplii, as inferred from their vertical distribution, are thus in accordance with observations on other inshore and shelf species (Marshall, 1983; Pillar *et al.*, 1989), as opposed to the classical developmental ascent of oceanic species (Makarov, 1979; Mauchline, 1980; Williams and Lindley, 1982). Ontogenetic migration, a common feature for most euphausiid species (Mauchline and Fisher, 1969; Mauchline, 1980; Hirota *et al.*, 1984; Pillar *et al.*, 1989), seems to occur from furcilia 3 + 4 onwards.

Habitat-partitioning was observed between the six species considered (Figure 5). Vertical separation of euphausiid species has been detected previously (Hirota *et al.*, 1984; Simmard *et al.*, 1986), although sometimes restricted to the non-migratory species (Baker, 1970). The relationship between potential prey vertical distribution and euphausiid distribution was studied by Sameoto *et al.* (1987). These authors observed that the largest concentration of euphausiids was found at the same depth as the main concentration of copepods, and concluded that maximum prey concentration may be more important in determining their depth rather than the temperature. Nevertheless, they considered that no competition for food occurred, because the species had a limited degree of overlap, suggesting that the major concentration of euphausiids was largely due to a single species. All the species studied in the present work are considered omnivorous (Mauchline, 1980), and stomach contents analysis revealed that copepods are the main prey item (M.Gibbons, personal communication). The lack of aggregation between euphausiids and potential prey may be due to high concentrations of food ($>18\text{ }\mu\text{g C m}^{-2}$). With food in excess other variables, especially water column structure, may act as controlling factors. Although most euphausiids have the ability to cross strong thermoclines (e.g. Williams and Frangopoulou, 1985), their existence may prevent some species from further upward swimming, despite poorer food concentrations at depth. Recent studies have suggested the important role of water column structure in regulating vertical distribution of zooplankters (Le Fèvre and Frontier, 1988; Frangopoulou and Likakis, 1990; Kiørboe *et al.*, 1990; Olla and Davis, 1990; Revelante and Gilmartin, 1990; Tremblay and Sinclair, 1990), especially in combination with potential prey distribution and light intensity (Olla and Davies, 1990).

The influence of the seasonal warm water intrusions in the zooplankton of the Benguela system needs some elaboration. The importance of the 1986 intrusion as a major oceanographic event was demonstrated by Boyd *et al.* (1987), who showed that the $35.5 \cdot 10^{-3}$ surface isohaline penetrated 4° south from January to April. 'El Niño' type intrusions have only been recorded recently in 1984 (Shannon *et al.*, 1986), but seasonal intrusions are recorded every year from late summer to early autumn (Boyd *et al.*, 1987). Short-term dynamics of the hydrographical parameters during the 1986 warm intrusion (Figure 9) suggest

that the intrusion process was non-homogeneous, consisting of irregular time-spaced pulses, that resulted in surface enrichment and sudden renewals of plankton populations. Further evidence of these short-term effects, regarding the euphausiid population, is provided in the present study. The marked increase in the number of *E. hansenii* calyptopis larvae observed during the major pulse of intrusion suggests that, despite the possible importance of the intrusion to the productivity of the northern Benguela system, these pulses of intrusion renewed the near-surface planktonic populations by both transporting some patches southward and bringing new populations into the system.

Briefly, strong night-time vertical segregation was observed between the major adult euphausiid species, regardless of food concentration, and appears to be related to water column structure and hydrographical discontinuities. Space partitioning between sexes of *E. hansenii* (but not other species) reveals that reproductive behavior may also play a role in regulating the vertical distribution of adult euphausiids.

Acknowledgements

I would like to thank Dr S.C. Pillar, Dr L. Hutchings, Dr H. Verheye and K.-A. Naish for their critical reviews on different drafts of the manuscript and their efforts to improve my English. Dr M.P. Olivar is also thanked for providing the copepod data. The cooperation of the crew of the R/S *Africana* and the members of the second SNEC cruise is appreciated. This research was supported by a grant under CAYCIT project number 1568/82.

References

- Allredge, A.L. and Hamner, W.M. (1980) Recurring aggregation of zooplankton by tidal currents. *Estuar. Coast. Mar. Sci.*, **10**, 31–37.
- Baker, A. de C. (1970) The vertical distribution of euphausiids near Fuerteventura, Canary Islands ('Discovery' Sond Cruise, 1965). *J. Mar. Biol. Assoc. U.K.*, **50**, 301–342.
- Barange, M. and Stuart, V. Distribution patterns, abundance and population dynamics of the euphausiids *Nyctiphanes capensis* and *Euphausia hansenii* in the northern Benguela upwelling system. Submitted.
- Bayly, I.A.E. (1986) Aspects of tidal migration in zooplankton, and its enigma variation. In De Decker, P. and Williams, W.D. (eds), *Limnology of Australia*. Dr W. Junk, Amsterdam. *Monogr. Biol.*, **61**, 349–368.
- Boyd, A.J., Salat, J. and Maso, M. (1987) The seasonal intrusion of relatively saline water on the shelf off northern and central Namibia. In Payne, A.I.L., Gulland, J.A. and Brink, K.H. (eds), *The Benguela and Comparable Ecosystems*. *S. Afr. J. Mar. Sci.*, **5**, 107–120.
- Brinton, E. (1967) Vertical migration and avoidance capability of euphausiids in the California current. *Limnol. Oceanogr.*, **12**, 451–483.
- Brinton, E. (1979) Parameters relating to the distributions of planktonic organisms, especially euphausiids, in the eastern tropical Pacific. *Prog. Oceanogr.*, **8**, 125–189.
- Frangopoulou, N. and Likakis, J.J. (1990) Vertical distribution and nocturnal migration of zooplankton in relation to the development of the seasonal thermocline in Patraikos Gulf. *Mar. Biol.*, **104**, 381–387.
- Forward, R.B. (1988) Diel vertical migration: zooplankton photobiology and behavior. *Oceanogr. Mar. Biol. Annu. Rev.*, **26**, 361–393.
- Hirota, Y., Nemoto, T. and Marumo, R. (1984) Vertical distribution of larvae of *Euphausia nana* and *Euphausia similis* (Crustacea: Euphausiacea) in Sagami bay and Suruga bay, Central Japan. *Mar. Biol.*, **81**, 131–137.

- Huntley, M. (1985) Experimental approaches to the study of vertical migration of zooplankton. In Rankin, M.A. (ed.), *Migration: Mechanisms and Adaptive Significance. Contributions in Marine Science*. Marine Science Institute, Texas, pp. 71–90.
- Kimmerer, W.J. and McKinnon, A.D. (1987) Zooplankton in a marine bay. II. Vertical migration to maintain horizontal distributions. *Mar. Ecol. Prog. Ser.*, **41**, 53–60.
- Kjørboe, T., Kaas, H., Kruse, B., Mohlenberg, F., Tiselius, P. and Aertebjerg, G. (1990) The structure of the pelagic food web in relation to water column structure in the Skagerrak. *Mar. Ecol. Prog. Ser.*, **59**, 19–32.
- Le Févre, J. and Frontier, S. (1988) Influence of temporal characteristics of physical phenomena on plankton dynamics, as shown by north-west European marine ecosystems. In Rothschild, B.J. (ed.), *Toward a Theory on Biology-Physical Interactions in the World's Ocean*. Kluwer Academic Publishers, Dordrecht, pp. 245–272.
- Longhurst, A.R. (1976) Vertical migration. In Cushing, D.H. and Walsh, J.J. (eds), *The Ecology of the Seas*. Blackwell Scientific Publications, Oxford, pp. 116–137.
- Makarov, R.R. (1979) Larval distribution and reproductive ecology of *Thysanoessa macrura* (Crustacea: Euphausiacea) in the Scotia Sea. *Mar. Biol.*, **52**, 377–386.
- Marschall, H.P. (1983) Sinking speed and size of Euphausiid eggs. *Meeresforschung*, **30**, 1–9.
- Maso, M. (1987) Preliminary hydrological results of the 'Spanish Namibian Environmental Cruise' survey 'SNEC-II'. *Collect. Sci. Pap. Int. Commn. S.E. Atlantic Fish.*, **14**, 113–124.
- Mauchline, J. (1980) The biology of mysids and euphausiids. *Adv. Mar. Biol.*, **18**, 1–681.
- Mauchline, J. and Fisher, L.R. (1969) The biology of euphausiids. *Adv. Mar. Biol.*, **7**, 1–454.
- Mostert, S.A. (1983) Procedures used in South Africa for the automatic photometric determination of micronutrients in seawater. *S. Afr. J. Mar. Sci.*, **1**, 189–198.
- Olla, B.L. and Davis, M.W. (1990) Behavioral responses of juvenile walleye pollock *Theragra chalcogramma* Pallas to light, thermoclines and food: possible role in vertical distribution. *J. Exp. Mar. Biol. Ecol.*, **135**, 59–68.
- Pearre, S. (1979) Problems of detection and interpretation of vertical migration. *J. Plankton Res.*, **1**, 20–44.
- Phillips, B.F. (1981) The circulation of the Southeastern Indian Ocean and the planktonic life of the western rock lobster. *Oceanogr. Mar. Biol. Annu. Rev.*, **19**, 11–39.
- Pillar, S.C., Armstrong, D.A. and Hutchings, L. (1989) Vertical migration, dispersal and transport of *Euphausia lucens* in the southern Benguela current. *Mar. Ecol. Prog. Ser.*, **53**, 179–190.
- Revelante, N. and Gilmartin, M. (1990) Vertical water column resource partitioning by a ciliated protozoan population under stratified conditions in the northern Adriatic. *J. Plankton Res.*, **12**, 89–107.
- Roe, H.S.J., Angel, M.V., Badcock, J., Domanski, P., James, P.T., Pugh, P.R. and Thurston, M.H. (1984a) The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 1. Introduction and sampling procedures. *Prog. Oceanogr.*, **13**, 245–260.
- Roe, H.S.J., James, P.T. and Thurston, M.H. (1984b) The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 6. Medusae, Ctenophores, Amphipods and Euphausiids. *Prog. Oceanogr.*, **13**, 425–460.
- Sameoto, D., Guglielmo, L. and Lewis, M.K. (1987) Day/night vertical distribution of euphausiids in the eastern tropical Pacific. *Mar. Biol.*, **96**, 235–245.
- Shanks, A.L. (1986) Vertical migration and cross-shelf dispersal of larval *Cancer* spp. and *Randallia ornata* (Crustacea: Brachyura) off the coast of southern California. *Mar. Biol.*, **92**, 189–199.
- Shannon, L.V., Boyd, A.J., Brundrit, G.B. and Tauton-Clark, J. (1986) On the existence of an El Niño-type phenomenon in the Benguela system. *J. Mar. Res.*, **44**, 495–520.
- Simmard, Y., Ladurantaye, R., Therrikault, J.-C. (1986) Aggregation of euphausiids along a coastal shelf in an upwelling environment. *Mar. Ecol. Prog. Ser.*, **32**, 203–215.
- Strickland, J.D.H. and Parsons, T.R. (1972) *A Practical Handbook of Seawater Analysis*, 2nd edn. *Bull. Fish. Res. Bd Canada*, **167**, 1–310.
- Tremblay, M.J. and Sinclair, M. (1990) Sea scallop larvae *Placopecten magellanicus* on Georges Bank: vertical distribution in relation to water column stratification and food. *Mar. Ecol. Prog. Ser.*, **61**, 1–15.
- Wiebe, P.H., Boyd, S.H., Dais, B.M. and Cox, J.L. (1982) Avoidance of towed nets by the euphausiid *Nematoscelis megalops*. *Fish. Bull.*, **80**, 75–91.
- Williams, R. and Frangopoulou, N. (1985) Vertical distribution and nocturnal migration of *Nyctiphanes couchii* (Crustacea: Euphausiacea) in relation to the summer thermocline in the Celtic Sea. *Mar. Biol.*, **89**, 257–262.
- Williams, R. and Lindley, J.A. (1982) Variability in abundance, vertical distribution and ontogenic

Vertical migration and distribution of euphausiids

- migrations of *Thysanoessa longicaudata* (Crustacea: Euphausiacea) in the North-Eastern Atlantic ocean. *Mar. Biol.*, **69**, 321–330.
- Wroblewski, J.S. (1982) Interaction of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone—a simulation. *Deep-Sea Res.*, **29**, 665–686.
- Youngbluth, M.J. (1975) The vertical distribution and diel migration of euphausiids in the central waters of the eastern South Pacific. *Deep-Sea Res.*, **22**, 519–536.
- Youngbluth, M.J. (1976) Vertical distribution and diel migration of euphausiids in the central region of the California current. *Fish. Bull.*, **74**, 925–936.

Received on January 24, 1990; accepted on July 17, 1990