Vol. 9: 267–277, 1995 | AQUATIC MICROBIAL ECOLOGY Aquat microb Ecol | Published December 21

Seasonal variations of pico- and nano-detrital particles (DAPI Yellow Particles, DYP) in the Ligurian Sea (NW Mediterranean)

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ABSTRACT: Seasonal variations of pico- and nano-sized marine detrital particles (DAPI Yellow Particles, DYP) and their relationships with components of the microbial food web were studied from April 1993 to March 1994 in the NW Mediterranean Sea. A hierarchical flexible clustering distinguished 2 major groups of DYP: ≤10 µm and 10–20 µm. Average abundance and total surface area of ≤10 µm DYP in surface waters were $21.6 \pm 3.2 \times 10^6$ l^{-1} and 153 ± 55 mm^2 l^{-1}, respectively, approximately an order of magnitude greater than abundances or total surface areas reported for larger detrital particles. Relationships of DYP, chlorophyll *a* and micro-organisms were investigated within and among 5 different hydrographic periods distinguished via vertical temperature gradients. Peak concentrations of ≤10 µm DYP occurred in early autumn at the end of stratification. In contrast, DYP 10–20 µm peaked at the beginning of the stratification period in early June. Correlation analysis revealed only weak relationships between DYP and abundance of bacteria, heterotrophic microflagellates and ciliates. However, declines in chlorophyll were generally followed by increases in DYP concentrations.

KEY WORDS: Detrital particles · Detritus · DAPI Yellow Particles (DYP) · Microbial populations · Mediterranean Sea

INTRODUCTION

The role of large detrital particles in oceanic biogeochemistry is quite well studied (Fowler & Knauer 1986). In contrast, small detrital particles have received little attention. The lack of simple methods of observing pico- and nano-sized detrital particles has likely hampered studies of these size fractions of detrital particles. However, some general trends were established in the 1960s in studies which considered particles down to the micro- and nano-size range.

Riley (1963) found a bimodal seasonal cycle of organic aggregates (5 µm to several mm) with peaks in winter and early summer which he related to the phytoplankton population in Long Island Sound, USA. Riley et al. (1964) showed the same phenomenon between Bermuda and the west coast of Africa. Later, Riley et al. (1965) observed that numbers of organic aggregates (5 µm to several mm) in surface waters of the Sargasso Sea were relatively small at all times but showed a slight seasonal variation, with highest values in winter and spring and lower ones in summer, in general agreement with the observed seasonal variations in phytoplankton. Kane (1967) followed the seasonal variations of organic aggregates in the Ligurian Sea (NW Mediterranean). Her data indicated a similar variation of detritus (10–260 µm) as found by Riley and his co-workers, in good agreement with phytoplankton variations. These studies all suggested, by grouping all particle size-classes together, that detrital particles are a homogenous pool and are closely linked with phytoplankton stocks. However, quantification of the stocks of pico- and nano-sized particles separately is of importance because they represent non-living organic matter with low to negligible sinking velocities.

In the companion paper we present a rapid method for the quantification of pico- and nano-detrital particles (Mostajir et al. 1995). Using the DAPI (4′6′-diamidino-2-phenylindole) stain, epifluorescence counts

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of DAPI Yellow Particles, DYP, can be made, particles without the characteristic blue fluorescence of DAPI conjugated with DNA rich in A-T base pairs. We showed that more than 90% of DYP are almost exclusively organic, enzyme-degradable matter and that they represent an abundant class of degradable organic particles. Preliminary data indicated that DYP were distributed very irregularly with depth along an offshore transect in the Ligurian Sea (Mostajir et al. 1995) suggesting that DYP represent a highly dynamic stock of particulate matter.

In the present paper we present data on pico- and nano-sized DYP detrital particles based on weekly sampling over 1 yr in the Ligurian Sea. Relationships among different size classes of pico- and nano-DYP were examined and stocks are compared to those of living particles in the microbial loop, and chlorophyll *a* (chl *a*) in distinct periods defined by water column structure. We were interested in examining the relationship of DYP stocks to chl *a* and determining whether periods in which DYP are abundant correspond with periods of high heterotrophic microbial biomass.

MATERIALS AND METHODS

Sampling. The study site, Point 'B', is a standard oceanographic station at the entrance of Villefranche Bay [43° 41′ 10″ N, 7° 19′ 00″ E; see Etienne et al. (1991) for site background]. Samples were taken once a week from March 31, 1993, to March 30, 1994. Temperature was measured with a Seabird CTD at 0, 10, 20, 30, 40, 50, 60 and 75 m. Using Niskin bottles, samples for chl *a* analysis were taken from 0, 10, 20, 30, 50 and 75 m. For enumeration of DYP and micro-organisms, samples were taken from 4 standard depths chosen to correspond with surface waters, the summer thermocline, the average depth of the chlorophyll maximum and deep water: 0, 20, 40 and 75 m.

Sample processing. Chl *a* was analysed following the protocols of SCOR/UNESCO (1964). DYP enumeration procedures are given in Mostajir et al. (1995). Briefly, 10 ml water samples were fixed with formalin (3% final conc.), stained with DAPI (final conc. 0.25 µg ml^{-1}) and immediately drawn down onto a 25 mm black Nuclepore polycarbonate membrane (0.2 µm pore size) using low vacuum (<0.2 bar). The filter was placed on a slide, and examined with an epifluorescence microscope with a 100× Neofluar objective. Particles were enumerated in size classes of 0.2–2, 2–5, 5–10, 10–15 and 15–20 µm. For each size class, 100 pico- and nano-DYP were counted. To calculate the surface area of particles they were considered as circles with diameters as follows for each of the above size classes, respectively: 1.25, 3.5, 7.5, 12.5 and 17.5 µm. The precision of particle counting is reported in Mostajir et al. (1995). The standard error, as a percentage of the mean, ranges from 3 to 66% with the relative error increasing with particle size class. On the same filters prepared for DYP counts, heterotrophic microorganisms, flagellates and bacteria were counted. Estimates of ciliate microzooplankton were made from 100 ml of sample water, preserved with acid Lugol (0.4% final concentration), sedimented for 24 h and examined with a Zeiss inverted microscope.

Data analysis. ***Characterisation of hydrographic conditions:*** Hydrographic periods were distinguished based on temperature differences between 0 and 75 m (Δt), similar to the procedure of Bustillos-Guzmán et al. (1995), used for the same site. A *MIX+* period was defined as positive Δt (deep layers were colder than surface waters) which occurred in early spring, from March 31 to April 29, 1993. Following this period, stratification of the water column began and the stratified period was divided into 3 subdivisions: *SEMI+* (semi-stratified+), a period of rapid increase in surface water temperature (from May to early June), *STRATIFIED*

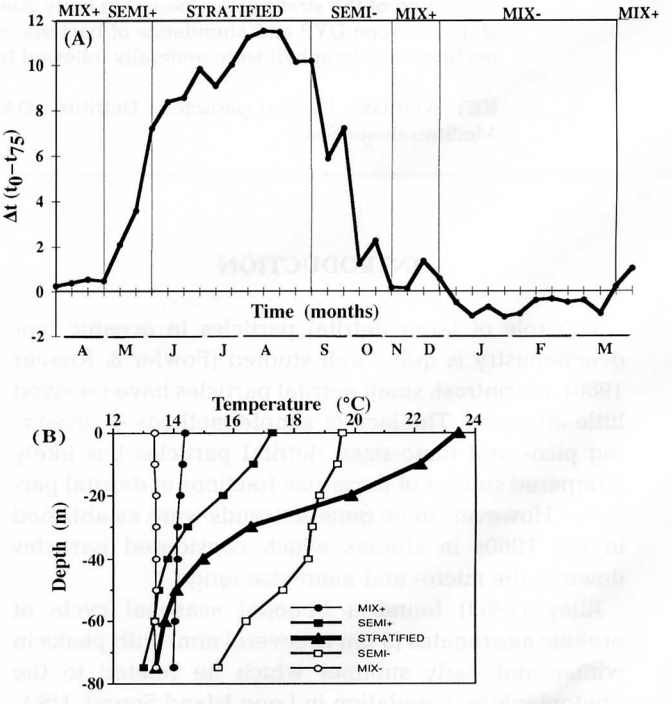

Fig. 1. (A) Seasonal temperature variations (Δt) at Point 'B', a standard oceanographical station at the mouth of Villefranche Bay (43° 41′ 10″ N, 7° 19′ 00″ E) from March 31, 1993 to March 30, 1994. Different hydrographic periods are indicated. (B) Vertical profile of temperature at different hydrographic conditions in 1993. Each point is the mean of all data for each period in each depth

(from June to September) and *SEMI–* (semistratified–) the beginning of destratification (from September to end of October). During the *SEMI–* period, water column temperature was significantly higher than during the *SEMI+* period. The stratified period merged into the second *MIX+* period (from November to end of December) as described above. Negative Δt, mixed water mass, is called here *MIX–* (from January to mid March 1994) with about 13°C at surface and a slight increase at deeper waters. This period gave way to the *MIX+* period at the end of our annual observation. Temperature variations in these 5 periods are summarised in Fig. 1A. Fig. 1B shows the vertical temperature profiles of these 5 periods with data obtained in 1993.

Classification of DYP particles: To investigate natural groupings among the different detrital size classes, the data set (5 size classes of DYP in water column with 52 dates) was standardized. Hierarchical flexible clustering, with $\beta = -0.25$ on a matrix of Euclidean distances among the standardized data was performed according to Legendre & Legendre (1984).

Correlation analyses: A correlation matrix was employed with 6 variables (≤10 µm DYP, 10–20 µm DYP, chl *a*, bacteria, heterotrophic flagellates and oligotrich ciliates) using integrated water column values for each hydrographic condition and for the whole study period.

RESULTS

Classification of DYP

Results of DYP classification are revealed that 2 major groups can be separated corresponding roughly to particles ≤10 µm and >10 µm. The ≤10 µm group can be further divided into subgroups by depths with particles at 0 and 20 m separated from 40 and 75 m (details not shown).

DYP number and surface area

The number of detrital particles (± SE) decreased remarkably with increase in size from $17 \pm 2 \times 10^3$ ml^{-1} to 9 ± 4 ml^{-1} for 0.2–2 µm DYP and 15–20 µm DYP, respectively. Fig. 2A illustrates abundance variations of DYP at the 4 depths sampled. Generally, particle concentrations did not differ with depth from 0 to 75 m (Fig. 2). Total surface area of 2–5 µm DYP was much larger than other size fraction of DYP at all depths. The surface area (± SE) of DYP 2–5 µm ranged from 76 ± 11 mm^2 l^{-1} in surface waters decreasing to 45 ± 4 mm^2 l^{-1} at 75 m (Fig. 2B).

General trends in DYP concentrations

Reflecting the classification analysis, particles ≤10 µm co-varied, all showing marked minima during the stratified season and peak concentrations often occurring during periods of transition from one hydrographic period to the next (Fig. 3). Among particles 10–20 µm in size, the larger size class (15–20 µm) occurred sporadically, obscuring general trends. The smaller size class (10–15 µm) appeared to be distinct from other size classes as it often showed subsurface peaks in concentration (Table 1).

General trends in concentrations of micro-organisms

Among microbial populations, bacteria showed the least variability with depth and a lack of clear seasonal trends (Fig. 4). Ciliates and heterotrophic microflagellates both generally decreased in abundance with depth and displayed pronounced periods of maximum concentration in early spring.

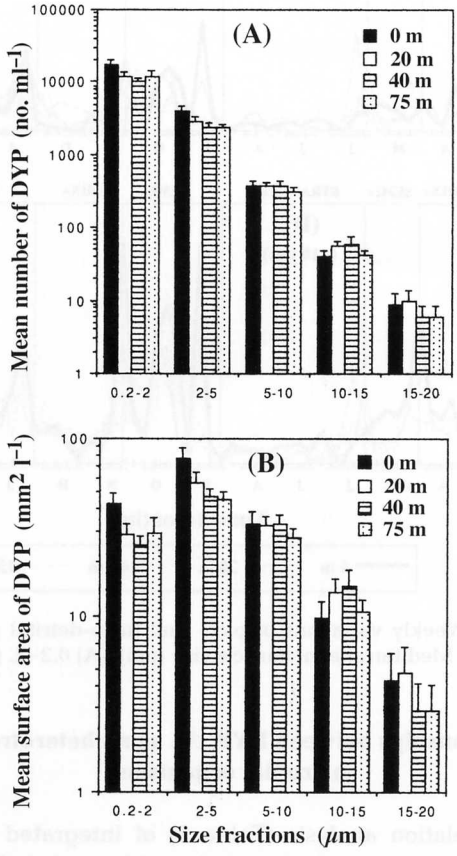

Fig. 2. Number and surface areas of different size classes of DYP. (A) Logarithmic plot of annual mean number of DYP; (B) logarithmic plot of annual mean surface of DYP. Bars represent standard errors

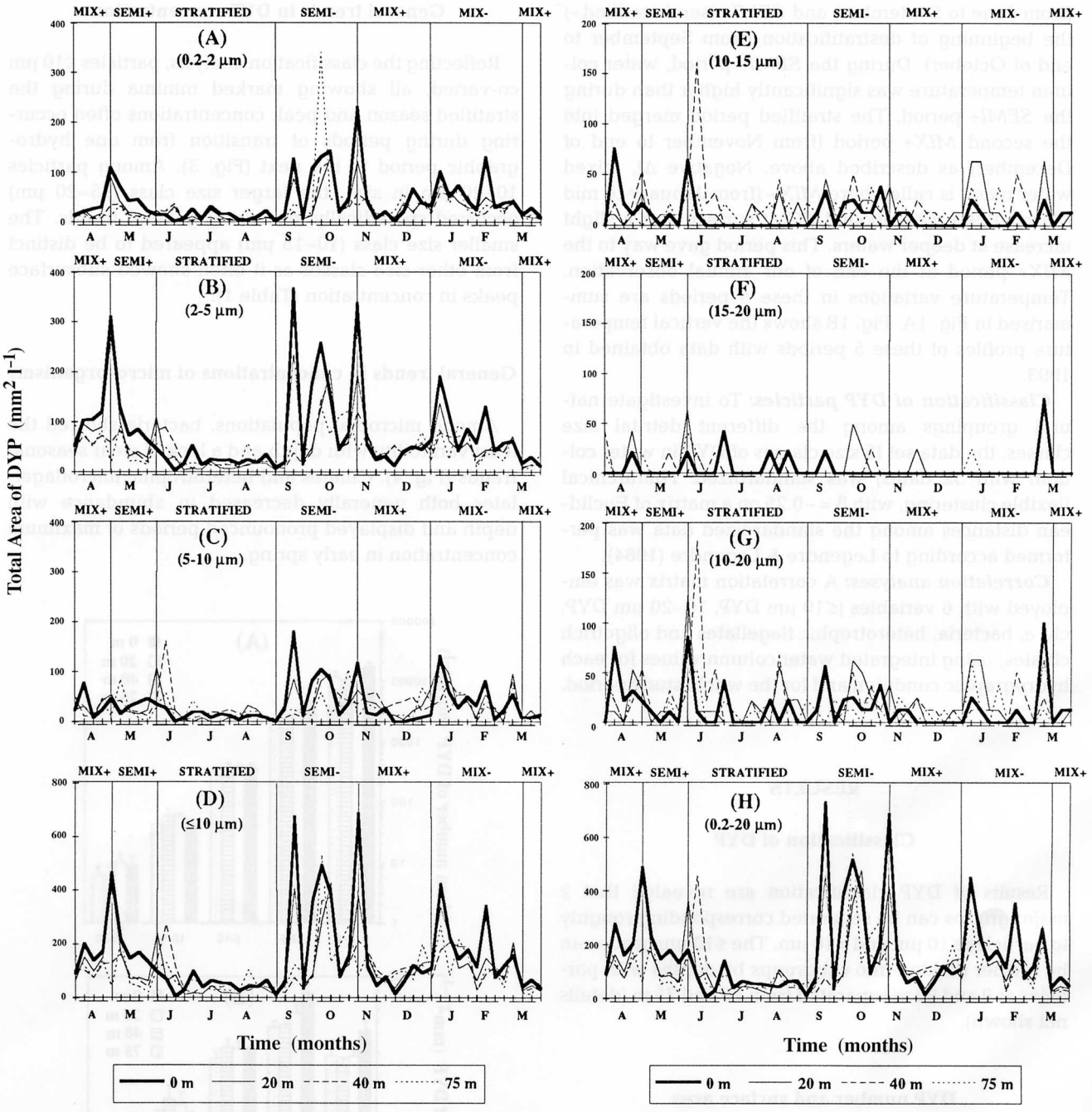

Fig. 3. Weekly variations of pico- and nano-detrital particles from March 31, 1993, to March 30, 1994, in the Ligurian Sea, NW Mediterranean. Particle size (µm): (A) 0.2–2, (B) 2–5, (C) 5–10, (D) ≤10, (E) 10–15, (F) 15–20, (G) 10–20, (H) 0.2–20

Relationships between DYP, chl *a* and heterotrophic microbial organisms

Correlation analysis (Table 2) of integrated water column values over the whole study period did not indicate any strong relationships between either of the major DYP groups and chl *a* or microbes. Concentrations of ≤10 µm and >10 µm particles were significantly related to each other as were chl *a* and heterotrophic microflagellates as well as ciliates and heterotrophic microflagellates. The correlations found overall were the result of strong relationships between ≤10 µm and >10 µm particles during the stratified period and the correlations of chl *a*, microflagellates and ciliates during mixed water column periods. Among the different hydrographic periods, the transitional periods between

Table 1. Total surface area ($mm^2\ l^{-1} \pm SE$) of different size fractions of DYP at 4 depths from March 31, 1993, to March 30, 1994, in the NW Mediterranean Sea. Each value corresponds to the mean of 4 or 5 samples taken for each month

Month	0.2–2 µm				2–5 µm				5–10 µm				≤10 µm			
	0 m	20 m	40 m	75 m	0 m	20 m	40 m	75 m	0 m	20 m	40 m	75 m	0 m	20 m	40 m	75 m
Apr	40±17	30±15	15±5	11±1	138±45	113±41	60±6	64±14	36±12	32±8	32±8	30±7	214±66	176±62	107±10	106±22
May	46±10	23±7	18±6	15±6	87±15	50±17	45±13	38±18	33±7	20±2	24±7	29±19	166±19	93±25	88±26	81±43
Jun	13±4	16±5	18±6	17±4	29±9	35±19	51±17	33±8	18±6	33±20	48±29	29±10	59±19	83±42	116±46	80±18
Jul	18±5	10±5	8±1	6±2	21±3	10±4	16±2	15±2	14±2	4±2	19±3	11±3	53±5	24±7	42±1	32±3
Aug	11±4	5±1	7±2	11±5	23±4	14±2	16±3	28±10	9±2	16±7	11±2	15±4	43±8	36±8	34±4	55±17
Sep	51±27	25±16	11±3	18±6	117±70	65±44	22±7	37±9	61±33	30±15	14±4	17±3	229±128	120±74	47±13	73±16
Oct	84±30	64±25	71±26	121±73	133±48	109±37	106±32	110±12	60±21	60±17	71±15	54±19	278±96	234±77	247±70	285±87
Nov	75±52	48±26	32±11	29±9	112±76	84±38	66±21	47±10	44±25	40±9	44±8	22±6	232±152	172±72	143±32	96±23
Dec	32±11	27±6	25±5	34±9	42±9	41±7	44±6	49±9	5±3	28±11	36±5	29±11	80±19	96±18	106±9	112±23
Jan	67±13	51±10	59±3	54±14	109±31	75±21	75±3	71±15	67±23	73±23	58±9	57±16	243±63	199±52	192±6	182±40
Feb	56±25	35±6	23±6	25±5	72±20	39±3	37±8	26±6	35±17	23±12	17±7	19±10	162±60	97±20	78±18	70±21
Mar	24±7	17±8	17±8	20±9	30±11	28±28	25±14	30±16	22±11	32±22	26±19	23±16	76±28	77±44	69±40	73±40

	10–15 µm				15–20 µm				10–20 µm				0.2–20 µm			
	0 m	20 m	40 m	75 m	0 m	20 m	40 m	75 m	0 m	20 m	40 m	75 m	0 m	20 m	40 m	75 m
Apr	26±13	13±5	19±10	13±6	4±4	8±8	8±8	13±5	30±12	21±9	28±9	26±9	244±68	197±66	135±18	131±29
May	5±3	5±3	8±3	8±5	0	0	5±5	0	5±3	5±3	13±7	8±5	172±21	99±23	101±25	89±45
Jun	15±13	19±11	49±29	11±7	13±8	13±13	8±5	13±8	28±16	32±24	58±32	23±11	87±33	115±65	174±75	103±29
Jul	0	8±5	5±5	8±3	0	0	0	0	0	8±5	5±5	8±3	53±5	32±7	48±5	40±5
Aug	0	14±9	11±11	11±7	11±6	11±6	6±6	0	11±6	25±12	17±17	11±7	55±6	61±19	51±15	66±14
Sep	14±7	11±9	2±2	14±4	4±4	0	0	0	18±10	11±9	2±2	14±4	247±139	131±83	49±15	86±14
Oct	22±6	19±4	19±11	16±8	0	19±12	6±6	0	22±6	38±11	25±12	16±8	300±96	271±86	273±74	301±88
Nov	6±4	13±9	9±6	9±6	0	6±6	0	0	6±4	19±8	9±6	9±6	238±150	191±77	152±29	107±29
Dec	0	5±3	8±3	5±3	0	0	0	0	0	5±3	8±3	5±3	80±19	101±21	113±11	117±21
Jan	9±6	38±15	13±0	22±9	0	0	0	6±6	9±6	38±15	13±0	28±14	252±68	237±65	205±6	210±49
Feb	3±3	0	19±12	0	0	0	0	0	3±3	0	19±12	0	166±64	97±20	97±27	70±21
Mar	13±5	19±15	6±6	9±3	19±19	0	0	0	31±23	19±15	6±6	9±3	107±51	96±58	75±46	82±42

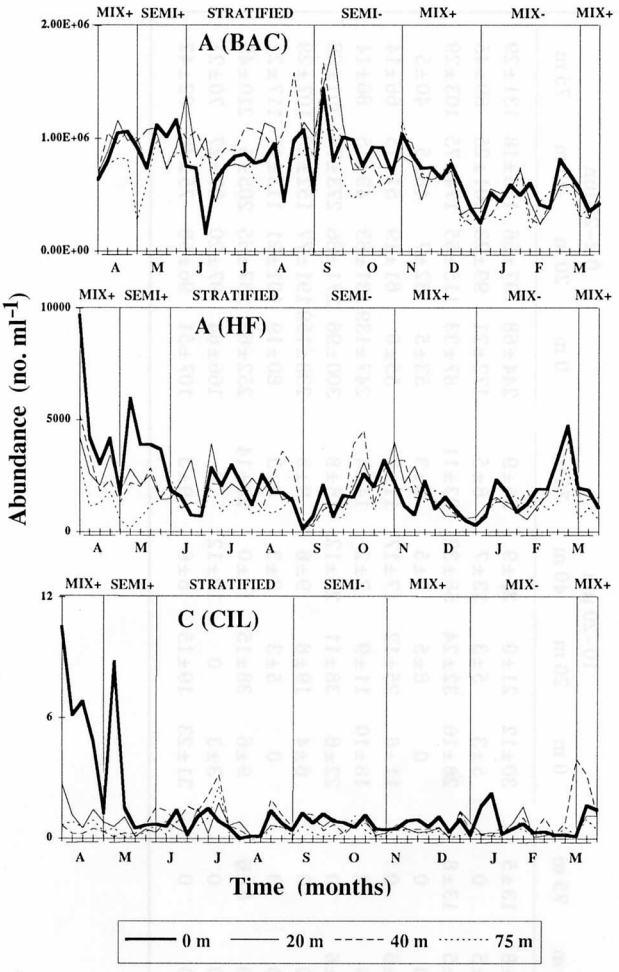

Fig. 4. Seasonal variations of (A) bacteria, (B) heterotrophic flagellates, (C) oligotrich ciliates in different hydrological conditions from March 31, 1993, to March 30, 1994, in the Ligurian Sea

stratified and mixed conditions (*SEMI+*, *SEMI–*) showed no strong significant relationship between any of the parameters. However, during the *SEMI–* period a significant relationship between ≤10 µm DYP and heterotrophic flagellates was detected as well as a relationship between ≤10 µm DYP and ciliates during the *SEMI+* period. Noteworthy was the apparent independence of bacterial concentrations except for a weak correlation with ≤10 µm DYP during the *MIX+* period of late autumn/early winter.

Analysis of temporal trends of chl *a* and concentrations of the 2 major groups of DYP (Fig. 5) showed qualitative similarities. DYP concentrations showed 'pulses' similar to those of chl *a*; marked declines in chl *a* concentrations were followed by increases in DYP in samples taken the following week. The relationship was qualitative; amplitudes of chl *a* oscillations were not quantitatively related to the amplitudes of DYP oscillations.

DISCUSSION

DYP compared to other particulate organic matter

DYP in the present investigation overlap the lower size range of detritus (≤20 µm) studied by Riley (1963), Riley et al. (1964, 1965), Kane (1967) and Gordon (1970) as well as the 'Transparent Exopolymer Particles' (TEP) reported by Passow & Alldredge (1994). Table 3 summarises data from earlier and recent studies of particulate matter, as well as for the DYP presented here. Number and total surface area of ≤10 µm DYP reported here are much higher than previously found for 'micro' organic aggregates in the NW Mediterranean (Kane 1967) and other systems as well (Riley 1963, Riley et al. 1964, 1965, Gordon 1970). Compared to data from more recent studies on marine snow, nano- and pico-DYP are considerably more abundant than 'macro'-sized aggregates, commonly

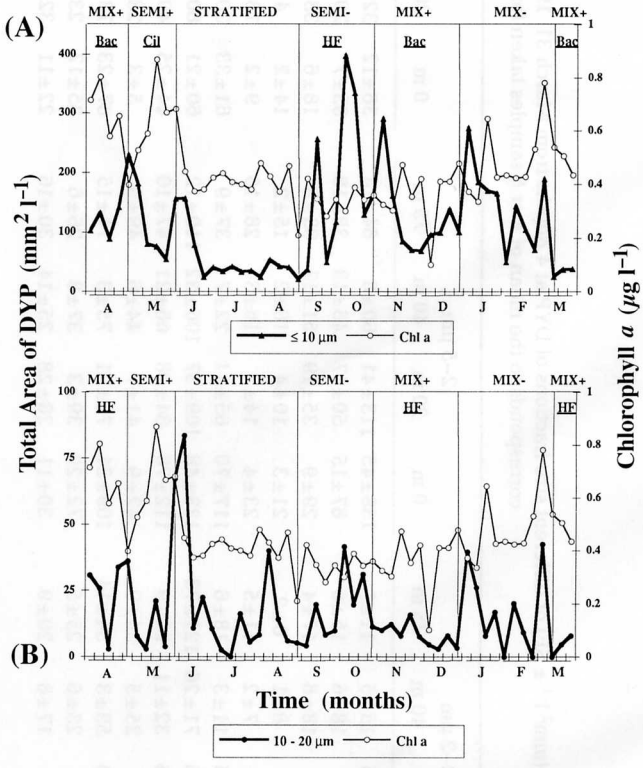

Fig. 5. Temporal changes of DYP and chl *a* during 5 hydrographic periods in Villefranche Bay from March 31, 1993, to March 30, 1994, based on weekly sampling. The values are integrated over the water column from surface waters to 75 m. (A) DYP ≤10 µm and chl *a*. Significant correlations between DYP ≤10 µm and bacteria (Bac) in *MIX+* periods, ciliates (Cil) in *SEMI+* period and heterotrophic flagellates (HF) in *SEMI–* period are underlined. (B) 10–20 µm DYP and chl *a*. Large DYP were significantly correlated with heterotrophic flagellates in *MIX+* periods (see text)

Table 2. Correlation matrix for 6 variables integrated throughout the water column from 0 to 75 m: chlorophyll *a* (chl), 2 size classes of DYP (≤10 and 10–20 µm), bacteria (Bac), heterotrophic flagellates (HF) and oligotrich ciliates (Cil) throughout the entire study period and within different hydrographic periods. Underlined values with * and ** are significant at p = 0.05 and p = 0.01 levels, respectively

WHOLE PERIOD (n = 52)

	Chl	≤10	10–20	Bac	HF	Cil
Chl	1					
≤10	−0.083	1				
10–20	0.19	0.454**	1			
Bac	0.062	−0.05	0.086	1		
HF	0.458**	0.297*	0.258	0.194	1	
Cil	0.309*	−0.143	−0.009	0.097	0.391**	1

STRATIFIED (n = 13)

	Chl	≤10	10–20	Bac	HF	Cil
Chl	1					
≤10	0.248	1				
10–20	0.228	0.854**	1			
Bac	0.17	0.029	−0.166	1		
HF	0.591*	0.09	−0.068	0.46	1	
Cil	0.077	0.051	−0.215	0.269	0.483	1

SEMI+ (n = 5)

	Chl	≤10	10–20	Bac	HF	Cil
Chl	1					
≤10	−0.484	1				
10–20	0.281	0.433	1			
Bac	−0.097	−0.418	0.201	1		
HF	0.323	0.319	−0.053	−0.896*	1	
Cil	−0.791	0.892*	0.087	−0.34	0.097	1

SEMI− (n = 8)

	Chl	≤10	10–20	Bac	HF	Cil
Chl	1					
≤10	−0.144	1				
10–20	−0.381	0.751*	1			
Bac	0.457	−0.376	−0.489	1		
HF	−0.056	0.803*	0.513	−0.641	1	
Cil	0.676	−0.133	−0.165	0.645	−0.343	1

MIX+ (n = 16)

	Chl	≤10	10–20	Bac	HF	Cil
Chl	1					
≤10	−0.134	1				
10–20	0.478	0.386	1			
Bac	0.107	0.515*	0.461	1		
HF	0.502*	0.247	0.574*	0.553*	1	
Cil	0.701**	−0.233	0.43	0.06	0.631**	1

MIX− (n = 10)

	Chl	≤10	10–20	Bac	HF	Cil
Chl	1					
≤10	−0.072	1				
10–20	0.079	0.874**	1			
Bac	0.472	0.166	0.148	1		
HF	0.773**	0.053	0.364	0.514	1	
Cil	0.252	−0.537	−0.278	−0.114	0.086	1

reported in concentrations of 1 to 10 l^{-1} (Alldredge & Silver 1988) and rarely more abundant than 291 to 489 l^{-1} (Wells & Shanks 1987). The size range of DYP overlaps the lower size range of TEP (Passow & Alldredge 1994), although the abundance of DYP in the Mediterranean Sea is higher than TEP reported from other systems. However, compared to smaller 'particles', colloid aggregates >1 µm have been reported with a concentration of 10^5 colloid aggregates ml^{-1} (Wells & Goldberg 1993), which is about the same order of magnitude as DYP ≤10 µm in the present study. It should be noted that smaller colloids are much more abundant than colloid aggregates (Table 3).

In terms of particle surface area, DYP ≤10 µm appear to be more abundant than, or about equal to, larger organic aggregates based on previous reports. For example, total area of DYP ≤10 µm given here compared to surface areas of organic aggregates reported by Riley (1963) for Long Island Sound are of the same order of magnitude (Table 3). The surface area of all other organic aggregates from other sites (reported by Riley et al. 1965, Kane 1967 and Gordon 1970) are about an order of magnitude less than those of DYP ≤10 µm reported here (Table 3).

Total area of DYP ≤10 µm and that of TEP reported by Passow & Alldredge (1994) from 3 different systems are also of the same order of magnitude (43 to 278 mm^2 l^{-1} of DYP compared with 0.2 to 650 mm^2 l^{-1} of TEP). However, the authors emphasized that total area of TEP can vary by 4 orders of magnitude (0.2 to 2000 mm^2 l^{-1}) and high concentrations of TEP were associated with flocculating diatom blooms (Alldredge et al. 1993).

DYP in the Ligurian Sea

The present investigation suggests a classification of DYP into 2 groups with possible different origins. Hierarchical clustering classification separated the small ≤10 µm DYP from the larger ones. Peaks of ≤10 µm DYP (Fig. 5A) were observed during hydrographic shift periods (e.g. between *MIX+* and *SEMI+*, *SEMI+* and *STRATIFIED*). In these periods, chl *a* decreased

Table 3. Comparison of the numbers and total surface areas of DYP ≤10 µm with reports of particulate matter from early and recent studies

Particles (size range)	Number ($\times 10^3$ l^{-1}) Range	Mean	Total area (mm^2 l^{-1}) Range	Mean	Study site	Source
Organic aggregates (5 µm to several mm)	30–100	–	23–167	–	Long Island Sound, USA (coastal)	Riley (1963)
Organic aggregates (5 µm to several mm)	8–40	11.32	3–9.9	–	N Equatorial Current (open sea)	Riley et al. (1965)
Organic aggregates (5 µm to several mm)	–	–	3–38	–	Guinea Current (open sea)	Riley et al. (1965)
Organic aggregates (5 µm to several mm)	30–100	–	–	–	Off west coast of Africa (coastal)	Riley et al. (1965)
Organic aggregates (10–260 µm)	1.9–64	12.5	1–52	11.5	Ligurian Sea, off Monaco (coastal)	Kane (1967)
Organic aggregates (10–260 µm)	1.9–15	6.3	1–10	4.6	Ligurian Sea, off Monaco (open sea)	Kane (1967)
Organic aggregates (<5 µm)	32–235	–	–	–	N Atlantic Ocean, from Sargasso Sea to Irminger Sea	Gordon (1970)
Marine snow (>500 µm)	$0–8 \times 10^{-3}$	–	–	–	Santa Barbara, CA, USA	Alldredge (1979). For more details see Alldredge & Silver (1988)
Marine snow (4 ± 5 mm)	–	$7.0 \pm 1.2 \times 10^{-3}$	–	–	NE Atlantic Ocean	Shanks & Trent (1980)
TEP (3 to several 100 µm)	10^0–10^4	–	0.2–2000	–	Monterey Bay–Santa Barbara–Bermuda	Passow & Alldredge (1994)
DYP (0.2–10 µm)	744–112516	21619±3237	43–278	153±55	Ligurian sea off Villefranche (coastal) surface waters	This study
Sub-micron particles (0.38–1 µm)	$5–8 \times 10^7$	–	–	–	N Pacific Ocean (top 40 m)	Koike et al. (1990)
Sub-micron particles (0.36–1.01 µm)	–	$1.43–2.35 \times 10^7$	–	–	NW Atlantic shelf water (offshore; 10 m)	Longhurst et al. (1992)
Colloid aggregates (>1.0 µm)	–	10^5	–	–	Atlantic and Pacific Oceans (mid-depth and deep waters)	Wells & Goldberg (1993)
Colloids (0.005–0.2 µm)	–	10^9	–	–	N Atlantic and Southern Oceans	Wells & Goldberg (1994)

sharply, presumably due to sedimentation of phytoplanktonic cells or intensive grazing by heterotrophic organisms. In either case the occurrence of large quantities of detrital particles (mortality of phytoplanktonic cells, faecal production and carcasses of organisms) is not surprising. In contrast to isolated peaks before stratification, at the end of long stratification in the *SEMI–* period, 2 large peaks of ≤10 µm DYP were also observed in September and October (the second one was the highest for the studied year). In this period, chl *a* was lowest (0.34 ± 0.01 µg l^{-1}) and did not show any sharp shifts. Therefore, in this period the high amount of ≤10 µm DYP cannot be explained by a drop in chl *a*. Thus, there was probably another source of ≤10 µm DYP in the *SEMI–* period. Abundance trends of DYP >10 µm appeared to track chl *a* more closely than smaller particles (Fig. 5B) but over the entire study period there was no significant correlation.

Sources of DYP and its trophic importance may vary seasonally. For example, large DYP (10–20 µm) were correlated only with heterotrophic flagellates in the *MIX+* period and no other correlation of these large DYP was observed at any time with microbes (see Table 2).

The ≤10 µm DYP correlation with bacteria, heterotrophic flagellates and ciliates is even more interesting. During the *MIX+* period, bacteria were significantly correlated with this small DYP. During the *SEMI–* period, heterotrophic flagellates were significantly correlated with ≤10 µm DYP and not with any other parameters investigated here (Table 2). This significant correlation occurred during the *SEMI+* period between ciliates and ≤10 µm DYP. This suggests a variable linkage of DYP with the microbial food web during certain periods.

Speculations on the origins and fates of DYP

The idea that particulate organic matter (POM) may be formed via coagulation by bubbling of dissolved organic carbon (DOC) has been discussed for over 30 yr. Riley (1963), Sutcliffe et al. (1963), Riley et al. (1964), Barber (1966), Batoosingh et al. (1969), Corner et al. (1974), Biddanda (1985), and Kepkay & Johnson (1988, 1989) all provided some evidence on the conversion of dissolved organic matter (DOM) to POM by bubbling. More recently, Wells & Goldberg (1994) proposed a likely primary source of marine colloids as the agglomeration of some fraction of the truly dissolved organic phase.

In the NW Mediterranean, at least, DOC concentrations appear dynamic. Copin-Montégut & Avril (1993) detailed monthly vertical profiles of DOC 28 miles offshore of Villefranche. These authors concluded that DOC accumulated in surface waters throughout the stratified period and was then dispersed through water column mixing. Thus, considering wind forcing at the end of the stratified period on water mass mixing, it may be hypothesized that adsorption on bubbles could produce directly or indirectly the DYP that we observed during destratification (e.g. DOC adsorption on bubbles and production of colloids, and then agglomeration of colloids giving DYP).

In the *SEMI–* period, surface waters cooled due to wind stress, and consequently water column mixing began. In this period, the high observed value of ≤10 µm DYP might be explained by physical mechanisms (conversion of DOC to DYP). Two peaks of ≤10 µm DYP in the *SEMI–* period were followed by a 10–20 µm DYP peak. The sharp decrease of ≤10 µm DYP at the end of this period coincided with a third peak of DYP 10–20 µm. These fluctuations could be explained by a scenario in which ≤10 µm DYP formation (in the way of coagulation of DOC on bubble surfaces) was followed by the formation of large DYP. Two high peaks of ≤10 µm DYP were followed by another one in the *MIX+* condition. During this period, chl *a* decreased. Disaggregation of 10–20 µm DYP formed at the end of *SEMI–* period could explain this peak of ≤10 µm DYP. This case fits in the detritus cycle scheme suggested by Biddanda & Pomeroy (1988) with distinct phases of aggregation, disaggregation, re-aggregation and finally sinking out of the water column.

In the *MIX–* period the peaks of DYP seem to be regular especially for 10–20 µm detrital particles. In other words, during the *MIX–* period, DYP variations correspond with the scheme proposed by Biddanda & Pomeroy (1988). Nevertheless, in contrast with the fate of detritus in Biddanda & Pomeroy's scheme, DYP do not seem to sink to the deep layer, at least in the NW Mediterranean. Miquel et al. (1994), employing sediment trap data, presented the dynamics of the downward flux of particles and carbon in the open NW Mediterranean Sea. These authors did not observe a high value of downward particulate mass flux at the end of the stratified condition where ≤10 µm DYP peaked sharply.

Another possible source of DYP could be protozoan egesta. This idea corresponds with the hypothesis of Nagata & Kirchman (1992) that flagellates release their own digestive enzymes and incompletely digested membranes and probably other cellular components from bacterial prey. Indeed, several authors have reported on small particle production by protozoa (Stoecker 1984, Nöthig & von Bodungen 1989, Buck et al. 1990, Elbrächter 1991, González 1992, Buck & Newton 1995).

Concerning possible settling rates of DYP, little comparative data is available. Some values of settling rates of organic aggregates have been given in the literature: 1 to 7 m d^{-1} (Riley et al. 1965), 0.14 to 12 m d^{-1} (Hobson 1967), 0.10 to 0.57 m d^{-1} for particles of 2 to 6 µm (Riley 1970). Such settling rates are much lower than those found for diatoms, 100 to 150 m d^{-1} (Billet et al. 1983), zooplankton faeces, 29 to 122 m d^{-1} (Lorenzen & Welschmeyer 1983, Fowler et al. 1987) and marine snow aggregates, 50 to 100 m d^{-1} (Shanks & Trent 1980, Alldredge & Gotschalk 1990). This suggests that small particles are probably distributed solely by advection; settling becomes more important with progressively larger particles (Gordon 1970).

Trophic interactions between detritus and microorganisms were investigated by several authors. Riley (1963) was among the first to suggest that organic aggregates provide a substrate for bacterial growth and probably food for zooplankton. Several authors reported a rapid bacterial colonization of detritus followed by the development of protozoa. Detrital particles, colonized by bacteria, can come from different sources including phytoplankton (Hoppe 1981, Linley & Newell 1984, Fukami et al. 1985), zooplankton (Fukami et al. 1985), faecal pellets (Pomeroy & Diebel 1980, Jacobsen & Azam 1984) and organic particle

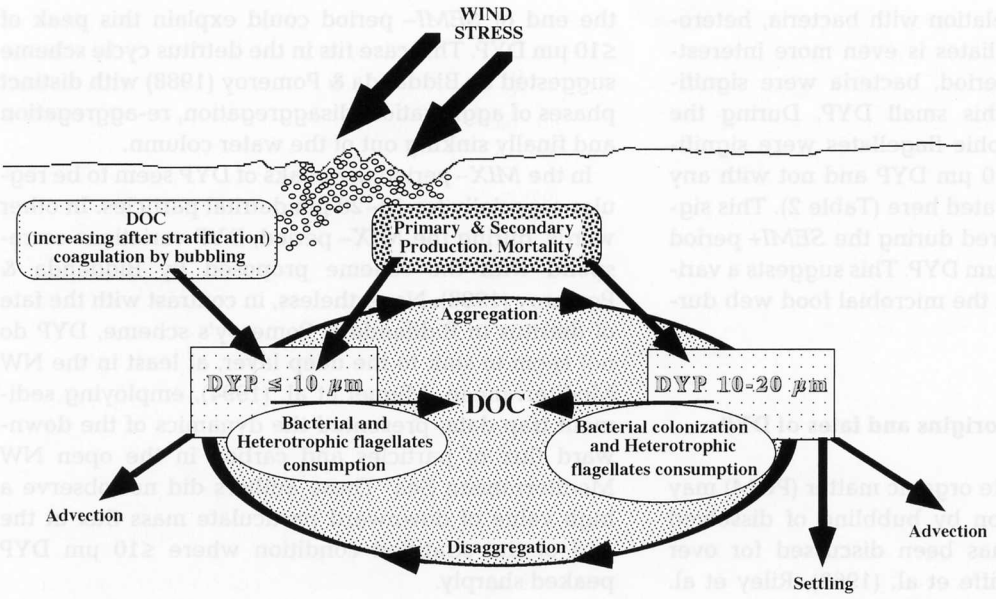

Fig. 6. Speculative schematic model of the 'detrital loop' indicating origins, trophic importance, fate and interactions of DYP in the microbial food web through the water column. See 'Discussion' for details

generation by surface coagulation (Kepkay & Johnson 1988, 1989). We think that DYP, with their seemingly negligible settling rate and their large surface/volume ratio, could be a significant resource in supplying nutrients for the regenerated production in planktonic systems. The relatively large amounts of DYP in the water column indicate a potentially important role for these particles as one of the sources for remineralization processes within the microbial food web.

Fig. 6 shows a speculative schematic model of a 'detrital loop' and summarises our discussion about origins, trophic importance, fate and interactions of DYP in the microbial food web through the water column. As this scheme illustrates, there are at least 2 possible origins of DYP formation. One is the primary and secondary production as suggested by Biddanda & Pomeroy (1988). Indeed, the mortality of organisms could add to this source. The second is DOC which can be converted to DYP ≤10 µm via coagulation by bubbling. This phenomenon could be important after a stratification period in which DOC increased in surface water followed by a period of wind-driven mixing. There appear to be qualitative differences between DYP ≤10 µm and larger DYP as smaller DYP are much less intensively colonized by bacteria (Mostajir et al. 1995). Aggregation of DYP ≤10 µm to DYP 10–20 µm could be either a purely physical phenomenon or a biological process or both. Some DYP ≤10 µm could leave the system by advection. The origin of DYP 10–20 µm is possibly the result of DYP ≤10 µm aggregation, or direct production by primary or secondary producers. The fate of DYP 10–20 µm is potentially disaggregation, producing DYP ≤10 µm, or exiting from the system via settling or advection.

Acknowledgements. We thank R. Charra for chlorophyll measurement, D. Betti and R. Charra for their regular sampling in Villefranche Bay, M. Perez Mediavilla for her help in counting of some ciliate slides, J. M. Fromentin and B. Planque for their help in statistical treatments, and P. Verity, M. Karner and B. Avril as well as 3 anonymous reviewers for their constructive comments on the manuscript. The work presented here is part of the doctoral dissertation of B.M. Financial support was provided by the CNRS/INSU (URA 716) and E.E.C. MAST II-MTP (Mediterranean Targeted Program, contract MAST II-CT93-0063, Medipelagos).

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Responsible Subject Editor: F. Azam, La Jolla, California, USA

Manuscript first received: July 31, 1995
Revised version accepted: October 19, 1995