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^{14}C-glucose uptake and ^{14}C-CO_2 production in surface microlayer and surface-water samples: influence of UV and visible radiation

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ABSTRACT: Sea-surface microlayer and surface water samples, collected in the Bay of Marseilles (France), were compared for ^{14}C-glucose incorporation and catabolism under natural radiation by means of incubation in glass and quartz tubes as compared to standard dark bottles. Beforehand, possible interference by phytoplankton during light exposure was investigated for one sample of each type by means of 1 µm size-fractionation and/or cycloheximide treatment. Though size-fractionation appeared to be unsuitable for the surface film sample, the cycloheximide experiment data suggested that the recorded activity was primarily due to bacteria. In a set of surface microlayer and associated underlying water samples, the former exhibited higher (ca 10-fold) heterotrophic activity. For both kinds of samples, a decrease in ^{14}C-CO_2 production (by 48 %) was observed in glass tubes but no difference was found between glass and quartz tubes. Since the remaining activity (> 50 %) could have been underestimated due to removal of produced ^{14}C-CO_2 by photoautotrophs during light exposure, this result is evidence of the extent of heterotrophic activity at the sea-air interface.

INTRODUCTION

Surface films are well known as sites of intensive accumulation of particulate and dissolved organic matter (for reviews see Liss 1975, Sieburth 1983). The accumulation of organic matter in association with greater abundances of living organisms induces enhanced biological activity, mostly heterotrophic-dominated (Harvey & Young 1980, Dahlbäck et al. 1982, de Souza-Lima & Chretiennot-Dinet 1984, Mimura et al. 1988). Therefore, this biologically active boundary layer may have an important effect on gaseous exchanges, particularly of CO_2, at the sea-air interface (Sieburth 1983).

Moreover, regarding the CO_2 budget, antagonistic processes – photosynthesis and respiration – are involved. Thus an attempt should be made to assess the relative importance of photosynthetic and respiratory mechanisms, or, roughly, phytoneustonic and bacterioneustonic responses.

The surface-film environment is subject to a high level of radiation, particularly UV radiation, which may affect to a greater or lesser degree part of the microneustonic activity. Studies conducted on this topic (see Norkrans 1989, Romano 1989) have reported on the characteristics of organisms present in surface film, such as their pigmentation and DNA with a high percentage of G-C pairs, which may represent responses to this detrimental factor.

The present study is focused on heterotrophic responses (^{14}C-glucose uptake and catabolism) of the microflora in natural surface water and sea-surface microlayer samples to solar radiation. The radioisotope technique was used to measure both the whole incorporated fraction and the production of respired ^{14}C-CO_2 (dissolved and/or ionic species), which is a product of biological transformation of the substrate. Possible interference by phytoplankton (e.g. ^{14}C-CO_2 recycling) was investigated beforehand.

MATERIALS AND METHODS

Sampling. Samples were collected in the Bay of Marseilles (northwestern Mediterranean Sea). Surface microlayers were collected in slicks using a Harvey's skimmer (Harvey 1966), and associated underlying water by pumping at 0.5 m depth. Sampling was

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always performed at dawn between 05:00 and 06:00 h GMT.

Heterotrophic activity measurement. Uptake and catabolism of a labelled organic substrate were measured according to the method of Hobbie & Crawford (1969). A slight modification of this method was necessary because of the particular characteristics of the surface microlayer (Garabétian 1990): D-[U-^{14}C]glucose (295 mCi mmol^{-1}; Commissariat à l'Energie Atomique) was diluted into cold glucose to reach a concentration of 100 µg C ml^{-1} with a specific activity of 0.014 µCi mmol^{-1}. Added substrate (100 µg C l^{-1}; see following paragraph) was monitored by measuring (1) ^{14}C incorporation in the particulate fraction collected on 0.2 µm pore size membranes (Sartorius), and (2) oxidation into ^{14}C-CO_2, which was liberated by acidification (0.5 ml H_2SO_4, 10 N) and then by blowing in gaseous N_2; the trapping agent used was phenetylamine. Both fractions were counted by liquid scintillation (10 ml ACS®, Amersham, USA), with quenching correction by means of 2 distinct quenching curves.

Experimental method. Labelled substrate was added to 100 ml subsamples (2 replicates) placed in bottles for dark incubation and in glass and/or quartz tubes for incubation under natural radiation (from 09:00 to 13:00 h GMT) using an in situ incubation device as described in Carlucci et al. (1985). The added concentration of glucose (100 µg C l^{-1}) might represent a high input as compared to the natural concentration (Garabétian 1990); thus, recorded activities must be considered as measurements of potential heterotrophic activity in a saturated concentration of substrate. The surface:volume ratio of tube-incubated subsamples was closer than that of bottle-incubated subsamples to the ratio of surface films in situ; thus, tube-incubated subsamples represented conditions of light incubation closer to natural conditions. In addition, glass (UV-opaque) and quartz tubes were used to distinguish between light intensity and UV effects. In one case, glass tubes masked with adhesive film (Mecanorma sheet, allowing 50% of transmission) were used to simulate non-inhibiting light conditions.

Six samples of sea-surface microlayer and associated surface waters (SF-1 to 6 and BW-1 to 6, respectively) were analysed for their response to glass and quartz tube incubation as compared to standard dark bottle incubation. In one case, by means of size-fractionation (Nuclepore, 1 µm) and/or cycloheximide inhibition (Sigma Chemicals; added concentration: 1 mM), an attempt was made to control the possible influence of phytoplankton. Cycloheximide is an inhibitor of eucaryotic cell protein synthesis (Vazquez 1974). It was used to avoid errors linked with particle size-fractionation in sea-surface microlayers (Laborde et al. 1986). For natural samples, the specificity of cycloheximide in inhibiting photosynthetic organisms is limited by the

Table 1. Particulate organic matter of surface film (SF) and bulk water (BW) samples: particulate organic carbon (POC) and nitrogen (PON), bacterial cell counts (Bact.) and chlorophyll *a* (Chl *a*)

Sample	Date	T (°C)	POC (mg l^{-1})	PON (mg l^{-1})	Bact. (10^9 l^{-1})	Chl *a* (µg l^{-1})
SF-1	May 1990	21.1	5.098	0.483	7.7	2.366
SF-2	Oct 1989	18.0	18.391	1.058	5.1	12.270
BW-1	May 1990	20.0	0.212	0.022	1.3	0.366
BW-2	Jun 1989	21.5	0.234	0.027	0.4	0.178
SF-3	Jun 1990	21.0	6.061	0.666	2.1	4.579
BW-3	Jun 1990	21.0	0.242	0.023	0.7	0.312
SF-4	Jun 1990	20.9	4.524	0.323	1.4	1.439
BW-4	Jun 1990	20.9	0.253	0.025	0.8	0.277
SF-5	Jul 1990	16.5	4.622	0.317	6.7	1.932
BW-5	Jul 1990	16.5	0.280	0.020	1.0	0.264
SF-6	Jul 1990	17.2	18.066	1.256	5.0	1.189
BW-6	Jul 1990	17.2	0.110	–	1.1	0.059
SF						
Mean		–	9.460	0.684	4.7	3.963
SD		–	6.814	0.393	2.5	4.246
n		–	6	6	6	6
BW						
Mean		–	0.222	0.023	0.9	0.243
SD		–	0.059	0.003	0.3	0.109
n		–	6	5	6	6

occurrence of cyanobacteria, as was pointed out by Wheeler & Kirchman (1986).

Complementary analyses. Prefiltered (150 µm) subsamples of each sample were taken for (1) bacterial counts according to Hobbie et al. (1977); (2) chlorophyll *a* measurement by the HPLC method of Mantoura & Llewellyn (1983) as modified by de la Giraudière et al. (1989); (3) particulate organic carbon and nitrogen measurement on a Perkin-Elmer elementary analyser. Temperature was measured by means of a calibrated thermistor.

RESULTS

Table 1 shows measured values for particulate organic matter content and temperature. Surface microlayer samples exhibited high chlorophyll *a* concentrations and bacterial counts as compared to those in underlying bulk water (0.5 m depth), and on the whole contained a higher particulate organic fraction. This has been widely reported in the literature, particularly the variability in enrichment from sample to sample, which explains the high standard deviations recorded in surface film samples. No differences in temperature were observed between associated surface-film and bulk-water samples, although Constans et al. (1984), using a more specific sensor, have recorded differences ranging from −0.6 to +1.2 °C between the microlayer and water from 0.5 m, which can be considered as negligible for biological processes.

Results from cycloheximide and size-fractionation experiments conducted on SF-1 and BW-1 are presented in Fig. 1. Bacterial densities of 1.7 and 0.4 × 10^9 cells l^{-1} were found for, respectively, surface microlayer and underlying water samples in the < 1 µm fraction. For each sample, a comparison of the total activity response in natural, cycloheximide-treated and < 1 µm fraction subsamples with respect to the 4 kinds of incubation glassware was done using the Friedman non-parametric 2-way analysis of variance (Siegel 1956). No significant differences were found between the matched subsamples in bulk water samples (N = 4, $k = 3$, $\chi^2_r = 2$, $p = 0.431$), indicating that neither cycloheximide nor filtration had significant effects relative to incubation conditions (dark bottles, unmasked or masked glass tubes and quartz tubes). On the other hand, in the surface microlayer sample the measured activity in the different vessels seemed to be strongly dependent on the treatment employed (N = 4, $k = 3$, $\chi^2_r = 10$, $p = 0.0046$). A considerable drop in activity (by > 90 %) was observed in the < 1 µm fraction as compared to the natural sample. The relative effect of treatment, calculated as [100 × (Treated − Natural)/Natural], ranged from −37 % (masked tube, SF-1) to +54 % (quartz tube, BW-1) for cycloheximide, and from −99 % (masked tube, SF-1) to +21 % (quartz, BW-1) for size-fractionation. For both SF-1 and BW-1 samples an important negative relative effect of treatment was observed in masked tubes.

Mean values (2 replicates) of ^{14}C-glucose utilization in surface microlayer and underlying (0.5 m) water samples are presented in Table 2. Comparison by the Mann-Whitney U-test (Siegel 1956) of total activity (Σ = uptake + catabolism, in µg C l^{-1} h^{-1}) showed a highly significant enhanced response in surface film samples (mean = 2.698, SD = 2.024, n = 5) as compared to bulk water samples (mean = 0.302, SD = 0.087, n = 6), both being incubated in standard dark bottles ($U = 0$, $n_1 = 5$, $n_2 = 6$, $p = 0.002$). The enhance-

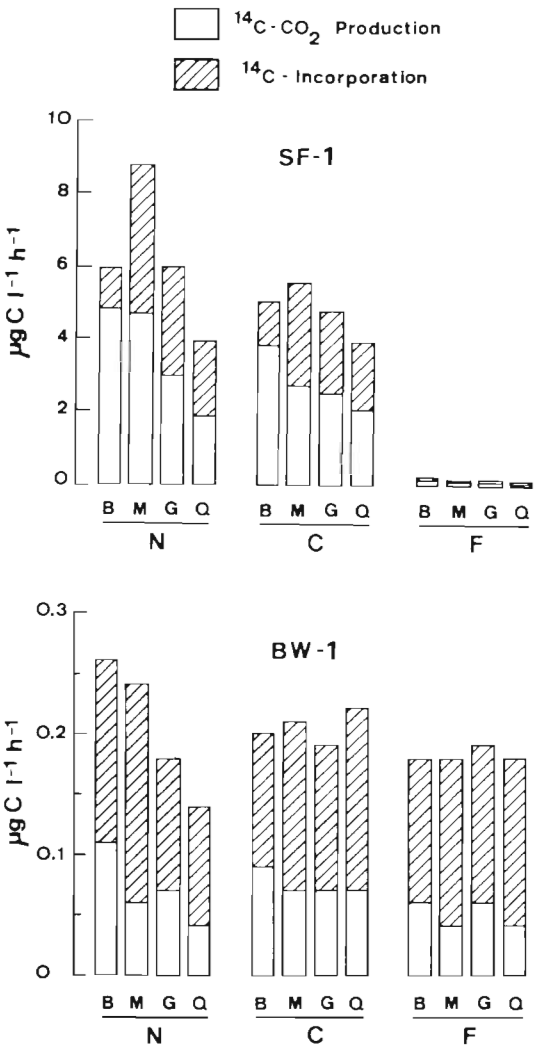

Fig. 1. ^{14}C-glucose utilisation in natural (N), cycloheximide-treated (C) and 1 µm size-fractionated (F) subsamples of surface film (SF-1), and surface (0.5 m) water (BW-1) samples incubated in dark bottles (B), in masked (M) and naked (G) glass tubes, and in quartz tubes (Q)

Table 2. Surface microlayer (SF) and bulk water (BW) samples. Mean values (2 replicates) of ^{14}C-CO^2 production (CO_2), ^{14}C incorporation (Inc.) and total activity (Σ = CO_2 + Inc.), in $\mu gC\ l^{-1}\ h^{-1}$, for incubations performed in situ at 0 m depth in glass and quartz tubes as compared to standard dark bottle incubation

Sample	Dark bottles			Glass tubes			Quartz tubes		
	CO_2	Inc.	Σ	CO_2	Inc.	Σ	CO_2	Inc.	Σ
SF-1	4.788	1.142	5.930	2.939	3.025	5.964	1.874	2.058	3.932
SF-2	2.694	0.194	2.888	0.899	0.124	1.023	1.000	0.149	1.149
BW-1	0.109	0.150	0.259	0.068	0.108	0.176	0.042	0.102	0.144
BW-2	0.174	0.156	0.330	0.045	0.032	0.077	0.030	0.028	0.058
SF-3	–	1.066	–	0.555	0.196	0.751	1.304	0.235	1.539
BW-3	0.261	0.190	0.451	0.076	0.115	0.191	0.070	0.147	0.217
SF-4	0.480	0.154	0.634	0.305	0.125	0.430	0.375	0.184	0.559
BW-4	0.141	0.141	0.282	0.118	0.177	0.295	0.096	0.174	0.270
SF-5	0.363	1.057	1.420	0.299	1.433	1.732	0.350	1.671	2.021
BW-5	0.070	0.233	0.303	0.079	0.196	0.275	0.071	0.175	0.246
SF-6	1.258	1.362	2.620	0.545	1.704	2.249	0.666	1.429	2.095
BW-6	0.057	0.132	0.189	0.065	0.121	0.186	0.063	0.134	0.197

ment factor ranged from 2 (SF-4 vs BW-4) to 14 (SF-6 vs BW-6) for associated samples. The same statistically significant enhancement of total activity in surface microlayer as compared to underlying water was observed in glass-tube- ($U = 0$, $n_1 = n_2 = 6$, $p = 0.001$) and/or quartz-tube- ($U = 0$, $n_1 = n_2 = 6$, $p = 0.001$) incubated sub-samples.

Concerning total activity on a cell basis [expressed in $\mu g\ C\ (10^9\ cells)^{-1}\ h^{-1}$], no statistical difference was found between surface film samples (mean = 0.57, SD = 0.20, n = 5) and underlying waters (mean = 0.27, SD = 0.22, n = 6) incubated in dark bottles.

The Wilcoxon matched-pairs signed-ranks test (Siegel 1956) was used to test for differences between dark-bottle- and glass-tube-incubated subsamples, pooling SW and BW samples. The calculated differences are presented in Table 3. Given the mean coefficient of variation of our measures (ca 15 %), differences of matched pairs within this range were considered to be null. No significant difference was found for total activity between dark-bottle- and glass-tube-incubated subsamples ($N = 8$, $T = 7$, $p > 0.05$); however, when ^{14}C-CO_2 production was taken into account irrespective of ^{14}C incorporation, a highly significant drop in activity was found in glass tubes as compared to dark bottles by the same test ($N = 9$, $T = 0$, $p < 0.01$). The mean percentage of the drop in ^{14}C-CO_2 production related to glass tube incubation was quite similar for surface microlayer and surface water samples (48 and 50 % respectively).

The same procedure was used in order to compare glass- and quartz-tube-incubated subsamples (Table 3). No statistically significant difference was found between the 2 kinds of tubes for either total activity ($N = 5$, $T = 7$, not applicable) or ^{14}C-CO_2 production

Table 3. Comparison of ^{14}C-CO_2 production and total activity (Σ = uptake + catabolism) between dark bottles and glass tubes (B – G) and between glass and quartz tubes (G – Q), showing differences of matched pairs for surface film (SF) and underlaying bulk water (BW) samples

Sample	B – G		G – Q	
	Σ	CO_2	Σ	CO_2
SF-1	0	+1.849	+2.032	+1.065
SF-2	+1.865	+1.795	0	0
SF-3	–	–	−0.788	−0.749
SF-4	+0.204	+0.175	−0.129	−0.070
SF-5	−0.312	+0.064	0	0
SF-6	+0.371	+0.713	0	−0.121
BW-1	+0.083	+0.041	+0.032	+0.026
BW-2	+0.253	+0.129	+0.019	+0.015
BW-3	+0.260	+0.146	0	0
BW-4	−0.053	+0.023	0	+0.022
BW-5	0	0	0	0
BW-6	0	0	0	0

($N = 7$, $T = 15$, $p > 0.05$), although some samples (e.g. SF-3; Table 3) exhibited an enhancement of activity recorded in quartz tubes as compared to glass tubes in surface microlayer samples.

DISCUSSION

Our results show, firstly, a high variability in surface-microlayer responses for all measured parameters. This has already been observed by Carlson (1982) and Romano & Laborde (1987). Our samples must therefore be considered as displaying a set of different sea-surface features irrespective of seasonal variations. Each of these microlayers exhibited unique charac-

teristics which might be related to variability in salinity and pollutants as well as irradiance. This should be kept in mind when cycloheximide inhibition and size-fractionation experiments are discussed.

Firstly, as compared to underlying bulk waters, the use of size-fractionation appears to be unsuitable for analyzing surface film samples, as observed by Laborde et al. (1986). This can be explained by a higher bacterial adsorption to > 1 µm size particles, which could be related to enhanced physico-chemical interactions between bacteria and particles in this highly loaded (see POC values in Table 1) environment (Norkrans 1989). Like Harvey & Young (1980), who found that 90% of bacteria were bound to particles, we observed that the removal of cells related to 1 µm filtration represented 78% of the initial cell count and affected more than 90% of the activity.

Possible interference by phytoplankton included passive ^{14}C-incorporation (Wright & Hobbie 1966, Williams & Askew 1968) and $^{14}CO_2$ recycling induced by light. Thus, in subsamples incubated in light (tubes), the possible occurrence of photoautotrophic ^{14}C-CO_2 recycling could have been a source of underestimation of heterotrophic ^{14}C-CO_2 production as compared to subsamples incubated in dark bottles. This might explain why, in the second experiment based on a set ($n = 6$) of surface film and associated underlying water samples, the difference between dark bottles and glass tubes was not significant when total activity was taken into account, and significant when only ^{14}C-CO_2 was considered.

Radiation conditions simulated in masked glass tubes should be non-inhibiting for phytoplankton and should thus emphazise phytoplankton interference as compared to that in dark bottles and/or unmasked tubes. The fact that a strong negative effect of cycloheximide treatment was observed for both samples in these tubes provides evidence for the effectiveness of the treatment. Though cycloheximide does not affect cyanobacteria, the recorded percentage of the cycloheximide-resistant activity (from 57% to > 100%) in both dark and light conditions for the 2 samples suggested that the activity observed was primarily due to bacteria.

Thus, the drop in ^{14}C-CO_2 production (by ca 48%) recorded for both samples in glass tubes as compared to dark bottles could be related to (1) interference by phytoplankton and/or (2) the deleterious effect of high radiation levels on heterotrophic activity.

For both surface microlayer and underlying water samples, no differences were found between quartz- and glass-tube-incubated subsamples. Mitamura & Matsumoto (1981), de Souza-Lima (1989) (for phytoplankton) and Carlucci et al. (1985) have found similar results, suggesting an adaptation to UV radiation. One possible reason for this is the occurrence of adapted strains as observed by Tsyban (1971) and Hermansson et al. (1987), who concluded that the higher frequency of pigmented bacteria they had observed in surface films could be a response to solar radiation.

Despite the high variability in ^{14}C-CO_2 production rates recorded from sample to sample in surface films, an enhancement was always observed as compared to underlying waters. On a cell basis, comparable mean values can be calculated for both kinds of samples. But from paired BW and SF samples, the recorded enhancement of heterotrophic activity was not systematically equal to the enhancement of bacterial density, which suggests either the occurrence of a partly inactive fraction within the counted cells and/or the inclusion of cyanobacteria in the epifluorescent cell counts. On the whole, light exposure did not affect the differences recorded between the 2 kinds of samples (SF and BW), which were ca 1 order of magnitude on a per liter basis.

Given that the percentage of activity remaining after light incubation (50%) was quite similar for both film and bulk water samples, this could suggest that the selective pressure related to irradiance acts on both kinds of samples. As care was taken to carry out sampling (at dawn) and incubations (around midday) at the same period of the day for each sample, we can assume that the responses do not represent previous short-term adaptations to the conditions of light prevailing at the interface just before sampling. This phenomenon might otherwise have increased differences of response between the 2 kinds of samples. Sieracki & Sieburth (1986) have mentioned the possible role of sunlight (particularly UV-A wavelengths) as a factor controlling diel cycle by inducing a growth delay. Thus, in terms of biological activity, the 'past' or 'history' of the sampled microlayers could be a possible source of variation, for it takes into account both the accumulation of matter and also the degree of previous biological adaptation. This could explain, regarding heterotrophic activity, why the conclusions of Dietz et al. (1976), Kjelleberg & Håkansson (1977) and Bell & Albright (1982), who found lower activity in surface microlayers as compared to underlying water, conflict with our results, which suggest, as did those of Williams et al. (1986) and Mimura et al. (1988), that in surface films, metabolizing cells are more active than in underlying waters because they are better adapted.

This experiment provides evidence for an enhanced heterotrophic activity in natural slicks as compared to underlying water, even after sunlight exposure in glass and quartz tubes. Since the hypothesis that photoautotrophs remove heterotrophic CO_2 production during light exposure cannot be rejected, the effect of sunlight exposure as measured by the drop in CO_2 production could have been overestimated. Moreover, the remaining activity (more than 50%) appeared to be unaffected by UV radiation. The occurrence in surface film of

better-adapted organisms reported in previous studies could explain these results. Nevertheless, this is evidence of the extent of heterotrophic activity at the sea-air interface and supports the hypothesis of an active boundary layer which may play a role in gaseous air-water exchanges, particularly for respired CO_2.

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