

**Vertical Migration and Feeding of Euphausia lucens
(Euphausiacea) in the Southern Benguela.**

M.J. Gibbons^{1,2}, M. Barange³ and S.C. Pillar².

1. Marine Biology Research Institute, Zoology Department, University of Cape Town, Rondebosch 7700, Cape Town, South Africa.

2. Sea Fisheries Research Institute, Private Bag X2, Roggebaai 8012, Cape town, South Africa.

3. Instituto de Ciencias del Mar, Paseo Nacional S/N, 08003 Barcelona, Spain.

ABSTRACT

Diel migration and feeding were examined for populations of Euphausia lucens living in the near- and offshore waters of the southern Benguela. Euphausiids at both stations displayed nocturnal diel vertical migration patterns. Animals ascended in a slow-fast-slow manner which seems to be related to differential food concentrations throughout the water column. Pronounced quantitative and qualitative changes in the diet of E. lucens were observed offshore but not inshore. These differences are discussed in relation to different ambient food environments.

INTRODUCTION

Vertical migration by euphausiids has been shown to be very strongly influenced by their feeding habits (Ponomareva, 1971; Hu, 1978; Willason and Cox, 1987). Most euphausiids are believed to be omnivorous and there is growing evidence to suggest that only by migration can feeding animals meet their metabolic requirements

(Ohman, 1984; McClatchie, 1985; Price *et al.*, 1988). Feeding shows a diel rhythm, with increased activity at night. The degree of diel change in feeding intensity differs between species and appears to be related in part to the length of distance migrated. Weak migrators which are often not exposed to large differences in food type and concentration exhibit less pronounced diel feeding rhythms than those species which migrate more extensively (Ponomareva, 1971; Hu, 1978; Willason and Cox, 1987).

Euphausia lucens is the most abundant euphausiid in the southern Benguela upwelling region and occurs across the shelf area along the west coast of South Africa (Pillar, 1986; Pillar and Stuart, 1988), sometimes forming large daytime surface swarms (Nicol *et al.*, 1987). It has been demonstrated that juvenile and adult stages of E. lucens migrate extensively throughout the water column, while the eggs and first feeding, early larval stages are generally confined to the surface layers (Pillar *et al.*, 1989). The different migratory behaviour of the various ontogenic stages of E. lucens are reflected by alternative feeding strategies (Stuart and Pillar, 1990). Older individuals show strong diel changes in gut pigment levels whereas younger stages do not. It has been suggested that E. lucens is a true omnivore (Stuart and Pillar, 1990), feeding carnivorously only when "in situ" phytoplankton levels are low. Such a strategy is considered optimal in upwelling areas such as the southern Benguela which is characterized by a fluctuating environment.

A limitation of previous *in situ* feeding studies (Ponomareva, 1971; Roger, 1975; Hu, 1978; Williams and Frangopoulou, 1985; Simard *et al.*, 1986; Willason and Cox, 1987) has been the lack of knowledge concerning the relationship between vertical movement and feeding activity under different food environments. The present study follows the nocturnal ascent of adult E. lucens from low to high food concentration, in order to examine concurrent changes in feeding activities. To determine whether food availability or

length of migration influenced the speed and feeding behaviour of migrating E. lucens, populations were examined at two contrasting sites. One inshore, in shallow but highly productive waters and the other offshore, in deeper but less productive waters.

MATERIAL AND METHODS

Sample collection

During October 1987 a transect of 10 stations from 5 to 120 miles offshore were sampled off the Olifants river, South Africa (31°37'S 18°18'E), in an attempt to locate high densities of E. lucens. Two stations (Fig. 10.1) were chosen for the diel migration and feeding studies, one 5 miles from the coast (inshore station) and the other 57 miles offshore (offshore station).

At each station a CTD/rosette cast provided continuous profiles of temperature and salinity. Water samples were collected at 6 depths (according to the temperature profile) throughout the water column during ascent of the rosette.

Zooplankton collections from each station were made at regular time intervals over 12hrs (Table 10.1), using a 200µm mesh 1m² multiple opening-closing Rectangular Midwater Trawl (RMT 1x6). The net was towed obliquely at 2 knots at 5 different depth strata, from just above the bottom to the surface (offshore; 200-100m, 100-60m, 60-40m, 40-20m, 20-0m: Inshore; 80-60m, 60-40m, 40-20m, 20-10m, 10-0m). The volume filtered was estimated by means of a digital flowmeter mounted centrally in the mouth of the net. Mesozooplankton was collected in the upper 80m from 6 depth strata using a diaphragm pump. Approximately 2m³ of water was delivered from each depth through a 7.6cm² pipe and filtered on deck through a 200µm mesh. All zooplankton samples were preserved in buffered (CaCO₃) saline formalin for later processing.

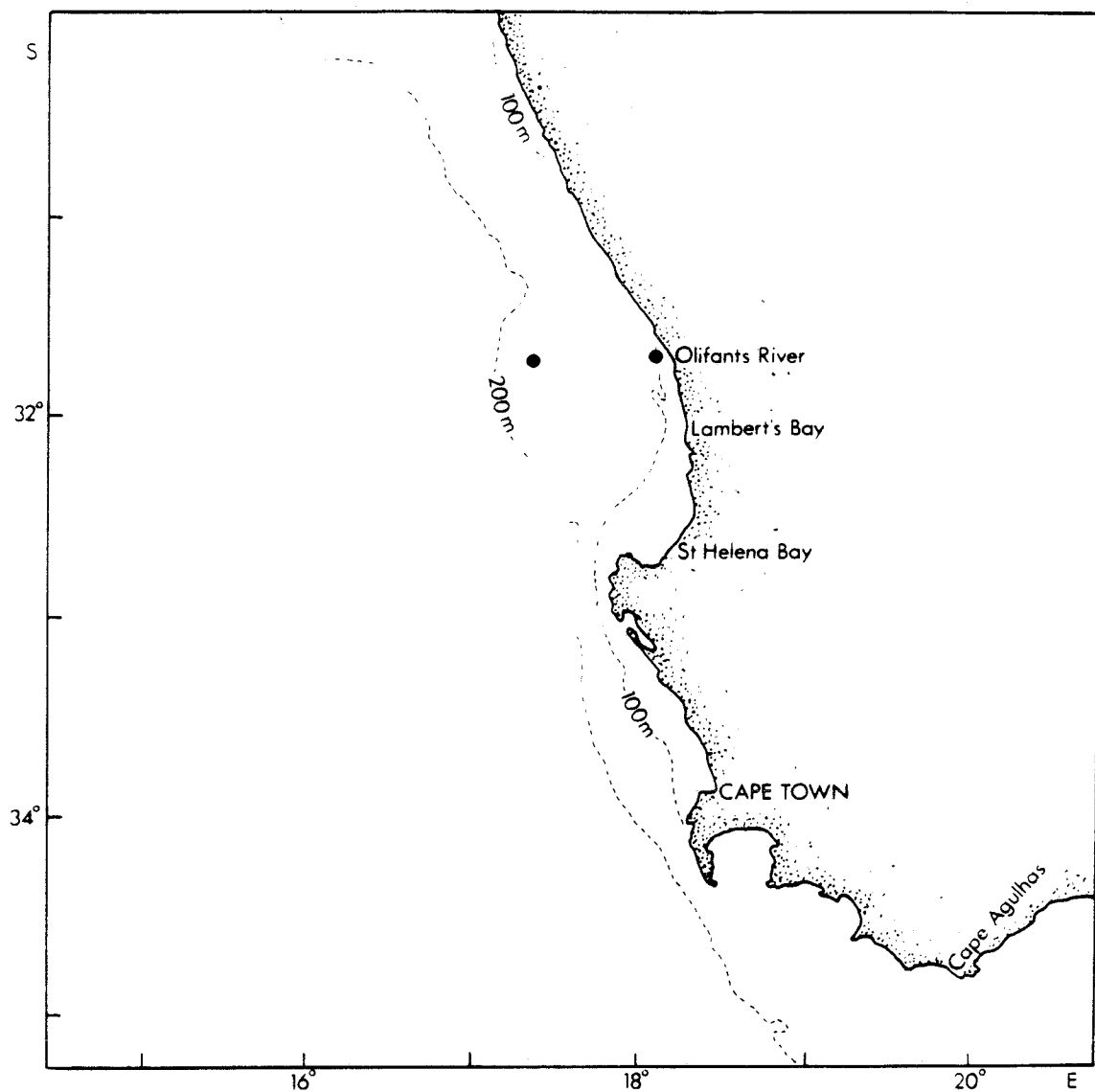


Figure 10.1. Map of St. Helena Bay showing the two sampling stations on a transect seaward of the Olifants River mouth.

Inshore migration speeds of E. lucens were estimated from echosounder (120kHz) traces. The targets of echo-sources were confirmed by RMT collections. Offshore, alternative techniques were used to calculate ascent speeds as no echo trace was available due to mechanical failure. These were estimated from RMT tows by: 1) following the upward movement of euphausiids at the different sampling layers and 2) following the movement of the Weighted Mean Depth (WMD, Roe et al., 1984a) of the population, at each sampling time.

$$WMD = (\sum N_i \cdot d_i) \div N$$

where d_i =depth of a sample (i); n_i =number of individuals at that depth; N =sum of the number of individuals over all sampling depths. The first method provides a "fastest" ascent speed estimate, while the second gives a speed of migration for the bulk of the population..which is comparable to the mode of ascent obtained using the echo-sounder. Since the stratum sampled below 100m was relatively large compared to those above it, no attempt has been made to include it in the calculations.

Sample processing

In determining vertical migration, all E.lucens were counted and mature individuals were sexed from all samples. Large collections were subsampled using a Folsom splitter and a minimum of 50 individuals counted per class (males, non-fertilised and fertilised females and juveniles). Data were standardized to numbers per square meter (250-600 adults.m⁻² offshore and 10-80 adults.m⁻² inshore) from a knowledge of the volume of water filtered by the nets (typically 90 m³ offshore and 45 m³ inshore), and the pump.

The diet of E. lucens was determined by stomach content analysis. As this is a very time consuming process, however, only animals

Table 10.1. The number of E. lucens stomach samples examined (n) at the different times and depths. Also shown is the type of sampling device.

STATION	TIME	DEPTH (m)	DEVICE	n
OFFSHORE	11.10	100-200	RMT	50
OFFSHORE	16.17	100-160	RMT	100
OFFSHORE	18.22	75-100	RMT	50
OFFSHORE	19.18	25-50	RMT	50
OFFSHORE	20.33	25-0	RMT	100
OFFSHORE	22.58	25-0	RMT	50
INSHORE	8.13	69	PUMP	100
INSHORE	13.12	62	PUMP	100
INSHORE	16.25	50-70	RMT	50
INSHORE	19.26	20-12	RMT	50
INSHORE	22.15	20-12	RMT	50

from depths corresponding to the estimated WMD for each collection time were examined (table 10.1). Euphausiids selected for stomach analysis were sexed and measured (rostrum-tip to telson-tip length) and the stomachs dissected out at X10 magnification. Visual estimates of stomach fullness (SF) were made at X20 magnification and indices scored on a 0 (completely empty) to 10 (completely full) basis (cf Ponomareva, 1971). The amount of phytoplankton consumed by individuals was calculated in a similar manner to stomach fullness indices, by estimating the proportion of "green mush" (Mauchline, 1960) in the stomach. These phytoplankton indices (PI) were also scored on a 0 to 10 basis. In the absence of detrital feeding, the application of this index yielded reproducible, relative data, although it should be noted that fullness is not always proportional to the amount of pigments in the gut (Willason and Cox, 1987). A total of 850 E. lucens were examined in this manner.

After dissection and estimation of fullness and phytoplankton indices, stomachs were placed onto glass slides in a drop of

glycerine. They were broken open and the contents examined at X160 magnification for copepod remains, especially mandibles. The width of each mandible blade was measured and the number of copepods consumed was estimated from the total number of matched pairs. Unmatched mandibles were considered to represent individual copepods. Stomachs without mandibles, but with copepod fragments were ignored in direct estimates of the number of copepods consumed, because very often more than one size of a particular fragment would be observed (eg. carapace). Such individuals were, however, scored as exhibiting carnivory, with the result that mean values quoted for numbers of copepods consumed are underestimated.

Single Factor Kruskal Wallis analyses were used to test for statistical significance between data. To determine relationships between phytoplankton and copepod consumption and euphausiid length, sex, depth of capture and ambient chlorophyll and copepod concentrations, stepwise multiple regressions (SMR's) were performed. As sex is a nominal variable, 2 "dummy" variables were substituted for each (Zar, 1984). Analyses were terminated when no additional variable was correlated at below the 5% level of significance. As estimated time-lagged food concentrations did not change, ambient data were used. All tests, means and 95% confidence limits were calculated using Statgraphics software.

RESULTS

Hydrography of the stations

Profiles of Chlorophyll a, salinity and temperature in the inshore and offshore stations are presented in figure 10.2. A strong thermocline existed at the inshore station between 10 and 20m, which was coincident with the chlorophyll maximum ($23 \mu\text{g.l}^{-1}$ at 20m). The thermocline was less marked at the offshore station. Although a sharp chlorophyll maximum was apparent at 20m, this was comparatively small ($6 \mu\text{g.l}^{-1}$) relative to the inshore station.

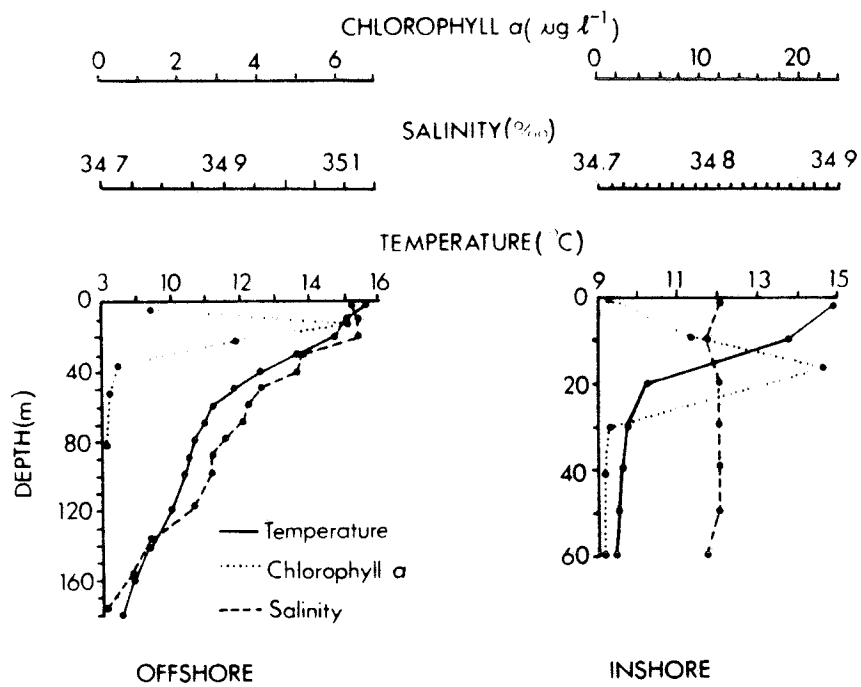


Figure 10.2. Profiles of temperature, salinity and chlorophyll a at the offshore and inshore stations. Note that the scales are different for both stations.

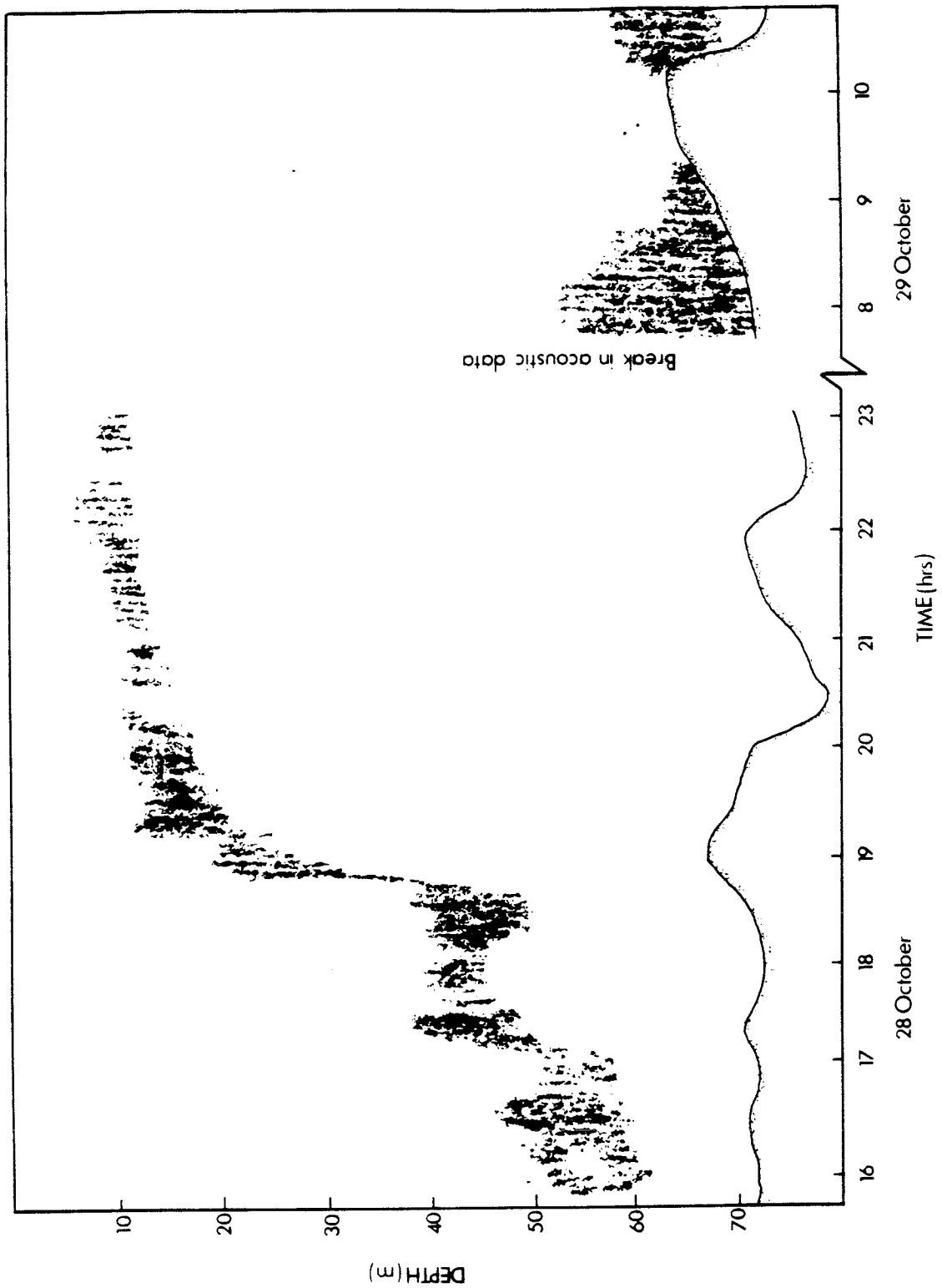


Figure 10.3. Condensed echogram of the E. lucens scattering layer at the inshore station (1cm horizontal axis represents 30 minutes).

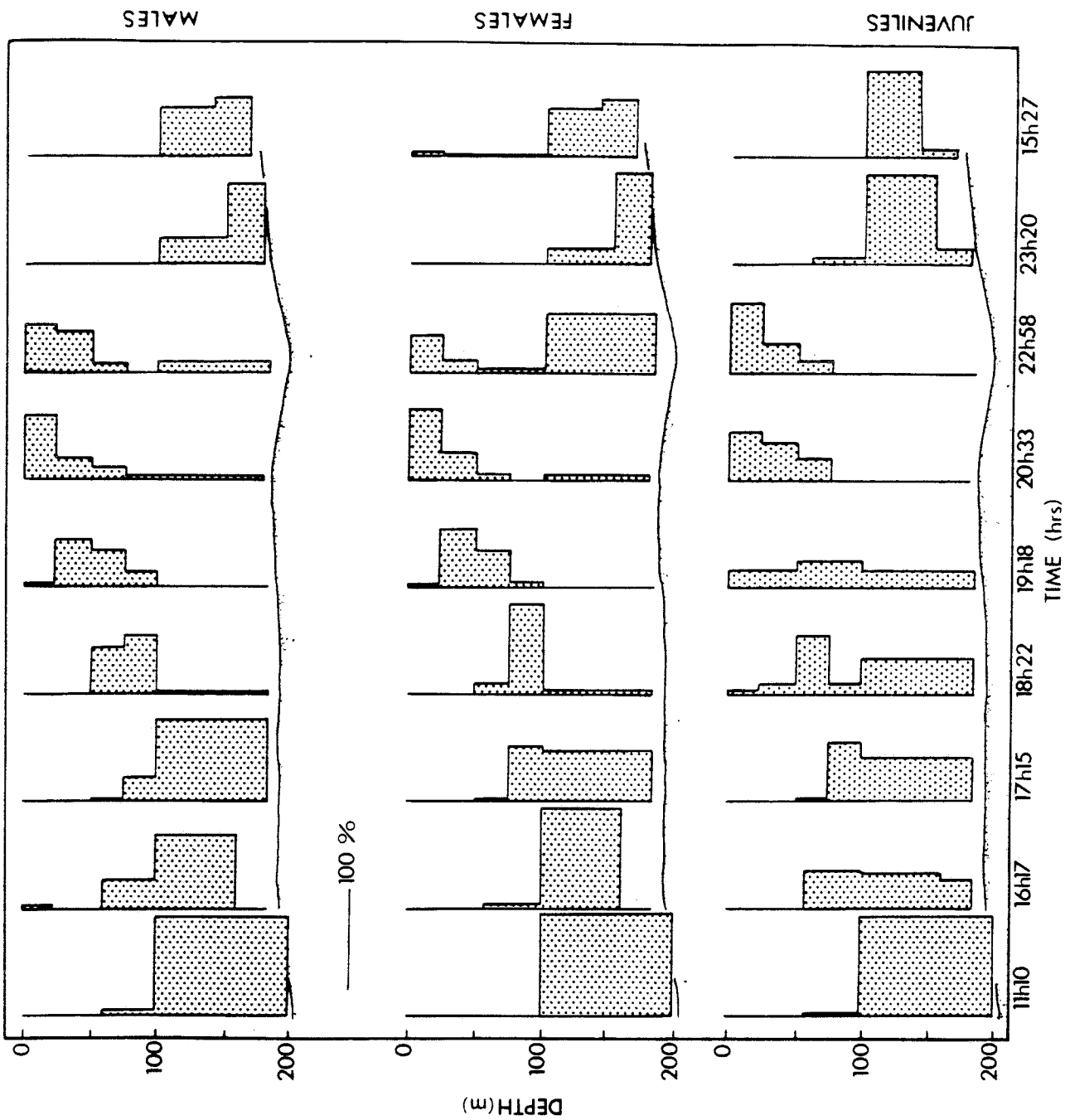


Figure 10.4. Vertical distribution of *E. Lucens* at the offshore station, by percent (of total numbers).

Copepod densities were significantly higher inshore than offshore and numbers peaked at the thermocline at both stations (Peterson *et al.*, 1990). Detailed descriptions of the copepod communities are provided by Peterson *et al.* (1990).

Vertical migration and swimming speeds of *E. lucens*

E. lucens remained at or near the bottom of the water column during the day and moved up towards the surface at night (Figs. 10.3 and 10.4). Although animals at the inshore station ascended at a mean speed of $0.37\text{cm}\cdot\text{s}^{-1}$ ($13.3\text{m}\cdot\text{h}^{-1}$) this was not constant, but varied in a slow-fast-slow manner. *E. lucens* migrated at a speed of $0.24\text{cm}\cdot\text{s}^{-1}$ from 55m to 40m; at $1.1\text{cm}\cdot\text{s}^{-1}$ from 40m to 20m and at $0.26\text{cm}\cdot\text{s}^{-1}$ from 20m to 9m (Fig. 10.3). This second relaxation coincided with the arrival of the population to the warmer, phytoplankton-rich layer.

Average speeds offshore, from 100m to the surface, were calculated as $1.18\text{ cm}\cdot\text{s}^{-1}$ ($42.5\text{ m}\cdot\text{h}^{-1}$) (Layer method) and $0.52\text{ cm}\cdot\text{s}^{-1}$ ($18.7\text{ m}\cdot\text{h}^{-1}$) (WMD method). Both methods showed that the offshore population migrated faster than the inshore population, and like the latter, animals reduced their speed near the water surface. WMD estimates of migrating speed between different layers at the offshore station were variable, being slower in deeper layers of the water column ($0.15\text{ cm}\cdot\text{s}^{-1}$ from 86.5m to 80.3m) than in the upper layers ($0.8\text{ cm}\cdot\text{s}^{-1}$ from 80.3m to 51.12m and $0.6\text{ cm}\cdot\text{s}^{-1}$ from 51.12m to 24.1m).

Animals from offshore samples were significantly larger (14.33mm) than those from nearshore samples (11.86mm: $p < 0.01$), and males were significantly smaller than females from both stations ($p < 0.01$).

Food and Feeding

The diet of *E. lucens* throughout the study period consisted largely of diatoms, tintinnids, dinoflagellates and copepods. Animals

collected offshore had significantly ($p < 0.05$) fuller stomachs ($SF = 6.92$ cf 5.01), higher phytoplankton indices ($PI = 5.74$ cf 4.57) and greater numbers of copepod mandibles (4.18 cf 1.13) in their stomachs than those inshore.

Animals at the offshore station fed continuously on copepods and phytoplankton throughout the sampling period and did not appear to change the qualitative composition of their diet during migration, although quantitatively pronounced diel feeding patterns were evident (Figs. 10.5 and 10.6). The results of the SMR (Table 10.2) suggest that the amount of phytoplankton in the stomachs of E. lucens at the offshore station was partly dependent on the concentrations of chlorophyll in the water column. It was low during the day, when the animals were at depth and ambient chlorophyll levels were low and increased significantly ($P < 0.01$) as they moved upwards (Fig. 10.5). Phytoplankton-full stomachs ($PI = 9.6$) were recorded during the first hour after reaching the surface waters, and appeared to decline thereafter. Females consumed significantly ($p < 0.01$) greater amounts of phytoplankton than males throughout the sampling period, except when the population moved through the phytoplankton-rich layer (Fig. 10.5).

The proportion of animals exhibiting carnivory at the offshore station remained high, even during the day (78.5%) and had reached 100% by 19.30hrs (Fig. 10.7). The number of copepod mandibles recovered from stomachs was significantly ($p < 0.001$) greater at night than during the day (Fig. 10.6), and results of the SMR (Table 10.2) regression suggest that this is in part attributable to ambient concentrations. Numbers of mandibles increased consistently as animals moved up in the water column and peaked (5.46 copepods per stomach) as individuals moved past the thermocline. Numbers of mandibles appeared to decline thereafter. Significantly ($p < 0.001$) greater numbers of mandibles were recovered from the stomachs of females (4.81) than males (3.33) over all strata except the thermocline layer (Fig. 10.6).

Table 10.2. Results of the stepwise multiple regression procedure. The dependent variable is the number of copepods recovered from *E. lucens* stomachs (offshore) and the amount of phytoplankton (as PI) (inshore).

OFFSHORE ($r^2 = 0.5561, n = 358$)		
INDEPENDENT VARIABLE	COEFFICIENT	Prob.
"in situ" no. of copepods	0.0003	0.0152
Euphausiid length	0.6576	0.0000
Euphausiid sex [†]	-0.4568	0.0168
Time	0.1852	0.0001
Constant	-8.9885	0.0000
INSHORE ($r^2 = 0.6962, n = 358$)		
INDEPENDENT VARIABLE	COEFFICIENT	P
Euphausiid length	0.4719	0.0000
Ambient Chlorophyll	1.4365	0.0000
Constant	-4.0935	0.0000

[†]. As sex is a nominal variable, dummy values have been substituted (see text).

Phytoplankton indices varied much more between individuals inshore than offshore, and no clear periodicity in herbivory was evident (Fig. 10.8). The amount of phytoplankton consumed appeared to increase from early morning and peak around noon (PI=6.39). Indices then declined as the population moved up in the water column at night to peak again only after arrival at the surface. There was no significant difference in the amount of phytoplankton consumed by males or females over the sampling period (Fig. 10.8). Neither ambient phytoplankton concentration nor copepod abundance were selected by the SMR procedure as accounting for variation in the observed stomach contents. This suggests that feeding appears to be largely independent of ambient levels of food.

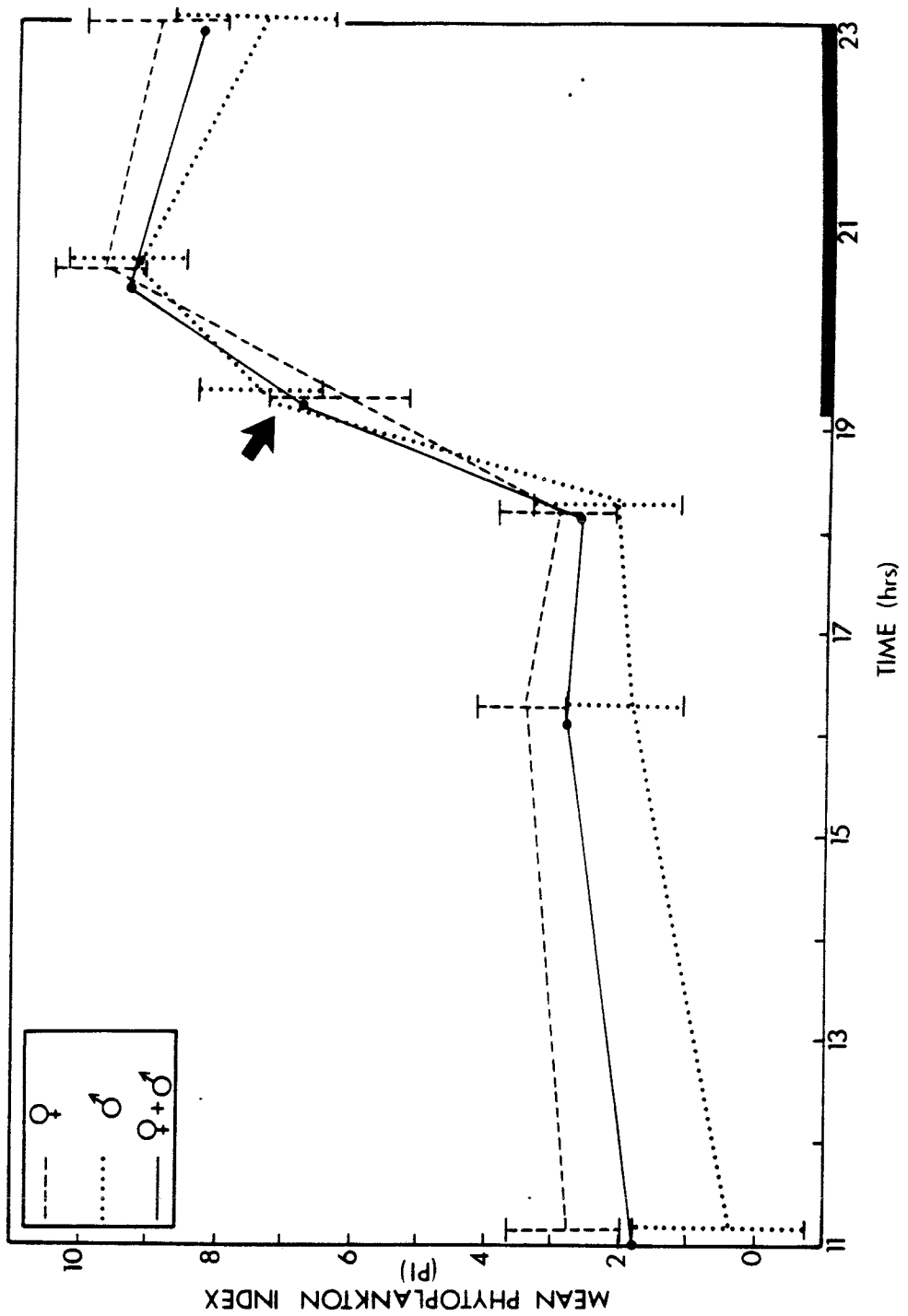


Figure 10.5. Diel changes in the mean amount of phytoplankton (as Phytoplankton Index, see text) gut contents of *E. lucens* at the offshore station. Data are presented for males and females separately and combined. Vertical bars represent 95% confidence limits about the mean. The arrow indicates the population which has just moved through the thermocline.

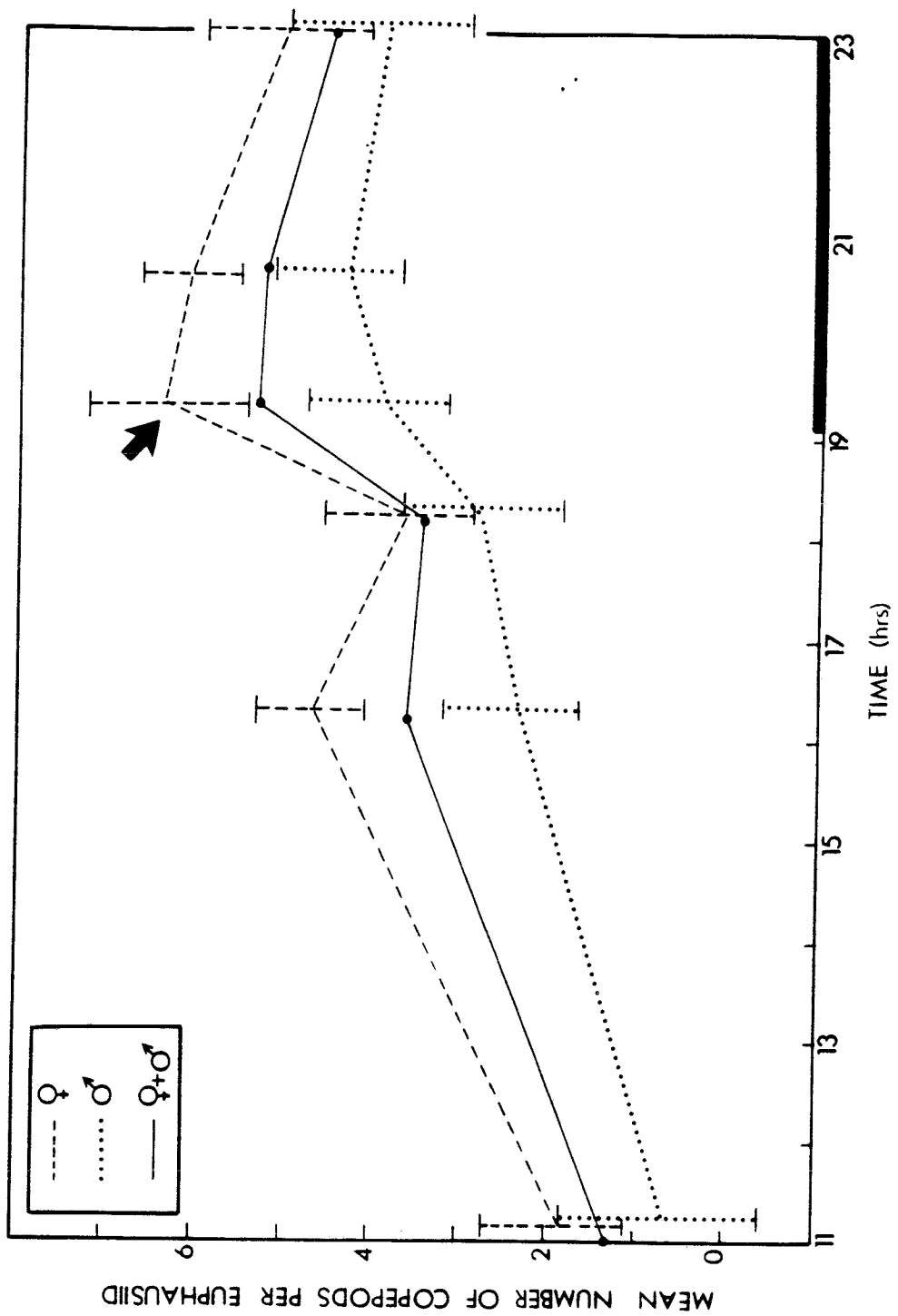


Figure 10.6. Diel changes in the mean number of copepods consumed by *E. lucens* individuals at the offshore station. Data are presented for males and females separately and combined. Vertical bars represent 95% confidence limits about the mean. The arrow indicates the population which has just moved through the thermocline.

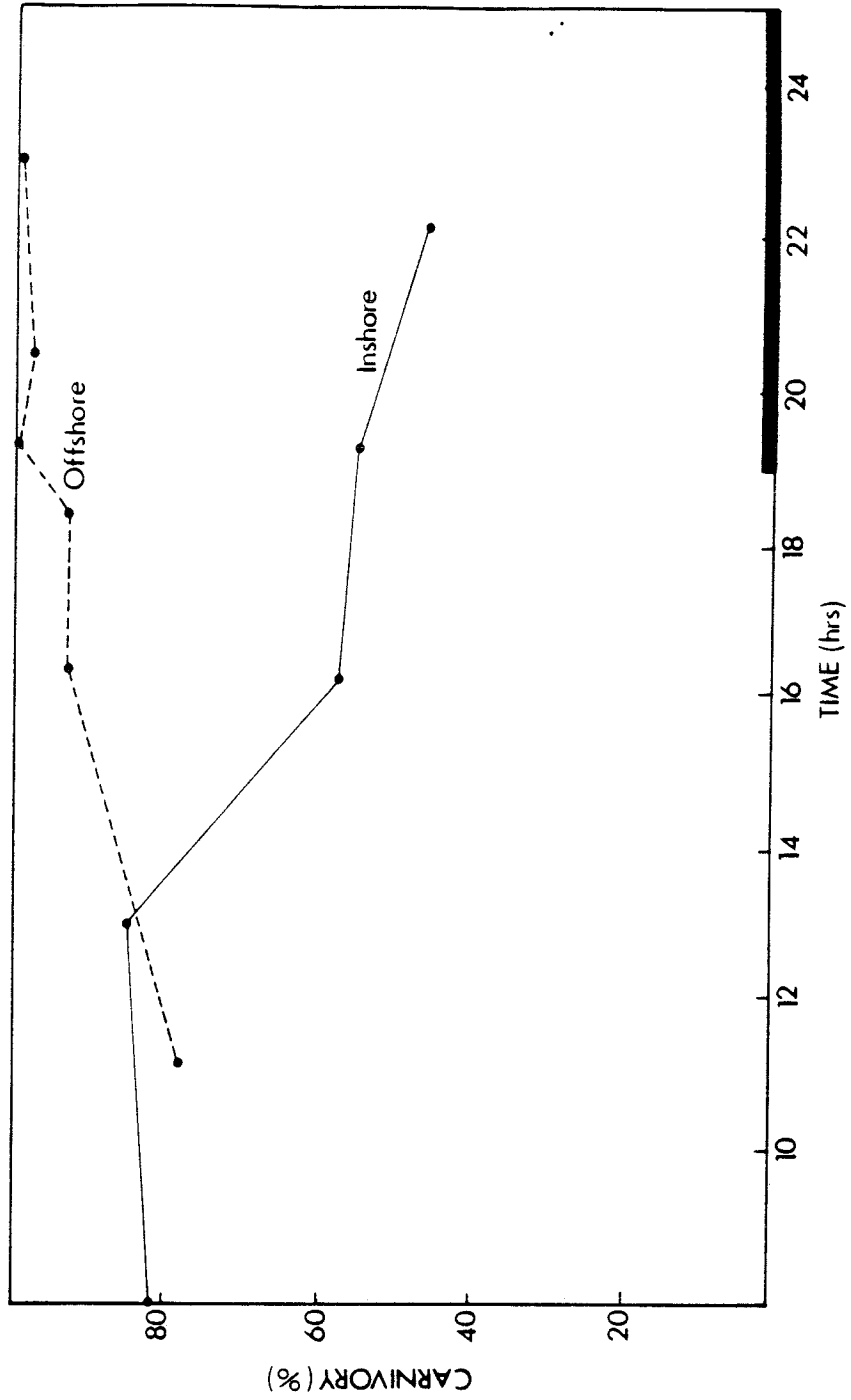


Figure 10.7. Diel changes in the proportion of *E. lucens* exhibiting carnivory, at the inshore and offshore stations.

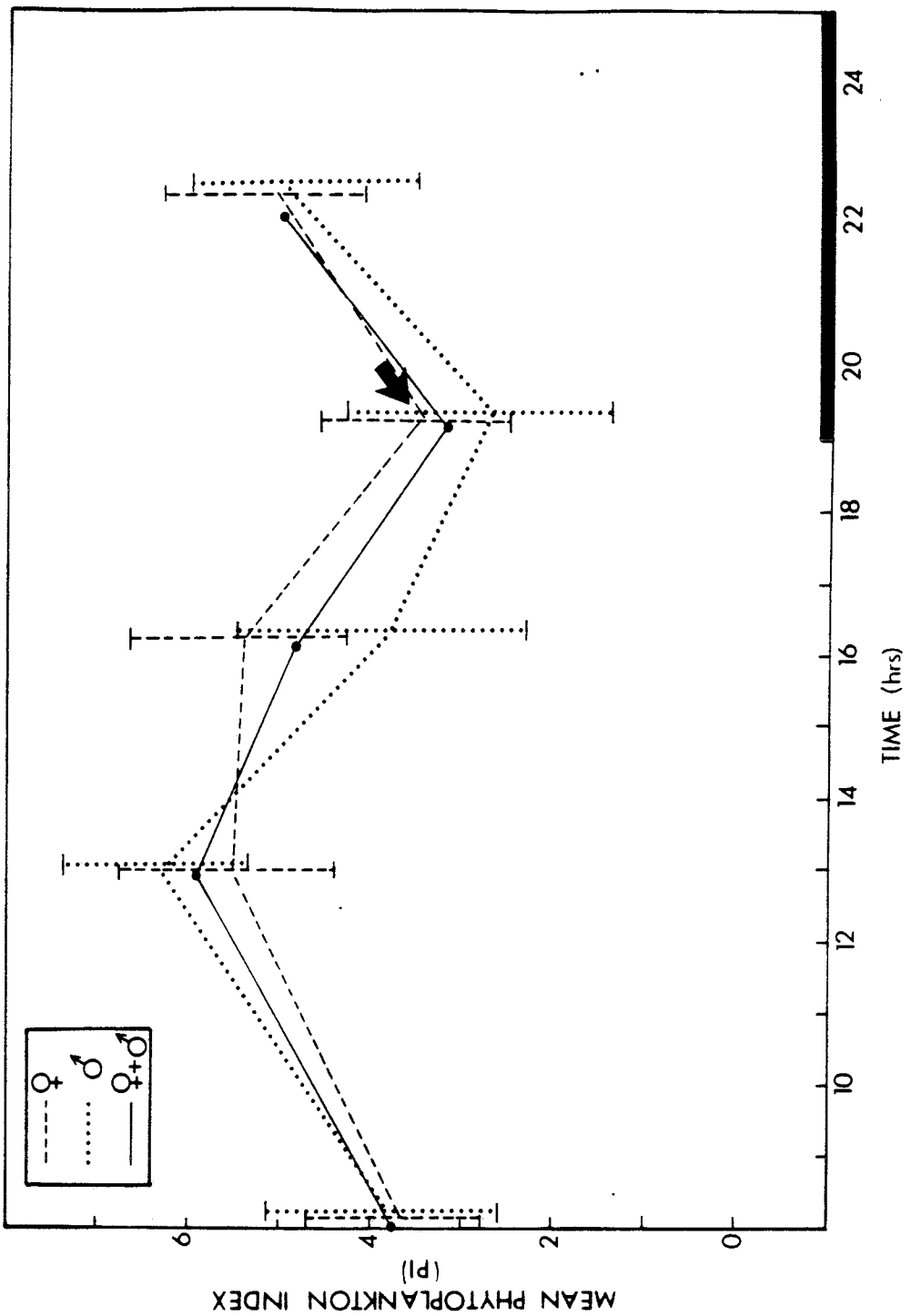


Figure 10.8. Diel changes in the mean amount of phytoplankton (as Phytoplankton Index, see text) consumed by *E. lucens* individuals at the inshore station. Data are presented for males and females separately and combined. Vertical bars represent 95% confidence limits about the mean. The arrow indicates the population which has just moved through the thermocline.

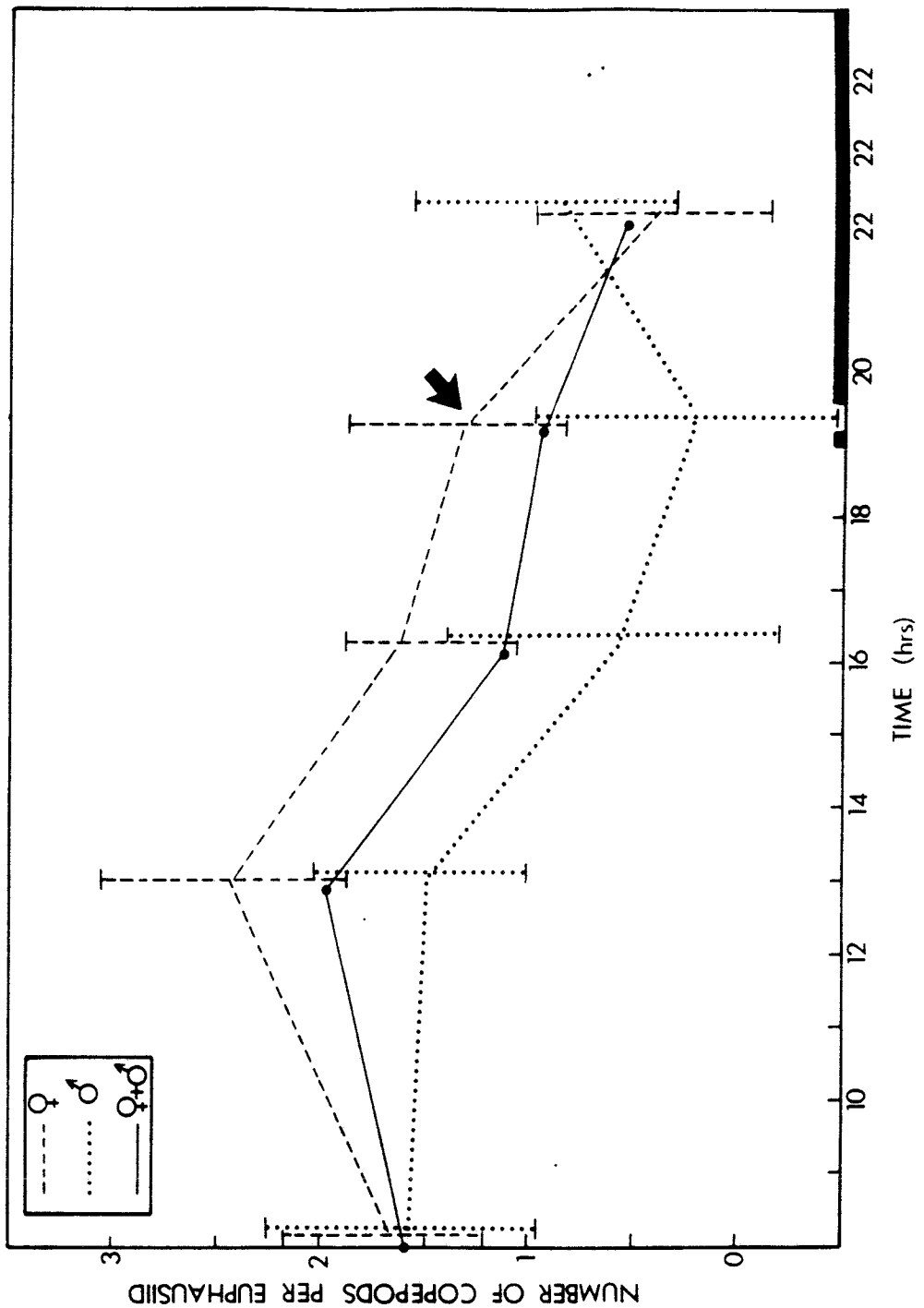


Figure 10.9. Diel changes in the mean number of copepods consumed by *E. lucens* individuals at the inshore station. Data are presented for males and females separately and combined. Vertical bars represent 95% confidence limits about the mean.

The proportion of animals exhibiting carnivory was greatest during the day at the inshore station (Fig. 10.7). The numbers of copepod mandibles in stomachs varied greatly but steadily decreased (1.9 to 0.41), as the animals moved up in the water column (Fig. 10.9). While females appeared to consume more copepods than males (Fig. 10.9), these differences were not significant ($p > 0.05$).

DISCUSSION

The speeds of vertically migrating E. lucens presented here are comparable to previous in situ estimates for other species (Hardy and Bainbridge, 1954; Kampa and Boden, 1954; Roe et al., 1984b; Williams and Frangopoulou, 1985). The slow movement and pronounced slow-fast-slow pattern of ascent, which occurred at the inshore station, (as E. pacifica; Kampa and Boden, 1954), can be viewed as a strategy to optimize food uptake in a vertically stratified food environment. The reduction in swimming speed at the chlorophyll maxima would allow E. lucens to remain for longer periods of time in regions of abundant food. Such an hypothesis is supported by the observations of McClatchie (1985) and Price (1989) that euphausiids achieved high intake rates by remaining in a patch of concentrated food rather than feeding faster. Euphausiids therefore seem to regulate their vertical speed as a strategy to remain for longer periods within "preferred" food regimes. Although regulation of vertical migration by food distribution and abundance has been previously postulated for Euphausia pacifica (Youngbluth, 1976), the influence of small scale changes in light intensity and cloudcover cannot be ignored, and the present conclusions should be viewed with caution.

The amount of phytoplankton and number of copepods in the stomachs of E. lucens at the offshore station generally reflected their relative concentrations in the water column. While the observations on herbivorous feeding are in general agreement with previous studies (eg Hu, 1978; Sameoto, 1981; Willason and Cox, 1987 but cf

Simard et al., 1986), those on carnivory are in conflict with data which suggest that euphausiids exhibit qualitative, diel changes in diet (eg. Hu, 1978; Sameoto, 1981). Stuart and Pillar (1990), have suggested, however, that E. lucens only prey on copepods when the concentrations of phytoplankton in the water column decline to below a certain threshold level (ie. at depths), and that the level of ambient chlorophyll cues a switch in feeding strategy. These conclusions were supported by their observations that when the amount of phytoplankton in the surface waters was too low to meet daily energy requirements E. lucens consumed copepods throughout the day and night.

Stomach contents reflect both the food eaten at the depth of capture and food eaten at prior depths to an equivalent of the gut passage time. It could be argued, therefore, that the timing and extent of feeding is smeared out by a long gut passage time. However, the gut passage time of copepods and phytoplankton in the stomachs of E. lucens is approximately 75 and 40 mins. respectively (Stuart and Pillar, 1990). That amounts of foodstuffs continue to increase over and above this time during migration suggests rapid feeding to the surface. Similarly, the shallow rate of decline in stomach contents once at the surface argues not a cessation of feeding but rather a reduction in feeding. It has previously been observed that migrating zooplankton exhibit elevated or rapid feeding on arrival at the surface (Lampert et al., 1988; Paffenhöfer, 1988) but then either become satiated (Simard et al., 1985; Simard et al., 1986) or reduce feeding to a lower level (Paffenhöfer, 1988). This is often tied in with an early descent of fed animals (Pearre, 1973) which in turn could account for the observed decline in stomach contents.

The inconsistent feeding pattern of E. lucens at shallower depths (inshore) has been reported previously for either weakly-migratory or non-migratory euphausiids (Ponomareva, 1971; Hu, 1978; Roger, 1975). High phytoplankton consumption and low copepod consumption

at night (but high during the day) has been frequently observed (eg. Hu, 1978) and related to food "preference" under conditions of high ambient chlorophyll (Stuart and Pillar, 1990). Elevated diurnal consumption of phytoplankton in a chlorophyll-poor environment (at depth) however, is unusual. While these results may be the artifact of an insensitive sampling index, they could also reflect the retention of nocturnally collected food (Willason and Cox, 1987) or the continued feeding on sinking, dead cells (see Mauchline and Fisher, 1969). Several euphausiids are thought to feed on detritus (see Mauchline and Fisher, 1969 for review) and Nicol et al. (1987) have previously recorded detrital material in the stomachs of E. lucens collected from daytime swarms.

Despite the increased size of animals offshore, size per-se does not explain the differences in copepod consumption between the two regions, especially as abundances of copepods were higher inshore. Although there is a very clear, positive relationship between euphausiid length and the number of copepods consumed (results of SMR and Gibbons et al., in press), large animals inshore had significantly fewer copepods in their stomachs, than offshore animals of the same size. Animals offshore may have been compensating for the relatively low concentrations of ambient chlorophyll by supplementing their diet with increased numbers of copepods, as suggested by Pillar and Stuart (1988), while the results inshore possibly reflect the "preference" of phytoplankton as a food source when it is in very high concentration (Stuart and Pillar, 1990). It could also be argued that the slightly lower temperature inshore resulted in depressed ingestion (Pearre, 1974). Alternatively, differences in physiological condition, especially reproductive, of animals at the two stations may account for the observed differences in copepod consumption. Pillar and Stuart (1988) noted a larger proportion of spawning E. lucens females offshore. Although females without eggs were rare in this study, the proportion of animals with spermatophores was higher offshore than inshore. Spawning stocks are likely to require very large

amounts of oils and proteins for incorporation into reproductive products. If phytoplankton alone cannot meet these requirements then the diet may have to be supplemented with zooplankton. This is borne out by the fact that offshore (but not inshore) females consumed significantly greater numbers of copepods (and phytoplankton) than males. Such differences in quantitative consumption are largely supported when sexual differences in size are adjusted for. The greater degree of sexual size overlap inshore, may account for the observed similarity in copepod consumption between males and females.

The results presented here demonstrate that feeding by E. lucens is very variable. Patterns of migration and diel feeding offshore were clear cut, while those inshore were less apparent. Feeding was probably continuous, and only offshore did quantitative and qualitative changes in ingestion reflect ambient food levels. Such variation may in part be due to differences in the food environment.

ACKNOWLEDGEMENTS

We would like to thank Dr L. Hutchings and the officers and crew of the R.S. Benguela for the collection of samples. We are also grateful to Drs L. Hutchings and V. Stuart as well as several anonymous referees for their useful comments on various drafts of the manuscript. We would also like to thank Mr A. van Dalsen for preparing the figures. Financial support for MJG was provided by the Benguela Ecology Programme of the Council for Scientific and Industrial Research.

REFERENCES

- GIBBONS, M.J., S.C. PILLAR AND V. STUART (in press) Selective carnivory by Euphausia lucens. Cont. Shelf Res.,
- HARDY, A.C. and R. BAINBRIDGE (1954) Experimental observations on the vertical migrations of plankton animals. J. Mar. Biol. Assoc. U.K., **33**, 409-448.
- HU, V.J.H. (1978) Relationships between vertical migration and diet in four species of euphausiids. Limnol. Oceanogr., **23**, 296-306.
- KAMPA, E.M. and B.P. BODEN (1954) Submarine illumination and the twilight movements of sonic scattering layer. Nature, **174**, 869-870.
- LAMPERT, W., R. SCHMITT AND P. MUCK (1988) Vertical migration of freshwater zooplankton: test of some hypotheses predicting a metabolic advantage. Bull. Mar. Sci., **43**, 620-640.
- MAUCHLINE, J. AND L.R. FISHER (1969) The biology of the euphausiids. Adv. Mar. Biol., **7**, 1-145.
- McCLATCHIE, S. (1985) Feeding behaviour in Meganyctiphanes norvegica (M. Sars) (Crustacea: Euphausiacea). J. Exp. Mar. Biol. Ecol., **86**, 271-284.
- NICOL, S., A. JAMES and G. PITCHER (1987) A first record of daytime surface swarming by Euphausia lucens in the southern Benguela region. Mar. Biol., **94**, 7-10.
- OHMAN, M.D. (1984) Omnivory by Euphausia pacifica: the role of copepod prey. Mar. Ecol. Prog. Ser., **19**, 125-131.
- PAFFENHÖFER, G. (1988) Feeding rates and behaviour of zooplankton. Bull. Mar. Sci., **43**, 430-445.
- PEARRE, S., Jr. (1973) Vertical migration and feeding in Sagitta elegans Verrill. Ecology, **54**, 300-314.
- PEARRE, S., Jr. (1974) Ecological studies of three west-Mediterranean chaetognaths. Inv. Pesq., **38**, 325-369.
- PETERSON, W.T., S.J. PAINTING AND L. HUTCHINGS (1990) Diel variations in gut content, diel vertical migration and estimates of grazing impact for copepods in the southern Benguela upwelling region, in October 1987. J. Plank. Res., **12**, 259-281
- PILLAR, S.C. (1986) Temporal and spatial variations in copepod and euphausiid biomass off the southern and southwestern coasts of South Africa in 1977/78. S. Afr. J. Mar. Sci., **4**, 219-229.

PILLAR, S.C. and V. STUART (1988) Population structure, reproductive biology and maintenance of Euphausia lucens in the southern Benguela Current. J. Plank. Res., **10**, 1083-1098.

PILLAR, S.C., D.A. ARMSTRONG AND L. HUTCHINGS (1989) Vertical migration, dispersal and transport of Euphausia lucens in the southern Benguela Current. Mar. Ecol. Prog. Ser., **53**, 179-190.

PONOMAREVA, L.A. (1971) Circadian migrations and feeding rhythm of some Indian Ocean euphausiid species. Oceanology, **11**, 226-231.

PRICE, H.J. (1989) Swimming behaviour of krill in response to algal patches: a mesocosm study. Limnol. Oceanogr., **34**, 649-659.

PRICE, H.J., K.R. BOYD AND C.M. BOYD (1988) Omnivorous feeding behaviour of the antarctic krill Euphausia superba. Mar. Biol., **97**, 67-77.

ROE, H.S.J. (1983) Vertical distributions of euphausiids and fish in relation to light intensity in the northeastern Atlantic. Mar. Biol., **77**, 287-298.

ROE, H.S.J., M.V. ANGEL, J. BADCOCK, P. DOMANSKI, P.T. JAMES, P.R. PUGH AND M.H. THURSTON (1984a) The diel migrations and distributions within a pelagic community in the north east Atlantic. 1. Introduction and sampling procedures. Prog. Oceanogr., **13**, 245-268.

ROE, H.S.J., P.T. JAMES AND M.H. THURSTON (1984b) The diel migrations and distributions within a pelagic community in the north east Atlantic. 6. Medusae, ctenophores, amphipods and euphausiids. Prog. Oceanogr., **13**, 425-460.

ROGER, C. (1975) Rhythms nutritionnels et organisation trophique d'une population de crustacés pelagiques (Euphausiacea). Mar. Biol., **32**, 365-378.

SAMEOTO, D.D. (1981) Relationships between stomach contents and vertical migration in Meganyctiphanes norvegica, Thysanoessa raschii and T. inermis (Crustacea Euphausiacea). J. Plank. Res., **2**, 129-143.

SIMARD, Y., G. LACROIX AND L. LEGENDRE (1985) In situ twilight grazing rhythm during diel vertical migrations of a scattering layer of Calanus finmarchicus. Limnol. Oceanogr., **30**, 598-606.

SIMARD, Y., G. LACROIX AND L. LEGENDRE (1986) Diel vertical migrations and nocturnal feeding of a dense coastal krill scattering layer (Thysanoessa raschii and Meganyctiphanes norvegica) in stratified surface waters. Mar. Biol., **91**, 93-105.

STUART, V. (1986) Feeding and metabolism of Euphausia lucens

(euphausiacea) in the southern Benguela current. Mar. Ecol. Prog. Ser., 30, 117-125.

STUART, V. AND S.C. PILLAR (1990) Diel grazing behaviour of all ontogenic stages of Euphausia lucens and in situ predation rates on copepods in the southern Benguela upwelling region. Mar. Ecol. Prog. Ser., 64, 227-241.

STONE, J.H. (1969) The chaetognatha community of the Agulhas current: its structure and related properties. Ecol. Monogr., 39, 433-463.

WILLASON, S.W. AND J.L. COX (1987) Diel feeding, laminarase activity and phytoplankton consumption by euphausiids. Biol. Oceanogr., 4, 1-24.

WILLIAMS, R. AND N. FRANGOPOULU (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.

YOUNGBLUTH, M.J. (1976) Vertical distribution and diel migration of euphausiids in the central region of the California Current. Fish. Bull., 74, 925-936.

ZAR, J.H. (1984) Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, N.J.