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Particulate nucleic acid dynamics in a highly oligotrophic system: the Cretan Sea (Eastern Mediterranean)

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ABSTRACT: Spatial and temporal variations of nucleic acid (DNA and RNA) concentrations and bacterioplankton density were investigated in a highly oligotrophic region of the Eastern Mediterranean in order to evaluate the relative contribution of the pico-, nano- and microparticulate fractions and to estimate bacterioplankton contribution to the nucleic acid pools. The oligotrophic conditions of the Cretan Sea were reflected by the extremely low particulate nucleic acid content. In particular, RNA concentrations (range: 0.1 to 3.8 µg l^{-1}) were the lowest reported so far in the marine environment. Particulate DNA concentrations (range: 0.8 to 5.9 µg l^{-1}) also displayed a reduced temporal variability. Picoparticulate RNA and bacterial secondary production displayed similar spatial patterns, suggesting that RNA concentrations increased as a result of enhanced metabolic activity. High DNA concentrations were generally associated with the high salinity (>38.95) Transition Mediterranean Waters (TMW) in summer (August 1994 and September 1995), whereas a sharp decrease in DNA concentrations was observed in non-stratified conditions (e.g. February 1995). Most of the DNA concentration was associated with picoparticles (more than 60% of total DNA pool), with a ratio of 1:3:6 for micro-, nano- and picoparticulate fractions, respectively. By contrast, particulate proteins and RNA displayed an average annual ratio of about 1:1:2 for micro-, nano-, and picoparticulate fractions, respectively. Bacterial densities in the Cretan Sea ranged from 1.1 to 8.8 × 10^8 cells l^{-1}. The bacterial DNA contribution to the total DNA pool in the Cretan Sea was on average 40%, but in February 1995 the living DNA fraction accounted for 85% of the total DNA pool. As phytoplankton DNA annually accounted on average for only 17% of the total DNA, we conclude that bacteria play a role of primary importance as a living DNA component in the Cretan Sea.

KEY WORDS: Particulate nucleic acids · Bacterioplankton · Eastern Mediterranean

INTRODUCTION

A large proportion of the particulate DNA in the water column and in the sediments (up to 90% of the total sedimentary DNA pools; Dell'Anno et al. 1998) is associated with dead cells and/or absorbed to particles (i.e. detrital DNA; Holm-Hansen et al. 1968, Winn & Karl 1986). The nature and diagenesis of such detrital DNA is, to a large extent, uncertain (Bailiff & Karl 1991). DNA composition is characterised by a large content of organic N and P relative to organic C (C:N:P = 10:4:1; Maruyama et al. 1993). Therefore, despite the relatively low concentrations of DNA in most marine environments, detrital nucleic acids might represent a potentially important trophic source (Paul et al. 1987), and in extremely oligotrophic environments, where N and P limit heterotrophic metabolism (Zweifel et al. 1993, Danovaro 1998), might become key source molecules. Previous studies have shown strongly decreasing gradients of particulate DNA concentrations from the coast to the open sea (i.e. with changing trophic conditions; Paul & Carlson 1984, Paul et al. 1985, Boheme et al. 1993). In surface oceanic waters, most of the particulate DNA and bacteria are associated with the smallest size fractions of the suspended particles

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Filter blanks were obtained from the 3 different pore size filters used. The detection limit was estimated through analysis of the blanks added with internal standards (final concentrations 0.5, 1.0, 1.5, 2.5, 5.0 µg ml^{-1}). The sensitivity of the method was ±2.0 µg.

Bacterial analyses. Bacterial abundance was determined by epifluorescence microscopy according to Hobbie et al. (1977). Subsamples were stained with Acridine Orange and filtered onto black Nuclepore 0.2 µm filters. Analyses were carried out for 3 to 5 replicates per sample. Two filters per replicate were processed. At least 400 cells were counted from each filter. Additional counts for bacteria attached to suspended particles larger than 2.0 µm were carried out in August 1994. Bacterial densities reported in this study must be considered as the sum of autotrophic and heterotrophic components. Bacterial DNA content was estimated assuming a conversion factor of 2.5 fg of DNA (Simon & Azam 1989) for cells displaying an average size similar to that encountered in this study (modal class 0.065 μm^3, data not shown).

RESULTS

Seasonal and spatial changes in total particulate DNA and RNA concentrations

To point out differences in nucleic acid concentrations and their distribution among the 3 different size classes, data were grouped according to hydrology and water column structure into: (1) surface concentrations (samples collected down to 100 m depth, i.e. particles associated with the surface waters, MAW and CIW); (2) deep water concentrations (>100 m depth, i.e. particles associated with TMW and the CDW). The depth of 100 m was also selected because it corresponded to the maximum depth of the photic layer (Psarra et al. 1996).

Spatial and temporal variations of total particulate DNA and RNA concentrations are illustrated in Fig. 3. Particulate DNA concentrations showed limited temporal changes ranging, on average over the entire data set, between 2.1 ± 1.0 (February 1995) and 3.1 ± 1.4 µg l^{-1} (August 1994). The highest value was measured in

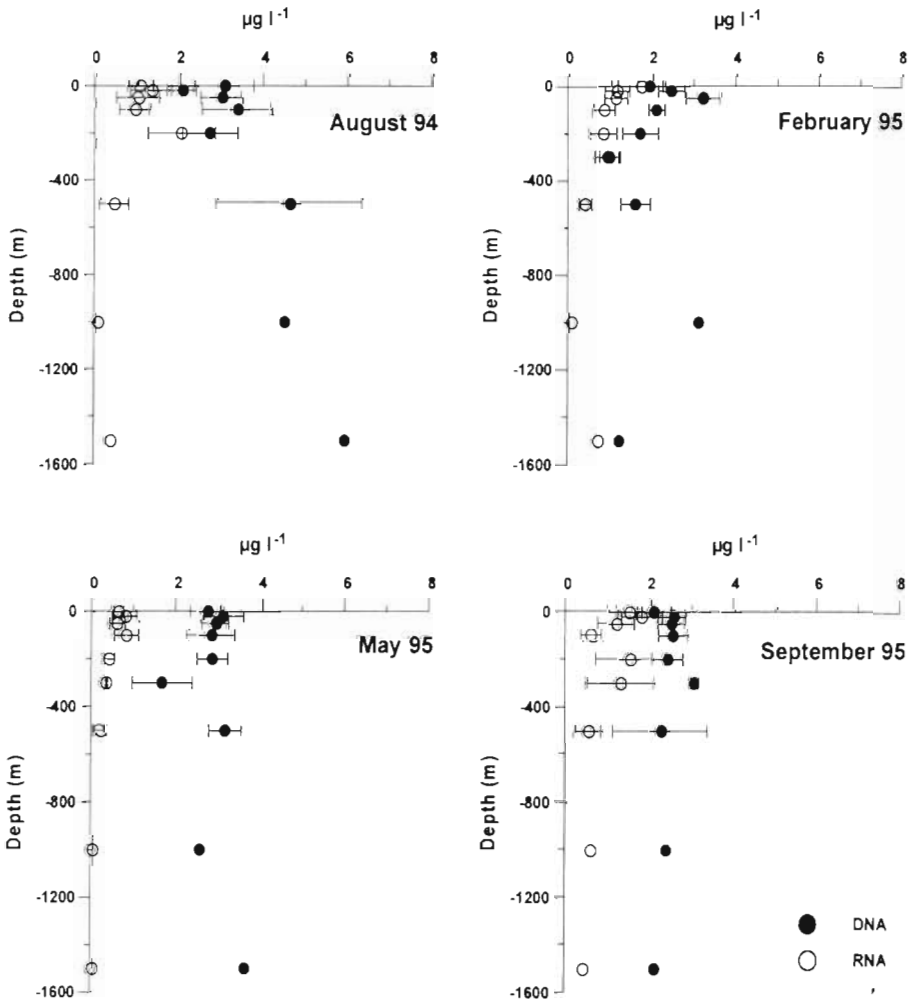

Fig. 3. Vertical profiles of DNA and RNA concentrations in the 4 sampling periods. Reported are average values of all sampled stations at each depth and relative standard errors

August 1994 at Stn D7 (7.9 µg l^{-1} at 500 m depth), while the lowest concentration was reported in February 1995 at Stn D6 (0.38 µg l^{-1} at 200 m depth). Surface DNA concentrations increased by about 4-fold from the coast to the open sea. DNA vertical distributions revealed significantly higher (*t*-test, $p < 0.01$) concentrations in surface waters (5.0 ± 0.7 µg l^{-1}) than in deeper water layers (2.5 ± 0.7 µg l^{-1}). Generally 2 main peaks were observed, one in surface waters and another in deeper water layers. These latter deep DNA peaks were particularly evident in August 1994 and May and September 1995, between 300 and 500 m depth.

RNA concentrations varied in a narrow range, on average over the entire data set, from 0.5 ± 0.5 (May 1995) to 1.2 ± 1.1 µg l^{-1} (September 1995). Integrated RNA concentrations in the surface waters did not show a clear coast to open sea pattern. RNA concentrations displayed a clear decrease with increasing water depth, being significantly higher (*t*-test, $p < 0.02$) in surface waters (2.7 ± 0.8 µg l^{-1}) than in deeper water layers (0.71 ± 0.3 µg l^{-1}).

Nucleic acids associated with different particle sizes

The distribution of total DNA concentrations (expressed as percentages) among the 3 particle size classes is reported in Fig. 4. DNA associated with the picoparticulate fraction (hereafter referred to as picoparticulate DNA) displayed the highest concentrations and was dominant in all sampling periods, accounting on average for 62% of total DNA annually. DNA associated with the nanoparticulate and microparticulate fractions accounted on average for 27 and 11% annually, respectively. In the top 100 m of the water column (Fig. 4a), no significant temporal changes were observed in the relative importance of the 3 size fractions. By contrast, below 100 m depth (Fig. 4b), significant changes ($F = 3.403$, $p = 0.02$) were observed between sampling periods (with picoparticulate DNA ranging from 43 to 70%).

The picoparticulate RNA annually accounted on average for 48% of the total RNA concentrations, followed by nano- (on average 29%) and microparticulate fractions (on average 23%; Fig. 5). The contribution of the microparticulate RNA to the total RNA pool was rather constant in all sampling periods (on average 23%, range 21 to 24%). Therefore, temporal changes in the contribution of the nanoparticulate RNA fraction (in May up to 43%) were balanced by changes in the picoparticulate RNA (minimum value in May, 34%).

Chloroplastic pigment concentrations

Chl *a* concentrations in September 1995 (Fig. 6) were very low (on average 0.06 µg l^{-1} in the top 100 m

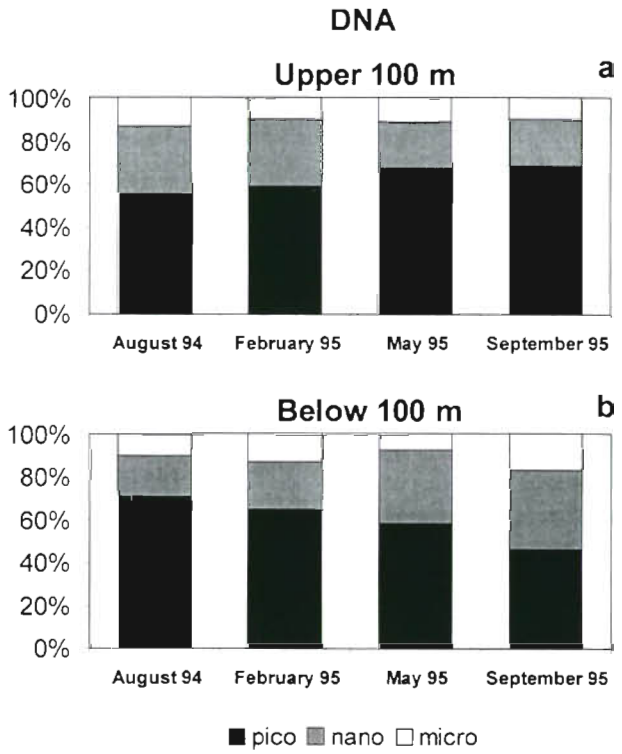

Fig. 4. Relative significance of the pico-, nano- and microparticulate fractions to the total particulate DNA pool (a) in the top 100 m of the water column and (b) below 100 m depth

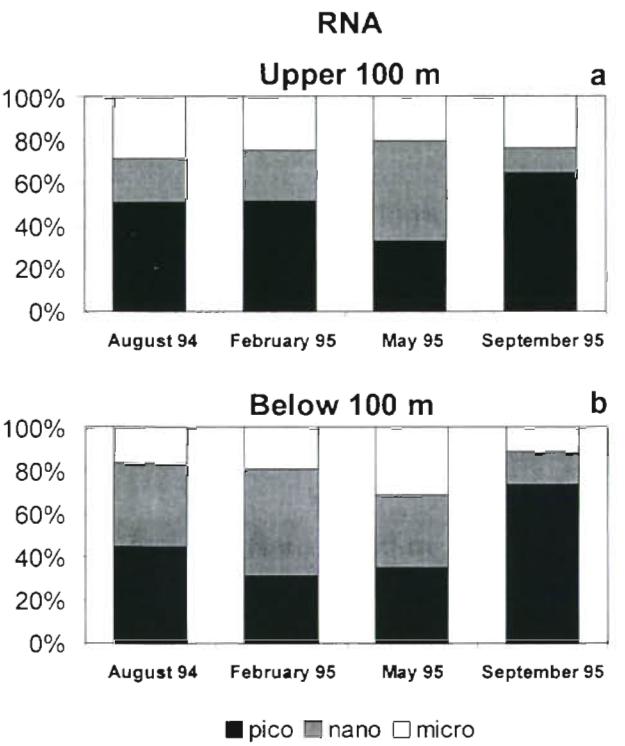

Fig. 5. Relative significance of the pico-, nano- and microparticulate fractions to the total particulate RNA pool (a) in the top 100 m of the water column and (b) below 100 m depth

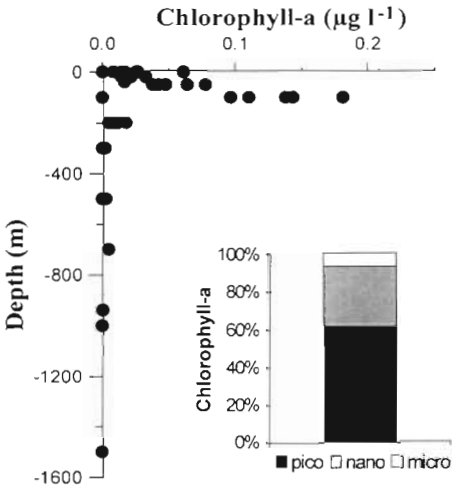

Fig. 6. Vertical profiles of chlorophyll *a* concentrations in September 1995. Inset: contribution of the different size classes to the total chlorophyll *a* content

depth). At Stns D2, D3, D4, D5 and D7 a deep chlorophyll maximum (0.07 to 0.16 µg l^{-1}) was observed at 100 m depth. As our data set was limited to September 1995, we used for comparison chl *a* concentration from synoptic sampling reported by Psarra et al. (1996). The same vertical pattern of chl *a* concentration was consistently and repeatedly reported in all vertical profiles. In the deeper water layers (below 100 m depth) chl *a* concentrations were generally <0.01 µg l^{-1}. The relative contribution of the different size classes to the total chl *a* pools is illustrated in Fig. 6. The largest fraction of chl *a* was associated with picophytoplankton, which accounted, on average, for 62% of the total chl *a* concentration, followed by nano- (on average 31%) and microparticulate chl *a* (on average 7%).

Phytoplankton DNA was estimated in the top 100 m of the water column using the conversion factor reported by Holm-Hansen (1969; 2 µg DNA μg^{-1} chl *a*). In order to provide phytoplankton DNA estimates for the 4 sampling periods the same factor was applied to data on chl *a* concentration summarised from Psarra et al. (1996). Phytoplankton DNA accounted on average for 17% of the total DNA, ranging from 10 to 28% in May and in February 1995, respectively.

Particulate protein concentrations

Spatial and temporal changes in particulate protein concentrations are reported in Fig. 7a. Protein concentrations did not change significantly among sampling periods and their distribution did not show a clear coast to open sea gradient. Protein concentrations decreased significantly (*t*-test, $p < 0.01$) with increasing water depth (on average 40.3 ± 2.3 µg l^{-1} in surface waters and 26.8 ± 3.5 µg l^{-1} in deeper water layers annually). The relative contribution of the different size classes to the total particulate protein pools is illustrated in Fig. 7b. Picoparticulate proteins dominated at all sampling periods, accounting on average for 45% of the total protein pool. Picoparticulate protein contribution to the total pool decreased from August 1994 (on average 55%) to September 1995 (on average 38%), whereas microparticulate proteins showed an opposite pattern, increasing from 17 to 34%. Nanoparticulate proteins did not show clear temporal changes.

Bacterial parameters

Bacterial density ranged from 0.94 to 9.52×10^8 cells l^{-1} (on average 3.6×10^8 cells l^{-1}) and showed large temporal changes, with highest values in February and September 1995 (on average 4.70 and 3.91×10^8 cells l^{-1}, respectively) and lowest values in August 1994 and May 1995 (2.76 and 2.58×10^8 cells l^{-1}, respectively). In August 1994, free living bacteria (0.2 to 2 µm) accounted for the large majority (about 80%) of the total bacterial density and picophytoplankton abundance was about 1 order of magnitude lower than total picoplankton abundance (data not shown). Vertical distribution of bacterial density showed clear decreasing patterns with depth in all sampling periods (Fig. 8), with the highest values in the top 50 m. Bacterial DNA contribution to the total DNA pool (Fig. 9) was annually, on average, 40%, but varied widely between sampling periods and with increasing distance from the coast. Highest bacterial DNA contributions were reported in February 1995 (on average 57%), and lowest in August 1994 and May 1995 (on average 29 and 28%, respectively). Bacterial DNA contribution to the total DNA pool decreased, although not significantly, from 43 ± 11% in the surface waters to 30 ± 12% in the deeper water layers.

DISCUSSION

Spatial and temporal changes in particulate nucleic acids

The Cretan Sea is among the most oligotrophic areas of the world, being characterised by the lowest primary production values of the entire Mediterranean (20 to 60 g C m^{-2} yr^{-1}; Dugdale & Wilkerson 1988, Psarra et al. 1996) and very low inorganic nutrient concentrations (0 to 0.76 µg-at. PO_4 l^{-1} and 0.2 to 0.9 µg-at. NO_3 l^{-1}; N:P > 25; Tselepides et al. 1996), chl *a* content (from 0.1 to 0.26 µg l^{-1}) and phytoplankton abundance (from

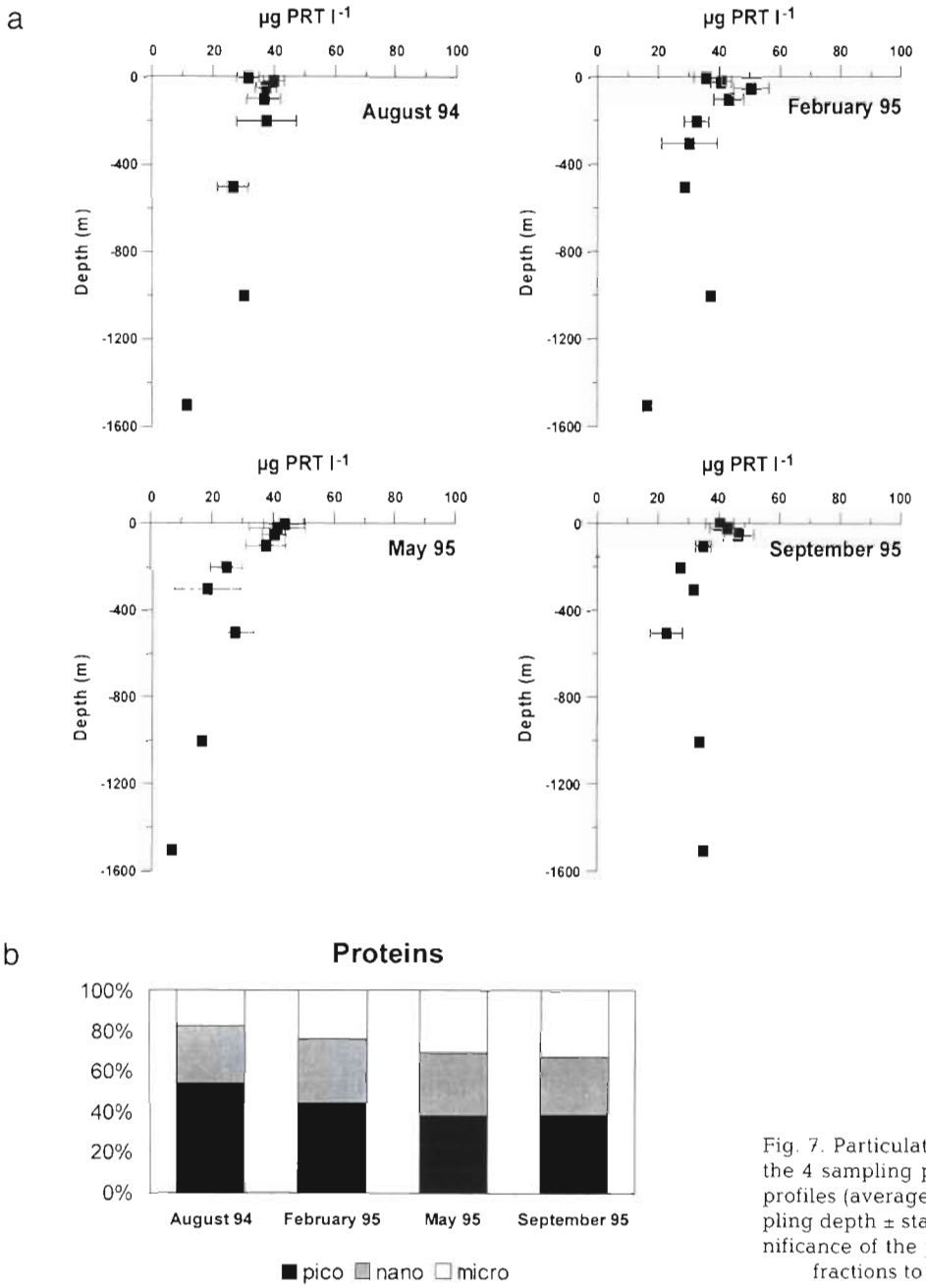

Fig. 7. Particulate protein concentrations (PRT) in the 4 sampling periods. Reported are: (a) vertical profiles (average values of all station at each sampling depth ± standard errors) and (b) relative significance of the pico-, nano- and microparticulate fractions to the total particulate proteins

0.8 to 3.9 × 10^3 cells l^{-1}, Psarra et al. 1996). These conditions are reflected by extremely low particulate organic matter concentrations (4 to 15 times lower than in other areas of the Mediterranean; Danovaro et al. in press a) and reduced POC fluxes (up to 2 orders of magnitude lower than in the Western Mediterranean; Chronis et al. 1996, Danovaro et al. in press b).

Nucleic acid concentrations reported in the present study confirm the oligotrophy of the Cretan Sea. In the top 100 m of the water column, total particulate DNA concentrations were comparable to those found in other highly oligotrophic systems, such as the Gulf of Mexico, but were up to 50 times lower than in estuarine environments (Table 1). On the other hand, particulate RNA concentrations were, together with those reported in offshore waters of the Western Mediterranean, the lowest reported so far in the marine environment (Table 1).

The reduced temporal variability in particulate DNA and protein concentrations (ratio of highest to lowest concentration: 1.3 and 1.1, respectively) reflected the limited temporal changes reported for most water col-

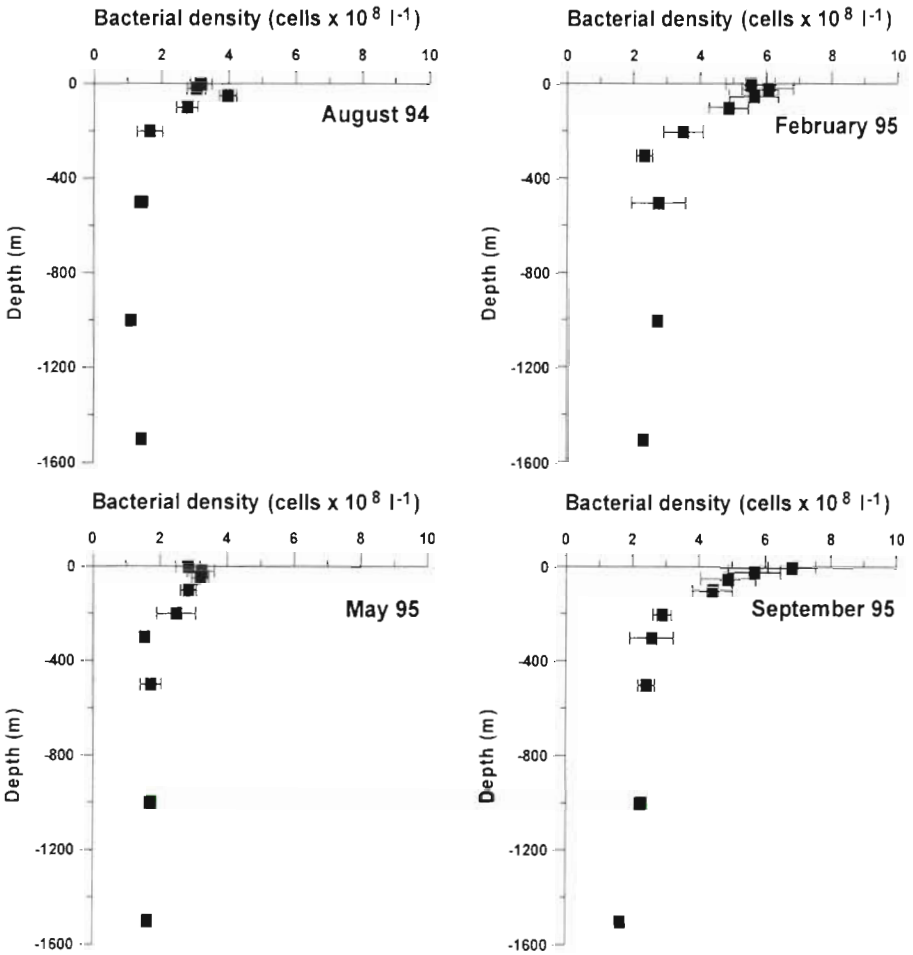

Fig. 8. Vertical distribution of bacterial density in the 4 sampling periods. Reported are average values of all sampled stations at each depth and relative standard errors

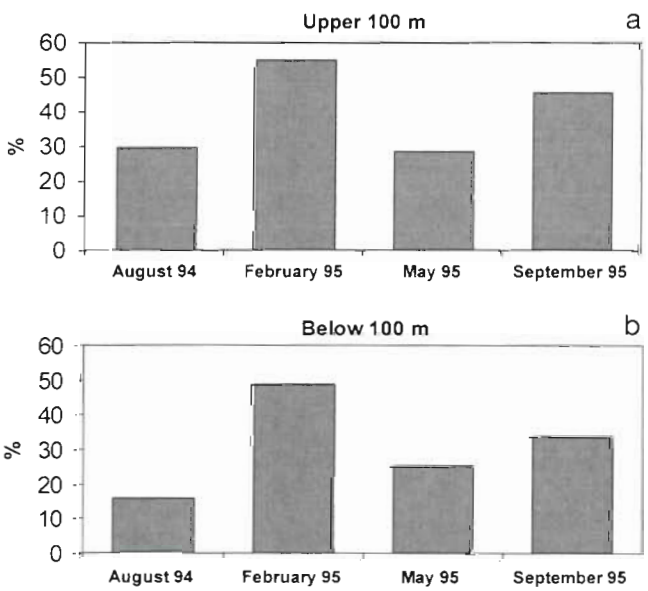

Fig. 9. Bacterial contribution to particulate DNA pools (a) in the top 100 m of the water column and (b) below 100 m depth

umn parameters such as POM concentrations (ratio of highest to lowest value: 1.3; Danovaro et al. in press a). By contrast, RNA concentrations displayed wider temporal changes (with a highest to lowest concentration ratio of 1.9). Similar temporal patterns and relatively higher variability were also reported for chl *a* and primary production values (highest to lowest ratio: 2.1 and 1.6, respectively; Psarra et al. 1996). Moreover, in this study, higher particulate RNA concentrations were found in the top 50 m of the water column, where higher primary production values and phytoplankton densities were reported (Psarra et al. 1996). These data, although based on 4 sampling periods, suggest a coupling between RNA concentrations and autotrophic processes in this system. According to Berdalet & Estrada (1993), who found similar relationships

between primary productivity and RNA concentrations in the Western Mediterranean, higher RNA concentrations accompanying increasing photosynthetic activity might be explained by the increase of RNA concentrations per cell. At the same time, increased RNA concentrations could be due to an enhanced bacterial and/or microheterotrophic growth induced by bloom conditions (Painchaud & Therriault 1989). In the Cretan Sea, bacterial secondary production (BSP) was coupled with primary production (PP) (both PP and BSP displayed highest values in February 1995: 252 and 131 mg C m^{-2} d^{-1} at D2, respectively, for PP and BSP; Psarra et al. 1996). Moreover, BSP values (from synoptic samplings at Stns D2, D4, D7, summarised from Van Wambeke et al. 1996) and picoparticulate RNA concentrations displayed similar spatial patterns (Fig. 10). These results further suggest that RNA concentrations increase as result of enhanced metabolic activity, both autotrophic and heterotrophic.

Previous studies have generally reported a strong decrease in particulate DNA concentrations with increasing water depth: concentrations lower than 1 µg DNA l^{-1} have been consistently reported below 300 m depth (Paul & Carlson 1984, Paul et al. 1985, DeFlaun et al. 1987, Boheme et al. 1993). By contrast, in the Cretan Sea the DNA vertical distribution did not show clear vertical patterns and appeared to be dependent upon physical water column structure. Higher DNA concentrations were generally associated with the high salinity (>38.95) TMW in summer, whereas a sharp decrease in DNA concentrations was observed in non-stratified conditions (i.e. February 1995). High levels of DNA in intermediate waters were also reported in the Sicily Straits between 300 and 500 m depth (Fabiano unpubl. data). The association between the highest DNA concentrations and TMW suggests the presence of an important input of allochthonous DNA into the Cretan Sea, probably deriving from lateral advection.

Table 1. Comparison of particulate DNA and RNA concentrations (µg l^{-1}) in areas characterised by different trophic conditions. NS = nearshore; OS = offshore; E = estuarine; UA = upwelling area; nd = not determined

Area	Location	DNA	RNA	Source
Antarctica				
Bransfield Strait	OS	1.2–5.4	nd	Bailiff & Karl (1991)
Ross Sea	OS	1.0–72.8	<1–170.5	Fabiano et al. (1993)
Terra Nova Bay	NS	13.7–94.6	<2–156.1	Fabiano et al. (1996)
Weddel Sea	NS	1.0–5.3	nd	Karl & Bailiff (1989)
Mediterranean				
W Mediterranean	OS	0.2–2.1	<0.1–6.7	Berdalet & Dortch (1991)
Ligurian Sea (NW Mediterranean)	NS	9.1–23.0	nd	Danovaro & Fabiano (1997)
Ligurian Sea (NW Mediterranean)	NS	8.8–19.9	2.8–59.8	Danovaro et al. (1995)
Catalan Sea (NW Mediterranean)	OS	0.5–2.6	1.2–12.2	Berdalet & Estrada (1993)
NW Mediterranean	OS	1.2–3.3	0.5–3.1	Fara et al. (1996)
Atlantic				
SE Gulf of Mexico	OS	<1–6.2	nd	Boheme et al. (1993)
SE Gulf of Mexico	OS	0.6–8.32	nd	DeFlaun et al.(1987)
SE Gulf of Mexico	NS	10.6–28.7	nd	DeFlaun et al. (1987)
Gulf Stream	OS	2.0–7.0	nd	Holm-Hansen et al. (1968)
Gulf Stream	OS	~8.6	nd	Holm-Hansen et al. (1968)
Gulf of Mexico	NS	<0.1–60.0[a]	<0.1–80.0[a]	Jeffrey et al. (1996)
Atlantic Ocean	OS	~27	nd	Paul & Myers (1982)
Gulf of Mexico and Tampa Bay	NS	10.6–19.6	nd	Paul et al. (1985)
Gulf of Mexico and Tampa Bay	OS	0.2–4.4	nd	Paul et al. (1985)
Oceanic waters				
Pacific Ocean	NS	4.0–30.0	nd	Holm-Hansen (1969)
California	UA	1.0–6.8	3.2–6.3	Mordy & Carlson (1991)
Pacific Ocean	OS	0.8–2.4	nd	Winn & Karl (1986)
Estuarine				
Chesapeake Bay	E	~47	nd	Paul & Carlson (1984)
Tampa Bay	E	17.5–42.6	nd	Paul et al. (1985)
This study				
Cretan Sea (E-Med) Stns D1–D3	NS	0.8–5.2[b]	<0.1–3.8[b]	This study
Cretan Sea (E-Med) Stns D4–D7	OS	0.8–5.9[b]	<0.1–3.4[b]	This study

[a]Data relative to the <0.8 µm particulate fraction
[b]Data relative to the upper 100 m of the water column

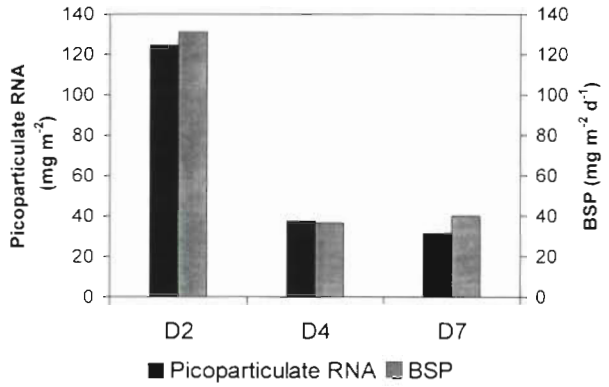

Fig. 10. Bacterial secondary production (BSP) versus picoparticulate RNA concentrations (values are integrated to the top 100 m of the water column) at Stns D2, D4 and D7. Data for BSP were summarised from Van Wambeke et al. (1996)

Nucleic acids in relation to particle size structure

The most evident characteristic of this oligotrophic environment is the dominance of DNA associated with picoparticles (more than 60% of the total DNA pool). The values found here are in agreement with those reported by Paul & Carlson (1984) and by Paul et al. (1985) for oceanic samples (picoparticulate DNA <1 µm accounting for more than 70% of the total DNA pool) and suggest that pico-particulate DNA dominance is a distinctive feature of oligotrophic systems. However, comparisons with previous studies must be viewed with caution. In fact, here picoparticulate DNA was defined according to Sieburth et al. (1978), as particles between 0.2 and 2 µm, while other authors identified the DNA associated with particles using different pore size filters (e.g. Paul & Carlson 1984, Paul et al. 1985: 0.2 to 1.0 µm, Jeffrey et al. 1996: 0.2 to 0.8 µm).

The relative significance of the 3 size classes reported for DNA (with a ratio 1:3:6 for micro-, nano- and picoparticulate DNA, respectively) was exactly the same as that of the chl *a* size fractions. By contrast, both particulate proteins and RNA displayed an average annual ratio of about 1:1:2. Therefore, parameters that might be utilised as indicators of metabolic activity (such as RNA and proteins) display higher relative importance in the larger size classes (nano- and microparticles), whereas DNA (which is likely to be more detrital) is mostly associated with the smallest particles (i.e. with picoparticles).

Previous studies carried out in other oligotrophic areas of the Mediterranean have demonstrated, for all biochemical components, significant temporal changes in the particle size to which they were associated, and such changes were particularly evident during phytoplankton blooms (Fabiano et al. 1994). In contrast, the relative significance of the different size classes of DNA in the present study did not display significant temporal changes in the top 100 m of the water column. The constancy of the DNA distribution among size classes in the photic layer might reflect the limited primary productivity of the system, related to the strong P deficiency (Berdalet et al. 1996, Tselepides et al. 1996). Interestingly, in May and September 1995 the nano- and microparticulate DNA fractions increased significantly below 100 m depth. There are 2 main explanations for this apparent anomaly: (1) DNA produced in the photic layer underwent aggregation during its sinking; (2) DNA concentrations observed under the photic layer originated from other areas being associated with specific water masses (e.g. TMW). This latter explanation is in agreement with evidence reported for the DNA vertical distribution described above.

Bacterioplankton contribution to the total DNA pool

In highly oligotrophic environments, where bacterioplankton largely dominates the system (Cho & Azam 1990), the concentration and relative importance of picoparticulate DNA are likely to be related to bacterial density. Data from the present study confirm this expectation, as bacterioplankton was significantly correlated to the total DNA concentrations ($n = 41$, $r = 0.452$, $p < 0.01$) in February 1995 (when living DNA—i.e. bacterial plus phytoplanktonic DNA—represented about 85% of the total DNA pool), whereas in other sampling periods no significant relationships were found.

In the northwestern Mediterranean, Berdalet & Estrada (1993) found significant relationships between particulate DNA (using the same fluorescent dyes utilised in the present study) and chl *a* concentrations in February, during the phytoplankton bloom, but not in May. They concluded that the lack of correlations in certain periods of the year might be due to an increase in the relative importance of detrital DNA.

Whether picoparticulate DNA is related to picophytoplankton assemblages or to bacterioplankton density is largely dependent upon their relative significance. Bacterial densities in the Cretan Sea (range: 1.1 to 8.8 $\times 10^8$ cells l^{-1}) were rather high and similar to those reported in the surface waters of the Central-North Pacific (range 3 to 15 $\times 10^8$ cells l^{-1}; Cho & Azam 1990) and in the Western Mediterranean (range 3 to 8 $\times 10^8$ cells l^{-1}; Danovaro & Fabiano 1997). Despite the large variability between sampling periods and due to the low nucleic acid concentrations, the bacterial DNA contribution to the total DNA pool in the Cretan Sea was high (on average 40%). This value is higher than the bacterial contribution to the particulate DNA re-

ported for the coastal waters of the Western Mediterranean (22%; Danovaro & Fabiano 1997), but matches exactly the contribution reported for the water surrounding a seagrass system of the Ligurian Sea (42%; Danovaro et al. 1998). Similar bacterial contributions (51%) were reported by Boheme et al. (1993) in the southeastern Gulf of Mexico, and even higher values were reported by other authors for surface oceanic samples (Paul & Carlson 1984, Paul et al. 1985). Discrepancies in the estimates of the bacterial DNA contribution to the DNA pool might be due to the use of different conversion factors. For instance, the conversion factor utilised in this study (2.5 fg DNA cell^{-1}) was about half of that utilised by Boheme et al. (1993) (i.e. 5.66 fg DNA cell^{-1}) and about one-fourth of that estimated by Paul & Carlson (1984) (on average 9.8 fg DNA cell^{-1}).

Paul et al. (1985) estimated the bacterial DNA content (i.e. 5.66 fg DNA cell^{-1}) from a linear regression between DNA content and bacterial counts (both in the fraction <1 µm) and reported an intercept value of 2.66 µg DNA l^{-1}, which was assumed to represent the detrital DNA fraction. Applying the same calculation methods (based on picoparticulate DNA vs bacterial density in February 1995) we found a DNA content per bacterial cell ranging from 1.9 to 3.0 fg DNA cell^{-1} (which is close to the one utilised) and an intercept of 0.51 µg DNA l^{-1} (which indicates that in February 1995, only 18% of the picoparticulate DNA was detrital; sensu Paul et al. 1985). Therefore, we might conclude that bacteria in the Cretan Sea played a role of primary importance as a living DNA component.

As phytoplankton DNA annually accounted on average for only 17% of the total DNA it can be concluded that in the Cretan Sea most of the living particulate DNA was associated with the heterotrophic bacterial component. Thus, as an annual average and for the entire water column, about 43% of the total DNA pool was associated with the microheterotrophic-detrital fraction.

Further studies, extended to the processes of transfer between particulate and dissolved DNA pools, will help clarify the importance of detrital DNA as a potential source of organic N and P for heterotrophic metabolism, especially in oligotrophic systems, where these nutrients might be limiting.

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