Small-scale distribution of macroplankton and micronekton in the Ligurian Sea (Mediterranean Sea) as observed from the manned submersible *Cyana*

Ph.Laval, J.-C.Braconnot, C.Carré, J.Goy¹, P/Morand and C.E.Mills² Unité associée au CNRS UA 716, Station zoologique, CEROV, BP 28, 06230 Villefranche-sur-Mer, France, ¹Laboratoire d'Ichtyologie générale et appliquée, Muséum national d'histoire naturelle, 43 rue Cuvier, 75231 Paris Cedex 05, France and ²Friday Harbor Laboratories, 620 University Road, Friday Harbor, WA 98250, USA

Abstract. A series of eight submersible dives (the MIGRAGEL I cruise) was made during late April 1986 using the French submersible Cyana to investigate macrozooplankton in the upper 400-700 m of the water column. Paired day and night dives were made at stations 3, 6, 13 and 23 nautical miles off Cape Ferrat, near Villefranche-sur-Mer, France; the distances represent different areas in the frontal system of the Ligurian Sea. Detailed day/night vertical distribution data are shown for the most abundant species; these include the narcomedusa Solmissus albescens, teleost fish Cyclothone spp., small appendicularians (primarily Oikopleura albicans), large appendicularians (an undescribed oikopleurid), diphyid siphonophores (mostly Chelophyes appendiculata) and an abundant lobate ctenophore. Salps, pyrosomes, amphipods (Phronima sedentaria), pteropods (Cavolinia inflexa), macroscopic 'star-like' protozoa and marine snow are also briefly discussed. The coastal zone was dominated by small appendicularians in the upper layers, with other filter feeders including large appendicularians in deeper water-these just above a non-migratory population of carnivorous Cyclothone. The carnivorous medusa Solmissus albescens moved throughout the upper 600 m in the course of its diel vertical migration. Offshore, carnivores were dominant throughout the water column, with numerous diphyid siphonophores in the upper layers, and Cyclothone, lobate ctenophores and macroprotozoa abundant in deeper water. Solmissus was also present, and was more numerous offshore than in the coastal zone.

Introduction

The gelatinous macroplankton mainly comprises fragile organisms that cannot be sampled adequately by conventional plankton nets. The most delicate forms may even be destroyed by such fishing devices. However, recent studies using SCUBA diving (e.g. Hamner *et al.*, 1975; Alldredge, 1976; Harbison *et al.*, 1978; Biggs *et al.*, 1981; Purcell, 1981; Madin, 1982) as well as submersibles (Mackie and Mills, 1983; Youngbluth, 1984; Genovese *et al.*, 1985; Mackie, 1985) have led to a reassessment of the numerical importance of gelatinous macroplankton and their role in pelagic ecosystems.

In order to understand the complex relationships existing between major constituents of pelagic ecosystems better, it is necessary to evaluate the importance of the 'gray area' formed by the organisms that are sparsely, or never, present in plankton samples. This paper reports the results of a series of submersible dives (MIGRAGEL I cruise) made simultaneously with a more conventional oceanographic cruise, TROPHOS II.

These cruises were made during the springtime in the Ligurian Sea. At this time of year the herbivorous macroplankton develops in response to the

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phytoplankton bloom. Large salp swarms usually invade the upper layers, as attested by more than 25 years of observations from the Zoological Station of Villefranche-sur-Mer. It was hoped that use of the submersible would allow us to watch the salp populations increase. Quite unexpectedly, salp swarms did not develop during the month-long oceanographic operations of 1986. However, valuable insights were gained on other macroplanktonic and micronectonic organisms that were present during the study.

Materials and methods

Sampling organization (Figure 1 and Table I)

Three ships were in the diving area at the same time.

(i) The tender ship, *Le Nadir*, carried the submersible *Cyana*. Eight submersible dives were made between April 22 and 27, 1986 (MIGRAGEL I cruise) at stations 3, 6, 13 and 23 nautical miles off Cape Ferrat, near Villefranche-sur-Mer, France.



Fig. 1. Location of the Cyana dives. Open circles, day; closed circles, night. The insert shows the relative position, for each dive Dn, of the stations made by the other ships: three by Le Noroit (N) and one by the Korotneff (K: pelagic trawls).

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(ii) The 50 m oceanographic ship, *Le Noroit*, provided the environmental parameters in a larger area before, during and after the submersible dives (TROPHOS II cruise, April 5–May 7, 1986). Oceanographic stations were made around each submersible dive location (Figure 1) during MIGRAGEL I. Openwater SCUBA diving was also performed from *Le Noroit*; these plankton investigations have been reported elsewhere (Biggs *et al.*, 1987).

(iii) The 20 m research ship of the Station Zoologique de Villefranche-sur-Mer, *Korotneff*, took midwater tows close to five of the eight diving points (PERIGEL cruise). These tows took place at the same time as, or <3 days later than, the corresponding MIGRAGEL I stations. Comparisons between the net sampling and the *Cyana* observations are covered in Laval and Carré (1988).

We made two preliminary dives using the Cyana in the same area, in December 1985 (PREMIGRAGEL cruise).

Submersible dives

The submersible *Cyana* carries three people (pilot, technical operator and scientist) to a maximum depth of 3000 m. The dives reported here represent the first cruise on which the *Cyana* had been used for scientific water column operations. It was necessary to modify the position of the submersible lights so that transparent organisms could be seen against a dark background. A rectangular frame with marks every 10 cm was placed in front of the observer porthole to help in estimating density, size, motion and speed of the organisms.

Dive	Position	Distance	Maximum dive depth	Date	Time	
			(m)	(4/86)	Start	End
D1	43°38.3 N 7°22.5 E	3	600	22	11:00	16:58
D2	43°24.0 N 7°42.5 E	23	700	23	10:48	15:56
D3	43°23.3 N 7°42.5 E	23	425	23–24	19:30	00:30
D4	43°51.5 N 7°34.6 E	13	430	24	09:50	14:36
D5	43°31.2 N 7°34.1 E	13	420	24–25	19:05	00:10
D6	43°38.0 N 7°22.3 E	3	500	25	19:30	24:00
D7	43°36.2 N 7°25.0 E	6	420	26	21:55	0 0:02
D8 '	43°36.0 N 7°25.0 E	6	1302	27	09:45	13:45

Table I. Station list for the eight Cyana dives

Distances are in nautical miles from Cape Ferrat. Hours are in local time (= GMT + 2).

A reduced diving speed ($\sim 5.55 \text{ cm s}^{-1}$) was necessary for careful midwater observations. In order to sample a given layer adequately, we found it necessary to follow a horizontal path so that a sufficiently large volume of water could be scanned. Thus it was not practical in the 5-6 h of each dive to execute a continuous profile to the bottom (which was $\sim 2000 \text{ m deep}$).

Based on the above findings, we designed a sampling scheme combining vertical and horizontal paths in a stepwise fashion in order to sample the upper 400-600 m of the water column adequately (Figure 2). We have included here only those observations made during the descent; during the ascent, turbulence created by the submersible's 'nose' which extends above the viewports, made accurate observations difficult.

Processing of video tapes

The video sound track, on which observers' identifications were recorded together with all sensor information (time, depth, temperature and submersible direction), formed the basis for processing the data.

For easier handling, everything on the sound track and on the screen was first transcribed onto paper. The depth indications, accurate only below ~ 600 m, were corrected for depths above this using a regression equation derived from calibrations made during the dives.

The water column, from the surface down to the maximum depth reached by the submersible, was then split into strata. The strata, as defined, correspond with some of the step limits. Each stratum is 50 m wide (except the uppermost, which is from 0 to 37.5 m), allowing the inclusion in each of two horizontal and two (1 + 2 halves) vertical paths (Figure 2), to allow for sampling a more representative water volume. We have made the first stratum narrower, because it represents a zone that was usually observed inadequately because of poor daylight visibility and general stabilization problems of the submersible.



Fig. 2. Sampling path resembling stairsteps, followed by the submersible during the descent. Each stratum except the first is 50 m wide; stratum no. 2 is shaded. The horizontal segments (not drawn to scale) were each 8 m long, and lasted 2 min 30 s. The vertical segments were 25 m deep, and lasted 7 min 30 s.

Submersible data

For the most frequent species, counts of identified organisms were summed in each stratum. All counts were converted to numbers per 1200 s (a duration close to the actual time spent in most layers, giving more realistic figures).

For any given species these values are indicative of the mean local density of the individuals (although the values may vary with the size, transparency or behaviour of the organisms). It is nevertheless interesting to calculate the corresponding numbers per m^3 , to allow a comparison with net data. This approximate calculation must take into account the volume of water scanned by the submersible, which depends on the submersible speed (from which the traveled distance is obtained) and the field of view. The former can be inferred from previous calibrations to a value close to 5.55 cm s⁻¹. The latter is more difficult to evaluate, and estimates varied from 1 to 4 m², depending on the lights and other factors, including size of the taxon in question. Even if the conservative upper estimate (4 m²) is used, the resulting animal densities are at least twice those inferred from the IKMT tows (Laval and Carré, 1988). These mean field of view (4 m²) and speed (5.55 cm s⁻¹) values will be used throughout this paper.

Many species were seen from the submersible, but the diving scheme, which was designed to scan regularly the different layers from the surface down to 400-600 m, did not permit stopping the submersible in order to observe individual specimens at length. We will thus present distributional data for only the most abundant species.

Observations

Hydrology of the area

The hydrology of the area is becoming better understood as a result of several recent cruises (Prieur, 1979; Béthoux and Prieur, 1983; Béthoux *et al.*, 1988). Its main characteristic is the presence of a gyre-shaped frontal zone that separates a coastal zone from a central zone. During the spring, the front is a turbulent boundary enriched by nutrients from the lower layers and giving rise to high seasonal phytoplankton growth (Boucher *et al.*, 1985).

As indicated by the TROPHOS II T/S diagrams and fluorescence profiles (not shown here), the 'frontal zone' lay (at the surface) between 13 and 23 nautical miles offshore, but not far from our 13 mile stations; in fact, the frontal interface is a plane tilted towards the coast, so that its depth is greater at 13 miles than further offshore. Our 23 mile stations are in the 'marginal zone' beyond the front. The 'central zone' of the Ligurian Sea was not reached during MIGRAGEL I.

The hydrology in the locality of the *Cyana* dives was investigated by CTD profiles made on the same days from *Le Noroit*. Isotherms and isohalines showed similar patterns, so only the former are depicted here. Temporal development of these patterns (Figure 3) is further known at this locality from two profiles made on April 11 and 19, 1986 by *Le Noroit* (before the submersible dives, which took place between April 22 and 27).



Fig. 3. Hydrological sections made with CTD. (A) April 11; (B) April 19; (C) during MIGRAGEL. Only isotherms are shown because they are fairly representative of the water masses. CTD casts were made at the geographical locations shown on the top line of each map (i.e. 3, 13 and 23 nautical miles for A).

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Between April 11 and 19 the meteorological situation was characterized by rough weather caused by a northwesterly displacement of the Azores anticyclone. A strong depression became established over the Western Mediterranean, leading to rough seas and low sunlight conditions. The surface warming that is usually observed at this time of year did not occur in 1986, as may be seen in the limited extension of water >13.4°C in Figure 3 (A, April 11; and B, April 19).

During MIGRAGEL I (Figure 3C) the Azores anticyclone returned to its usual position, and the surface warming re-established, but was not much more developed than it had been on April 11. The temperature profile in Figure 3C is similar to the one measured in May 1982 during TROPHOS I (Groupe TROPHOS, 1983).

Distributions of dominant species

Solmissus albescens (Gegenbaur) (Narcomedusae, Cuninidae). Described for the first time by Péron and Lesueur in 1810 from specimens collected near Nice (Goy, 1980), this species is endemic to the Mediterranean Sea and occurs in both the western and eastern basins (distribution reviewed by Mills and Goy, 1988). There is no doubt about the identifications (\sim 500 specimens seen) made from the submersible: one specimen was caught with a sucking device in PREMIGRAGEL and was identified as *S.albescens*, and all of the specimens (1062) collected during PERIGEL net tows (Laval and Carré, 1988) belonged to this species; the other species of this genus have never been seen in Mediterranean samples (see Kramp, 1961; Benović, 1973; Goy, 1983).

Behavioural observations on *Solmissus* made during the MIGRAGEL I dives are analyzed by Mills and Goy (1988).

Evidence of vertical migration of *S.albescens*. The depth distribution of *S.albescens* is clearly shallower at night than during the day (Figure 4). Vertical migrations of *S.albescens* have been shown already by Franqueville (1971), Benović (1973) and Goy and Thiriot (1976) from net data, and by Genovese *et al.* (1985) using the submersible *Forel* off Messina. This species was present in all night net tows from the upper 200 m, during the second part of TROPHOS II, at three stations around most of the *Cyana* diving positions. These combined tows span a 24 h period and show that *S.albescens* stays in the upper 200 m from 20.20 to 06.40 h (local time). The Isaacs-Kidd trawls made during PERIGEL show a similar pattern.

Submersible observations may both disclose the precise timing of the vertical migration and give an indication of its speed. In determining these factors for *S.albescens*, we used the depth of the mean population density maximum (Table II).

Timing of the migration. The rising time may be inferred from Figure 5, where the data in Table II are plotted against time. Solmissus appears to begin its ascent at \sim 15:00-16:00 h and arrives in the superficial layers towards 00:00 h.

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Fig. 4. Bathymetric distribution of the narcomedusa Solmissus albescens during the eight Cyana. dives (D1-8). The visual counts of medusae are summed over 50 m strata (21 of which are shown on the graph). Each histogram bar is proportional in length to the number of individuals seen in each stratum, standardized to numbers per 1200 s of observation time. The scale bar at the bottom of the graph represents 10 individuals per 1200 s; corresponding estimates per 1000 m³ are given in Table III. The histograms for night dives are shaded. Hours above the surface line indicate the beginnings of dives; ending times of the descents are shown below a short horizontal line drawn at the maximum diving depth (rounded to the nearest stratum; dive D8 reached the bottom at 1302 m).

Dive	Depth of max. den	sity (m)	Direction ^a		
	Submersible going down	Submersible going up			
 D1	460 m	460 m	towards the end of descent		
D2	560 m	_	presumably at its lowest depth		
D3	310 m	25 m	rising		
D4	460 m	460 m	towards the end of descent		
D5	225 m	25 m	rising		
D6	210 m	_	rising		
D7	60 m	25 m	towards the end of ascent		
D8	290 m	-	going down		

Table II. Location of the population density maximum of Solmissus albescens as seen from Cyana

"'Direction' indicates the migratory state of the population at the time of the submersible descent.

This yields a 9–10 h ascent time over 500 m, i.e. $45-50 \text{ m h}^{-1}$. This is close to the figures which can be calculated from Benovic (1973). Mills and Goy (1988), using videotaped observations of individual *Solmissus* seen on the MIGRAGEL



Fig. 5. Solmissus albescens. Depth of maximum density (from Table II) plotted against time. Closed circles, from counts made during descent of the submersible; open circles, during ascent. Broken line, hypothetical migration schedule (see text for explanations). D1-8, dive numbers. Hours in local time (= GMT + 2).

I cruise, obtained a maximum possible speed of up to 144 m h⁻¹, but observed that medusae can swim in any direction during the migration, and concluded that the migratory swimming path may be circuitous rather than direct. If we make the assumption that the descent is accomplished at 45–50 m h⁻¹, there remains 4–6 h per day not spent in migration. This lag time may be residence time near the surface, as suggested by Goy and Thiriot (1976) from tow-net data; this is also consistent with our direct observations of night feeding by *S.albescens* on the pteropod *Cavolinia inflexa* in the upper layers (discussed in Mills and Goy, 1988). If we allow 1–2 h at depth for reversing the direction of migration, we are led to the schedule of Figure 5, which attempts to conciliate our submersible data with the above observations.

Correction of the bias due to the vertical migration. The delayed temporal aspect of a vertical submersible transect requires correction of the observed depths of migrating species. If the *Solmissus* population is going upward at 50 m h^{-1} , while the submersible descends at 200 m h^{-1} , when the upper individuals are encountered the deepest ones are perhaps 300 m below. But hours later, these deepest specimens are at a higher position when they are met by the descending submersible. Simple geometric considerations show that a correction factor equal to the ratio of the medusa speed of ascent to the submersible speed of descent should be applied. In other words, the depth range observed by *Cyana* is, in this case, narrowed by 50/200, or 25%. This situation occurred during the descent in dives D3, D5 and D6. The overall spreading range of the

population is therefore not 200-300 m, as shown by Figure 4, but 250-375 m. The opposite case (submersible and *Solmissus* on the way down) occurred only in dive D8 (because we made no late night or early morning dives); in this case the actual range is shorter than the observed range by 25%. Dives D1, D2, D4 and D7 need little or no correction. The range discrepancies which occur between night and day, and between dives, are thus mostly observational artifacts. The actual spreading range of the *Solmissus* populations for all dives is about 250-300 m.

Density estimates. The submersible data allow estimation of the population density of *S.albescens* in great detail. Using the parameters 5.55 cm s^{-1} submersible cruising speed and 4 m² field of view as stated above, densities of 15->200 individuals 1000 m^{-3} were seen in the stratum of greatest abundance (Figure 4 and Table III). Note that the bias correction due to the migration applies only to the depth limits (i.e. the width of the strata) and not to the population densities themselves.

Instead of focusing on the stratum of greatest concentration, one may also integrate over the depth range occupied by *Solmissus* to obtain a mean population density (Table III). The distributional limits need to be corrected according to the direction of migration. For example, in dive D3 the whole population was seen between strata 4 and 8 (Figure 4), but because the submersible was going down while the medusae were ascending, they were actually distributed over a 25% larger range.

Behaviour. In contrast to *Pelagia noctiluca* (Goy, 1984; Morand *et al.*, 1987), *S.albescens* does not appear to form dense swarms. Its swimming and feeding behaviour, insofar as they are known, have been reported elsewhere (Mills and Goy, 1988).

Cyclothone (Teleostei, Gonostomatidae). Only two species of Cyclothone occur in the Mediterranean: C.braueri Jespersen and Tåning, a small, transparent species that is considered to be mesopelagic (Badcock, 1984); and C.pygmaea Jespersen and Tåning, a smaller, dark Mediterranean endemic species, with a bathypelagic distribution. We did not attempt to differentiate between the two species, all individuals appearing similar when observed from the submersible. Of the 625 specimens caught in the 25 IKMT tows made during PERIGEL at the time of the submersible dives, only 51 (8.2%) were C.pygmaea, and all came from the deeper (600-0 m) tows. It is likely that most of the Cyclothone seen during the submersible dives were C.braueri, with perhaps a few C.pygmaea seen in the lower layers.

Vertical and horizontal distribution. *Cyclothone* are absent from the upper 200 m, as determined both from our submersible observations (Figure 6) and the IKMT samples. The population seems to be concentrated between 200 and 550 m, with a peak at 300-400 m, although we cannot define its lower limit since only one dive went deeper than 600 m. Neither the submersible data (Figure 6)

Dive	Solmissus		Cyclothone		Big app. houses		Lobates		Diphyidae	
	D_{mean}	D _{max}	D _{mean}	D _{max}						
D1	24 (37)	59 (12)	38 (71)	134 (37)	0 (0)	0 (0)	23 + (37)	42 (12)	11 (15)	23 (6)
D2	47 + (69)	175 (21)	55 (118)	133 (39)	21 + (4)	38 + (1)	113 + (207)	317 (38)	24 (36)	62 (17)
D3	46 (79)	118 (33)	108 + (84)	140 (39)	0 (0)	0 (0)	32 + (37)	117 + (25)	13 (18)	32 (8)
D4	78 + (58)	208 (18)	116 + (133)	272 (38)	4 (1)	4 (1)	187 + (96)	416 (36)	71 (61)	211 (34)
D5	9 (13)	15 (4)	45 + (61)	99 (27)	5 + (9)	6 + (4)	34 + (62)	113 (27)	18 (21)	58 (17)
D6	13 (22)	35 (10)	10 + (15)	20 + (3)	34 (40)	54 (14)	19 + (20)	42 (10)	4 (1)	4 (1)
D7	32 (18)	70 (14)	16 (9)	21 (4)	36 + (19)	59 (14)	23 + (20)	31 (10)	6 (2)	8 (1)
D8	89 (25)	150 (10)	15 (14)	45 (3)	30 (11)	48 (4)	28 (13)	56 🤍 (4)	33 (4)	53 (2)

Table III. Organism densities (in individuals per 1000 m³) computed from submersible data (parameters: speed = 5.55 cm s^{-1} ; field of view = 4 m²)

 D_{max} = density in the densest stratum. D_{mean} = mean population density (average computed over all non-zero strata). The number in parentheses is the total number observed. For D_{mean} , the plus sign means that the deepest stratum yielded a non-zero count; for D_{max} it means that the densest stratum is also the last.



Fig. 6. Bathymetric distribution of the pelagic fish Cyclothone (mostly C.braueri). Legend as for Figure 4.

nor the IKMT tows showed convincing evidence of diel vertical migrations of these fish.

A similar, but slightly deeper, distribution was observed for *Cyclothone* in the Straits of Messina in May, by Baguet *et al.* (1983) and by Genovese *et al.* (1985) from the submersible *Forel*, which conducted deeper observations. They, too, found no vertical migration. Palma (1982), using net tows to study the distribution of *C.braueri* on an annual basis in the Ligurian Sea, found a population maximum at \sim 700 m, and Geistdoerfer *et al.* (1974) found that 24% of the population was as deep as 1500 m.

The population density of *Cyclothone* as estimated from the submersible data is shown in Table III. This density was higher in the frontal zone and towards the margin of the central zone, where it reached a maximum value in some layers of slightly more than 100 individuals 1000 m^{-3} in dive D4, 13 miles offshore.

Small appendicularian houses. High densities of small (5–10 mm) appendicularian houses, many of them occupied, were observed in the upper layers (Figure 7). SCUBA divers, operating from TROPHOS II at the same time as MIGRAGEL I, also reported seeing hundreds of Oikopleura houses (Biggs et al., 1987).

The most abundant species in this bloom was *O.albicans* (Leuckart). This identification is corroborated by the plankton tows made during TROPHOS II

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Fig. 7. Bathymetric distribution of small appendicularian houses (probably primarily from *Oikopleura albicans*). Due to the high density of houses, the numbers observed have been coded, with 4, 3, 2 and 1 circles corresponding to 'very high', 'high', 'medium' and 'moderate' density respectively. For each stratum except the uppermost, two rows of circles are drawn. Equivalence with numbers per 1000 m³ is given in the text. For dive D6 the circles in parentheses refer to observations made during the ascent; otherwise, all observations were made during the descent.

and SCUBA dives made at the same time in the nearby Bay of Villefranche (G.Gorsky, personal communication).

It is difficult to estimate the proportion of empty houses among the total number of houses we saw from the submersible, but we assume >50% were empty. House density in some layers was so high that it was not practical to illustrate it using the linear scale of the previous figures. We have instead adopted a coded scale for Figure 7, with four classes: very high density, corresponding to houses spaced from 5–10 to 50 cm apart $(10^4-10^6 \text{ per } 1000 \text{ m}^3)$; high density: houses 50 cm–1 m apart $(10^3-10^4 \text{ per } 1000 \text{ m}^3)$; medium density, houses >1 m apart $(200-10^3 \text{ per } 1000 \text{ m}^3)$, but too numerous to be counted; and moderate density, corresponding to houses in the same density range as the other dominant organisms in this paper (~10-200 per 1000 m³). These density estimates were computed assuming a simple cubic arrangement of the houses; formulae based on hexagonal or isahedronal packing [used respectively by Mackie and Mills (1983) and Hamner and Carleton (1979)] may overestimate numerical density, because the actual arrangement is not so tight.

In the uppermost stratum, appendicularian house densities were difficult to observe. The submersible was not stable in surface waters and was often moving vertically too fast for good observation. Also, during daytime dives the light in

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the upper layer was too strong and diffuse for good illumination of the houses, which show up best with back- or side-lighting (as is accomplished by the submersible lights in deep water or at night). During some dives, houses went unnoticed by the observer at the beginning of the descent, but were reported as very numerous in the same layer at the end of the dive. Vertical migrations are excluded as a cause for such discrepancies, as neither the other data (Figure 7) nor the literature (Fenaux, 1966) support such an interpretation. Patchiness may play a role, but it is more likely that the observers learned to distinguish the houses during the course of the dive or that surface lighting conditions were more easily adapted to form the darker depths than upon immersion of the submersible in the daylight.

To supplement the weakness of our submersible observations in the first stratum, we can use SCUBA diving data from nearby in the same week. The upper 20 m were scanned by SCUBA divers operating from *Le Noroit* (Biggs *et al.*, 1987). Converting their figures, given in houses min⁻¹, to our coding scheme, we assign (for dive D1) a 'moderate' rating for the uppermost few meters, increasing to 'medium' within the first 10 m, and continuing with the same intensity down to 20 m.

As shown by Figure 7, O.albicans was more abundant in the coastal and frontal zones than near the central zone [this was also noticed by Biggs et al. (1987)]. Its high density at 3, 6 and 13 miles is a situation which sometimes occurs just after the phytoplankton spring bloom in the Ligurian Sea.

Large appendicularian houses. In addition to the small houses occurring in the upper layers, larger (~4 cm) appendicularian houses were observed in deeper waters (300-450 m) (Figure 8). In most cases the main filters of these houses were very distinct, appearing as a pair of white patches; sometimes the undulating movements of the animal's tail were discernible inside. Two large species of appendicularians have been recorded in the area (Fenaux, 1966): Megalocercus abyssorum Chun, which has a distinctive red or orange-yellow colour, not seen from the submersible, and Stegosoma magnum (Langerhans), which makes slightly smaller houses (2-3 cm) and has a shallower depth range [above 150 m, according to Fenaux (1966)]. No large appendicularians were caught in the plankton tows taken nearby at the same time as the submersible dives during the TROPHOS II cruise. In fact, specimens similar to those we observed were captured during the May 1988 MIGRAGEL II cruise and proved to be an undescribed oikopleurid (R.Fenaux, personal communication).

The vertical range, 300-450 m, of the large oikopleurid houses is clearly below the euphotic zone (Figure 8). They were most abundant in the coastal area (3 and 6 nautical miles). Their apparent absence at 3 miles by day (D1) and abundance at the same location by night (D6) is surprising; the first observer was perhaps not prepared to see such large houses, and dismissed them as 'large aggregates'.

The high number of houses per 1000 m^3 (Table III) is surprising for a filterfeeder living below the euphotic zone; this warrants further investigation on the food these appendicularians find at this depth.

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Fig. 8. Bathymetric distribution of the large appendicularian houses. Legend as for Figure 4.

Siphonophores. Ten species of siphonophores were observed. Those belonging to the suborder Calycophorae (only the polygastric phase was identified) were Chelophyes appendiculata (Eschscholtz), Lensia conoidea (Keferstein and Ehlers), L.subtilis (Chun), Muggiaea sp., Abylopsis tetragona (Otto), Hippopodius hippopus (Forsskål) and Lilyopsis rosea Chun. The suborder Physonectae was represented by Agalma elegans (Sars), Nanomia bijuga (Delle Chiaje) and Forskalia edwardsi Kölliker.

Only C.appendiculata occurred in relatively large numbers—the figures in Table III under 'Diphyidae' refer almost entirely to this species. Lensia conoidea ranked second in abundance; we saw only $\sim \frac{1}{6}$ as many L.conoidea as C.appendiculata, a ratio close to the one found in the IKMT samples. In the remainder of this section, we will consider only C.appendiculata.

Chelophyes appendiculata. This species has the same overall shape as *L.conoidea*, but is easily distinguished from the latter when in resting position, the position most often seen from the submersible. In *C.appendiculata* both the stem and the nectophores are held nearly vertically, whereas in *L.conoidea* only the stem hangs vertically, perpendicular to the horizontal axis of the nectophores.

During all our morning dives, *C.appendiculata* was restricted to a mean depth range of 100-250 m (Figure 9), where it occupied a layer $\sim 100-200$ m wide on any one dive. Between 19.00 and 21.00 h, the range narrowed slightly to

100-200 m, with a band width of 100-150 m on each dive. In the middle of the night, this species was observed close to the surface.

The pair of dives D4/D5 shows clear evidence of a diel vertical migration, with a 100-150 m range. Such a migration is less clear in the other pairs of dives, but this may be due to the relative scarcity of clearly identified specimens. Franqueville (1970) found a similar migration range in the Mediterranean near Toulon in June. Pugh (1974) also described a slow vertical migration of ~200 m for this species in the North Atlantic. From all the dives data, we may conclude that *C.appendiculata* stays at the subsurface during the dark hours, and then descends to ~200 m between 7 and 11 h.

This species was seen in all dives, with higher mean densities at 13 and 23 nautical miles (Figure 9 and Table III).

Ctenophores. Several species of ctenophores were seen from the submersible, but only one, a lobate, was present in large numbers. Other ctenophore species were very scarce, and included some easily identifiable taxa (*Pleurobrachia rhodopis* Chun, *Cestum veneris* Lesueur, *Beroe ovata* Eschscholtz), as well as juvenile forms or organisms not positively identified by all the observers. Only observations of the abundant lobate will be discussed here.

Individuals of the lobate species were estimated to be up to 5 cm in length. They were observed during all of the PREMIGRAGEL and MIGRAGEL I dives. Although we were unable in this cruise to collect any specimens, these



Fig. 9. Bathymetric distribution of the diphyid siphonophores (mostly *Chelophyes appendiculata*). Legend as for Figure 4.

ctenophores looked like *Bathocyroe* sp., based on their general appearance and distinctive swimming behaviour [this conclusion was agreed with by M.J.Youngbluth, on a May 1988 dive in the same area (personal communication)]. Most specimens were motionless when first seen, with the lobes either open and extended, or closed; when disturbed, this ctenophore swam away by flapping its lobes together in a flap and glide rhythm. A patch of red pigmentation was evident on the gut walls. A similar ctenophore has been described as *B.fosteri* by Madin and Harbison (1978) from the mesopelagic North Atlantic (336–980 m deep).

The swimming lobate ctenophore was one of the most abundant species seen in the MIGRAGEL I cruise (Table III). Most of the specimens were observed at 13 and 23 nautical miles from the coast (Figure 10). There was no evidence of vertical migration. It occurred from ~ 200 m to >750 m deep. No specimens were found in the PERIGEL samples; the trawl is obviously too destructive for collection of these fragile organisms.

Remarks on other species and organic material

Salps were unexpectedly very rare for this time of the year and this area, and were limited to the upper 400 m; only a few specimens of *Salpa fusiformis* Cuvier were seen on dives D3, D4, D5 and D7. Pyrosomes were also very scarce: only seven colonies were seen during all the dives, all in the upper 350 m.



Fig. 10. Bathymetric distribution of lobate ctenophores (primarily *Bathocyroe* sp., with a small number of *Thalassocalyce* sp. included). Legend as for Figure 4.

However, a number of females of the hyperiid amphipod *Phronima sedentaria* (Forsskål) were observed (at stations D1, D2, D5, D6 and D7) inside the typical barrels they make from salps and pyrosomes (Laval, 1978)—on one occasion the observer (Ph.L.) even saw distinctly on a barrel the tubercles characteristic of a pyrosomian origin. The observation of *Phronima* in the apparent absence of Thaliacea may be due to the attraction of the amphipods by the submersible lights from very far away.

Thecosome molluscs, mostly *Cavolinia inflexa* (Lesueur), were seen only in the upper 300 m. *Cavolinia* egg masses were also present, but their transparency made them almost invisible in the daylight-illuminated upper layers and thereby difficult to quantify. Patchy distribution, which seems to be a characteristic feature of this species, may explain why only egg masses and no adults were seen during dives D6 (3 miles, night) and D2 (23 miles, day). A few individuals of the genus *Clio* were also observed.

'Star-like' protozoa, measuring $\sim 1-3$ cm in diameter including spines, were easily visible. The more numerous form appeared to have 5-8 rather heavy spines and occurred either singly or as double 'stars'. A second form had many more, thinner, spines. These protozoa were abundant at the 13 and 23 mile stations, with a maximum in the 200-400 m layer. They were seen as deep as 800 m on dive D8. No differences in day/night distribution were evident.

This cruise was not aimed at the study of marine snow, but its abundance and ubiquity struck all of the observers. In each dive, particles from a few millimetres to 1 cm, as well as mucous aggregates of several centimetres and filaments up to 60 cm long, were present at all depths. In dive D8, which reached the bottom at 1302 m, marine snow was present during the entire dive. In any one dive there was no clear gradient of abundance; we observed only local variations, and no obvious tendency towards accumulation at depth.

Conclusion

The submersible appears to be an invaluable tool for disclosing the abundance and exact position of deep macroplanktonic and micronektonic organisms. Animals ordinarily caught by nets and pelagic trawls, such as *Solmissus* or *Cyclothone*, are spotted precisely in time and space in the water column; this is a definitive advantage over nets, which mix the microdistributions of these organisms in a single sample. Moreover, the submersible is unique in providing the opportunity to observe and count very fragile organisms, such as ctenophores and large appendicularians (and their houses), which leave no recognizable remains in net samples.

By only using plankton nets, and focusing on mesoplankton, an important part of the Mediterranean ecosystem has been missed. For instance, abundant species like the lobate ctenophores and the large appendicularians we saw in MIGRAGEL I had not previously been recorded in spite of more than 25 years of regular plankton tows made in this area.

The fauna of fragile organisms that we saw during this cruise was distributed as follows.

(i) The coastal area (3 and 6 miles) differs from the offshore area (13 and 23 miles), and in each there is a marked change in community structure at 300-400 m.

(ii) In the coastal area, the upper layers are dominated by the herbivorous *Oikopleura albicans*, while the carnivorous diphyid siphonophores are not numerous. Fenaux (1966) reported that in some years *O.albicans* may form swarms as dense as salp swarms. MIGRAGEL I took place in such a 'non-salp year', at least in the coastal area of the Ligurian Sea. The hydrological conditions in 1986 may well have impeded the more typical explosive growth of salp aggregates, leaving an open ecological niche for the oikopleurids. Such a trade-off constitutes an interesting area for future research.

(iii) The lower layers of the coastal area were characterized by a nonmigratory population of *Cyclothone braueri*, and below, by an unexpected presence of large appendicularians. At 300 m there is not enough light to sustain the growth of algae, so that these filter-feeders may rely on the downward transport of phytoplankton by the frontal convergence or on the sedimentation of fecal pellets, or they may feed on fine detrital material. The overwhelming presence of marine snow at these depths is an indication that non-algal material may play an important role. More investigations are needed on the flux of organic matter at these depths.

(iv) The carnivorous medusa *Solmissus albescens* spanned both the upper and lower layers during the course of its diel vertical migration—its effect on the rest of the community cannot be ascertained at this time. It was a little less abundant at 3 miles than further offshore.

(v) The offshore area was dominated by carnivores: diphyid siphonophores were numerous in the upper layers, and *Cyclothone* and the lobate ctenophore resembling *Bathocyroe* sp. were abundant in the lower layers. *Solmissus albescens* moved throughout the upper 600 m on its diel migrations as it did in the coastal zone.

The cost and logistics of submersible dives preclude their use on a routine basis. But we are now in position to argue that a major oceanographic cruise aimed at the study of a planktonic ecosystem should be supplemented if at all possible by submersible dives. With special equipment and sensors specially designed for the water column and for the collection of fragile and transparent organisms, submersibles may provide crucial elements for understanding ocean fluxes.

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