Influence of the thermocline on the vertical migration of medusae during a 48 h sampling period

F. Pagès * and J.-M. Gili

Institut de Ciències del Mar (C.S.I.C.), Passeig Nacional s/n, 08039 Barcelona, Spain

The vertical distribution and migratory movements of epiplanktonic medusae were studied at an oceanic station off northern Namibia (18°00'S / 10°30'E). Samples were collected from five separate depth strata (200–100 m, 100–60 m, 60–40 m, 40–20 m, and 20–0 m) using a multiple opening and closing RMT 1×6 net over a 48-h period. The area was characterized by mixing of the Angola Current surface waters with the northernmost subsurface waters of the Benguela Current. During the sampling period there was a continuous flow of water from Angola, giving rise to a strong thermocline between 20 and 40 m depth. A total of 17 species of medusae were captured, of which *Aglaura hemistoma, Liriope tetraphylla*, and *Solmundella bitentaculata* were the most abundant. Both the number of species and the number of individuals were higher on the second than on the first day of sampling, chiefly in the 20–0 stratum. Differences in abundance appeared to be related to the patch size of each species. The depth diistribution of the medusae population was characterized by the existence of two assemblages, one associated with each current, and by the presence of the thermocline, which acted as a boundary between the two water masses and did not facilitate migratory movements of the most abundant species. The non-migratory distribution pattern of most of the species was attributable to the high concentration of potential prey items and to the absence of predators in the layer above the thermocline throughout the sampling period.

Die vertikale verspreiding en migratoriese bewegings van epiplanktoniese meduse is bestudeer by 'n oseaanstasie in Noord-Namibië (18°00'S / 10°30'0). Monsters is versamel vanaf vyf verskillende dieptestrata (200–100 m, 100–60 m, 60–40 m, 40–20 m, and 20–0 m) deur gebruik te maak van 'n veelvuldige oop- en toemaak RMT 1×6 net oor 'n tydperk van 48 h. Die gebied is gekenmerk deur die vermenging van oppervlakwater van die Angolastroom met die mees noordelike onderoppervlakwater van die Benguelastroom. Gedurende die bemonsteringstydperk was daar 'n aanhoudende vloei van water vanaf Angola, wat tot die vorming van 'n sterk termoklien tussen 20 en 40 m diepte aanleiding gegee het. 'n Totaal van 17 medusae-spesies is gevang, waarvan *Aglaura hemistoma, Liriope tetraphylla*, en *Solmundella bitentaculata* die talrykste was. Die aantal spesies sowel as die aantal individue was hoër op die tweede as die eerste dag van monsterneming, hoofsaaklik in die 20–0 stratum. Verskille in die talrykheid het geblyk 'n verwantskap te toon met die kolgrootte van elke spesie. Die diepteverspreiding van die medusaebevolking is gekenmerk deur die bestaan vam twee groeperings, een geassosieer met elke seestroom, en deur die teenwoordigheid van die termoklien wat as grens tussen die twee waterliggame gedien het en nie die migratoriese bewegings van die mees talryke spesies vergemaklik het nie. Die nie-migratoriese verspreidingspatroon van die meeste van die spesies kon toegeskryf word aan die hoë konsentrasie van potensiële prooi-items en die afwesigheid van predatore in die laag bokant die termoklien tydens die hele bemonsteringsperiode.

* To whom correspondence should be addressed

One of the most important phenomena in the small-scale distribution of zooplankton takes place in the upper layers of the water column, where species may remain in discrete depth strata or migrate vertically scores of metres in a short period. Investigations into the causes of such vertical migrations have been reported in numerous studies, but there is no general theory that accounts for vertical migrations. Light intensity seems to be the mechanism that triggers the migrations (Forward 1988), yet other processes also appear to be directly related to whether or not medusae need to carry out vertical migrations. Certain researchers consider the search for prey to be the cause of vertical migrations (Enright 1977; Longhurst & Harrison 1989), while others consider the need to escape from predators to be the regulatory mechanism underlying such migrations (Dagg 1985; Gabriel & Thomas 1988).

Although medusae have in some instances been observed to respond to light stimuli (Arkett 1985), there is no clear evidence of any mechanism regulating medusae migrations. Some evidence of active migration by certain species has been reported (e.g. Mackie, Larson, Larson & Passano

1981), but other workers have reported evidence of the converse (e.g. Roe, James & Thurston 1984). In any event, it seems that different species may or may not perform migrations depending upon both the hydrographic and trophic characteristics prevailing in the environment.

The role of the thermocline as a physical barrier to the vertical migration and distribution of zooplanktonic organisms is a subject of constant interest to planktologists. The findings of past studies (Angel 1968; Sameoto 1984, 1986; Williams & Fragopoulu 1985; Fragopoulu & Lykakis 1990) have been inconclusive, owing to the differing physical and chemical characteristics of the water masses considered in different studies and the diverse biology and ethology of the components of the zooplankton. Concomitantly, the vertical structure of the water column seems to play a role in regulating the activity of zooplanktonic organisms, to the point of assisting or impeding migrations (Pillar, Armstrong & Hutchings 1989; Kiørboe, Kaas, Kruse, Mohlenbrg, Tiselius & Aertebjerg 1990).

The influence of the thermocline on the vertical distribution and migratory movement of medusae has been studied

in the laboratory (Arai 1976) and at sea (Southward & Barret 1983), but the number of species considered was quite limited compared with the number of known species and, furthermore, medusae display a wide variety of locomotive (Gladfelter 1972; Mills 1981; Larson, Mills & Harbison 1989) and migratory movements (Williams & Conway 1981; Mills 1983; Mills & Goy 1988).

Data on the depth distributions of the most common species have been published in a number of papers, but few studies have analysed the vertical distribution within discrete depth intervals (Moreira 1973; Benovic 1976; Roe *et al.* 1984).

The present study was carried out at an oceanic station where a strong thermocline was produced by the meeting of two oceanic currents with differing hydrographic characteristics, with the waters of the Angola Current circulating above the waters of the Benguela Current. The object was to examine the vertical distribution and migratory movement of medusae during a 48 h sampling period in various depth strata in the upper 200 m of the water column.

The waters off Namibia are characterized by their origin in South Atlantic Central waters and by the Benguela Current, which flows along the entire coast (Shannon 1985). The limit to the influence of the Benguela Current is situated at around 17°S near the northern border of Namibia. Continuous intrusions by the Angola Current, carrying warmer, more saline water than the Benguela Current, occur all year long. Although the intensity of such intrusions is highly variable, the intrusion that took place in April 1986 was exceptionally intense (Boyd, Salat & Masó 1987), giving rise to a marked boundary between the two water masses.

Materials and Methods

The sampling station was located 96 km from the coast at 18°00'S / 10°30'E, where bottom depth was 3550 m. It was the last of a series of stations located along transects perpendicular to the Namibian coast occupied during the second Spanish Namibian Environmental Cruise (SNEC II) [for additional information, see Olivar (1990) and Pagès & Gili (1991)]. This station was selected after preliminary sampling, during which visual examination of the trawls indicated higher concentrations of planktonic cnidarians than at other stations. The hauls carried out in this 48 h sampling period employed the same strategy and methodology used in the remainder of the cruise.

The sampling period commenced at 8:30 on 24 April 1986 and ended at 6:20 on 26 April 1986. Tows were effected every 2–3 h, the shortest feasible period between hauls. A 1 m² multiple opening-closing RMT 1×6 net with a mesh size of 200 μm was used to collect the samples. The depth strata sampled were 200–100 m, 100–60 m, 60–40 m, 40–20 m, and 20–0 m. Hauls were oblique, and towing speed was 0,35 m s⁻¹; vessel speed during the hauls was 2 knots. All the medusae caught were removed, counted, and sorted, and the data were standardized to number of individuals per 1000 m³ based on the flow of water through
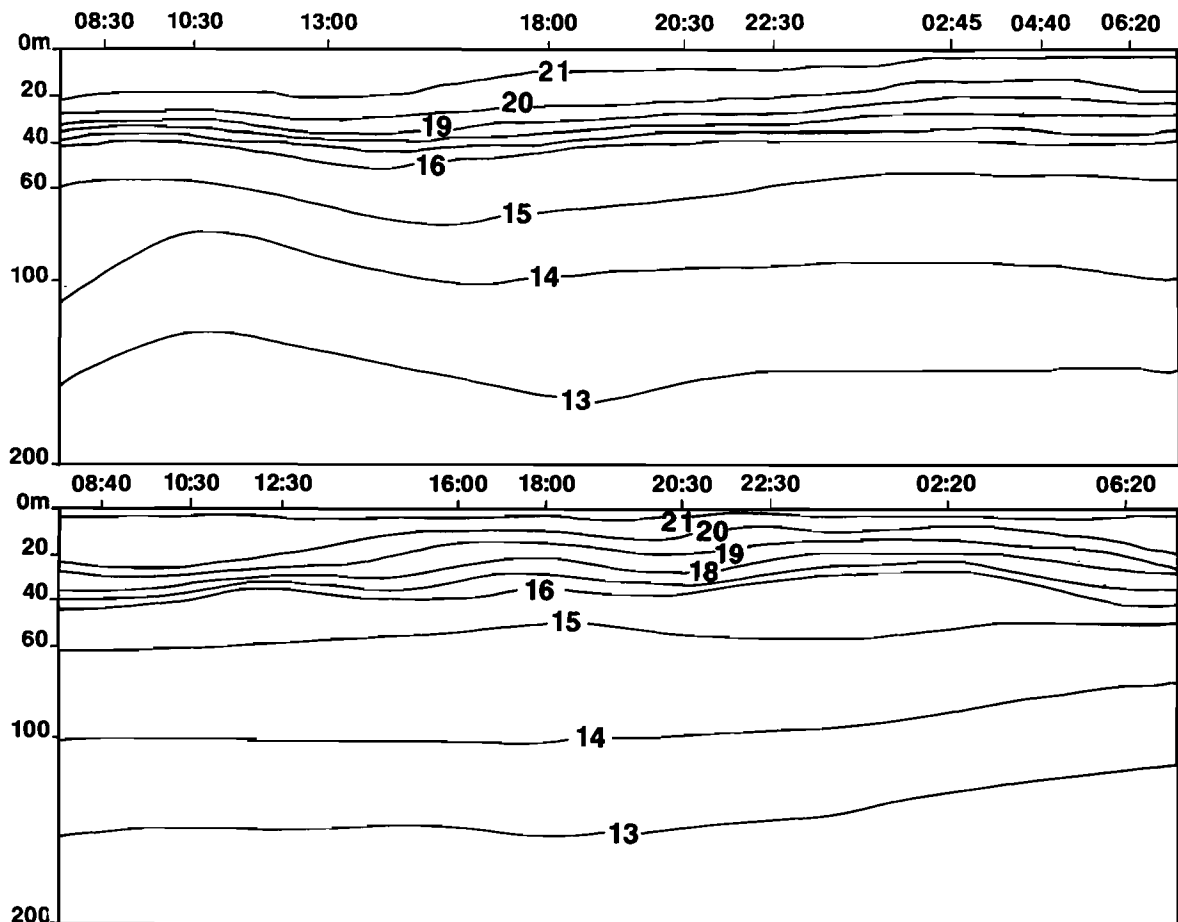

Figure 1 Temperature (°C) variations with depth at the sampling station over the 48 h sampling period.

the meshes during each tow. Flow was estimated by means of digital flowmeters mounted centrally in the mouth of each of the six 200 μm-mesh nets and externally on the net frame. Between plankton tows temperature and salinity data were collected at 5-m intervals in the upper 200 m by means of a calibrated CTD probe, with simultaneous sampling of the water column at various depths using a rosette system.

Results

The temperature values recorded at the sampling station over the two days of sampling were indicative of pronounced vertical stratification (Figure 1), with a thermocline located at a depth of between 20 and 40 m. The salinity values displayed a similar but less intense pattern of stratification, with a slight penetration by more saline water at depths above 100 m on the first day (Figure 2).

In all, 17 species of medusae were caught, namely, one anthomedusa, four leptomedusae, three trachymedusae, six narcomedusae, and three scyphomedusae species (Table 1). The species composition indicated a higher proportion of oceanic species.

In order to define the space occupied by each species over the water column, the weighted mean depth (WMD) was calculated (Roe et al. 1984). On the basis of Figure 3 and Table 1, only three species, C. hysoscella, A. aequorea, and R. velatum, appeared to carry out vertical migrations. For the rest of the species there was no evidence of migration

within the water column, and these species were preferentially located above the thermocline. Moreover, a few species remained at depths below 100 m; these were mesopelagic species, and the individuals captured were located at the upper limit of their vertical distribution range.

Aglaura hemistoma (2 mm high) was by far the most abundant species during the sampling period. On the first day the species was concentrated in the 20–0-m stratum, with some individuals penetrating down to 60 m (Figure 4). Concentration increased from dusk on the first day, rising to a maximum value of 32 individuals per m³ during daylight hours on the second day. At the same time, certain individuals migrated to deeper layers, so that the entire sampled water column was occupied. This situation ceased at sunset. Individual abundance decreased over the rest of the sampling period (seven individuals per m³) but remained higher than values for the other species, which aggregated in the top 20 m at night.

Specimens of Liriope tetraphylla (3–4 mm wide) were caught only in the 20–0-m stratum during the first 24 h (Figure 5). At the start of the second day individual concentration increased, and the vertical distribution expanded down to 100 m. At night the population again aggregated in the 20–0-m stratum, where it stabilized.

Aequorea aequorea (5-15 mm wide) was frequent throughout the sampling cycle above the thermocline and occasionally present in and just beneath the thermal gradient (Figure 6). The distribution in the 200–100-m stratum was
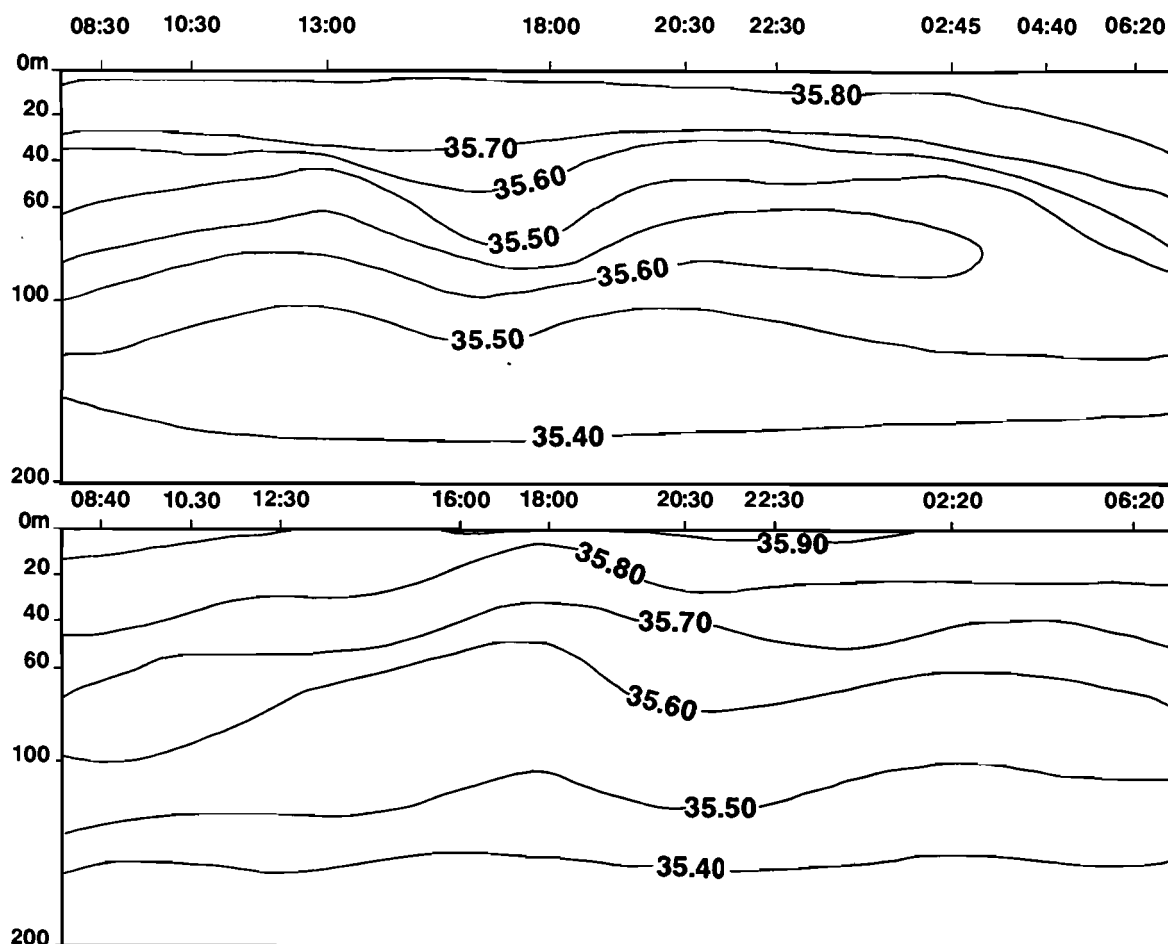

Figure 2 Salinity variations with depth at the sampling station over the 48 h sampling period.

Table 1 Average weighted mean depth (WMD, in metres) and standard deviation during the day and at night for the species collected during the 48 h sampling period

	Day (n = 9)		Night (n = 9)	
	x̄	SD	x̄	SD
Cl Hydrozoa				
SC1 Anthomedusae				
Porpita porpita	10	0	10	0
SC1 Leptomedusae				
Clytia simplex	10	0	10	0
Aequorea aequorea	59,6	37,9	53,2	36,7
Laodicea undulata	10	0	–	–
Eirene sp.	150	0	–	–
SC1 Trachymedusae				
Rhopalonema velatum	50	0	21,6	24,1
Aglaura hemistoma	13,4	8,0	11,5	1,9
Liriope tetraphylla	13,1	5,0	10	0
SC1 Narcomedusae				
Aegina citrea	150	0	150	0
Solmundella bitentaculata	96,8	59,4	124,8	21,9
Cunina sp.	–	–	10	0
Pegantha martagon	–	–	10	0
Solmaris corona	–	–	10	0
Solmissus marshalli	10	0	20	17,3
Cl Scyphozoa				
Nausithoë sp.	0	0	20	10
Chrysaora hysoscella ephyrae	9,9	0,1	16,2	8,8
juvenile	45,4	29,5	61,6	49,5
Periphylla periphylla	–	–	150	0

markedly different on the two days. *A. aequorea* was absent from this stratum during daylight hours on the first day but was present in all the nocturnal hauls. The opposite situation occurred on the following day, when the species was present in the deepest stratum throughout the daylight hours but rose to around the thermocline at dusk. There is evidence that the vertical migrations of this species through the water column extended beyond the sampling water column, which spanned the upper 200 m (unpublished data). It is therefore reasonable to expect some of the individuals to have entered the 200 to 100-m interval from deeper depths. The size of the specimens collected was rather similar over the entire 48 h sampling period, which reduces the likelihood of a possible ontogenetic basis for these migrations.

Solmundella bitentaculata (3 mm wide) was caught practically over the entire sampling period, mainly at night in the 200–100-m stratum, where concentration was highest (Figure 7). Small numbers were also taken sporadically in the remaining depth strata.

Chrysaora hysoscella was collected from all the depth strata sampled, but chiefly in the top 20 m (Figure 8). Individual size of the juveniles was small (up to 3 cm in diameter). The proportion of juveniles was higher than that of ephyrae by day but it was lower at night (Table 2). Juveniles were caught at all levels in the water column, whereas the ephyrae were almost all located above the thermocline.

Individuals of the remaining species were present only in

small densities (less than 0,003 individuals per m³ throughout the 200–0 depth stratum), and their mean abundances and depth distributions are set out in Table 2 and Figure 3. Their vertical distributions were difficult to establish on account of the low abundance levels.

Discussion

Three general patterns of medusae distribution were found.

(i) Species associated with the Angola Current. The warm waters of the Angola Current were populated by greater numbers of species and of individuals and were (characterized by the extremely high abundance of *A. hemistoma* (up to 32 individuals per m³ in the upper 20 m, Figure 4) and, to a lesser extent, *L. tetraphylla* (up to 0,3 individuals per m³ in the upper 20 m).

(ii) Species associated with the Benguela Current. This medusae community was composed of mesopelagic species. *S. bitentaculata* was the most abundant species (up to 0,17 individuals per m³ in the 200–100 depth interval) and it was the only species with a clearly defined depth distribution.

(iii) Species associated with both currents. *C. hysoscella* and *A. aequorea* were the most important of these species. The two species were continuously present in both currents throughout the entire sampling cycle; each current bore its own population of each species, but an exchange of individuals between the two water masses took place thanks to migration. *Rhopalonema velatum* was a third, but less abundant species that followed this general pattern.

The highest temperature and salinity values were consistent with the characteristic values for the Angolan Current (Boyd *et al.* 1987). These warmer, more saline waters flowed on top of the water from northern Namibia (under the influence of the Benguela Current), giving rise to a strong thermocline that formed a boundary between the two water masses. The surface layer contained high zooplankton concentrations, particularly of copepods, with densities greater than 2×10^6. $1000\ m^{-3}$ (Olivar & Barangé 1990).

The most abundant species (*A. hemistoma, L. tetraphylla, and S. bitentaculata*) exhibited more well-defined vertical distributions, whereas the species that presented lower abundance values over a wider depth range (*A. aequorea, C. hysoscella*) exhibited more irregular distribution patterns. The vertical distributions of the different species suggested that each current had its own medusan community and that the thermocline acted as a boundary between the two currents, restricting the exchange of species and individuals.

Differences in the density values for most species recorded on the first and second days were very probably due to the patch size of each species. The patch size of *A. hemistoma* was greater than 19,4 km, based on the surface current speed of 15–20 cm.s⁻¹ (Salat, Masó & Boyd 1992) and individuals were collected continuously over more than 36 h. The core of this species's patch may have been sampled on the morning of the second day, when a density of 32 m⁻³ was recorded. This value is higher than the values previously recorded in other seas: up to 2,3 m⁻³ in the Red Sea (Schmidt 1973), up to 2,4 m⁻³ on the Brazilian coast (Moreira 1973) and up to 27 m⁻³ on the western Mediterranean (Gili, Pagès & Vives 1987).

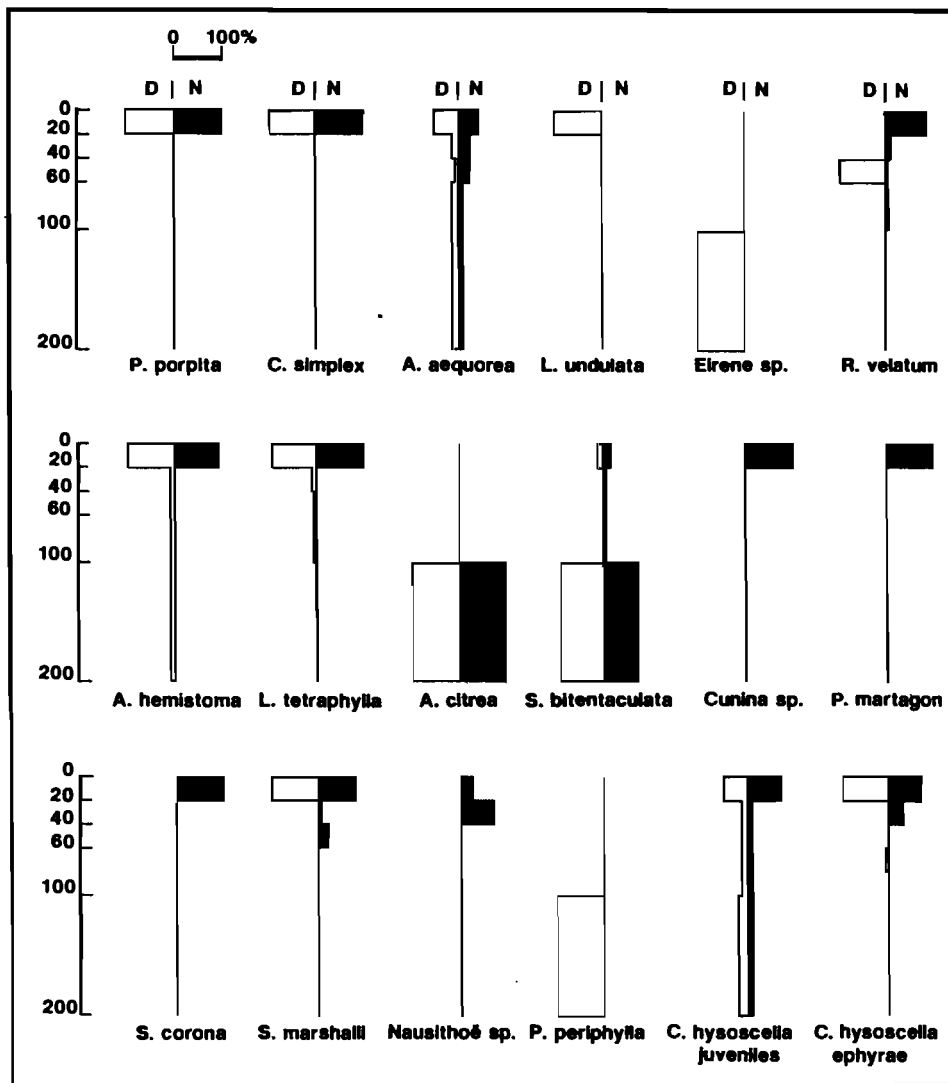Although the daily vertical migrations by *A. hemistoma*

Figure 3 Depth (m) distribution of the medusae species plotted as a percentage at each depth interval by day (outlined) and night (shaded).

and *L. tetraphylla* in areas where the water column is homogeneous is influenced by the cycle of daylight, with individuals descending to greater depths during the day and rising towards the surface at night, this pattern was not followed during the sampling period at the 48-h station. Schmidt (1973) reported this pattern for these two species in the upper 300 m using 50 m depth strata in the Red-Sea. Vertical distribution data collected on the SNEC II survey (Pagès & Gili 1991), which was carried out just prior to the 48 h sampling period considered herein, indicated a similar pattern. Based on data for all the stations sampled on the SNEC II survey from the Cunene River to Lüderitz, these two species carried out vertical migrations whenever no strong thermocline was present (Figure 9). On the first day the greater part of the population was concentrated in the surface stratum, while on the second day, although a very small portion of the population crossed the thermocline and remained below it during daylight hours, most of the *A. hemistoma* and *L. tetraphylla* populations stayed above the thermocline.

Many workers have considered vertical migrations to be related to the search for food (e.g. Conover 1968; Longhurst

& Harrison 1989). Such migrations do not seem to occur when the concentration of potential prey items is adequate (Pearre 1979), and this is even more true when the need to cross the thermocline in search of prey requires a high energy expenditure (Ohman 1990). The absence of predators is another factor that reduces the likelihood of migrations taking place (Gabriel & Thomas 1988). Both these conditions were recorded during the 48 h sampling period considered herein, in which prey abundance and the low density of potential predators in and above the thermocline (pers. obs.) may in large measure account for the weak migratory movements of the medusae; only the species that possessed more highly developed locomotive systems, like *A. aequorea* and *C. hysoscella* were able to traverse the thermocline. In contrast, in areas where the water column is less stratified, medusae may alter their behaviour and spread out over a broader vertical distribution range (e.g. Moreira 1973; Roe *et al.* 1984).

The pattern of distribution of *S. bitentaculata* could well suggest diel vertical migration with marked nocturnal ascent from below 200 m into the 200–100-m layer. This species is widely distributed and very common in the oceans (Kramp
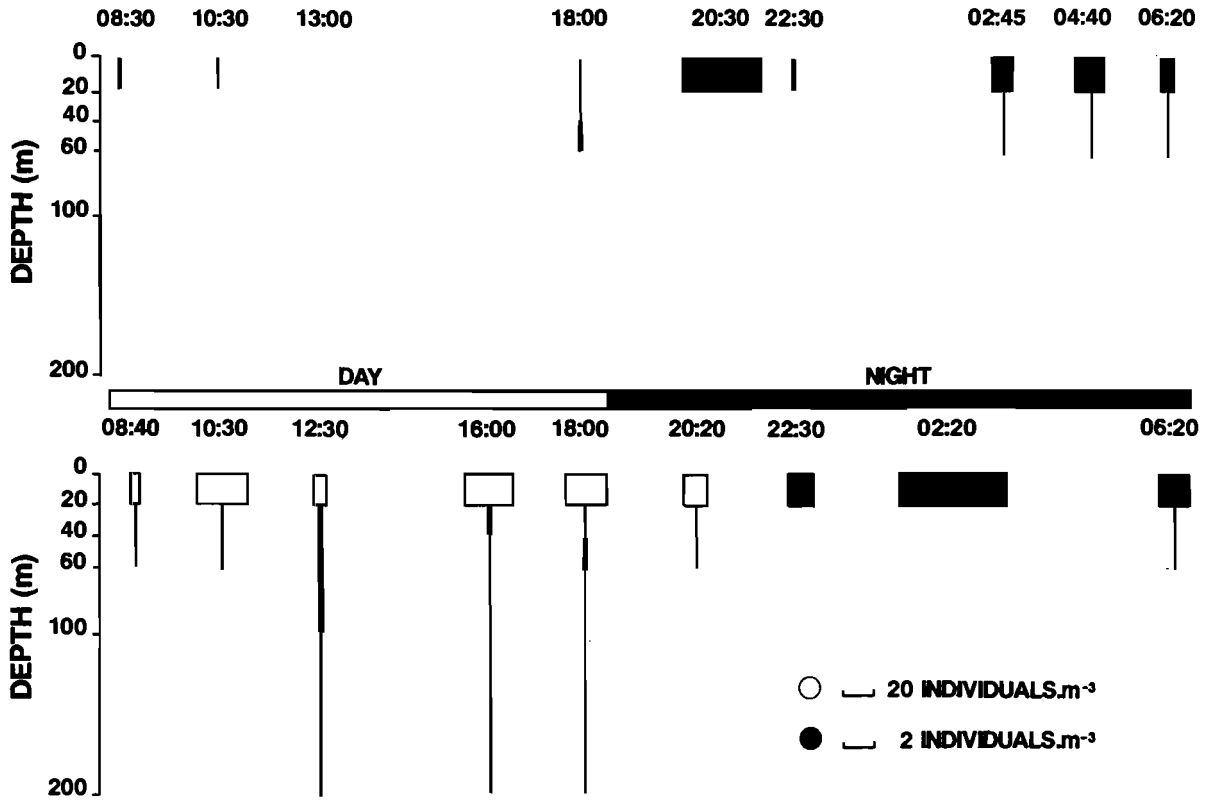
Figure 4 Depth (m) distribution and concentration of *Aglaura hemistoma* during the 48 h sampling period.
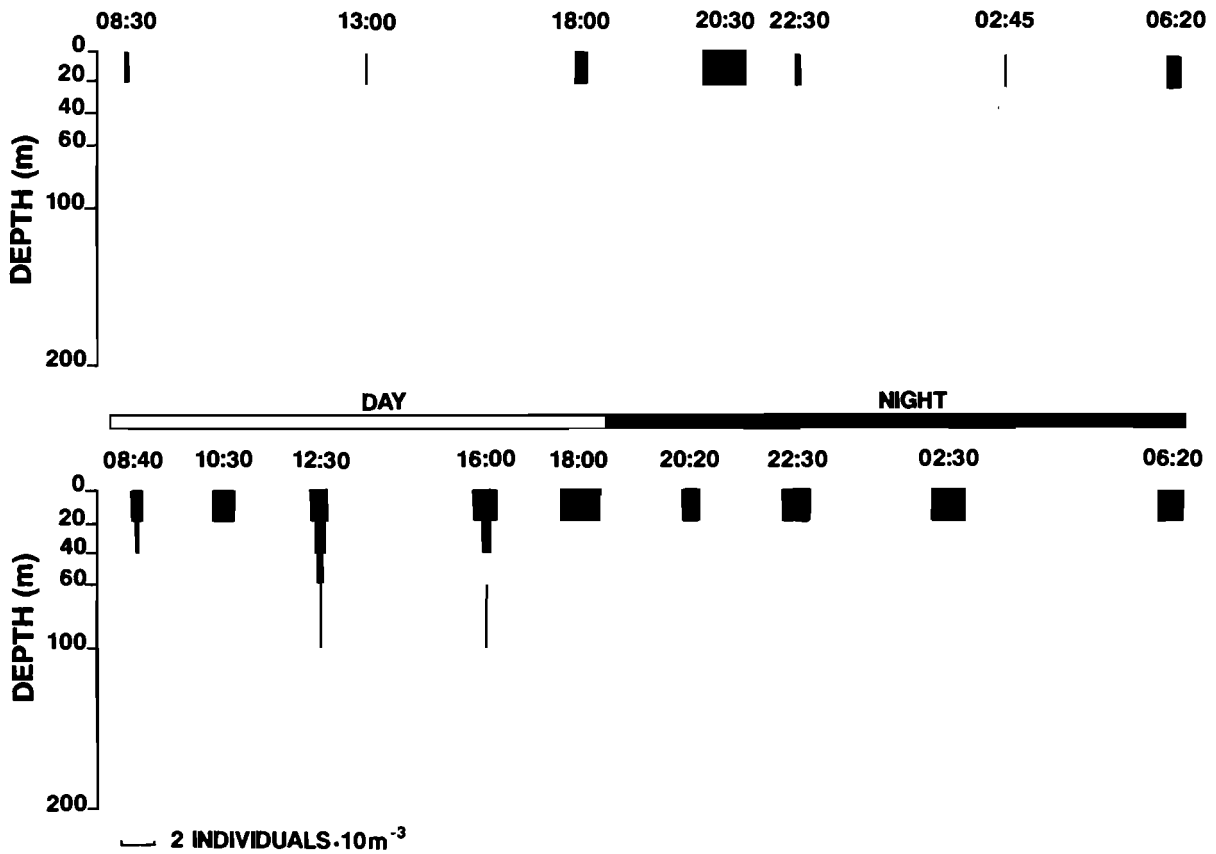
Figure 5 Depth (m) distribution and concentration of *Liriope tetraphylla* during the 48 h sampling period.

1965) showing a broad vertical distribution that reaches 700 m in depth (Casanova 1980).

It is not clear which factors were responsible for regulating *A. aequorea* distribution. Satterlie (1985) reported this
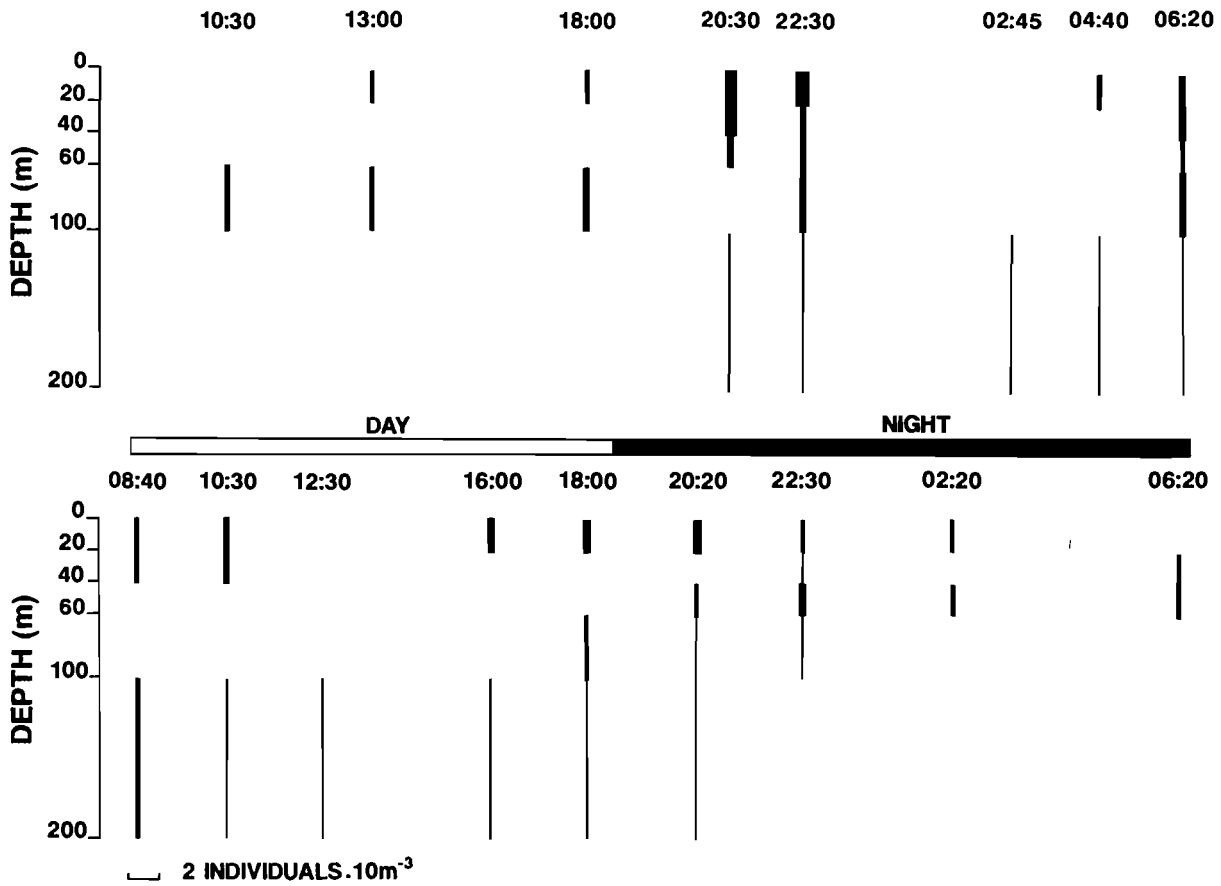
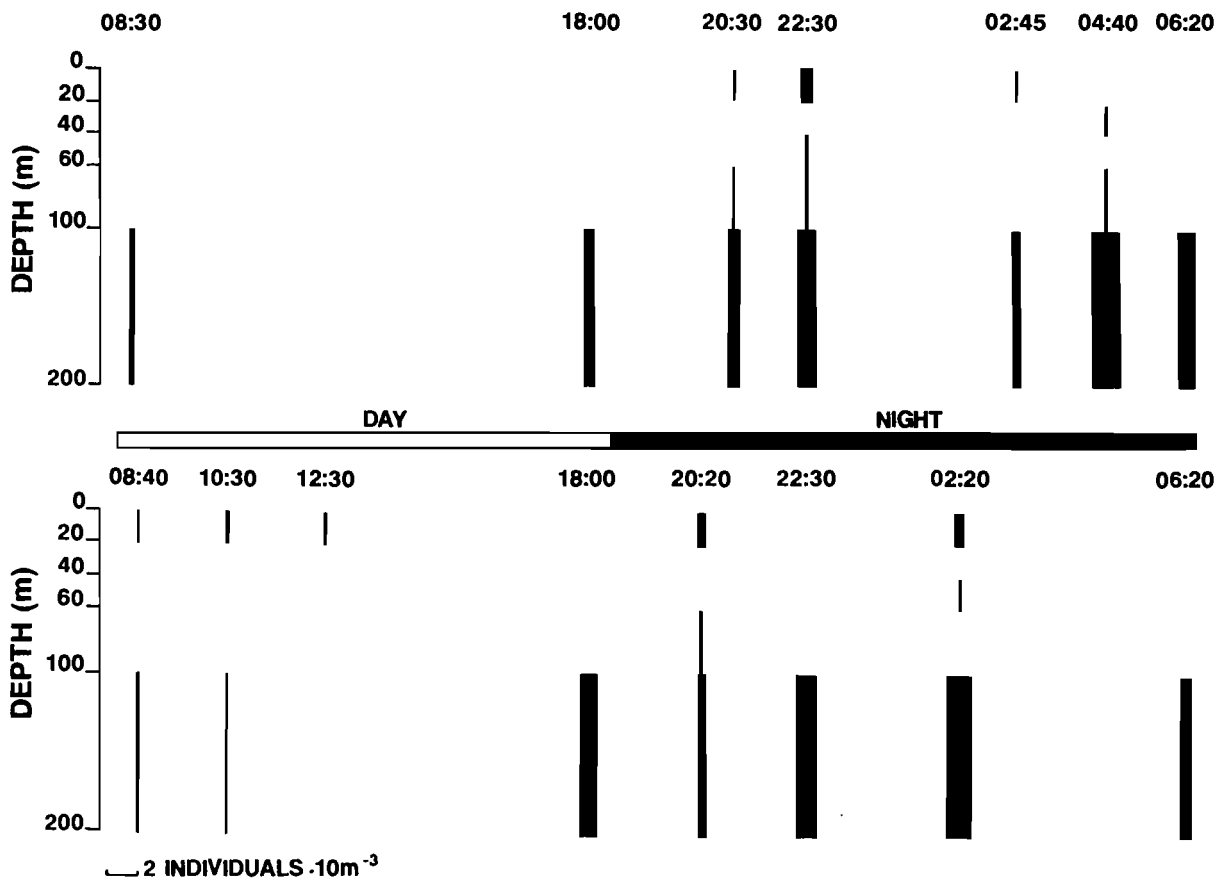**Figure 6** Depth (m) distribution and concentration of *Aequorea aequorea* during the 48 h sampling period.

Figure 7 Depth (m) distribution and concentration of *Solmundella bitentaculata* during the 48 h sampling period.
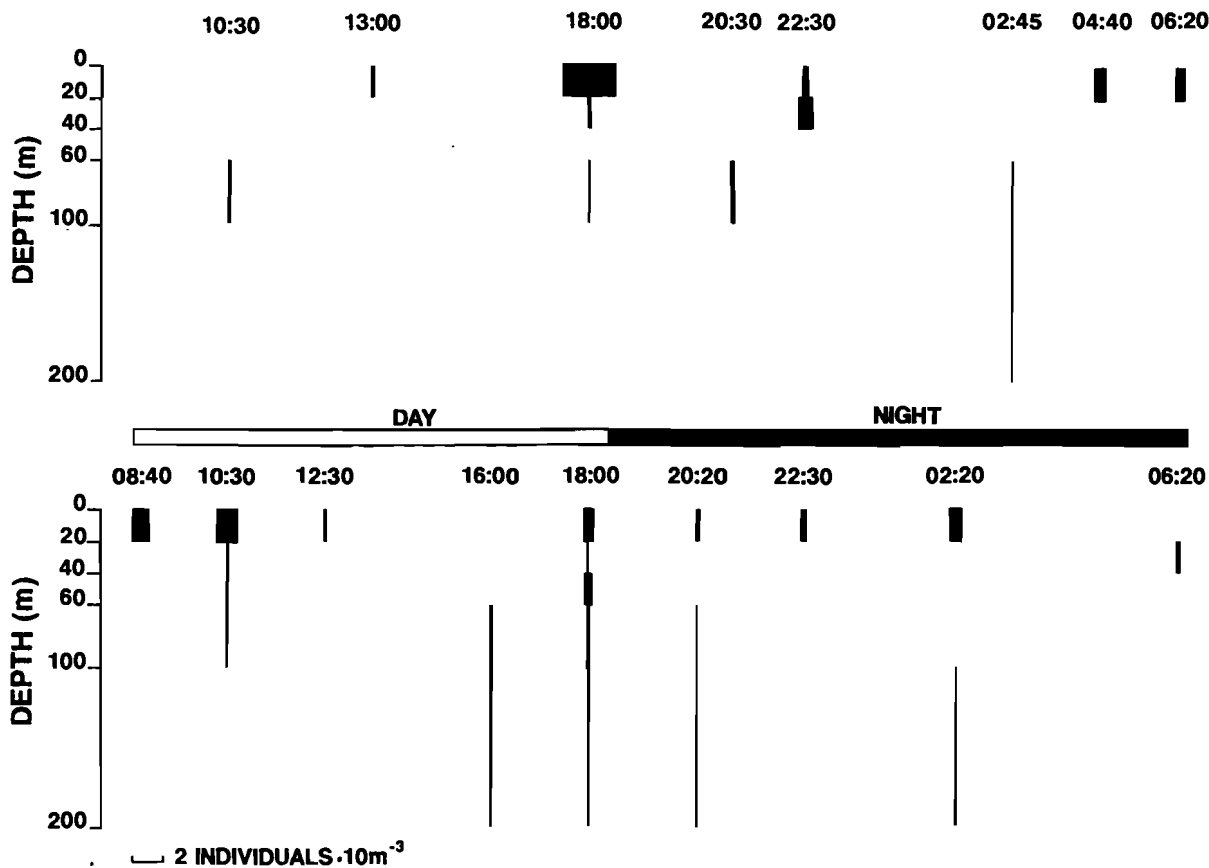
Figure 8 Depth (m) distribution and concentration of *Chrysaora hysoscella* during the 48 h sampling period.
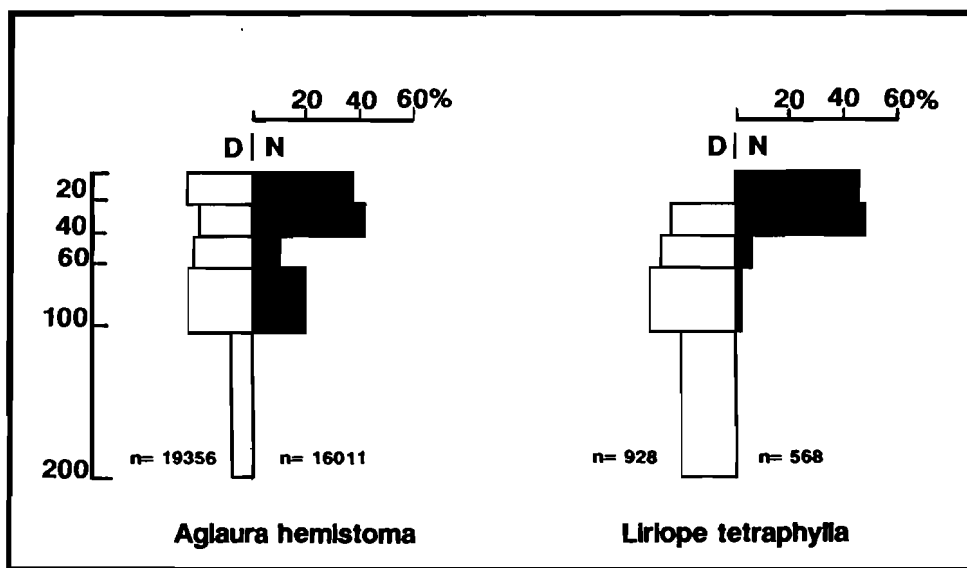

Figure 9 Depth (m) distribution and concentration (plotted as a percentage at each depth interval by day and night) of the species *Aglaura hemistoma* and *Liriope tetraphylla* based on data from all the stations sampled on the SNEC II survey carried out just prior the 48 h sampling period; *n* is the number of individuals of each species collected by day and night.

species to be an irregular swimmer that floats motionless for long periods and is capable of self-activation with no need of external stimulation, since the swimming motor neurons apparently do not react to light, inasmuch as no response of these medusae to changes in light intensity could be elicited. The results of this study also showed *A. aequorea* to be an irregular swimmer, though it was capable of crossing the thermocline. It is not clear what kind of stimuli originated the vertical migration on the second day which is related to the possible endogenous production of swimming activity by the swimming motor-neuron network as Satterlie (1985) pointed out.

Table 2 Mean densities of individuals per 1000 m³ and standard deviation from 200 m to surface, collected from day and night samples during the 48 h sampling period

	Day (n = 9)		Night (n = 9)	
	x̄	SD	x̄	SD
Cl Hydrozoa				
SCl Anthomedusae				
Porpita porpita	0,8	2,4	1,5	4,3
SCl Leptomedusae				
Clytia simplex	0,3	0,6	8,1	11,8
Aequorea aequorea	4,4	3,3	10,4	7,5
Laodicea undulata	1,4	4,0	–	–
Eirene sp.	0,1	0,2	–	–
SCl Trachymedusae				
Rhopalonema velatum	0,2	0,6	0,1	0,2
Aglaura hemistoma	1870,1	2280,4	854,1	886,1
Liriope tetraphylla	12,6	10,3	28,8	24,1
SCl Narcomedusae				
Aegina citrea	0,1	0,2	0,1	0,2
Solmundella bitentaculata	5,6	5,8	23,4	10,5
Cunina sp.	–	–	0,2	0,7
Pegantha martagon	–	–	0,6	0,7
Solmaris corona	–	–	0,5	1,7
Solmissus marshalli	–	–	1,1	1,2
Cl Scyphozoa				
Nausithöe sp.	–	–	1,1	2,0
Chrysaora hysoscella ephyrae	6,6	8,4	6,6	6,8
juvenile	11,7	20,9	2,0	1,9
Periphylla periphylla	–	–	0,1	0,2

The low abundance of *C. hysoscella* is related to its horizontal distribution pattern. The highest densities of ephyrae and juveniles occur in coastal waters (Pagès 1992) decreasing offshore where the adults are more abundant. The ephyrae which drifted offshore were concentrated in surface waters while the juveniles, with a more developed locomotion, showed a broader vertical distribution. This vertical distribution pattern can be regarded as ontogenetic since the ephyrae exhibited a different vertical distribution from the juveniles. Although the vertical distribution pattern for *C. hysoscella* seems to be more difficult to elucidate than that of *A. aequorea*, the results obtained were in conformity with existing knowledge of this species, i.e., that it is epipelagic and that its vertical distribution is prey-related, since it is an opportunistic feeder (Larson 1986). Its irregular distribution through the entire sampling interval in the water column may have been the result of sinusoidal locomotive movements in search of food; such movements were studied *in situ* in a similar species, *Pelagia noctiluca*, by Rottini Sandrini & Avian (1989). The highest concentrations of copepods were located just in and above the thermocline (Olivar & Barangé 1990) but significant densities were recorded throughout the water column.

In summary, the depth distribution of the medusae community was characterized by the existence of separate populations associated with each current system and by the presence of a thermocline that acted as a boundary, keeping the populations apart. It is interesting to note that, unlike other groups in the region, such as euphausiids (Barangé 1990), medusae hardly display any vertical movement and tend to aggregate near the surface. This behaviour would appear to be an adaptation to the special hydrographic (thermocline) and trophic (abundance of potential prey items and absence of predators) conditions that prevailed in the region during the sampling period. This non-migratory behaviour may change when the water column is not stratified and prey density is more uniformly distributed throughout the water column.

Acknowledgements

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