

# Deep planktonic filter-feeders found in the aphotic zone with the Cyana submersible in the Ligurian Sea (NW Mediterranean)

Philippe Laval, Jean Claude Braconnot, Nadja Lins da Silva

Observatoire Océanologique, URA 716 du CNRS, Station zoologique, BP 28, F-06230 Villefranche-sur-Mer, France

**ABSTRACT:** Dives made during spring 1988 in the Ligurian Sea with the Cyana submersible uncovered a deep layer of active salps *Salpa fusiformis* and large appendicularians (a new species of *Oikopleura*). These zooplanktonic organisms stayed at a depth of about 400 m, and did not perform vertical migrations. There was a substantial amount of living micro- and nanoplankton, transported by the strong downwelling due to the Ligurian convergence, at the depth of the layer where the filter-feeders were. We believe that this circulation process occurs year-round and provides sufficient particulate matter to sustain midwater populations of salps and appendicularians.

## INTRODUCTION

Deep fragile macroplanktonic organisms may in most cases be observed and sampled only with submersibles. Plankton nets destroy many ctenophores or such delicate structures as larvacean houses; long salp chains are broken and are not effectively collected by fine mesh nets.

In April 1986, dives were conducted with the submersible 'Cyana' in the Ligurian Sea during the MIGRAGEL I cruise (Laval et al. 1989) to observe fragile macroplankton that are poorly represented in net-collected samples. One of the main objectives was to study the development of a salp bloom, an event which regularly occurs in spring in this area (Braconnot 1971). Unfortunately, 1986 happened to be an exceptional year. There was no salp bloom. Instead, a deep population of large appendicularians (houses 4 to 5 cm in diameter) was observed for the first time in this area.

In May 1988, a second submersible cruise, MIGRAGEL II, was undertaken in the same area. This time, salps were present in large numbers, as well as the large appendicularians. These appendicularians co-occurred in the mesopelagic zone with a deep population of salps. This paper reports the distribution of both these filter-feeders and the specific composition of their trophic environment.

## METHODS

**Sampling.** Eight submersible dives (Table 1; MG1 to MG8) were made in the area of the Ligurian Sea already sampled during MIGRAGEL I. A map showing these stations may be found in Gorsky et al. (1991). The Cyana was equipped with two 6.5 l 'detritus samplers' (Youngbluth 1984).

**Distribution of macroplanktonic animals.** Standing stocks were determined using the same method as for MIGRAGEL I (Laval et al. 1989). However, results are reported here in a semi-quantitative coded form more suitable for depicting population densities (see legend to Fig. 1). For each layer, the code corresponds to the maximum abundance observed. Small variations between observers, in illumination of the field of view, or in time spent in the layers are greatly smoothed with this coding. This depiction is nevertheless representative of the relative abundance of zooplankton that exhibit a high level of patchiness.

Average densities corresponding to each code were estimated as follows. The surface scanned by the observer from the porthole was measured before the MIGRAGEL II cruise by submerging the vessel in a test basin. At a mean observational distance of 1.5 m, this surface was 4.6 m<sup>2</sup>; it had been estimated (with less precision) in a previous paper to be about 4 m<sup>2</sup> (Laval & Carré 1988). Because counting encompassed

Table 1. Characteristics of dives in the Ligurian Sea

Dive	Date (May 1988)	Location	Nautical miles from Cape Ferrat	Start–End (UT + 2 h)	Max. dive depth (m)
MG1	14	43°37.7' N, 7°26.6' E	6	21:41–02:00	615
MG2	15	43°35.6' N, 7°29.4' E	8	21:40–01:53	625
MG3	16	43°37.2' N, 7°26.6' E	6	21:11–01:30	625
MG4	17	43°35.6' N, 7°29.4' E	8	14:50–19:22	590
MG5	19	43°27.8' N, 7°46.8' E	23	09:33–14:16	692
MG6	20	43°32.8' N, 7°35.2' E	13	10:30–15:10	610
MG7	21	43°35.9' N, 7°28.8' E	8	09:48–14:45	970
MG8	22	43°36.0' N, 7°39.2' E	8	09:15–11:25	457

animals situated from 0.5 m to about 4 m from the port-hole, we took 5 m<sup>2</sup> as a coarse estimate. For calculating densities, the water column was divided in layers 20 m thick. The volume scanned along a 20 m vertical path was thus roughly 100 m<sup>3</sup>. When many individuals were close together, we assumed a cubic arrangement (as was done in Laval et al. 1989). An inter-individual spacing of 1.5 m corresponds to about 300 individuals per 1000 m<sup>3</sup>.

#### Distribution of microplankton and nanoplankton.

After the dives, a fraction of the water contained in the 'detritus samplers' was kept for counting; these samplers were usually closed with a large appendicularian inside, except for MG8, during which a large planktonic foraminifer was caught, and MG6, when only water from the appendicularian layer was taken.

One hydrological cast with Niskin bottles at 0, 50, 100, 200, 300, 400, 550, and 600 m was also made from the research ship of the Station zoologique, RV 'Korotneff', at a station (Stn H) close to dive MG6, but 1 nautical mile away, for safety reasons.

Samples were preserved with Lugol's solution and counted after settling in a 100 ml Utermöhl chamber. For phytoplankton, only pigmented cells were considered. Cells were also counted in samples from the 'detritus samplers' for all dives, and in surface samples for dives MG7 and MG8.

## RESULTS

### Distribution of salps (Fig. 1)

Two species were abundant in the upper layers: *Ihleia punctata* (Forsskål – usually but erroneously spelled Forskål; see Hureau & Monod 1973, p. 322), and *Salpa fusiformis* Cuvier. The former occupied the first 100 m, while the latter extended from 0 to 150 or 200 m.

Below the upper layers occupied by salps, there was in almost all dives, between 150 and 250 m, a layer

almost devoid of conspicuous organisms, which the observers called the 'desert zone'. This layer was seen in many submersible campaigns in this area.

Below the desert zone, the submersible dives uncovered an unforeseen aspect of the *Salpa fusiformis* distribution. A population of this species was observed between 400 and 600 m during all dives except MG1 and MG5 (Fig. 1). Live oozoids (solitaries) and blastozoids (chains) were present and were swimming slowly, in the same way they normally filter water for feeding. Some blastozoids carried embryos, an indication that the population was healthy. This deep population did not reach high densities (as is apparent from the absence of Code 3 in Fig. 1), but was regularly present. Its abundance increased from the station at 6 nautical miles from Cape Ferrat to those at 8 and 13 miles; it was deeper at these offshore stations (500 to 550 m). No deep *S. fusiformis* were observed at the 23-mile station, MG5, where the maximum dive depth was 692 m.

### Distribution of *Phronima sedentaria* (Fig. 1)

Results concerning the hyperiid amphipod *Phronima sedentaria* (Forssk.) are presented here together with those of the salps because, in the Ligurian Sea, this parasitoid crustacean depends on them for feeding and making its 'barrel' (Laval 1978, 1981). The consequences of this feature are discussed below.

For the deep layer, the distribution of *Phronima sedentaria* corresponded closely to that of the salps, with 2 notable exceptions. In dive MG1, no *Salpa fusiformis* were observed below 300 m, while *P. sedentaria* was abundant between 340 and 520 m (there were also some *P. sedentaria* between 10 and 280 m). In dive MG5, there were a few *P. sedentaria* individuals in the 420 to 440 m layer, but a continuous population, increasing in density with depth, was seen from 640 to 692 m, the end-of-dive limit.

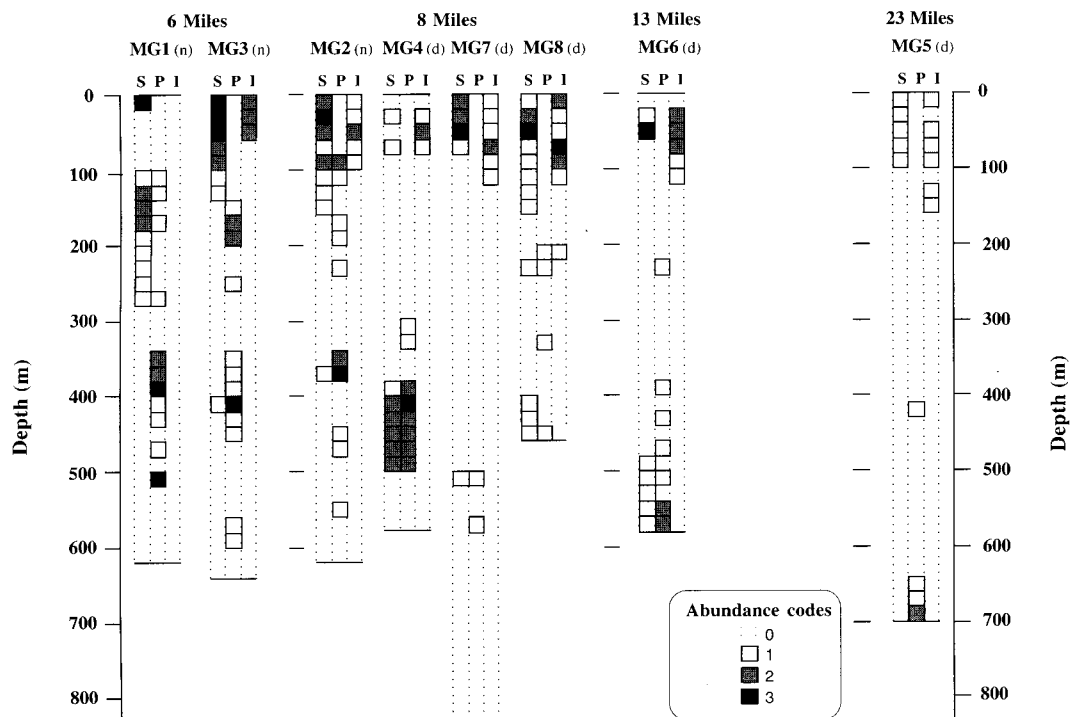


Fig. 1. *Salpa fusiformis*, *Phronima sedentaria*, *Ihlea punctata*. Depth distribution of 2 species of salps and an amphipod during the MIGRAGEL II cruise, at Stns MG1 to MG8. (d) or (n): day or night dive. S: *S. fusiformis*; P: *P. sedentaria*; I: *I. punctata*. For each 20 m layer, the abundance codes are as follows: (0) absence; (1) corresponds to 1–5 animals in the field of view; (2) and (3) correspond to > 5 animals, with inter-individual distances > 1.5 m and ≤ 1.5 m. Dive MG7 reached 970 m. The horizontal spacing of the dives is not drawn to scale

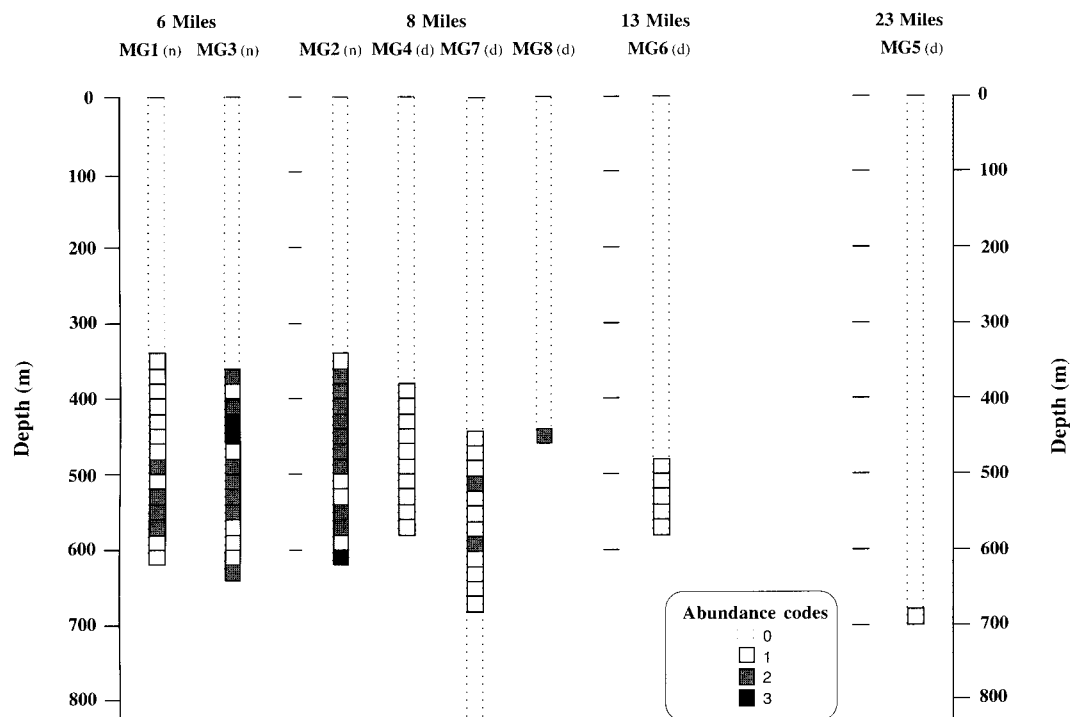


Fig. 2. *Oikopleura* sp. Depth distribution of a large new appendicularian species. Codes and abbreviations as in Fig. 1

### Distribution of large appendicularians (Fig. 2)

The deep population of a large species of *Oikopleura* found during MIGRAGEL I (Laval et al. 1989) occurred at the same place during MIGRAGEL II [according to R. Fenaux (pers. comm.) it is a new species, which will be described as *O. villafrancae*]. This species was always present in moderate numbers below 320 m, down to 600 m and more. Its upper limit deepened as the distance from the coast increased, and it is apparent from Fig. 2 that the dive MG5 reached only the top of its depth range.

### Distribution of microplankton and nanoplankton

The diatoms *Leptocylindrus danicus* Cl. and *Nitzschia seriata* Cl. reached densities of 1700 cells  $l^{-1}$  in surface water at Stn H. Other abundant species in the surface water were *Rhizosolenia alata* (Bright) and *R. fragilissima* Bergon (240 and 280 cells  $l^{-1}$ , respectively). These species were rare or absent below the surface.

The composition of micro- and nanoplankton populations at the depth of the deep filter-feeder's layer is given in Table 2. Five species were present at densities  $\geq 100$  cells  $l^{-1}$ , some at depths  $> 500$  m.

## DISCUSSION

### Presence of a deep population of *Salpa fusiformis*

The salps *Ihlea punctata* and *Salpa fusiformis* are frequently seen in the upper layers of this area and in the Bay of Villefranche in spring. However, direct observation of numerous *S. fusiformis* below 400 m, in the aphotic zone of the Ligurian Sea, was unexpected. To understand this, it is helpful to consider previous observations, which at the time were dismissed because of the uncertainty attached to the collecting devices, especially for deep operations.

*Salpa fusiformis* was present in vertical opening-closing plankton tows made in May 1963 in the same area, 10 and 15 nautical miles off Villefranche, in layers at 1000–600, 1500–300, and 300–100 m depth (Braconnot et al. 1965). Franqueville (1971) also caught this species in (non-closing) IKMT pelagic trawls between 300 and 800 m, not far from this area. In the tropical Atlantic, Godeaux & Goffinet (1968) found *S. fusiformis* below 300 m in 42 samples out of 91.

Even in our MIGRAGEL I submersible dives (Laval et al. 1989), when there were no salps in the surface layers, we observed a few individuals (oozooids and blastozooids) of *Salpa fusiformis* between 150 and

500 m; they were not reported in that paper because of their scarcity. Retrospectively, these observations appear significant, because they showed the persistency of a sparse deep population even in the absence of a surface spring bloom.

### Do *Salpa fusiformis* undergo diel vertical migrations in the Ligurian Sea?

By 'diel vertical migrations', we mean that the bulk of the population is found in the upper layers at night, and is found at much greater depths during the daytime. Long-range vertical migrations are known for the closely related species *Salpa aspera* (Wiebe et al. 1979). Our data do not show any clear evidence of such behavior for *S. fusiformis*. During the daytime dives (MG4 to MG8), as well as during the nighttime dives, *S. fusiformis* was present in significant numbers in the upper layers. Except in MG1, the deep population was also always present, both day and night (although in low numbers during the 2 nighttime dives, MG2 and MG3). Its absence at depth in MG1 was not accompanied by a corresponding absence of *Phronima sedentaria* (see below).

These underwater observations are consistent with results from several years of plankton net collections in the same area (Braconnot 1971, Braconnot et al. 1990), which show the presence of *Salpa fusiformis*, often in large numbers, in the upper layers during daytime. However, it should be noted that no systematic sampling has been conducted with an opening-closing net for the purpose of studying any possible vertical migration of this species in this area. There is no doubt that *S. fusiformis* occurs in abundance in the upper layers during daytime in the Ligurian Sea. This does not appear to be the case in the North Atlantic. Here Harbison & Campenot (1979), using SCUBA, almost never found *S. fusiformis* (or *S. aspera*) in the upper layers during daytime.

Franqueville (1971) claimed that *Salpa fusiformis* undergoes diel vertical migration. This assertion has been repeated by all subsequent workers, but it is suggested only by the illustrations in Franqueville's paper: the data for daytime did not include the 100 to 0 m layer, while night hauls did, and the Isaacs-Kidd trawl used had no closing device, so that specimens plotted at depth may well have been caught all along the way up. Visually an upward migration seemed to take place at night, but this was not supported by the underlying data.

We are not saying here that *Salpa fusiformis* does not migrate vertically in the Ligurian Sea, only that the bulk of the population does not move up and down on a nycthemeral basis. This does not preclude that a few

Table 2. Abundance (cells l<sup>-1</sup>) of living microplankton and nanoplankton below 300 m during the MIGRAGEL II cruise. Values  $\geq 100$  are underlined. H: hydrological station sampled from the RV 'Korotneff', 1 nautical mile from dive MG6, at the same time; Distance: distance from coast (nautical miles); Sampling devices: S, detritus sampler attached to the submersible; N, Niskin bottle; Depth: depth of sample (m)

Species	Dive:	MG3	MG4	MG7	MG7	MG8	H	H	H	H	MG6	MG5	MG5
	Distance:	8	8	8	8	8	12	12	12	12	13	23	23
	Sampling device:	S	S	S	S	S	N	N	N	N	S	S	S
	Depth:	450	418	490	509	450	300	400	500	600	570	300	680
<b>Diatoms</b>													
<i>Amphora</i> sp.		20	10										
<i>Asterionella glacialis</i> Castr.						20							
<i>Asteromphalus</i> sp.					10								
<i>Bacteriastrium delicatulum</i> Cleve							10				10		
<i>Coscinodiscus</i> sp.		<u>260</u>						10		10			50
<i>Coscinodiscus radiatus</i> Ehr.		20											
<i>Ditylum brightwelli</i> (West) Grunow		20	10	10			20		10	30	10		20
<i>Leptocylindrus danicus</i> Cleve					10	10							
<i>Nitzschia delicatissima</i> Cleve						20							
<i>Nitzschia seriata</i> Cleve												<u>160</u>	
<i>Nitzschia</i> sp.		<u>420</u>						30		20	<u>170</u>	10	10
<i>Pleurosigma</i> sp.							20		20				
<i>Rhaphoneis</i> sp.		80								10			
<i>Rhizosolenia setigera</i> Bright.													10
<i>Rhizosolenia styliformis</i> Bright.												10	
<i>Skeletonema costatum</i> (Grev.) Cleve											40		
<i>Thalassiosira eccentrica</i> (Ehr.) Cleve		<u>120</u>											
<i>Thalassiosira</i> sp.		20	<u>110</u>	10	70	<u>110</u>	<u>100</u>	<u>170</u>	<u>220</u>	40	<u>280</u>	<u>190</u>	<u>111</u>
<i>Thalassionema nitzschioides</i> Grunow												20	
<i>Thalassiotrix frauenfeldi</i> Grunow					20								
<i>Triceratium alternans</i> Bailey										20			
<b>Dinoflagellates</b>													
<i>Gymnodinium</i> sp.						10					30		
<i>Gyrodinium spirale</i> (Bergh.) Kofoid & Swezy					10				60				
<b>Silicoflagellates</b>													
<i>Dictyocha fibula</i> Ehr.					10		10	10			20		
<b>Tintinnids</b>													
<i>Dadayella ganymedes</i> (Entz Sr.)												10	
<i>Tintinnopsis nana</i> Lohmann							10	10		10			
<b>Ciliates</b>													
<i>Mesodinium rubrum</i> Lohmann			10	30			40	50	10				10
Total		960	140	50	130	170	210	280	320	140	560	400	210

individuals move vertically, essentially when the hydrological conditions become homogeneous at the end of winter.

#### *Phronima sedentaria* as an aid in salp detection

The close correlation noted between the depth distributions of *Salpa fusiformis* and *Phronima sedentaria* is not surprising, owing to the peculiar biology of phronimids. It was mentioned above that these amphipods live in tunicate 'barrels'. For *P. sedentaria*, these barrels come from salps (and also pyrosomes). The amphipod uses them to protect and rear their off-

spring. Salps are sought for making barrels, and are part of the amphipod diet.

In the northwestern Mediterranean Sea, *Phronima sedentaria* is found in the upper layers at night, and below 200 m during daytime (Vu Do 1981). This was confirmed by our results: its upper limit was higher during the night dives (MG1 to MG3) than during the daytime dives (MG4 to MG8). It did not co-occur with *Ihleia punctata*. This is consistent with the fact that its barrel comes from the oozoid of *Salpa fusiformis* (Laval 1978). It may also be built from *Pyrosoma atlanticum* (Péron), but only one individual of this species was seen from Cyana during MIGRAGEL II (Stn MG1, at 108 m depth).

The fact that hyperiid amphipods are attracted by the submersible lights is a common observation made from submersibles (own obs., and M. Youngbluth pers. comm.). Sometimes 'clouds' of amphipods such as *Brachyscelus cruscum* Spence Bate follow the descent of the submersible for over more than 100 m; if the lights are switched off several minutes while the submersible goes down, the amphipods are 'lost' when the lights are switched on again, but they soon reappear in numbers. Amphipods such as *Phronima sedentaria* or *Platyscelus ovoides* (Claus) do not form very dense clouds, but they follow the submersible's descent, and their numbers increase when the descent pauses.

If we assume that (1) the distribution of salps is patchy, (2) the amphipod can detect the submersible lights from a great distance, and (3) *Phronima sedentaria* stays inside, or close to, patches of *Salpa fusiformis*, then the presence of a few *P. sedentaria* is an indication that a salp patch is present at some distance from the submersible. This explanation may account for the fact that no deep *S. fusiformis* were observed in dive MG1, while numerous *P. sedentaria* were attracted by the submersible lights (Fig. 1). Also, *S. fusiformis* was not observed below 650 m in MG5, but the presence of *P. sedentaria* may indicate that this was indeed the top of the salp layer.

The patchiness of the distribution of *Salpa fusiformis* is apparent in some studies (Braconnot 1971, Nival et al. 1990). This may be a consequence of its asexual reproduction (one solitary giving birth in a short time to several chains of aggregates). It is likely that the eyes of *Phronima* spp. are very sensitive, as well as capable of high resolution, as shown by histological studies (Ball 1977, Land 1981).

#### What happens to *Salpa fusiformis* between the spring blooms?

Our findings of a deep population of *Salpa fusiformis* may provide an explanation of the 'disappearance' of the species in the plankton collections from the upper layers between spring blooms (Andersen & Nival 1986, Nival et al. 1990). These authors suggested that either (1) a small population of old salps takes refuge in deep layers, persisting there until the spring, or (2) they remain offshore, where they are not sampled, during winter. Regarding the first case, they observed that 'salps do not seem to have sufficient reserves to maintain a basal metabolism in these conditions'.

The complete salp life-cycle, including the solitary and the aggregate phase, lasts 20 to 25 d at 15 °C (Braconnot et al. 1988). There is a rapid succession of generations during the spring bloom, and the salps

spread over the entire Ligurian Basin. They disappear from the upper layers at the beginning of summer (Braconnot 1971).

As shown by Braconnot et al. (1988), a density of only 1 individual of *Salpa fusiformis* per 100 m<sup>3</sup> is enough, in February, to produce a very dense population (1000 to 1500 ind. per 100 m<sup>3</sup>) 2 mo later. In February, the water column is homogeneous from the surface down to at least 600 m. It is thus not hard to suppose that a few individuals may then swim from the deep layer to the upper layers, where they may take advantage of the highly favorable conditions for re-initiating the spring bloom.

#### The deep filter-feeder layer

Salps and large appendicularians co-occurred in the deep layer, with the same distributional pattern relative to the frontal zone (i.e. they were found deeper at the 23-mile station than in the more coastal station, the frontal zone itself being near the 13-mile station).

The presence of a healthy deep population of *Salpa fusiformis* raises some questions about their source of food. In the absence of light, there was still a significant number of living phytoplanktonic cells at the depth of the salp layer (Table 2). It is very likely that they were transported by the convergence induced by the frontal circulation (Sournia et al. 1990). Smayda (1971) recognized that downwelling may play an important role in the transport of phytoplankton to great depths. However, the amount of phytoplankton found in the salp layer does not seem sufficient to satisfy the food requirements of *S. fusiformis*, as calculated by Cetta et al. 1986. But *S. fusiformis* is also able to collect particles as small as 1 µm (Morris et al. 1988, Bone et al. 1991), and this may account for the survival of the deep population between spring blooms.

For the large appendicularian species, measurements (Gorsky et al. 1991) showed that deep phytoplankton could provide less than 1/10 of carbon requirements. To survive, the appendicularians must ingest substantial amounts of particulate organic matter. This point is fully discussed in Gorsky et al. (1991).

The above hypothesis concerning the presence of a small, perennial deep salp population requires that food be available over the entire year, not only during the spring bloom. Thus phytoplankton cannot be the only food source for these deep salps. Particulate matter originating from the Ligurian frontal zone, of which the micro- and nanoplankton found at depth is only a part, may provide a continuous flux sufficient to explain the persistence of the deep filter-feeder population.

**Acknowledgements.** We thank I. Palazzoli for her help with video and photo manipulations during and after the cruise. G. Gorsky was a member of the scientific party, and also contributed with helpful discussions. M. J. Youngbluth conducted the MG7 dive; he kindly supplied the detritus samplers mounted on Cyana; he also helped to improve the manuscript. S. Dallot provided critical comments. The technical support of the Cyana pilots and crew was greatly appreciated. J. Goy (Muséum, Paris) informed us about the correct spelling of Forsskal. The cruise was supported by CNRS/INSU and IFREMER.

#### LITERATURE CITED

- Andersen, V., Nival, P. (1986). A model of the population dynamics of salps in coastal waters of the Ligurian Sea. *J. Plankton Res.* 8: 1091–1110
- Ball, E. (1977). Fine structure of the compound eyes of the midwater amphipod *Phronima* in relation to behavior and habitat. *Tissue Cell* 9: 521–536
- Bone, Q., Braconnot, J. C., Ryan, K. P. (1991). On the pharyngeal feeding filter of the salp *Pegea confoederata*. *Acta zool. (Stockholm)* 72: 55–60
- Braconnot, J. C., Carré, C., Goy, J., Sentz-Braconnot, E. (1965). Campagnes planctoniques en mer de Ligurie. *Cah. océanogr.* 17: 185–206
- Braconnot, J. C. (1971). Contribution à l'étude biologique et écologique des Tuniciers pélagiques Salpides et Dolioïdes. I. Hydrologie et écologie des Salpides. *Vie Milieu* 22: 257–286
- Braconnot, J. C., Choe, S. M., Nival, P. (1988). La croissance et le développement de *Salpa fusiformis*. *Annls Inst. océanogr.*, Paris 64: 101–114
- Braconnot, J. C., Étienne, M., Moitié, M. (1990). Distribution du Tunicier pélagique *Salpa fusiformis* Cuvier à Villefranche: 13 années d'observations. *Rapp. P.-v. Réunion. Commn int. Explor. scient. Mer Méditerran.* 32: 225
- Cetta, C. M., Madin, L. P., Kremer, P. (1986). Respiration and excretion by oceanic salps. *Mar. Biol.* 91: 529–537
- Franqueville, C. (1971). Macroplankton profond (Invertébrés) de la Méditerranée nord-occidentale. *Tethys* 3: 11–56
- Godeaux, J., Goffinet, G. (1968). Données sur la faune pélagique au large des côtes du Gabon, du Congo et de l'Angola. Tuniciers pélagiques. I. Salpidae. *Annls Soc. r. Belg.* 98: 49–86
- Gorsky, G., Lins da Silva, N., Dallot, S., Laval, P., Braconnot, J. C., Prieur, L. (1991). Midwater tunicates: are they related to the permanent coastal front of the Ligurian Sea (NW Mediterranean)? *Mar. Ecol. Prog. Ser.* 74: 195–204
- Harbison, G. R., Campenot, R. B. (1979). Effects of temperature on the swimming of salps (Tunicata, Thaliacea): implications for vertical migration. *Limnol. Oceanogr.* 24: 1081–1091
- Hureau, J.-C., Monod, T. (eds.) (1973). Catalogue des Poissons de l'Atlantique du Nord-Est et de la Méditerranée. CLOFNAM II, UNESCO, Paris
- Land, M. F. (1981). Optics of the eyes of *Phronima* and other deep-sea amphipods. *J. comp. Physiol. (Sect. A)* 145: 209–226
- Laval, P. (1978). The barrel of the pelagic amphipod *Phronima sedentaria* (Forsk.) (Crustacea: Hyperidae). *J. exp. mar. Biol. Ecol.* 33: 187–211
- Laval, P. (1981). Relations entre la femelle et le tonnelet chez *Phronima sedentaria* (Forsk.) (Amphipode Hypéride). *Rapp. P.-v. Réunion. Commn int. Explor. scient. Mer Méditerran.* 27: 193–194
- Laval, P., Braconnot, J. C., Carré, C., Goy, J., Morand, P., Mills, C. E. (1989). Small-scale distribution of macroplankton and micronekton in the Ligurian Sea (Mediterranean Sea) as observed from the manned submersible *Cyana*. *J. Plankton Res.* 11: 665–685
- Laval, P., Carré, C. (1988). Comparaisons entre les observations faites depuis le submersible CYANA et les pêches au chalut pélagique pendant la campagne MIGRAGEL I en mer Ligure (Méditerranée nord-occidentale). *Bull. Soc. r. Liège* 4/5: 249–257
- Morris, R. J., Bone, Q., Head, R., Braconnot, J. C., Nival, P. (1988). Role of salps in the flux of organic matter to the bottom of the Ligurian Sea. *Mar. Biol.* 97: 237–241
- Nival, P., Brancourt, J. C., Oberdorff, T. (1990). Structure démographique d'une population de salpes en mer Ligure. *Mar. Nature* 3: 1–8
- Smayda, T. J. (1971). Normal and accelerated sinking of phytoplankton in the sea. *Mar. Geol.* 11: 105–122
- Sournia, A., Brylinski, J.-M., Dallot, S., Le Corre, P., Leveau, M., Prieur, L., Froget, C. (1990). Fronts hydrologiques au large des côtes françaises: les sites-ateliers du programme Frontal. *Oceanol. Acta* 13: 413–438
- Vu Do, Q. (1981). Crustacés micronektoniques en Mer Ligure. *Rapp. P.-v. Réunion. Commn int. Explor. scient. Mer Méditerran.* 27: 143–144
- Wiebe, P. H., Madin, L. P., Haury, L. R., Harbison, G. R., Philbin, L. M. (1979). Diel vertical migration by *Salpa aspera* and its potential for large-scale particulate organic matter transport to the deep-sea. *Mar. Biol.* 53: 249–255
- Youngbluth, M. J. (1984). Water column ecology: in situ observations of marine zooplankton from a manned submersible. In: Flemming, N. C. (ed.) *Divers, submersibles and marine science*. Mem. Univ. Newfoundland, Occ. Pap. Biol. 9: 45–57

*This article was submitted to the editor*

*Manuscript first received: July 5, 1991*

*Revised version accepted: December 13, 1991*