Vertical distribution of epipelagic siphonophores at the confluence between Benguela waters and the Angola Current over 48 hours

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Abstract

The diel distribution of epipelagic siphonophores at a station off northern Namibia (18°00' S 10°30' E) was studied. This area is characterized by the mixing of surface waters of the Angola Current with the waters of the northernmost Benguela region. During the sampling period, the continuous flow of the Angola Current gave rise to a marked thermocline at *ca* 30 m depth. In order to study the diel vertical distribution patterns of epipelagic species under these hydrographic conditions, narrow depth horizons in the top 200 m of the water column were sampled repeatedly over a 48 h period. Thirty-four species were collected. *Sphaeronectes gracilis* and *Chelophyes appendiculata* predominated. Increasing numbers of species and individuals were observed on the second day of sampling, particularly in the layers above the thermocline. Only a few species showed an upward nocturnal migration that crossed the boundary between 2 water masses. The differences in the depth distributions of the various species were related to 3 distinct phenomena: the existence of 2 separate siphonophore populations associated with each of the 2 water masses; vertical migration by the most abundant species, which were able to cross the thermocline; and differences in patch size for the most epipelagic species.

Introduction

The vertical distribution of siphonophores, primarily related to swimming ability or migration, has been a subject of growing interest. Several authors have given information on species abundance and the depth ranges in which they were taken (e.g., Alvariño, 1971). However, the use of nets that sampled broad depth intervals for extended periods has made it difficult to determine the exact depth ranges of species and populations. More recent work based on improved sampling methods, that is on hauls carried out over narrow depth ranges over short time spans, has demonstrated daily vertical migrations by some species

(Pugh, 1977; Casanova, 1980). Such studies, particularly that by Pugh (1984), have furnished valuable information but have acknowledged the uncertainty in assessing the small-scale vertical distribution of siphonophores.

When interpreting the diel vertical distribution patterns of siphonophores it is important to take account of the prevailing hydrographic conditions. Although there have been few studies on siphonophore populations (Mackie *et al.*, 1987), it is known that the existence of boundaries between different water masses, particularly in the near-surface region, can greatly influenced such distribution patterns.

The present study was undertaken to examine

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the diel variation in depth distribution of the siphonophore population at a site off Namibia, when there was a pronounced boundary between different water masses. The waters off Namibia are characterized both by their origin in the South Atlantic Central waters and by the influence of the Benguela Current (Shannon, 1985). The limit of the latter current's influence is situated near the northern edge of Namibia, around 18° S. Continuous intrusions by the Angola Current occur, bringing warmer and more saline water than that of the Benguela Current. Although the intensity of such intrusions is highly variable, its magnitude in April 1986 was exceptionally high (Boyd *et al.*, 1987). During this period the surface waters were highly stratified, presenting a pronounced boundary between the 2 water masses (Angolan waters and northernmost Namibian waters).

Material and methods

The sampling station was *ca* 96 km offshore at 18°00' S 10°30' E. The bottom was at 3 550 m. Sampling was made along a series of transects perpendicular to the coast of Namibia included in the SNEC (Spanish Namibian Environment Cruise) II oceanographic survey. The station was selected after a preliminary sampling survey during which visual examination of the haul indicated the presence of higher concentrations of planktonic cnidarians than at other stations.

The sampling cycle commenced at 08.30 h on 24 April 1986 and ended at 06.20 h on 26 April. A 1 × 6 rectangular midwater trawl multiple opening/closing net with a 200 μm mesh was employed, and 18 hauls were made. In order, the depth intervals sampled were 200–100, 100–60,

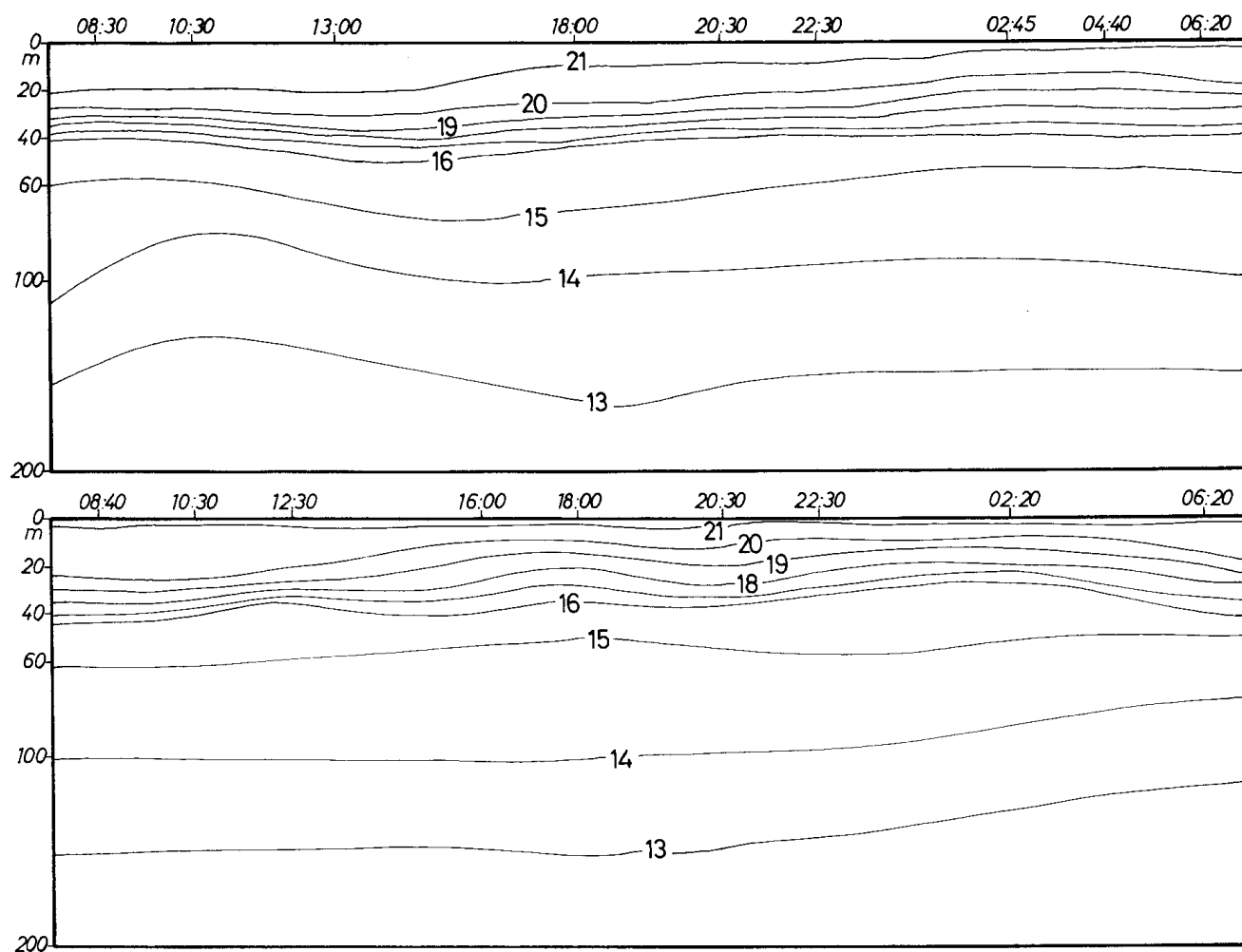*Fig. 1.* Temperature (° C) variations with depth at the sampling station over the 48 h sampling period.

60–40, 40–20, and 20–0 m (one net was not used). Hauls were oblique at an average towing speed of 0.35 m s^{-1}.

All siphonophores were identified and both the asexual (polygastric) and sexual (eudoxid) stages of calycophores were counted. Authorities for species names are as given by Totton (1965). As suggested by Pugh (1984), the numbers of phy-sonects and hippopodiids present in the samples were divided by 10 to approximate the actual number of colonies sampled. The number of nec-tophores of *Rosacea plicata*, however, was not halved because most were larval. Hydrographic data were obtained from conductivity-tempera-ture-depth casts carried out before each haul during the 48 h cycle.

Principal component analysis (PCA) was applied in order to obtain an objective description of the distribution pattern of the multispecific population sampled. The PCA was performed on the species correlation matrix after smoothing of the data by logarithmic transformation.

Results and discussion

Temperatures taken during the zooplankton hauls revealed pronounced vertical stratification (Fig. 1). Salinities exhibited a similar, though less pronounced, stratification pattern, with a slight intrusion of somewhat more saline water just above 100 m on the first day of sampling only (Fig. 2). The highest surface temperature and salinity values were consistent with characteristic values from Angolan waters (Boyd *et al.*, 1987). This warm, saline water was flowing above the
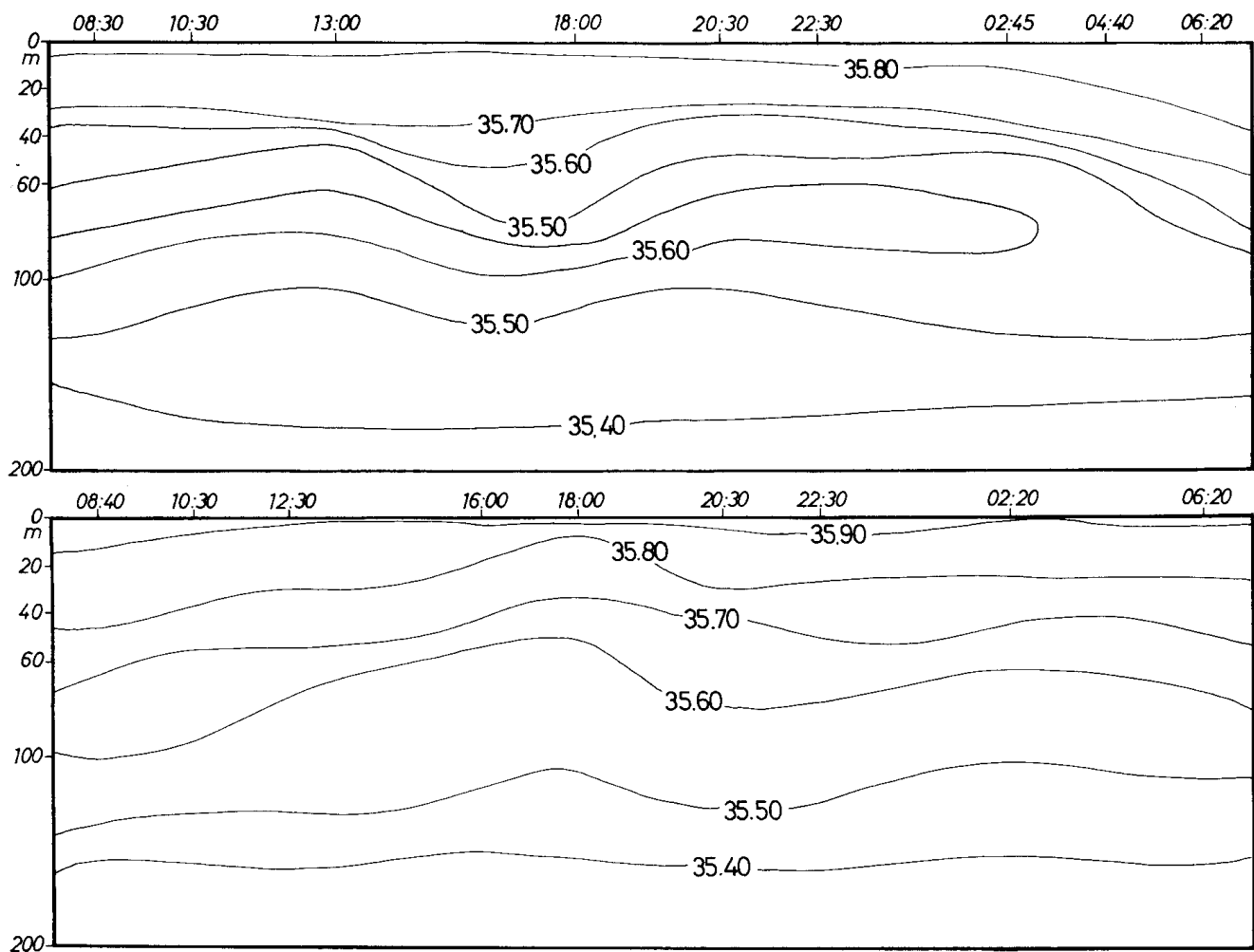

Fig. 2. Salinity (‰) variations with depth at the sampling station over the 48 h sampling period.

northernmost Namibian waters, influenced by the Benguela Current, resulting in a marked thermocline.

Thirty-four species (1 cystonect; 6 physonects; and 27 calycophores, 8 of which included the eudoxid stage) were identified. Of *Praya dubia*, the eudoxid stage only was present. A list of species, in systematic order and ranked for abundance, appears in Table 1. The numbers of calycophore and physonect species and individuals were highest on the second day. The main concentration of individuals of both these suborders occurred in the top-most depth interval, above the thermocline, calycophores increasing from 0.79 to 1.18 individuals m^{-3}, and physonects from 0.10 to 0.30 m^{-3}. In and below the thermocline layer calycophore abundance remained constant, while the physonect population decreased sharply with depth. The rise in the siphonophore population on the second day mainly resulted from increases in the numbers of *S. gracilis*, *C. appendiculata*, *A. okeni* and *N. bijuga*.

The siphonophore population shallower than 40 m comprised both sexual and asexual stages, whereas below 40 m eudoxids were extremely scarce. The average number ($\pm$ SD) of species in the 0–200 m sampling range was 13.3 $\pm$ 2.2 species on day one and 16.3 $\pm$ 1.0 species on day two, including respectively 10.8 $\pm$ 1.8 and 12.2 $\pm$ 3.1 calycophore species. Calycophores accounted for the highest number of species in the top 20 m of the water column on each day (5.0 $\pm$ 2.0 and 7.7 $\pm$ 1.3 species).

Three main distribution patterns were recognized:

1) Species inhabiting the Angola Current waters, and thereby remaining above 40 m depth (e.g., *A. tetragona, B. bassensis, N. bijuga* and *D. dispar*), were highly correlated with the positive values of the first factor of the PCA. The eudoxids of these species were the most abundant calycophores in the top 20 m, suggesting that the warm temperatures of the Angola current were favourable for their spawning.

2) Species associated with Benguela Current waters and correlated with the negative values of the first factor of the PCA were *L. conoidea, R.*

plicata and *V. glabra*, which were collected mainly at depths below 60 m.

3) Species found in both water masses, although primarily concentrated in the surface layers and highly correlated with the positive values of the first factor of the PCA were *C. appendiculata* (Fig. 3), *S. gracilis* and *A. okeni*. These were the only species that displayed distinct migratory behaviour. *S. gracilis* was extremely abundant above 40 m. However, it did not exhibit a clear migratory pattern, although obviously able to cross the thermocline, probably due to its swimming ability (Purcell, 1980). The migratory patterns of *C. appendiculata* and *A. okeni* were similar. The behaviour of *C. appendiculata* coincided with that predicted by Pugh (1977). The behaviour of *A. okeni* matched that described by Biggs (1976).

The first factor in the PCA accounted for 36 % of the variance described. In Fig. 4 the sample scores for this factor are plotted against depth and time. They show that on both days positive values were in all cases located around or above a depth of 30 m, while the negative values were all located below the thermocline. The positive values on day 2 were somewhat higher than those on day 1, whereas the negative values were similar on both days. The –0.2 contour showed a diel fluctuation, being closer to the surface at night, as would be expected from the diel vertical migration pattern of certain species. The positive values in the first factor of the PCA correspond with the highest values of individual concentrations and the major numbers of species, whereas the negative values correspond with low concentrations of individuals.

The results also point to the important effect of the thermocline on vertical distribution, particularly when the thermocline results from the superposition of two water masses of different temperatures, one overlying the other. The absence of *C. appendiculata* and *A. okeni* from the region of the boundary during daylight hours suggests that each water mass had separate populations of each species. The thermocline probably acted as a boundary, but at dusk the urge to feed was probably strong enough for individuals to swim through it towards the surface. Here they appar-

Table 1. Siphonophore species collected during the 2d sampling period. Columns A-E show, for each depth interval (in metres), the numbers of individuals of each species collected during each day (1 or 2) divided by the number of hauls within that depth interval expressed as percentages of the totals of the means for each species collected. (Hence the total of each column A1 to E2 equals ca 100.) Column F shows the means of the values for each species on day 1 or 2 from columns A-E. Column H shows the species ranked by abundance by computing the means of days 1 and 2 in column F. (For the calycophores of which both polygastric and eudoxid stages were found, the numbers of each stage were summed before computing the daily means.) Column G is based upon the same raw data as are columns A-E and the computations are similar to those in column F but are grouped into day and night periods instead of into separate days. The order of ranking (not shown) based upon column G is not statistically significantly different from that shown in column H. (1 = 1st day; 2 = 2nd day; D = day-time; N = night-time.)

	A		B		C		D		E		F		G		H
Species	20–0		40–20		60–40		100–60		200–100		Means		Means		Rank
	1	2	1	2	1	2	1	2	1	2	1	2	D	N	
Suborder Cystonectae															
Rhizophysa eysenhardti	–	0.05	–	–	–	–	–	–	–	–	–	0.01	–	0.01	34
Suborder Physonectae															
Apolemia uvaria	–	–	–	–	–	–	–	–	0.40	–	0.08	–	–	0.10	28
Agalma okeni	4.11	8.20	2.91	3.15	7.75	7.66	4.87	6.57	2.51	1.93	4.43	5.50	4.87	3.95	7
Halistemma rubrum	–	–	–	4.84	–	–	–	3.68	–	0.14	–	1.73	0.02	2.45	15
Nanomia bijuga	6.88	18.80	0.33	3.80	–	–	–	–	–	–	1.44	4.52	2.48	3.42	10
Physophora hydrostatica	–	–	1.22	–	2.80	0.67	1.09	–	–	0.09	1.02	0.15	0.07	1.22	18
Forskalia leuckarti	0.01	0.27	–	2.00	20.68	3.76	2.92	1.36	–	0.09	4.71	1.49	2.35	2.92	9
Suborder Calycophorae															
Amphicaryon acaule	0.05	–	–	–	–	–	2.92	–	–	–	1.49	–	–	0.79	16
Rosacea plicata	–	–	–	–	–	–	2.43	–	64.03	42.85	13.29	8.57	9.50	13.22	4
Praya dubia	–	–	–	–	–	–	–	–	3.12	6.68	0.62	1.33	1.09	0.81	12
Hippopodius hippopus	0.02	–	–	–	–	–	–	0.32	–	–	0.01	0.06	0.05	–	31
Sulculeolaria quadrivalvis	–	0.43	–	–	–	1.61	–	–	–	–	–	0.40	0.36	0.05	22
Sulculeolaria turgida	–	0.09	–	–	–	–	–	–	–	–	–	0.01	–	0.01	33
Sulculeolaria chuni	0.18	0.15	–	–	–	–	–	–	–	–	0.03	0.03	0.09	–	30
Sulculeolaria monoica	0.07	–	–	–	–	–	–	–	–	–	0.01	–	–	0.01	32
Lensia conoidea	–	–	1.09	–	–	6.18	13.29	5.67	10.37	19.97	4.95	6.35	5.45	6.28	6
Lensia multicristata	0.32	–	–	0.38	–	–	–	–	6.39	2.22	1.34	0.52	1.71	0.78	13
Lensia hardy	–	–	–	–	6.08	4.56	12.43	5.93	1.86	0.96	4.07	2.29	1.91	4.42	8
Lensia subtilis	–	–	–	0.92	–	–	–	–	–	–	–	0.18	0.20	–	26
Chelophyes appendiculata	16.90	34.94	7.22	14.91	6.46	22.31	10.60	25.02	7.65	13.47	9.76	22.10	19.35	10.86	2
Muggiaea kochi	0.15	1.44	3.21	–	–	–	–	–	–	–	0.67	0.28	0.35	0.63	19
Muggiaea atlantica	0.70	0.12	0.92	–	–	–	–	–	–	0.48	0.32	0.12	0.21	0.23	21
Eudoxoides spiralis	–	0.05	–	–	–	–	–	–	1.05	0.58	0.21	0.11	0.16	0.16	24
Eudoxoides mitra	–	0.26	–	–	–	–	–	–	–	–	–	0.05	–	0.04 ⎫	29
eudoxid	0.15	–	–	–	–	–	–	–	–	–	0.03	–	–	0.02 ⎬	
Diphyes dispar	3.56	–	–	–	–	–	–	–	–	–	0.71	–	0.13	0.43 ⎫	11
eudoxid	20.60	–	–	–	–	–	–	–	–	–	4.12	–	–	3.01 ⎬	
Diphyes bojani	0.31	0.62	–	–	–	–	–	–	–	–	0.06	0.12	0.17	0.04	23
Vogtia glabra	–	–	–	–	–	–	–	–	–	2.24	1.41	2.61	0.58	0.79	17
Ceratocymba sagittata	–	–	1.09	–	–	–	1.82	–	–	–	0.58	–	0.20	0.19 ⎫	20
eudoxid	–	–	–	–	–	3.49	–	–	–	–	–	0.69	–	1.06 ⎬	
Abyla schmidti	–	0.11	–	–	–	–	–	–	–	–	–	0.02	0.03	– ⎫	27
eudoxid	–	0.36	–	–	–	–	–	–	–	–	–	0.07	0.10	– ⎬	
Abyla ingeborgae	–	–	–	–	–	–	–	1.12	–	–	–	0.22	0.19	–	25
Abylopsis tetragona	3.23	1.15	9.46	4.84	–	–	1.70	0.64	–	–	2.87	1.32	1.28	2.83 ⎫	3
eudoxid	20.60	11.80	36.50	12.45	14.56	–	5.12	–	–	–	15.35	4.85	11.76	7.09 ⎬	
Bassia bassensis	2.03	1.27	3.67	0.84	–	–	–	–	–	–	1.14	0.42	1.41	0.23 ⎫	5
eudoxid	17.12	7.89	24.92	9.15	6.46	6.72	–	–	–	–	9.70	4.75	10.63	3.93 ⎬	
Enneagonum hyalinum	–	0.32	–	1.00	4.34	–	–	0.96	0.25	–	0.91	0.45	0.23	1.04 ⎫	14
eudoxid	–	0.35	–	1.00	–	–	–	–	–	–	–	0.27	0.07	0.21 ⎬	
Sphaeronectes gracilis	2.83	11.1	7.35	40.90	31.03	43.01	41.40	46.59	0.90	7.84	16.70	29.88	23.54	26.88	1

ently remained on the following day since there was no evidence of a downward migration. In general, the thermocline at 20–40 m acted as a boundary separating the siphonophore populations associated with each water mass. Only a small fraction of the species, although they were the most abundant on either side of the thermocline, passed through this boundary.

Besides variations in vertical distribution, differences in horizontal distribution were observed. Some species showed similar concentrations in the surface layer (Angola Current) on both days, whereas others presented variations independent of any diel rhythm. The Angola Current flow was slow but constant, and the effect of drift was the same for all individuals. Hence the different concentrations recorded resulted from differences in

species' patch sizes. Accordingly, species such as *A. tetragona* and *B. bassensis* had larger patch sizes than the rest of the species.

In conclusion, vertical variations in abundance are considered to be caused by 3 phenomena: the existence of 2 separate siphonophore populations, associated with each of the 2 water masses separated by a thermocline; vertical migration by the most abundant species, which were able to cross the thermocline; and, for the most epipelagic species, differences in patch size.
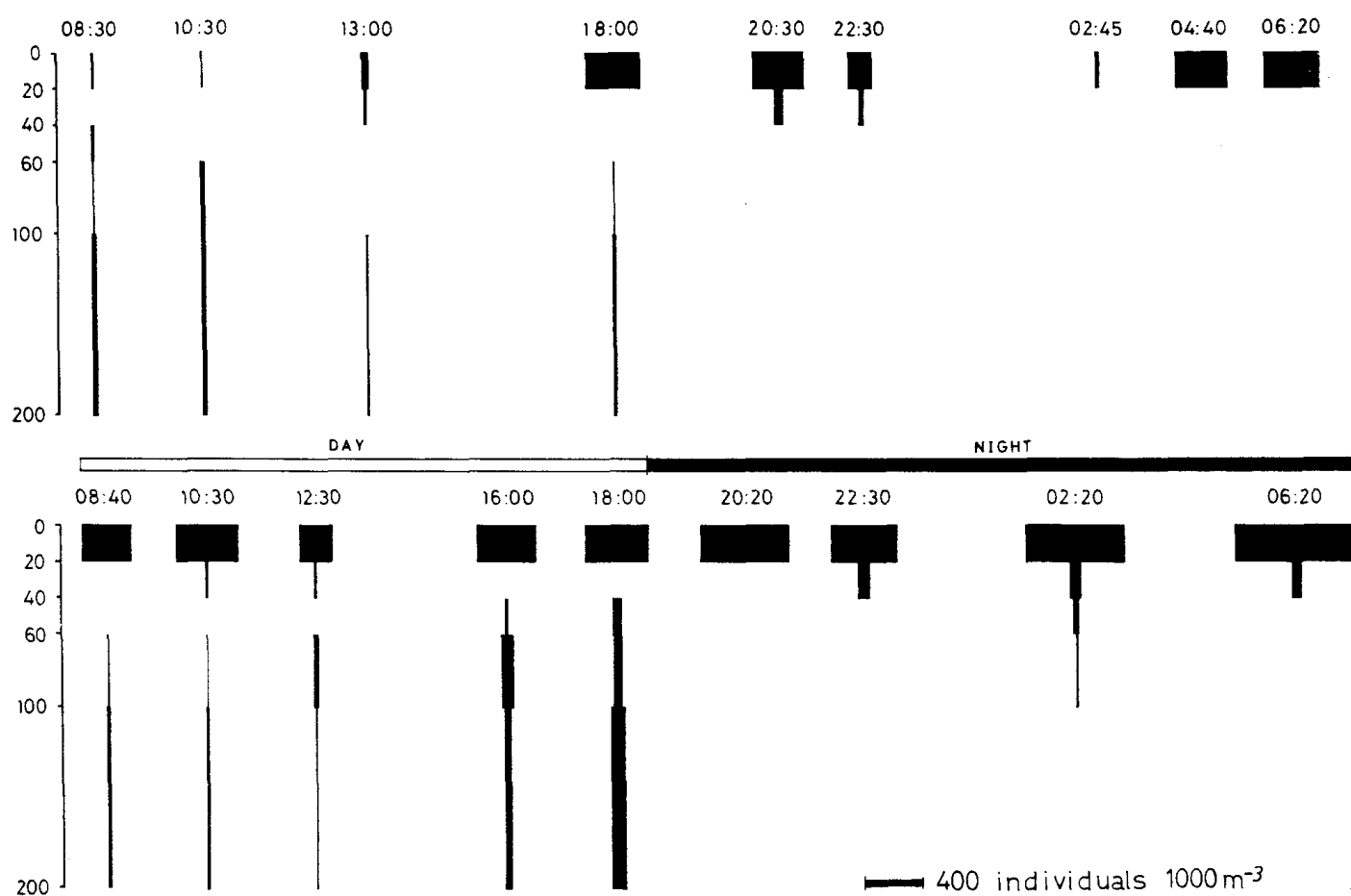
Acknowledgements

Fig. 3. Depth (m) distribution and concentration of *Chelophyes appendiculata* during the 48 h sampling period. Vertical scale in metres.
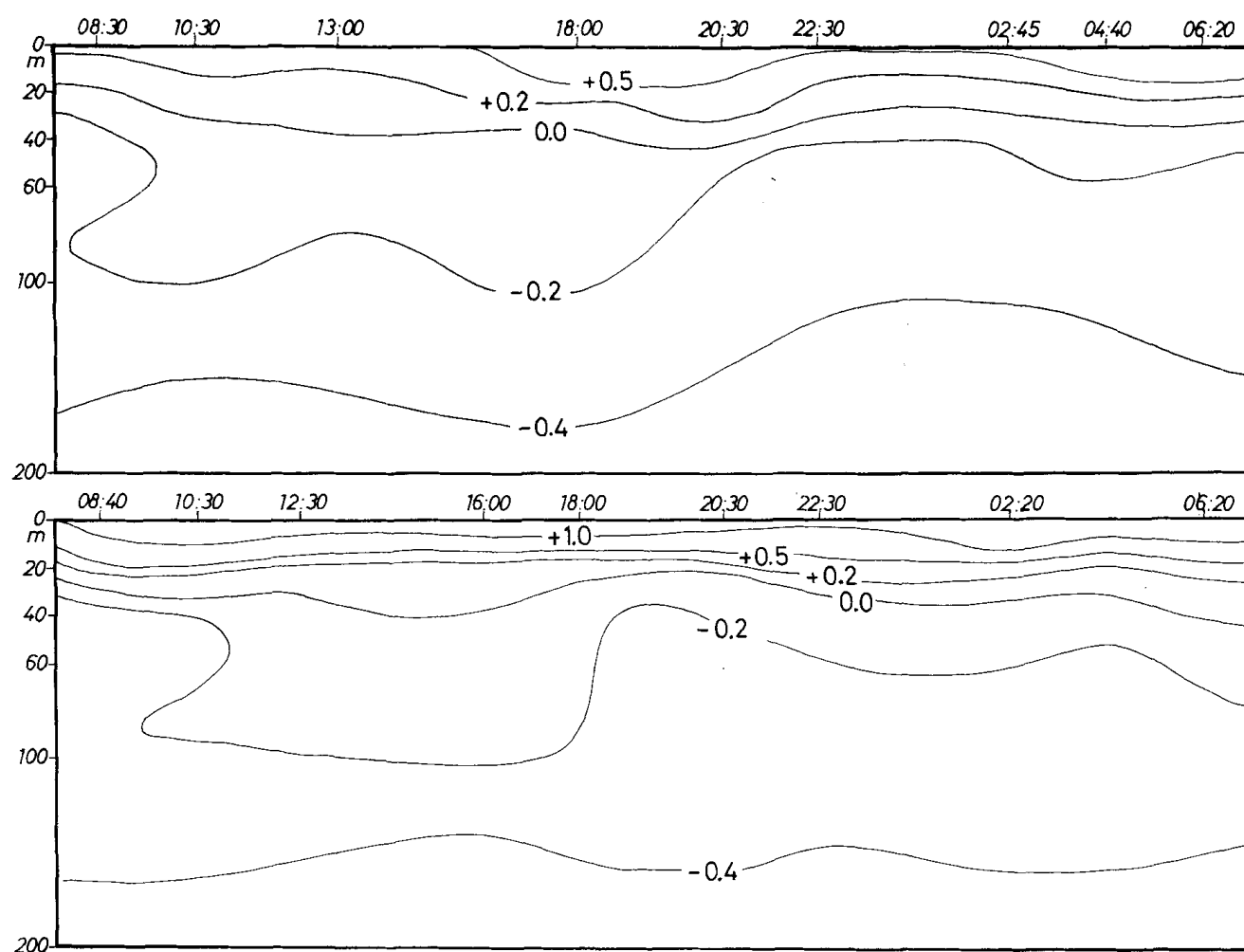
Fig. 4. Distribution of the f-scores from the first factor of the PCA over the 48 h sampling period. Positive values were located above the thermocline, negative values below.

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