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On the vertical distribution of siphonophores in the upwelling area off NW Africa (Auftriebs-Expedition R.V. "Meteor", cruise 26, 1972)

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With 2 figures and 8 tables

Über die Vertikalverbreitung der Siphonophoren im Auftriebsgebiet vor NW Afrika (Auftriebs-Expedition F.S. „Meteor", Fahrt 26, 1972)

Zusammenfassung

Die vorliegende Untersuchung über die Vertikalverteilung der Siphonophoren im Seegebiet vor Cap Mirik (19° N) an der Mauretanischen Küste erfolgte in Schräghols mit einem Bongo-Netz mit 6-facher Wechselbecher-Einrichtung in 100 m Intervallen von 0—500 m Tiefe. Das Verbreitungsmuster der beobachteten 15 Siphonophoren-Arten wird bezüglich der hydrographischen Verhältnisse des Auftriebsgebietes diskutiert. Im wesentlichen wurden im Vergleich zum wärmeren küstenfernen Wasser folgende Beobachtungen gemacht: 1. eine geringere Diversität der Siphonophoren, 2. eine flachere Verbreitung einiger sonst meso- und bathypelagisch lebender Arten, bedingt durch niedrigere Temperaturen in den oberen 300 m und einer geringeren Lichtdurchlässigkeit des Wassers, 3. keine Beteiligung physonectider Siphonophoren als Echostreuer in echogebenden Schichten.

Abstract

Using a Bongo-Net equipped with a multiple cod-end closing device, the vertical distribution of siphonophores has been observed in 100 m depth intervals at 13 stations off Cap Mirik (19° N) (from 0—500 m depth). The distributional pattern of the 15 siphonophores species found is discussed in relationship to the hydrography of this upwelling region. The following main features have been observed in comparison with the warmer oceanic water offshore: (1) a lower diversity, (2) a shallower distribution of some of the deep living species due to the lower temperature in the upper 300 m and a lower transparency, (3) no contribution to acoustic scattering by physonect siphonophores.

Introduction

Our knowledge on the vertical distribution of siphonophores is still very incomplete. Most data originate from the larger oceanographic expeditions, with descriptions limited to the geographical distribution of the plankton organisms. With few exceptions sampling was done with open nets and only during the last decades, with progress in the development of opening-closing nets and depth recording devices, has the bathymetric distribution of siphonophores been described more precisely (ALVARIÑO 1967, PUGH 1974, 1975).

The study of vertical distribution of siphonophores has attracted particular attention in faunal studies of the deep scattering layers (DSL), particularly with the discovery of acoustic scattering caused by physonect siphonophores (BARHAM 1963). Most of these investigations contributing to our knowledge of the DSL have been done in few restricted areas

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of the eastern Pacific Ocean. In the Atlantic Ocean, faunistic DSL-studies refer only briefly to the distribution of siphonophores species (KINZER 1969, 1971).

The present study describes the vertical distribution of siphonophores in the upper 500 m off the Mauretanian coast. The distribution of siphonophores from areas of coastal upwelling have not yet been described. As their "ecological importance is far from being insignificant" (PUGH 1974), is seems worthwhile to give a short description of the vertical distribution of siphonophores with reference to the hydrography of the area where sampling was carried out.

Material and methods

The biological sampling was carried out on 13 stations during the Auftriebs-Expedition (Upwelling-Expedition of R.V. "Meteor" from 26 February until 9 March 1972). The location of plankton stations off the Mauretanian coast is shown in Fig 1. The stations 9, 11, 12 are situated in two of the canyons cut into the continental shelf and slope, the other stations are oceanic.

Sampling was carried out with the Bongo Net (McGOWAN & BROWN 1967) of 71 cm net opening and a monofilament gauze of 500 μ mesh size. One of the twin nets was equipped with a revolving-buckets system (6 buckets) similar to the gear described by KINZER & HEMPEL (1970) which allowed five discrete depth layers to be sampled in a single haul. The nets were towed at a speed of 2 knots. Sampling was carried out by means of oblique hauls from 500 m depth to the surface. The change of buckets was triggered from on board the ship so that, in each haul, the following depth horizons were fished, 500—400, 400—300, 300—200, 200—100, 100—0 m. The flow of water and the rotation of the buckets were monitored on the ship by means of a conducting cable. The depth of the net was telemetered by a depth pinger (manufactured by Benthos, Inc. USA). Each of the five 100 m-depth horizons was sampled for an average of 9—12 min. Clogging of the net occurred only occasionally in the 100—0 m depth interval.

The samples were preserved in 4 % formalin, buffered with hexamine. Each sample was sorted in total, except for the surface samples, where for the most part, only a subsample was examined.

For recording the DSL an ELAC echo-sounder was used, operated at a frequency of 15 kHz and at a power-output of 4.5 kW. The pulse length averaged 40 msec.

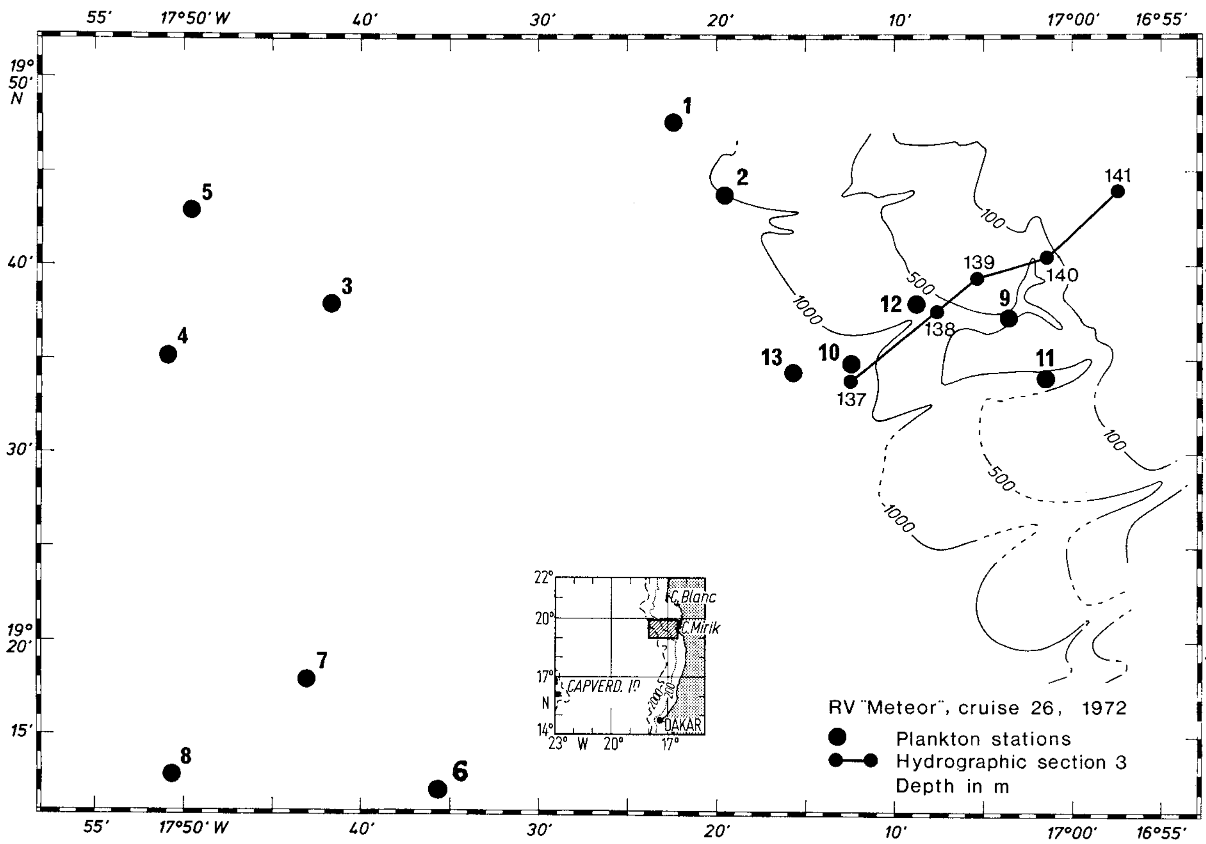

Fig. 1. Location of plankton and hydrographic stations during the "Auftriebs-Expedition" of R. V. "Meteor" 1972.

Results

Siphonophores have been collected at all 13 plankton stations and at all depths from the surface to 500 m. Most of the 15 siphonophore species occurred during the daytime between 100 to 400 m depth. The relatively low number of siphonophores in the upper 100 m might be due to clogging of the net.

The samples at stations 8, 9 and 10 were collected during the night. The following species have been observed:

Halistemma rubrum (VOGT, 1852)

25 nectophores were caught on station 3 at 400—500 m depth and another 3 nectophores at station 9 in 200—300 m depth (Table 1). A wellknown species from warm-water regions of all oceans, including the Mediterranean Sea (KINZER 1965), its depth distribution is still quite uncertain. ALVARIÑO (1967) describes it as mesopelagic, while PUGH (1974) in the Canary Islands area found it most common between 40 and 940 m depth, with some fragments even in the neuston net.

Species of Siphonophora collected at stations 1 to 13 from 26 February until 9 March 1972:

Table 1
Halistemma rubrum (nectophores) = ○
Bargmannia elongata (nectophores)
Physophora hydrostatica (nectophores) = □

depth (m)	1	2	3	4	5	6	7	8	9	10	11	12	13
0 - 100								2					
100 - 200													
200 - 300									3				
300 - 400									14		3		
400 - 500			25						26			34	

Nanomia bijuga (CHIAJE, 1841)

Seven nectophores were collected at stations 8 and 9 at 0—100 m and 200—300 m depth respectively (Table 5). It is common in all oceans (ALVARIÑO 1971) and has also been observed in the Mediterranean Sea. According to ALVARIÑO (1971) und PUGH (1974) it lives mostly near the surface and possibly should be considered neritic. The depth of water at station 9 was 500 m, whereas station 8 was further off-shore at 2460 m.

Bargmannia elongata TOTTON, 1954

A total of 77 nectophores were found at stations 9, 11 and 12 at depths between 300 and 500 m (Table 1). The highest concentration occurred at station 12 with 34 nectophores at 400—500 depth. From all the samples collected it evidently was the deepest living siphonophore (below 400 m). *B. elongata* has been described only a few times from the Indian and Atlantic Oceans (TOTTON 1954) and the Azores region (LELOUP 1955). STEPANYANTS (1967, 1970, see PUPGH 1974) and ALVARIÑO (1967) considered this species to be bathypelagic. This corresponds well with the observations by PUGH (1974) who caught nectophores between 360 and 950 m, but as most of his specimens were caught in the 500—625 m depth range, then perhaps *B. elongata* should be considered as a mesopelagic form.

Physophora hydrostatica FORSKAL, 1775

Only two nectophores were found in the sample from the upper 100 m at station 8 (Table 1). Most probably, the absence of specimens is due to the clogging and insufficient washing of the net after each haul, as also other typical surface dwelling species were missing. Additional samples collected with the Rectangular Midwater Trawl (RMT 8) contained nectophores of this species at several stations.

Ph. hydrostatica has a worldwide distribution. It has also been described from the Mediterranean Sea. PUGH (1974) found that, in the region of the Canary Islands, most nectophores were present in the catches from the upper 250 m, although at one station he found nectophores as deep as 950 m.

Praya dubia (QUOY & GAIMARD (1833), 1834)

Eudoxid bracts of *P. dubia* have been found quite abundantly between 100 and 300 m depth with two additional specimens at 300—400 m (Table 2).

Table 2
Praya dubia (eudoxid bracts)
Bassia bassensis (ant. nectophores) = ○

depth (m)	1	2	3	4	5	6	7	8	9	10	11	12	13
0 - 100		43	38		25			34				23	
100 - 200											49	21	16
200 - 300							20	11	2		9		
300 - 400				2									
400 - 500													

The species is known from the Atlantic and Pacific Oceans (PUGH 1974) but little data are available about its vertical distribution. PUGH observed a few eudoxid bracts in IKMT-catches centering at 435 m depth while TOTTON (1965) describes a few nectophores and bracts from open net-hauls between 460 m and the surface. More recent evidence of *P. dubia* in the Atlantic Ocean is indicated by PUGH (1976) from preliminary observations of material from "Discovery"-cruises with sampling stations between 11° and 60° N.

Rosacea spp.

Due to the soft tissue of the *Rosacea* species, most nectophores have been damaged. Therefore the separation of the three species has not been possible. According to PUGH (1974), only the two widespread species *R. cymbiformis* and *R. plicata* should be abundant in this area. The third species, "*R. villafrancae* is little known and so far restricted to a very small area of the Mediterranea Sea" (PUGH 1974).

Except for one station, nectophores and eudoxid bracts of *Rosacea* were numerous at depths from 100 to 300 m (Table 3). At six stations eudoxid bracts were found with a maximum of 32 bracts at station 1.

From previous studies (see PUGH 1974) it appears that *Rosacea* spp. have a wide depth distribution. Neither species has been found shallower than 85 m depth. BIGELOW & SEARS (1937) have observed that their distribution is related to temperatures below 20° C.

Table 3
Rosacea spp. (nectophores)
Rosacea spp. (eudoxid bracts) = □
Nectopyramis thetis (eudoxid) = ○ x = sample lost

depth (m)	1	2	3	4	5	6	7	8	9	10	11	12	13
0 - 100													
100 - 200	$\boxed{21}$	2		$\boxed{4}$					$\boxed{25}$	x	3 $\boxed{3}$		
200 - 300	$\boxed{32}$	6	5		2 $\boxed{5}$	2	7	1 $\boxed{4}$	7		3	1	2
300 - 400				4								1	
400 - 500													

Nectopyramis thetis BIGELOW, 1911

Only at station 12 was a single eudoxid isolated from the sample collected at 200 to 300 m depth (Table 3). *N. thetis* is well known from the Atlantic Ocean but has also been collected in the Indian and Pacific Oceans (see PUGH 1974 for further details). He has observed numerous polygastric and eudoxid stages near the Canary Island in the 570—800 m depth range.

Vogtia glabra BIGELOW, 1918

Among the Hippopodiidae, *V. glabra* appeared to be the most abundant *Vogtia* species in the area of investigation. As also observed by PUGH (1974), *V. glabra* has a broad vertical distribution. Nectophores have been isolated from all stations between 100 and 500 m depth, but they were rarely found between 400 and 500 m (see Table 4).

The distribution of *V. glabra* in the Atlantic Ocean and Mediterranean Sea has been described by several authors (see PUGH 1974). During the daytime it has a wide depth range from 40—950 m, with a maximum between 560 and 600 m (PUGH 1974). In the

Table 4
Vogtia glabra (nectophores)

depth (m)	1	2	3	4	5	6	7	8	9	10	11	12	13
0 - 100													2
100 - 200	5		9		6	7	4	1			11	24	22
200 - 300	9			21		13	1	1	1	1	13		12
300 - 400		12	8	16	4	24	1	6	10	12		6	
400 - 500													

Mediterranean Sea the species presumably is bathypelagic (BIGELOW & SEARS 1937).

Vogtia serrata (MOSER, 1925)

As is the case with *Vogtia pentacantha*, *V. serrata* has a rather restricted vertical distribution. Except for station 2 with 8 nectophores from 100—200 m depth, only the samples from between 200 and 400 m depth at six other stations contained nectophores (Table 5). A maximum of 12 nectophores was collected in one sample at station 2 in 200—300 m depth.

The rich material investigated by PUGH (1974) at the Canary Islands stations gives clear evidence for a bathypelagic distribution. He collected most nectophores between 560 and 650 m depth. BIGELOW & SEARS (1937) recorded the largest depth of nectophores between 1066 to 2900 m.

Table 5
Vogtia serrata (nectophores)
Nanomia bijuga (nectophores) = ○

depth (m)	1	2	3	4	5	6	7	8	9	10	11	12	13
0 - 100								4					
100 - 200		8											
200 - 300		12							3				3
300 - 400						3	6					1	
400 - 500													

Vogtia pentacantha KÖLLICKER, 1853

Next to *V. glabra*, the nectophores of *V. pentacantha* appeared most abundantly. Their vertical depth-range reached from 100 to 300 m (Table 6). At several stations, particularly station 3, and in the slope area, *V. pentacantha* was the dominant siphonophore species.

Table 6
Vogtia pentacantha (nectophores)
Sulculeolaria quadrivalvis (ant. nectophores) = ○
Lensia achilles (nectophores) = □

depth (m)	1	2	3	4	5	6	7	8	9	10	11	12	13
0 - 100													
100 - 200		2	3				2				35+2	14	
200 - 300			37	3	3	9	1	20		$\boxed{3}$	15	18	17
300 - 400												1	
400 - 500													

PUGH (1974) observed nectophores at 150—660 m, their abundance increasing with depth. BIGELOW & SEARS (1937) collected most nectophores between 665 and 933 m depth, but also a few from near the surface. In the Gulf of Naples a single nectophore of *V. pentacantha* was caught in the upper 50 m (KINZER 1965).

Sulculeolaria quadrivalvis BLAINVILLE, 1834

Only two anterior nectophores were collected at station 7 (100—200 m depth, Table 6). *S. quadrivalvis* has a worldwide distribution, mostly described as a species from the surface water (LELOUP 1932, 1933, BIGELOW & SEARS 1937). PUGH (1974) found upper and lower nectophores between 40—415 m, but predominately in the upper 85 m.

Lensia achilles TOTTON, 1941

Three anterior nectophores were isolated from the sample at station 10 from a depth of 200—300 m (Table 6).) Its vertical range has been described by TOTTON (1941), for the Atlantic Ocean, as from 900 to 2500 m depth. PUGH (1974) collected large numbers of *L. achilles* in the 500 to 625 m depth range, and occasionally at depths down to 1000 m.

Chelophyes appendiculata (ESCHSCHOLTZ, 1829)

This species was most abundant in the upper 100 m, both anterior and posterior nectophores being present (see Table 7). Only at station 10 did the sample from 200—300 m contain any nectophores.

Table 7

Chelophyes appendiculata (ant./post. nectophores)
Abylopsis tetragona (ant./post. nectophores) = $\boxed{}$

depth (m)	1	2	3	4	5	6	7	8	9	10	11	12	13
0 - 100	3/2	8/6	5/2		1/1	2/4		0/6		1/1		4/4	1/1
100 - 200					$\boxed{0/2}$	$\boxed{0/2}$	$\boxed{1/1}$						
200 - 300										3/0			
300 - 400													
400 - 500													

PUGH (1974) describes *Ch. appendiculata* as "probably the commonest and most widely distributed species of siphonophores". From his rich material, from the Canary Islands area, he describes the dial vertical migration of *Ch. appendiculata*, from which it appears that this species prefers a daytime depth of about 250 m. At night it migrates to the surface.

LELOUP & HENTSCHEL (1935) describe the presence of nectophores of *Ch. appendiculata*, from the Southern Atlantic Ocean, in the upper 100 m, but with a second maximum about 400 to 600 m depth. MOORE (1949, 1953) found this species to be "fairly common" at Bermuda and off Florida. From the Mediterranean Sea BIGELOW & SEARS (1937) described *Ch. appendiculata* to be most common at the 200 m level. This corresponds also to my observations from the Gulf of Naples (KINZER 1965). FURNESTIN (1957) found this species to occur off the Moroccan coast at depths where the temperature ranged from 16.15° to 20.8° C.

Abylopsis tetragona (OTTO, 1823)

At three stations located off the shelf anterior and posterior nectophores were collected at depths from 100—200 m (Table 7).

A. tetragona is an abundant species from the surface waters of the Atlantic Ocean. FURNESTIN (1957) collected nectophores in the coastal waters off Morocco. PUGH (1974) found nectophores in the 50 to 110 m depth range, and a single specimen at 615 m. In the Gulf of Naples it occurred at most stations from depths of 0—50m (KINZER 1965). Off the Mauretanian coast *A. tetragona* was collected during the daytime at temperatures ranging from 12.5 to 14.3 C. As the upper 100 m was not sampled efficiently (see above, *Physophora hydrostatica*), a later analysis of the RMT 8 samples might give evidence of *A. tetragona* appearing also in the near surface waters.

Bassia bassensis (QUOY and GAIMARD (1833), 1834)

Next to *Chelophyes appendiculata*, this species appeared to be most abundant in the upper 100 m depth horizon, although it was collected only at five stations (Table 2). Anterior nectophores and complete polygastric stages were sampled.

B. bassensis has been described from all the oceans, the Mediterranean Sea and the Moroccan coast (FURNESTIN 1957) at depths ranging from the surface to 200 m. PUGH (1974) from his large collection of nectophores near the Canary Islands observed most specimens in the upper 100 m. During the day he sampled polygastric stages at 40 to 85 m depth, while at night they moved closer to the surface. A few have even been caught in the neuston net.

Discussion

Although only plankton hauls of 13 stations are included in this study, the low number of siphonophore species in the area is quite evident. A reduced diversity of species seems to be typical of areas with upwelling cold water. Also the number of euphausiid species sampled in the same area was markedly smaller than in the warm oceanic water further offshore (WEIGMANN, pers. communication).

Comparing the vertical distribution of the 15 siphonophores species described above to the data collected by PUGH (1974), from sampling stations

600 miles to the north in the region of Canary Islands, it becomes evident that the depth range of most of the deeper living siphonophores from the Mauretanian coast is shifted by approximately 200 m towards the surface. This is probably due to the lower temperature in the upper 300 m of the water column, in contrast to the warmer offshore water.

Along the slope there are several deep canyons (Fig. 1). According to SHAFFER (1974) upwelling is strongly influenced by the bottom topography and occurs mostly within these canyons. The patches of upwelling are only about 10 km in diameter. Further offshore, the surface temperature measured > 17 °C, indicating „older“ upwelled and oceanic water.

Comparing the distributional pattern of siphonophores to the hydrographic data described above, upwelling along the coastal shelf seems to influence the horizontal and vertical distribution of only a few species. The physonectid siphonophore *Bargmannia elongata* appeared mostly in a canyon (sta. 9) at depths between 300 and 500 m and also on the slope at a depth of 400—500 m (sta. 12), possibly because of the presence of cold upwelling water. PUGH (1974) describes this species as mesopelagic, predominating at depths from 500—625 m. Temperatures at his sampling depths at Fuerteventura, Canary Island, ranged from about 11.6° to 10.6 °C (Table 8), which correspond well to the temperatures recorded off the NW African shelf at 300—500 m depth (Fig. 2). Unfortunately, depths below 500 m have not been sampled during this cruise.

Table 8. The distribution of temperature at station 5796, 16 Oct. 1965 off Fuerteventura, Canary Islands. British SOND cruise, RRS "Discovery" (from CURRIE et al. 1969).

Depth (m)	t (°C)
1	21.99
20	21.37
40	20.79
60	20.46
79	18.91
98	16.85
148	16.00
198	15.38
246	14.50
296	13.59
345	12.90
393	12.37
440	11.88
486	11.44
532	10.89
579	10.39
626	9.80

Similar to *Bargmannia elongata*, *Vogtia glabra* and *Vogtia serrata* also have been caught at shallower depths (100—400 m) than at the Canary Islands (population maximum at 560—650 m), these species being described by PUGH (1974) as bathypelagic. Another related species, *V. pentacantha*, has also been collected closer to the surface (see above). BIGELOW & SEARS (1937) have reported this species from the surface layer in the upwelling waters off Messina, Mediterranean Sea.

Apart from temperature and salinity (MARGULIS 1972, PUGH 1975), another important factor deter-

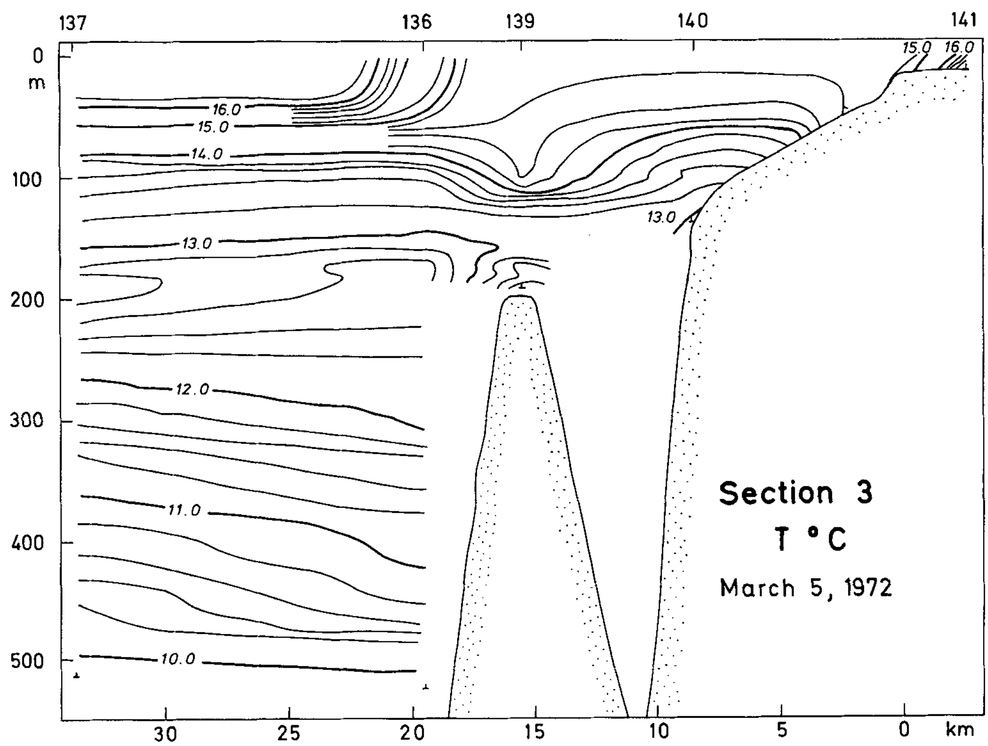

Fig. 2. The vertical distribution of temperature at section 3. See Fig. 1 for location of hydrographic stations (from SHAFFER 1974).

mining the vertical distribution of siphonophores is probably the depth of certain isolumes (ALVARIÑO 1971). Along the NW African coast the transparency of the water is considerably reduced, compared to the more distant oceanic areas (DICKSON 1972). This is, for the most part, due to patches of high phytoplankton biomass.

The low transparency is also reflected by the shallower depths of the deep scattering layers (DSL) along the NW African coast (HAIGH 1970). In the area of investigation, the DSL recorded at 15 kHz, had a depth range from 150 to 450 m. Mostly it consisted of two migratory layers. Typically for areas with upwelling water, its pattern and depth range changed very suddenly. Sometimes the change in depth was correlated with changes in surface temperature and/or the colour of the surface water, i. e. transparency. At the shelf break for instance, in a cold water patch of 14.8 °C, the DSL was recorded as two distinct layers at 150—210 and at 300—400 m depth. After the vessel passed from this cold water patch into warmer oceanic water of 16.1 °C, the DSL was observed at 200—300 and 400—500 m depth.

Of the physonect siphonophores, only four species have been observed: *Halistemma rubrum*, *Nanomia bijuga*, *Bargmannia elongata* and *Physophora hydrostatica*. Only *B. elongata* appeared in large numbers, but mostly at a depth of 400—500 m (Table 1) which was far below the DSL (15—250 m). Evidently, therefore, siphonophores did not contribute to the sound scattering layer in the area investigated.

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