

Midwater tunicates: are they related to the permanent front of the Ligurian Sea (NW Mediterranean)?

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ABSTRACT: Midwater filter feeders may play an important role in the downward carbon flux by aggregating particulate organic matter into large, slowly sinking mucoid aggregates or rapidly sinking fecal material. Successive submersible cruises made in the frontal zone of the Ligurian Sea showed the presence of midwater (400 to 800 m) populations of a not yet described larvacean species of the genus *Oikopleura* and of the thaliacean *Salpa fusiformis* Cuvier. The vertical stratification of autotrophic and heterotrophic organisms and the occurrence of autotrophic microphytoplankton at aphotic depths suggested that food supply for midwater filter feeders was actively transported by the frontal circulation from the subsurface layers along the inclined isopycnals. Minimum flow velocity for renewal of organic carbon at the midwater stratum was estimated to be 20 m d⁻¹. The vertical distribution of the midwater filter-feeder community corresponded to the deep origins of peripheral (near the coast) and central divergences and may indicate the deep junction of convection cells.

INTRODUCTION

Our concepts of oceanic mesopelagic life are based mainly on samples taken with trawls, nets and pumps. These techniques unfortunately destroy fragile organisms, whose identity and ecological roles frequently remain unknown. In order to better understand midwater biological activity, more information and new methods are needed. The use of manned submersibles for observation and sampling of pelagic organisms is a technique that alleviates these problems (Youngbluth et al. 1990). Bathyscaphe observations made in the mid-1950's (Suzuki & Kato 1953) and later (for review see Mills & Goy 1988) revealed diverse and often abundant populations of macroplankton in deep layers. New species are still being collected and described (Madin & Harbison 1978, Mackie & Mills 1983, Mills et al. 1987, Pugh & Harbison 1987, Pugh & Youngbluth 1988, Fenaux & Youngbluth 1990). In situ studies allow vertical stratification and population densities of mesozooplankton to be analyzed (Youngbluth 1984, Mackie 1985, Mills & Goy 1988, Laval et al. 1989), and their metabolic rates measured (Youngbluth et al. 1988). Submersibles have also been utilized for investigations of marine snow (Silver & Alldredge 1981, Alldredge & Youngbluth 1985).

We report here results from the MIGRAGEL II sub-

mersible cruise carried out from 14 to 22 May 1988 in the Ligurian Sea (NW Mediterranean). Reports of a previous cruise, MIGRAGEL I, indicated the presence of an unexpected larvacean population in midwater depths (Laval et al. 1989). During the MIGRAGEL II cruise these observations were confirmed and extended. A population of filter-feeding tunicates, including a new larvacean species, *Oikopleura villafrancae**, and the salp *Salpa fusiformis* Cuvier, were found at midwater depths. The following characteristics of these pelagic tunicates suggest that their roles in the pelagic ecosystem may be important:

(1) In optimal feeding conditions larvaceans and salps form dense blooms (Braconnot 1971, Seki 1973, Taguchi 1982, Le Borgne 1983, Deibel 1985). High individual growth rates and short life cycles yield rapid population growth (Heron 1972, Fenaux 1976, Heron & Benham 1985, Fenaux et al. 1986, Le Borgne & Moll 1986, Braconnot et al. 1988, Gorsky & Palazzoli 1989). (2) Both groups are important producers of organic matter and have high defecation rates (Bruland & Silver 1981, Iseki 1981, Madin 1982, Taguchi 1982). Larvaceans can secrete and discard as many as 15

* A description of this new midwater oikopleurid is currently being prepared by R. Fenaux

houses per day (Gorsky 1980, Fenaux 1985). The size of a mucous house is species- and age-dependent and varies from 1 mm to more than 1 m in diameter (Barham 1979). (3) Larvaceans and salps can retain particles as small as 0.1 and 0.7 μm respectively (Hamner et al. 1975, Flood 1979, Deibel & Turner 1985). Both groups show high filtering rates (Harbison & Gilmer 1976, Paffenhöfer 1976, Harbison & McAlister 1979, Alldredge 1981, Mullin 1983, Madin & Cetta 1984, Andersen 1985, Deibel 1988). (4) About 30% of particles filtered by the larvacean are not ingested but remain in the discarded house (Gorsky et al. 1984). Larvaceans filter non-selectively and thus microbial populations are introduced and develop in the house (Davoll & Silver 1986). The house forms, therefore, a rich organic particulate environment.

Considering the above, high larvacean and salp abundances observed at midwater depths during the I and II cruises suggest: (a) that the dietary requirements of these populations were satisfied, (b) that by aggregation of small particles, they may influence the size distribution and the composition of particles in suspension in the water column. The purposes of this paper are: (i) to describe the nature and the origin of the trophic environment harvested by these organisms, and (ii) to discuss the role of the Ligurian front in the maintenance of this population.

MATERIAL AND METHODS

During the 'MIGRAGEL II' cruise 8 dives were conducted to a maximum depth of 970 m using the submersible 'Cyana' (IFREMER, France). Accompanying research vessels were 'Le Suroit' and 'Korotneff'. The

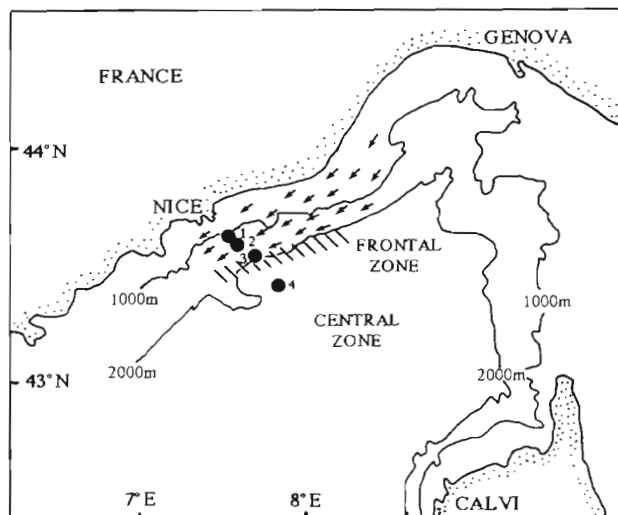


Fig. 1 The Ligurian Sea, showing the diving locations of the MIGRAGEL II cruise. Ligurian Current is shown by arrows; frontal zone is hatched

dive stations were located between Cape Ferrat (France) and Calvi (Corsica) (Fig. 1). Stns 1, 2, 3 and 4 were situated 6, 8, 13 and 23 nautical miles, respectively, offshore from Cape Ferrat (Table 1). Three submersible dives were performed during the night and 5 during the day. All dives were video-recorded. One CTD cast (0 to 800 m) was performed at each of the 4 stations with a Guildline probe, model 8705. On 20 May 1988, a vertical profile of water (0 to 600 m) was taken at Stn 3 using Niskin bottles by RV 'Korotneff'. Since the time spent at each diving station (6 to 12 h) was not sufficient for a complete CTD section through the frontal zone, we also used data obtained from the PROS VI program (PROSpection mer Ligure; Prieur et al. 1990) carried out at the beginning of June 1988. Fortunately, the meteorological and hydrological conditions were remarkably stable between the second half of May 1988 and 1 June. On this latter date, a series of hydrological profiles were performed as a part of the PROS VI program 3, 8, 13, 18, 23 and 28 n miles offshore. We used this complete section across the frontal structure for Fig. 2. The similarity of hydrological structures between mid-May and 1 June is shown in Table 2.

Gelatinous filter-feeder concentrations (mean distances between individuals) were estimated according to a modified method of Mackie & Mills (1983). Two 500 W spotlights were directed towards a 50 cm long graduated bar (10 cm graduations) mounted 120 cm in front of the observer. One of the cameras was focused on the bar and this 2-dimensional surface was used for density calculations during horizontal sections of the stair-like descent of the submersible (Laval et al. 1989). Two 6.5 l translucent detritus samplers (Tietze & Clark 1986) were employed to trap organisms. On board, captured organisms were rapidly transferred from the samplers and fixed in 4% buffered formaldehyde. Samples for bacterio-, pico- and nanoplankton counting were fixed in Borax-buffered formalin (final concentration 4%) and processed according to Porter & Feig's DAPI method (1980). Microphytoplankton and ciliates were preserved in Lugol's iodine solution 2% v/v, and counted using the Utermöhl sedimentation technique. Chlorophyll *a* was measured using a Turner 111 fluorometer. Particulate matter from water samples was filtered first through 100 μm Nyltel net and finally through precombusted Whatman GF/C filters, and frozen in liquid nitrogen.

We partitioned the living components of the marine food web into 6 groups: (a) microphytoplankton (MPH), unicellular phytoplankton of the size range $> 20 \mu\text{m}$, consisting mainly of diatoms, dinoflagellates and silicoflagellates, (b) autotrophic nanoflagellates (ANF), plastidic flagellates of a diameter from 2 to 20 μm , (c) cyanobacteria (CYA), (d) heterotrophic bacteria (HBE), (e) heterotrophic nanoflagellates (HNF), aplastidic flagellates with diameters from 2 to 20 μm , and (f)

Table 1. Summary of diving stations and shallowest observations of mesopelagic filter-feeders. *O. v.* *Oikopleura villafrancae*

Dive No.	Date (1988)	Station	Miles offshore	Location	Dive start (h)	Dive end (h)	Max. depth (m)	Shallowest <i>O. v.</i> (m)	Shallowest salp (m)
1	14 May	1	6	43°37.7'N, 7°26.6'E	21:41	02:00	615	350	410
2	15 May	2	8	43°35.6'N, 7°29.4'E	21:40	01:53	625	370	380
3	16 May	1	6	43°37.2'N, 7°26.6'E	21:11	01:30	625	360	400
4	17 May	2	8	43°35.6'N, 7°29.4'E	14:50	19:22	590	400	380
5	19 May	4	23	43°27.8'N, 7°46.8'E	09:33	14:16	692	650	680
6	20 May	3	13	43°32.8'N, 7°35.2'E	10:30	15:10	610	510	480
7	21 May	2	8	43°35.9'N, 7°28.8'E	09:48	14:45	970	440	500
8	22 May	2	8	43°36.0'N, 7°39.2'E	09:15	11:25	457	450	400

Table 2. Location, date and isopycnal depths obtained by CTD casts during the MIGRAGEL II cruise in mid-May and the PROS VI cruise on 1 June 1988. Station numbers are those of the PROS VI cruise. Geographic location and distance from Cape Ferrat are indicated in local time [UT (Universal Time) + 2]. MIGRAGEL dive no. corresponds to the submersible dive number from Table 1. Subheadings under 'Isopycnal depths' are density excesses (kg m^{-3})

PROS VI cast no.	Cruise	Location	MIGRAGEL dive no.	Date (1988)	Local time (h)	Distance from shore (miles)	Isopycnal depths (m)		
							28.80	28.90	29.00
6	PROS VI	43°38.1'N, 7°23.2'E	–	1 June	09:55	3	140	200	350
–	MIGRAGEL	43°37.2'N, 7°26.6'E	3	16 May	23:46	6	158	198	295
5	PROS VI	43°35.2'N, 7°28.6'E	–	1 June	11:44	8	71	100	250
–	MIGRAGEL	43°35.6'N, 7°29.4'E	4	17 May	21:49	8	142	192	270
4	PROS VI	43°32.6'N, 7°34.5'E	–	1 June	14:08	13	45	79	180
–	MIGRAGEL	43°32.8'N, 7°35.2'E	6	20 May	16:35	13	42	84	158
3	PROS VI	43°30.1'N, 7°40.9'E	–	1 June	16:01	18	43	49	60
2	PROS VI	43°27.6'N, 7°46.9'E	–	1 June	17:46	23	48	55	71
–	MIGRAGEL	43°27.8'N, 7°46.8'E	5	19 May	23:19	23	48	55	66
1	PROS VI	43°24.7'N, 7°52.5'E	–	1 June	20:01	28	28	39	70

oligotrichous ciliates and tintinnids (CIL). The biomass of these groups in each sample is given in Table 3.

Conversion factors for calculation of carbon biomass from biovolume (C. Vol. ratio) were used according to Fuhrman & Azam (1980), Strathmann (1967), Putt & Stoecker (1989), Wiadnyana & Lins da Silva (unpubl.) and Verity & Langdon (1984), for bacteria, flagellates, oligotrichous ciliates, phytoplankton and tintinnids, respectively.

RESULTS

Distribution of filter feeders

The MIGRAGEL I and MIGRAGEL II cruises found and confirmed previously unknown spatial stratifications of the midwater zooplankton community. Visual observations made in the aphotic zone during the MIGRAGEL II cruise revealed the presence of several larvacean and salp species from the surface down to 970 m. A high density (2 to 3 chains m^{-3}) of salps, mainly *Salpa fusiformis* Cuvier and *Ihleia punctata* (Forssk.), was observed in the upper 50 m at Stns 1 and

2. Just below this layer 2 larvacean species were numerous in the water column, *Oikopleura albicans* Leuckart and *O. fusiformis* Fol. The diameter of the most frequently observed houses was ca 3 cm.

Starting at a depth of ca 350 m near the coast at Stn 1 and at ca 650 m at Stn 4 (23 miles offshore; Fig. 2), a larvacean population belonging to a new species, *Oikopleura villafrancae* (Fig. 3), became dominant. The spatial distribution of this population was patchy and its population density varied between 1 and 10 ind. m^{-3} during the MIGRAGEL II cruise (detailed information on the spatial distribution of zooplankton will be published elsewhere; Laval, Braconnot & Lins da Silva unpubl.). The diameter of observed houses was estimated to vary between 3 and 6 cm. The upper limit of occurrence of these filter feeders descended with increasing distance from the shore. Five specimens of the new species were collected. Their trunk size varied between 3 and 4 mm. The mouth opening of this size class reached ca 300 μm diameter.

In the same layer different developmental stages of *Salpa fusiformis*, short blastozooid chains, oozoids and blastozooids with embryos were observed with a swim-

Table 3. Composition of water samples taken by the submersible 'Cyana' during the MIGRAGEL II cruise and by Niskin bottles from the RV 'Korotneff' on 20 May 1988 (*). MPH: microphytoplankton (> 20 µm); ANF: plastidic nanoflagellates (2 to 20 µm); CYA: cyanobacteria; HBE: heterotrophic bacteria; HNF: aplastidic nanoflagellates (2 to 20 µm); CIL: oligotrichous ciliates and tintinnids; AFDW: ash-free dry weight; ml⁻¹: organisms per ml

Station	Date (1988)	Depth (m)	HBE (ppm)	CYA (ppm)	ANF (ppm)	HNF (ppm)	CIL (ppm)	MPH (ppm)	AFDW (mg l ⁻¹)	Chl a (µg l ⁻¹)
1	16 May	450	0.005	3.00 × 10 ⁻⁵	0.00	2.00 × 10 ⁻⁵	0.00	0.026	–	0.03
2	22 May	0	0.010	2.80 × 10 ⁻³	1.74 × 10 ⁻²	6.15 × 10 ⁻²	2.39 × 10 ⁻³	0.117	0.417	0.23
2	22 May	75	0.021	2.30 × 10 ⁻³	5.07 × 10 ⁻²	7.30 × 10 ⁻²	1.00 × 10 ⁻³	0.001	0.468	0.65
2	17 May	418	0.004	2.00 × 10 ⁻³	9.00 × 10 ⁻⁴	3.20 × 10 ⁻³	8.00 × 10 ⁻⁵	0.006	0.411	0.04
2	22 May	450	0.009	1.60 × 10 ⁻³	3.54 × 10 ⁻²	3.11 × 10 ⁻²	4.60 × 10 ⁻⁴	0.000	0.313	0.03
2	21 May	490	0.004	3.00 × 10 ⁻⁵	1.25 × 10 ⁻²	5.62 × 10 ⁻²	3.90 × 10 ⁻⁴	0.006	0.127	0.02
3	21 May	509	0.004	2.00 × 10 ⁻⁵	0.00	2.10 × 10 ⁻³	5.60 × 10 ⁻⁴	0.000	–	–
3	20 May*	0	0.010	2.10 × 10 ⁻³	2.09 × 10 ⁻²	7.76 × 10 ⁻²	5.00 × 10 ⁻⁴	0.031	0.611	0.18
3	20 May*	50	0.012	1.90 × 10 ⁻³	7.95 × 10 ⁻²	8.10 × 10 ⁻²	8.90 × 10 ⁻³	0.001	–	0.39
3	20 May*	100	0.001	1.00 × 10 ⁻⁴	1.29 × 10 ⁻²	1.88 × 10 ⁻²	3.20 × 10 ⁻³	0.001	–	0.08
3	20 May*	200	0.005	4.00 × 10 ⁻⁵	1.70 × 10 ⁻³	8.80 × 10 ⁻³	2.39 × 10 ⁻³	0.006	–	0.06
3	20 May*	300	0.005	2.00 × 10 ⁻⁵	7.06 × 10 ⁻⁴	7.01 × 10 ⁻³	2.05 × 10 ⁻⁴	0.012	–	0.03
3	20 May*	400	0.006	1.00 × 10 ⁻⁵	9.00 × 10 ⁻⁴	6.10 × 10 ⁻³	2.95 × 10 ⁻³	0.001	–	0.01
3	20 May*	500	0.005	0.00	7.00 × 10 ⁻⁴	7.70 × 10 ⁻³	8.44 × 10 ⁻⁴	0.007	–	0.02
3	20 May*	570	0.004	0.00	0.00	1.60 × 10 ⁻³	4.00 × 10 ⁻⁵	0.006	0.251	0.02
3	20 May*	600	0.005	1.00 × 10 ⁻⁵	2.00 × 10 ⁻⁴	5.20 × 10 ⁻³	2.74 × 10 ⁻⁴	0.018	–	0.02
4	19 May	0	–	–	–	–	–	–	0.635	0.34
4	19 May	300	0.006	1.30 × 10 ⁻⁴	1.10 × 10 ⁻³	7.10 × 10 ⁻³	1.00 × 10 ⁻⁴	0.002	–	–
4	19 May	680	0.004	1.00 × 10 ⁻⁵	2.00 × 10 ⁻⁴	4.50 × 10 ⁻³	1.10 × 10 ⁻⁴	0.012	0.218	0.04
Station	Date (1988)	Depth (m)	HBE (ml ⁻¹)	CYA (ml ⁻¹)	ANF (ml ⁻¹)	HNF (ml ⁻¹)	CIL (ml ⁻¹)	MPH (ml ⁻¹)	AFDW (mg l ⁻¹)	Chl a (µg l ⁻¹)
1	16 May	450	1.18 × 10 ⁵	1.43 × 10 ²	0.00	9.98	0.00	0.96	–	0.03
2	22 May	0	2.54 × 10 ⁵	1.38 × 10 ⁴	2.23 × 10 ²	9.58 × 10 ³	2.90	1.53	0.417	0.23
2	22 May	75	5.17 × 10 ⁵	1.17 × 10 ⁴	1.05 × 10 ³	1.68 × 10 ³	1.00 × 10 ⁻³	0.21	0.468	0.65
2	17 May	418	1.08 × 10 ⁵	1.10 × 10 ²	4.86 × 10 ²	1.23 × 10 ²	2.00 × 10 ⁻²	0.16	0.411	0.04
2	22 May	450	2.35 × 10 ⁵	8.10 × 10 ³	8.05 × 10 ²	8.35 × 10 ²	3.00 × 10 ⁻²	0.17	0.313	0.03
2	21 May	490	1.04 × 10 ⁵	1.40 × 10 ²	1.33 × 10 ¹	9.98	6.00 × 10 ⁻²	0.05	0.127	0.02
3	21 May	509	1.02 × 10 ⁵	3.66 × 10 ¹	0.00	8.65 × 10 ¹	4.00 × 10 ⁻⁵	0.13	–	–
3	20 May*	0	2.59 × 10 ⁵	1.05 × 10 ⁴	5.25 × 10 ²	2.61 × 10 ³	4.00 × 10 ⁻²	4.10	0.611	0.18
3	20 May*	50	1.98 × 10 ⁵	9.28 × 10 ³	2.57 × 10 ³	3.05 × 10 ³	1.39	0.10	–	0.39
3	20 May*	100	1.69 × 10 ⁴	6.02 × 10 ²	2.56 × 10 ²	4.13 × 10 ²	3.00 × 10 ⁻²	0.12	–	0.08
3	20 May*	200	1.35 × 10 ⁵	2.13 × 10 ²	2.50 × 10 ²	2.76 × 10 ²	5.00 × 10 ⁻²	0.20	–	0.06
3	20 May*	300	1.28 × 10 ⁵	9.31 × 10 ¹	1.33 × 10 ¹	1.66 × 10 ²	2.05 × 10 ⁻⁴	0.16	–	0.03
3	20 May*	400	1.60 × 10 ⁵	5.99 × 10 ¹	1.33 × 10 ¹	1.66 × 10 ²	1.00 × 10 ⁻²	0.23	–	0.01
3	20 May*	500	1.28 × 10 ⁵	1.66 × 10 ¹	9.98	1.73 × 10 ²	1.20 × 10 ⁻¹	0.31	–	0.02
3	20 May	570	1.04 × 10 ⁵	0.00	0.00	5.99 × 10 ¹	2.00 × 10 ⁻²	0.56	0.251	0.02
3	20 May*	600	1.19 × 10 ⁵	6.65 × 10 ¹	3.33	1.87 × 10 ²	3.00 × 10 ⁻²	0.13	–	0.02
4	19 May	0	–	–	–	–	–	–	0.635	0.34
4	19 May	300	1.59 × 10 ⁵	6.32 × 10 ¹	1.66 × 10 ¹	2.86 × 10 ²	1.00 × 10 ⁻²	0.43	–	–
4	19 May	680	9.81 × 10 ⁴	5.32 × 10 ¹	3.33	1.36 × 10 ²	4.00 × 10 ⁻²	0.22	0.218	0.04

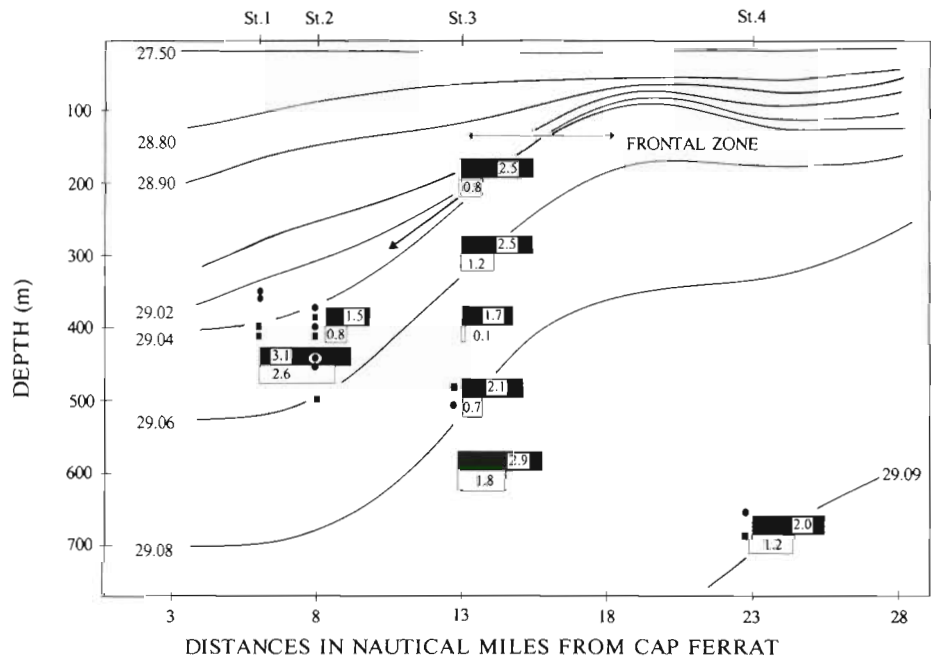
ming pattern characteristic of feeding individuals. The size of the observed oozoids exceeded 15 mm and the size of blastozooids exceeded 25 mm. The concentration of *S. fusiformis* in midwater depths was highest at the 8 mile location, where the estimated number varied between 5 and 30 per 100 m³. At other stations the concentration varied between 1 and 5 ind. 100 m⁻³.

Composition of water column

At Stns 1 and 2, the mid-water filter feeders were observed in a layer which corresponded to a water mass situated between the thermal minimum of the cold,

winter water (density excess of ca 28.90 kg m⁻³) and the thermal maximum of the intermediate water (29.06 kg m⁻³). At Stn 1, the top of the midwater layer containing filter feeders began at 350 m (larvaceans at 350 m, salps at 400 m). At 450 m depth, where the highest concentration of tunicates was observed, microphytoplankton was relatively abundant (0.026 × 10⁶ µm³ ml⁻¹; Table 3, Fig. 2). At Stn 2, *Oikopleura villafrancae* appeared at 360 m depth and *S. fusiformis* 20 m deeper. The layer between 400 and 500 m was rich in plastidic and aplastidic nanoflagellates (ANF and HNF), 0.035 × 10⁶ µm³ ml⁻¹ at 450 m and 0.056 × 10⁶ µm³ ml⁻¹ at 490 m, respectively. At Stn 2 below 800 m another larvacean species, *Pelagopleura* sp., became dominant (ca 1 house

Fig. 2. Vertical section (0 to 800 m) of density excess (kg m^{-3}) on the Cape Ferrat – Calvi transect as obtained from the PROS VI data, 1 June 1988. Under the pycnocline the density front was located between 13 and 18 miles offshore. The advective circulation was situated along isopycnal lines having a slope greater than 1% between 18 and 8 miles offshore (arrow). Black histogram = total living biomass (ppm \times 100) in the sample, open histogram = biomass (ppm \times 100) of autotrophic microphytoplankton (MPH) in the sample. (●) Shallowest observation of the larvacean *Oikopleura villafrancae*; (■) shallowest midwater observation of the thaliacean *Salpa fusiformis*. Note that the depth of the midwater tunicate layer increased with distance from shore



m^{-3} , ca 3 cm diameter; observation by M. Youngbluth). At Stn 3 the upper limit of the salp stratum began at 480 m depth. The mesopelagic *O. villafrancae* population appeared at 510 m depth. At these latter depths the hydrological conditions are characterized by a weakly stratified layer of intermediate and deep water having a density excess of more than 29.08 kg m^{-3} . At 510 m we found a biomass of $0.018 \times 10^6 \mu\text{m}^3 \text{ ml}^{-1}$ of microphytoplankton cells apparently in good living conditions. At Stn 4, mesopelagic larvaceans were observed at 650 m and salps appeared 30 m deeper. At this 680 m depth the biomass of the living microphytoplankton was $0.012 \times 10^6 \mu\text{m}^3 \text{ ml}^{-1}$.

In 20 May profiles of chlorophyll *a*, estimated carbon biomass of autotrophs (MPH, ANF, CYA) and heterotrophs (HBE, HNF, CIL) at Stn 3 (13 miles; Fig. 4), reached their maximum values at a depth of 50 m. The numerical domination of heterotrophic organisms over the autotrophic ones is common in a post-bloom period. The minimum values for the autotroph MPH and ANF occurred at 400 m, where an increase was observed for the heterotrophic component.

DISCUSSION

Hydrology

In the study area, the Ligurian Current, which is about 30 km wide and ca 150 m deep (Béthoux & Prieur 1984, Béthoux et al. 1988), flows southwestward along the coast. A subsurface density front (Sournia et al. 1990) separates the central water mass from the Ligu-

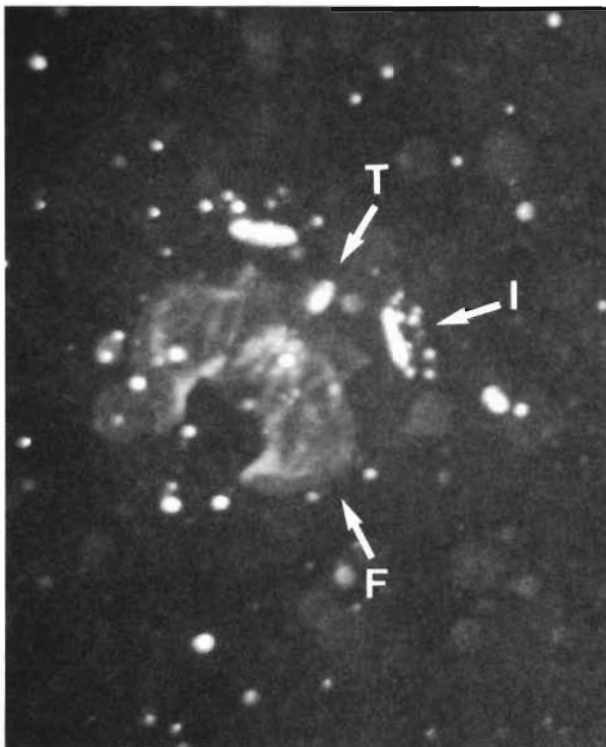


Fig. 3. Photograph taken at 500 m depth from the submersible 'Cyana' showing an *Oikopleura villafrancae* (house ca 5 cm in diameter). Note the high concentration of particles in its environment. I: Incurrent coarse filter; F: food-concentrating filter; T: trunk of the larvacean

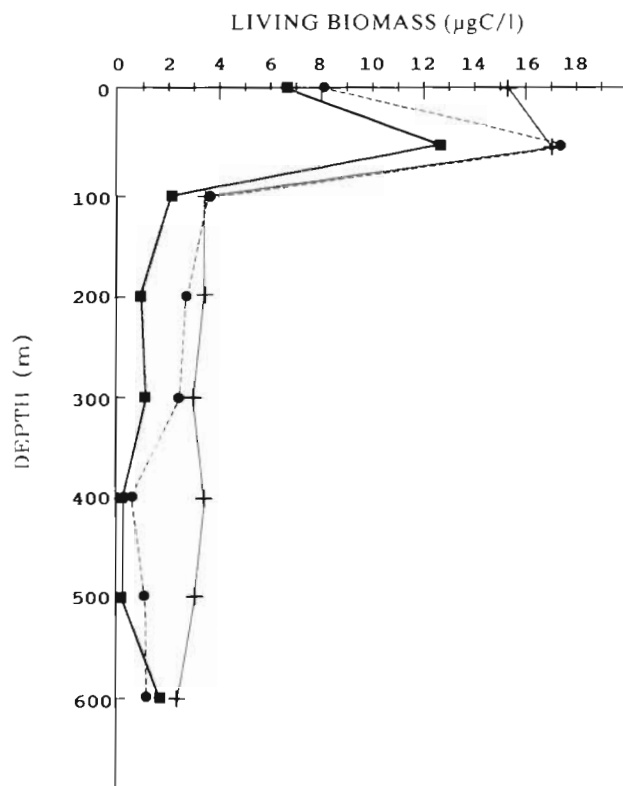


Fig. 4. Vertical profiles of living biomass ($\mu\text{g C l}^{-1}$) at Stn 3 sampled by RV 'Korotneff' on 20 May 1988. (■) Autotrophs, (+) heterotrophs, (●) chlorophyll $a \times 45$ (constant used for the Mediterranean phytoplankton)

rian Current (Fig. 1). The Ligurian Current, defined as the primary circulation, induces a secondary circulation, which is assumed to be constituted by 2 convection cells with a common downwelling convergent part along the inclined isopycnals. Boucher et al. (1987) presented a vertical circulation scheme mainly active in the frontal zone as suggested by the recurrently observed spatial distribution of physical, chemical and biological parameters. The convergence which mediates the biomass downward (Fig. 2) is generally encountered in the maximum of the horizontal density gradient (see Boucher et al. 1987, Figs. 4, 5 & 6). During the MIGRAGEL II cruise this maximum was located between 13 and 18 miles offshore at depths between 50 and 150 m. This maximum of the horizontal density gradient is considered to constitute the origin of the downwelled biomass (indicated by an arrow in Fig. 2). Temperature and salinity values observed at the diving stations are consistent with those obtained on 1 June. To facilitate the comparisons, the same isopycnals were drawn in Fig. 2 (PROS VI casts, 1 June) and in Fig. 5 (diving stations, mid-May). Comparison of isopycnal depths are shown in Table 2. The differences observed at the 8 mile location are probably due to the meandering of the Ligurian Current (Sournia et al. 1990). Data

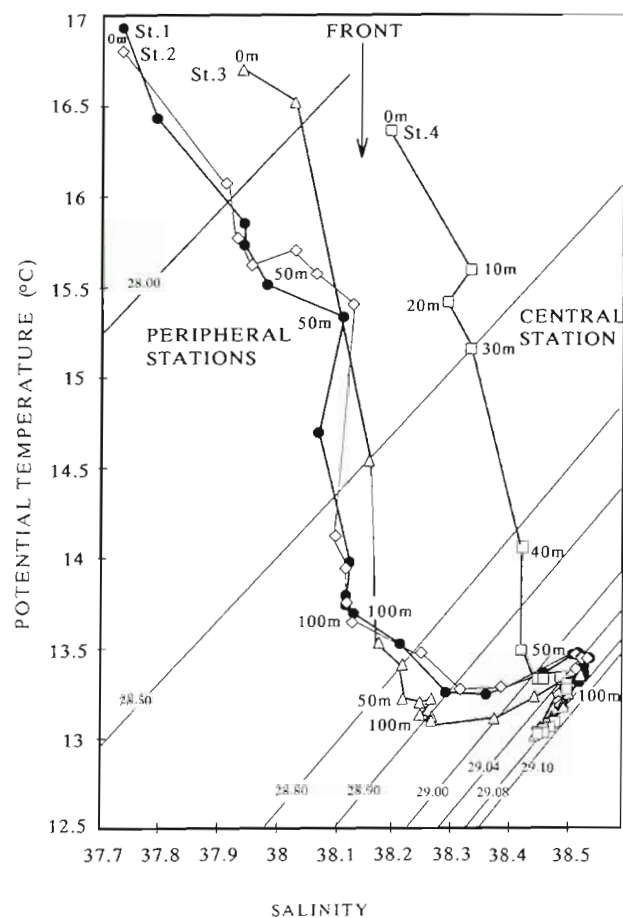


Fig. 5. T-S profiles of the 4 diving stations, drawn from data taken every 10 m in the upper 100 m layer and every 50 m between 100 and 800 m. Isopycnals are drawn here for comparison with the isopycnals in Fig. 2. Stns 1, 2 & 3 are peripheral (near the coast) stations and have similar T-S profiles. Stn 4 is central (outer side of the front) and is characterized by surface salinity (38.2) much higher than at the 3 peripheral stations. Note that the densities at similar depths are lower at peripheral stations than at the central one

from the long-term survey program PROS VI (Prieur et al. 1990) suggest that this hydrological structure of the Ligurian front is permanent. This feature is essential for the development of the specific zooplankton community described in the present paper.

Ecological considerations

Similar estimates for the cold water *Oikopleura vanhoffeni* Lohmann and warm water *Stegosoma magnum* Langerhans indicate that the clearance rate of species acclimated to a given temperature is more size-temperature-dependent (Alldredge 1981, Deibel 1988). In addition, Knoechel & Steel-Flynn (1989) found a negative relationship between filtering rate and temperature for *O. vanhoffeni*. However, it is

extremely difficult to assess the behavioral stress of larvaceans during experimental work in situ or in the laboratory (Alldredge 1976, pers. obs.). *O. villafrancae* belongs to the family Oikopleuridae, as do *Stegosoma magnum* and *O. vanhoffeni*, and has a similar feeding behavior. We estimate then the filtration rate of a non-mature *O. villafrancae* of 3 mm trunk length as 300 ml h^{-1} , in the range of values published for the 2 former species.

The carbon content of ingestible sized living cells in aphotic depths at Stn 3 was ca $4 \mu\text{g C l}^{-1}$ (Fig. 4). At this concentration the upper limit of the daily filtering rate would be $28.8 \mu\text{g C}$ per individual. If 30% of filtered material remains in the abandoned house and is not ingested by the larvacean (Gorsky et al. 1984 for *Oikopleura dioica* Fol.), the daily ingestion rate of living carbon will attain $20.2 \mu\text{g ind.}^{-1}$. During the MIGRAGEL II cruise we observed a population of large larvacean *Oikopleura albicans* in the upper 600 m of the water column. We suppose that the metabolic activities of *O. albicans* and *O. villafrancae* harvesting at the same time in a similar environment are comparable. An *O. albicans* of 3 mm trunk length contains $210 \mu\text{g C}$ (G. Gorsky unpubl.). The percentage of daily ration ($\mu\text{g ingested C} \times \mu\text{g body C}^{-1} \times 100$) derived from the living biomass available at the sampled depths will then reach 9.8% of body carbon. According to Deibel (1986) and Alldredge (1976) the carbon content of a clean house without filtered material represents 10 to 20% of the body weight. It is therefore clear that the living food biomass found at midwater depths is not the main nutritional source of the midwater larvaceans.

Larvaceans are non-selective suspension feeders. If the ash free dry weight/organic carbon ratio of the organic matter at the studied area is 2.5 (G. Copin-Montégut pers. comm.), then 418 m deep (Stn 2) the water contains $160 \mu\text{g organic C l}^{-1}$ and at 680 m (Stn 4), $80 \mu\text{g C l}^{-1}$. After multiplying the filtration ratio by 0.70 (non-ingested particles), the maximum potential daily ration attains $806 \mu\text{g C}$ or 384% of body carbon for an individual at depth 418 m and $403 \mu\text{g C}$ or 192% of body carbon at 680 m. If mesopelagic larvaceans discard 4 houses per day (observed for *Oikopleura albicans* at 13°C), then 40 to 80% of body carbon is used daily for house secretion and the remaining part of the ration for metabolism, growth and reproduction.

The presence of living microphytoplankton in aphotic layers indicated that organic matter, which allowed development of filter-feeders at the observed depths, originated from the surface or from the subsurface layers and was transported to deeper layers.

Our observations show that: (1) a non-negligible biomass of living algal cells was observed in the apho-

tic layer containing a permanent and specific filter-feeder community; (2) organic particulate matter in suspension and not living cells constituted the main diet of midwater larvaceans; (3) *Oikopleura villafrancae* did not appear above an inclined layer, 350 m near the coast at Stn 1 and 680 m at Stn 4 (Fig. 2).

Fowler et al. (1987), using an automatic time-series particle trap moored 15 miles off the coast of Calvi (Corsica), reported a rapid removal of Chernobyl fallout from surface waters to deeper layers. The presence of these radionuclides at 200 m a few days after the fallout could not be explained by settling of small particles.

Assuming that the entire food supply for midwater tunicates is of surface origin, we can estimate the minimum vertical flow velocity required to renew the organic carbon stock which maintains the populations of midwater filter-feeders. Net vertical flux is equal to the consumption rate of these filter-feeders and can be estimated from:

$$W(C_1 - C_2)S = nRSH,$$

where W = the vertical component of the velocity; C_1 = concentration of organic carbon entering the tunicate stratum; C_2 = concentration of organic carbon leaving this layer; S = entry and outlet surface; n = number of filter-feeders per unit volume; R = daily carbon ration of filter-feeders; H = vertical extent of the tunicate stratum (Fig. 6).

At Stn 2 the tunicate stratum began at a depth of ca 400 m and ended at a depth of about 800 m. The mean estimated daily ration of an individual was about

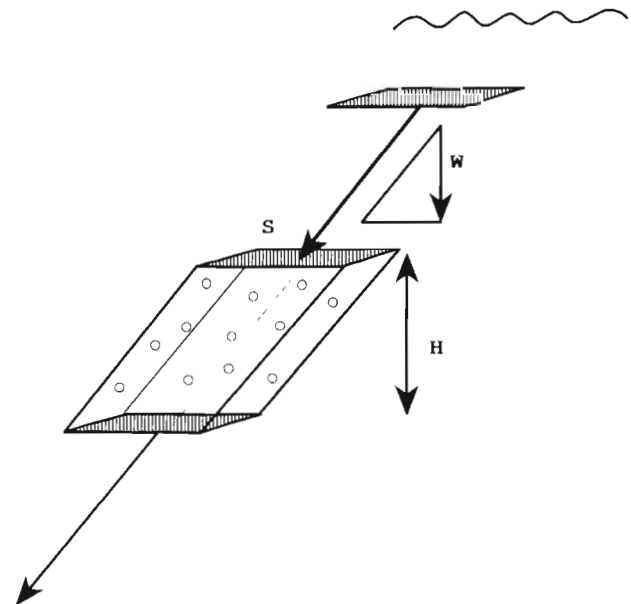


Fig. 6. Scheme of the midwater tunicate layer and of the water flow induced by the frontal circulation. S: Surface; W: vertical component of the flow velocity; H: depth of midwater filter-feeder stratum

0.8 mg C d⁻¹ and the subsurface carbon concentration was determined to be about 160 mg C m⁻³. If we consider that $C_2 = 0$ or $C_1 - C_2 = 160$ mg C m⁻³, then $W = nRH/(C_1 - C_2) = 10 \times 0.8$ mg C \times 400/160 mg C = 20 m d⁻¹. Thus 15 d are required for transport of organic matter from subsurface layers (100 m deep) down to the tunicate stratum (400 m). Our calculation concerns the high density estimate of tunicates, because they exhibited a patchy distribution which may correspond to the non-homogeneous arrival of food particles. On the other hand, the proximity of mature individuals may be considered as important for the preservation of the population (Holland et al. 1988). As we have assumed that no organic carbon of digestible size is leaving the midwater tunicate layer, our vertical flux value should be an underestimate.

The downward movement of particulate matter can be generated by vertical sedimentation, or by active transport induced by the frontal secondary circulation. The sedimentation rate of living and senescent algal cells of ingestible diameter (2 to 40 μ m for larvaceans) varies from 1 to 5 m d⁻¹. This rate can however vary (Smayda 1971, Bienfang 1980, 1981, Smayda & Bienfang 1983). The rate is insufficient to support nutritional needs of midwater filter-feeders at maximal observed concentrations and does not support a vertical sedimentation hypothesis. In the case of active transport, organic particles are moved from subsurface layers about 18 miles offshore to midwater depths at Stns 1 and 2 (6 and 8 miles) nearshore along the inclined isopycnals. The vertical distribution of microphytoplankton (MPH) at Stn 3 (Fig. 2) agrees with the scheme suggested for a vertical circulation of the Liguro-Provençal sea front (Boucher et al. 1987): the high values of MPH observed 300 m deep at Stn 3, 418 m deep at Stn 2 and 450 m deep at Stn 1 could be indicative of the downwelled water mass due to frontal circulation and may constitute a nutritional source for midwater communities at Stns 1 and 2. The second peak observed at 600 m (Stn 3) and the high value of MPH at 680 m (Stn 4) could indicate deep closure of the offshore convection cell or diffusion and sedimentation of living and non-living particles downwelled by the frontal circulation in the weakly stratified water mass (Fig. 2). As the deep closure flow cannot be measured directly by conventional methods such as with current meters or by the use of tracers, we suggest that the midwater larvaceans can be considered as indicators of layers rich in organic matter, and in the case described above, indicate the deep closure of the secondary circulation cell.

Karl & Knauer (1984), analyzing sediment trap data from northeast Pacific, found midwater layers containing high concentrations of suspended particulate matter. They suggested that the accumulation of organic

matter is the result of in situ metabolic activity, but the question concerning the source of carbon supporting this activity remained open.

The slow sinking rate of small particles and the strong vertical stratification of marine snow and pico-, nano- and microplankton lead us to conclude that the existence of midwater filter-feeder populations in the Ligurian frontal zone is closely related to an downward convective flux of organic matter from subsurface layers to midwater depths. The population of the new mesopelagic larvacean *Oikopleura villafrancae* is associated with this persistent convergent flow which produces localized concentrations of food particles. It is not yet clear if the population dynamics of this new species are controlled exclusively by the frontal structure.

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LITERATURE CITED

- Allredge, A. (1976). Field behavior and adaptive strategies of appendicularians (Chordata: Tunicata). *Mar. Biol.* 38: 29–39
- Allredge, A. (1981). The impact of appendicularian grazing on natural food concentration in situ. *Limnol. Oceanogr.* 26: 247–257
- Allredge, A., Youngbluth, M. J. (1985). The significance of macroscopic aggregates (marine snow) as sites for heterotrophic bacterial production in the mesopelagic zone of the subtropical Atlantic. *Deep Sea Res.* 32: 1445–1456
- Andersen, V. (1985). Filtration and ingestion rates of *Salpa fusiformis* Cuvier (Tunicata: Thaliacea): effects of size, individual weight and algal concentration. *J. exp. mar. Biol. Ecol.* 87: 13–29
- Barham, E. G. (1979). Giant larvacean houses. *Science* 205: 1129–1131
- Béthoux, J. P., Prieur, L. (1984). Hydrologie et circulation en Méditerranée Nord-Occidentale. In: Bizon, J. J., Burolet, P. F. (eds.) *Ecologie des microorganismes en Méditerranée occidentale*. ASTP, Paris, p. 13–22
- Béthoux, J. P., Prieur, L., Bong, J. H. (1988). Le courant Ligure au large de Nice. *Oceanol. Acta* 9: 59–67
- Bienfang, P. K. (1980). Phytoplankton sinking rates in oligotrophic waters off Hawaii, USA. *Mar. Biol.* 61: 69–77
- Bienfang, P. K. (1981). Sinking rates of heterogeneous, temperate phytoplankton populations. *J. Plankton Res.* 3: 235–253
- Boucher, J., Ibanez, F., Prieur, L. (1987). Daily and seasonal variations in the spatial distribution of zooplankton populations in relation to the physical structure in the Ligurian Sea Front. *J. mar. Res.* 45: 133–173
- Braconnot, J. C. (1971). Contribution à l'étude biologique et écologique des tuniciers plagiés salpides et doliolides. *Vie Milieu* 22: 257–286

- Braconnot, J. C., Choe, S. M., Nival, P. (1988). La croissance et le développement de *Salpa fusiformis* Cuvier (Tunicata, Thaliacea). Ann. Inst. Océanogr., Paris 64: 101–114
- Bruland, K. W., Silver, M. W. (1981). Sinking rates of fecal pellets from gelatinous zooplankton (salps, pteropods, doliolids). Mar. Biol. 63: 295–300
- Davoll, P. J., Silver, M. W. (1986). Marine snow aggregates: life history sequence and microbial community of abandoned larvacean houses from Monterey Bay, California. Mar. Ecol. Prog. Ser. 33: 111–120
- Deibel, D. (1985). Blooms of pelagic tunicate, *Doliolitta gegenbaueri*: are they associated with Gulf Stream frontal eddies? J. mar. Res. 43: 211–236
- Deibel, D. (1986). Feeding mechanism and house of the appendicularian *Oikopleura vanhoeffeni*. Mar. Biol. 93: 429–436
- Deibel, D. (1988). Filter feeding by *Oikopleura vanhoeffeni*: grazing impact on suspended particles in cold ocean waters. Mar. Biol. 99: 177–187
- Deibel, D., Turner, J. T. (1985). Zooplankton feeding ecology: contents of fecal pellets of the appendicularian *Oikopleura vanhoeffeni*. Mar. Ecol. Prog. Ser. 27: 67–78
- Fenaux, R. (1976). Cycle vital d'un appendiculaire *Oikopleura dioica* Fol. 1872. Description et biologie. Ann. Inst. Océanogr., Paris 52, 1: 89–101
- Fenaux, R. (1985). Rhythm of secretion of oikopleurids' houses. Bull. mar. Sci. 37: 498–503
- Fenaux, R., Bedo, A., Gorsky, G. (1986). Premières données sur la dynamique d'une population d'*Oikopleura dioica* Fol. 1872 (Appendiculaire) en élevage. Can. J. Zool. 64: 1745–1749
- Fenaux, R., Youngbluth, M. J. (1990). A new mesopelagic appendicularian, *Mesochordeus bahamasi* gen. nov., sp. nov. J. mar. biol. Ass. U.K. 70: 755–760
- Flood, P. R. (1979). Filters characteristics of appendicularian food catching nets. Experientia 34: 173–175
- Fowler, S. W., Buat-Ménard, P., Yokoyama, Y., Ballestra, S., Holm, E., Nguyen, H. V. (1987). Rapid removal of Chernobyl fallout from Mediterranean surface waters by biological activity. Nature, Lond. 329: 56–58
- Fuhrman, J. A., Azam, F. (1980). Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica and California. Appl. environ. Microbiol. 39: 1085–1095
- Gorsky, G. (1980). Optimisation des cultures d'appendiculaires. Approche du métabolisme de *O. dioica*. Thèse Doctorate de 3^e cycle. Université de P. et M. Curie Paris VI
- Gorsky, G., Fisher, F. S., Fowler, S. W. (1984). Biogenic debris from the pelagic tunicate, *O. dioica*, and its role in the vertical transport of a transuranium element. Estuar. coast. Shelf Sci. 18: 13–23
- Gorsky, G., Palazzoli, I. (1989). Aspects de la biologie de l'appendiculaire *Oikopleura dioica* Fol. 1872 (Chordata: Tunicata). Oceanis 15: 39–49
- Hamner, W. M., Madin, L. P., Alldredge, A. L., Gilmer, R. W., Hamner, P. P. (1975). Underwater observations of gelatinous zooplankton: sampling problems, feeding biology and behavior. Limnol. Oceanogr. 20: 907–917
- Harbison, G. R., Gilmer, R. W. (1976). The feeding rates of the pelagic tunicate *Pegea confederata* and two other salps. Limnol. Oceanogr. 21: 517–528
- Harbison, G. R., McAlister, V. L. (1979). The filter-feeding rates and particle retention efficiencies of three species of *Cyclosalpa* (Tunicata, Thaliacea). Limnol. Oceanogr. 24: 875–892
- Heron, A. C. (1972). Population ecology of a colonizing species: the pelagic tunicate *Thalia democratica* I. Individual growth rates and generation time. Oecologia (Berl.) 10: 269–293
- Heron, A. C., Benham, E. E. (1985). Life history parameters as indicators of growth rate in three salp populations. J. Plankton Res. 7: 365–379
- Holland, L. Z., Gorsky, G., Fenaux, R. (1988). Fertilisation in *Oikopleura dioica* (Tunicata, Appendicularia): acrosome reaction and sperm-egg fusion. Zoomorphology 108: 229–243
- Iseki, K. (1981). Particulate organic matter transport to the deep sea by salp fecal pellets. Mar. Ecol. Prog. Ser. 5: 55–60
- Karl, D. M., Knauer, G. A. (1984). Vertical distribution, transport, and exchange of carbon in the northeast Pacific Ocean: evidence for multiple zones of biological activity. Deep Sea Res. 31: 221–243
- Knoechel, R., Steel-Flynn, D. (1989). Clearance rates of *Oikopleura* in cold coastal Newfoundland waters: a predictive model and its trophodynamic implications. Mar. Ecol. Prog. Ser. 53: 257–266
- Laval, Ph., Braconnot, J. C., Carré, C., Goy, J., Mills, C., Morand, P. (1989). Small scale distribution of macroplankton in the Ligurian Sea (Mediterranea) as observed from the manned submersible CYANA. J. Plankton Res. 11: 665–675
- Le Borgne, R. (1983). Note sur les proliférations de Thaliacés dans le golfe de Guinée. Océanogr. trop. 18: 49–54
- Le Borgne, R., Moll, Ph. (1986). Growth rates of the salp *Thalia democratica* in Tikehau atoll (Tuamotu Is.). Océanogr. trop. 21: 23–29
- Mackie, G. O. (1985). Midwater macroplankton of British Columbia studied by submersible PISCES IV. J. Plankton Res. 7: 753–777
- Mackie, G. O., Mills, C. E. (1983). Use of the PISCES IV submersible for zooplankton studies in coastal waters of British Columbia. Can. J. Fish. Aquat. Sci. 40: 763–766
- Madin, L. P. (1982). Production, composition and sedimentation of salp pellets in oceanic waters. Mar. Biol. 67: 39–45
- Madin, L. P., Cetta, C. M. (1984). The use of gut fluorescence to estimate grazing by oceanic salps. J. Plankton Res. 6: 475–497
- Madin, L. P., Harbison, G. R. (1978). *Bathocyroe fosteri* gen. nov. sp. nov.: a mesopelagic ctenophore observed and collected from a submersible. J. mar. biol. Ass. U.K. 58: 559–564
- Mills, C. E., Goy, J. (1988). *In situ* observations of the behavior of the mesopelagic *Solmissus* Narcomedusae (Cnidaria, Hydrozoa). Bull. mar. Sci. 43: 914–937
- Mills, C. E., Larson, R. J., Youngbluth, M. J. (1987). A new species of coronate scyphomedusa from Bahamas, *Atorella octogonos*, new species. Bull. mar. Sci. 40: 423–427
- Mullin, M. W. (1983). *In situ* measurement of filtering rates of the salp, *Thalia democratica*, on phytoplankton and bacteria. J. Plankton Res. 5: 279–288
- Paffenhöfer, G. A. (1976). On the biology of Appendicularia of the south-eastern North Sea. In: Persoone, G., Jaspers, E. (eds.) Proc. 10th Eur. Mar. Biol. Symp., Vol. 2. Universa Press, Wetteren, 437–455
- Porter, K. G., Feig, Y. S. (1980). The use of DAPI for identifying and counting aquatic nanoflora. Limnol. Oceanogr. 25: 943–948
- Prieur, L., Raunet, J., Taillez, D. (1990). Radiale PROS VI 1981–1989. Rapport interne L.P.C.M. (Laboratoire de Physique et Chimie marines), 600 p.
- Pugh, P. R., Harbison, G. R. (1987). Three new species of prayine siphonophore (Calycephorae, Prayidae) collected by submersible, with notes on related species. Bull. mar. Sci. 41: 68–91

- Pugh, P. R., Youngbluth, M. J. (1988). A new species of *Halistema* (Siphonophora, Physionectae, Agalmidae) collected by submersible. *J. mar. biol. Ass. U.K.* 68: 1–14
- Putt, M., Stoecker, D. K. (1989). An experimentally determined carbon:volume ratio for marine 'oligotrichous' ciliates from estuarine and coastal waters. *Limnol. Oceanogr.* 34: 1097–1103
- Silver, M. W., Alldredge, A. L. (1981). Bathypelagic marine snow: deep-sea algal and detrital community. *J. mar. Res.* 39: 501–530
- Seki, H. (1973). Red tide of *Oikopleura* in Saanich Inlet. *Bull. Soc. franco-jap. Océanogr.* 11: 153–159
- Smayda, T. J. (1971). Normal and accelerated sinking of phytoplankton in the sea. *Mar. Geol.* 11: 105–122
- Smayda, T. J., Bienfang, P. K. (1983). Suspension properties of various phyletic groups of phytoplankton and tintinnids in an oligotrophic, subtropical system. *P.S.Z.N.I.: Mar. Ecol.* 4: 289–300
- Sournia, A., Brylinsky, 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
- Strathmann, R. R. (1967). Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. *Limnol. Oceanogr.* 12: 411–418
- Suzuki, N., Kato, K. (1953). Studies on suspended materials. Marine snow in the sea. I. Sources of marine snow. *Bull. Fac. Fish. Hokkaido Univ.* 4: 132–135
- Taguchi, S. (1982). Seasonal study of fecal pellets and discarded houses of appendicularia in a subtropical inlet, Kaneohe Bay, Hawaii. *Estuar. coast. Shelf Sci.* 14: 545–555
- Tietze, R. C., Clark, A. M. (1986). Remotely operated tools for undersea vehicles. In: McGuinness, T. (ed.) *Current practices and new technology in ocean engineering*. American Society of Mechanical Engineers, New York, p. 219–223
- Verity, P. G., Langdon, C. (1984). Relationships between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. *J. Plankton Res.* 6: 859–868
- Youngbluth, M. J. (1984). Water column ecology: *in situ* observations of marine zooplankton from a manned submersible. In: Fleming, N. C. (ed.) *Divers, submersibles, and marine science*. Mem. Univ. Newfld. Occ. Pap. Biol. 9: 45–57
- Youngbluth, M. J., Bailey, T. G., Jacoby, C. A. (1990). Biological explorations in the mid-ocean realm: food webs, particle flux, and technological advancements. In: Lin, Y. C., Shida, K. K. (eds.) *Proc. 2nd Int. Symp. on Man in the Sea*, Honolulu, Hawaii. Best Publishing, p. 191–208
- Youngbluth, M. J., Kremer, P., Bailey, T. G., Jacoby, C. A. (1988). Chemical composition, metabolic rates and feeding behavior of midwater ctenophore *Bathocyroe fosteri*. *Mar. Biol.* 98: 87–94

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