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

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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 nanoplancton, 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 I cruise by submerging the vessel in a test basin. At a mean observational distance of 1.5 m, this surface was 4.6 m²; it had been estimated (with less precision) in a previous paper to be about 4 m² (Laval & Carré 1988). Because counting encompassed
animals situated from 0.5 m to about 4 m from the port-
hole, we took 5 m² 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 m³. 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 m³.

Distribution of microplankton and nanoplankton.

After the dives, a fraction of the water contained in the
‘detritus samplers’ was kept for counting; these sam-
plers were usually closed with a large appendicularian
inside, except for MG8, during which a large plank-
tonic 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, 500, 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 con-
sidered. 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:
Ihlea punctata (Forsskål – usually but erroneously
spelled Forskal; 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 fus-
iformis distribution. A population of this species was
observed between 400 and 600 m during all dives
except MG1 and MG5 (Fig. 1). Live oozooids (solit-
taries) and blastozooids (chains) were present and
were filtering slowly, in the same way they
normally filter water for feeding. Some blastozooids
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 con-
sequences 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 fus-
iformis 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 appendiculanan 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. villaifrancae*]. 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 1000–500, 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
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 offspring. 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 *Ihlea punctata*. This is consistent with the fact that its barrel comes from the oozooid 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 crusculum 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 m³ is enough, in February, to produce a very dense population (1000 to 1500 ind. per 100 m³) 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 nanoplancton found at depth is only a part, may provide a continuous flux sufficient to explain the persistense of the deep filter-feeder population.
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