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The Cousteau Society

April 16, 1991

Dear Katy:

The neuston workshop report just arrived. I copied salient pages for you to browse through. Even if this doesn't address your specific interests, it might provide some contacts who would know more about what is being done currently.

Hope the ozone-CFC package I mailed finally reached you. The April Log has a good article by Barbara Prezelin explaining how the UVB affects plankton.

Let me know if we can help further.

Yours truly,

PROCEEDINGS OF THE WORKSHOP ON
THE SEA-SURFACE MICROLAYER IN
RELATION TO OCEAN DISPOSAL
December 18-19, 1985
Airlie, Virginia

October 1986

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EXECUTIVE SUMMARY

A workshop was convened to identify information needs concerning the sea-surface microlayer (SSM) that would assist the U.S. Environmental Protection Agency in the ocean disposal regulatory process. Twenty-two participants from a wide diversity of disciplines, including technical experts on the sea-surface microlayer, identified and ranked over 30 relevant information needs. Top priority was given to determining: 1) residence times for components in the SSM and their alteration by inputs from disposal, 2) the importance of the SSM as a biological habitat, and 3) the toxicity of disposal wastes applied in a realistic way to the SSM. A research and monitoring plan based on a decision-tree and containing short- and long-term tasks was outlined. The first step involves sampling and analysis of the SSM during research ocean disposal activities. Measured SSM contaminant concentrations would then be compared with data on toxicity to surface organisms such as neustonic (floating) fish eggs.

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INTRODUCTION

The sea-surface microlayer (SSM) (upper millimeter or less of the water surface) is a vital biological habitat. Neuston form an important element of the ecosystem in subtropical and boreal offshore waters (Hempel and Weikert 1972). Many fish and shellfish, including cod, sole, flounder, hake, anchovy, crab, and lobster, have egg or larval stages that develop in this layer. More information is available from nearshore studies; however, available data suggest that, even far off the east and west coasts of North America, ichthyoneuston concentrate at the surface at certain times (Ahlstrom and Stevens 1975; Grant et al. 1979). For example, neuston net tows found densities of larvae of Pacific saury over 250 miles offshore that were equal to or greater than densities nearshore (Kendall and Clark 1982). Contaminants from atmospheric deposition, urban runoff, wastewater outfalls, industrial point sources, and ocean dumping enter coastal waters and partition. A large portion of these contaminants associate with suspended particles and deposit in the bottom sediments. However, contaminants that have low water solubility or that associate with floatable particles concentrate at the air-water interface. Consequently, high concentrations of toxic PAHs, PCBs, and metals have been found in the surface microlayer at some coastal sites (Hardy et al. 1985, 1986). At present, the spatial distribution of this SSM contamination remains unknown. Also, the relative contribution that incineration or disposal of wastes at sea may make to SSM contamination remains to be assessed.

An initial assessment of the potential impacts of ocean disposal suggested a need for further information on the fate and effects of wastes vis-a-vis the SSM (Hardy 1985). In order to meet this need, the U.S. Environmental Protection Agency (EPA) convened a workshop of technical experts, science advisors and agency representatives (see Appendix A). This report contains the technical papers presented at the workshop and summarizes the proceedings, results, and recommendations of this workshop.

SYNOPSIS OF TECHNICAL PRESENTATIONS AND DISCUSSIONS

Darrell Brown (EPA) provided a brief summary of the background and rationale that led to the convening of the workshop. The need for the workshop became apparent following comments from both the public and the EPA Science Advisory Board concerning the sea-surface microlayer as an interface that could play a significant role in the transport and concentration of materials from waste disposal at sea.

Frank Herr, Office of Naval Research (ONR), then provided a description of a new research initiative on the SSM at the ONR. The ONR plans to sponsor a number of research projects to examine the biological, chemical, and physical processes that influence the optical properties of the SSM. Particular emphasis will be on how processes such as the production of biogenic organic films modify infrared and microwave remote sensing signals. He encouraged a coordination and sharing of information between different SSM research programs to provide a better understanding of the basic processes involved at the air-sea interface.

Physical processes of the SSM were described by Duncan Blanchard (SUNY-Albany). Breaking waves, which on average cover about 1% of the world ocean, inject bubbles into the water column. As they rise to the surface, the bubbles scavenge surface-active material from the water column. When they reach the surface and burst, this material becomes concentrated on the seawater aerosol that is ejected into the atmosphere.

Dave Carlson (Oregon State University) emphasized that basic research on the natural organic chemistry of the SSM is a prerequisite to understanding how contaminants from ocean disposal will behave. Observed chemical enrichments of the SSM reflect a balance between diffusive and advective input processes and removals by mixing, chemical alteration, or evaporation. Materials added to the SSM from ocean disposal will likely partition in ways similar to naturally occurring compounds. Enrichments are often still observed at sea states of Beaufort 4 or even 5, but above this, there are no reliable measurements.

Recent studies on physical mixing processes in the upper water column were described by Robert Weller (Woods Hole Oceanographic Institution). A number of

innovative approaches and instrumentation were used to quantify the current velocities in the region of Langmuir cells. Weather conditions frequently lead to the formation of circulation patterns (Langmuir cells) with strong horizontal surface convergences and vertical downwelling. The depth of these cells may vary between a few centimeters to the base of the mixed layer. Bubbles and surface particles (and possibly associated contaminants) may follow these current patterns. However, sufficient information is not yet available to provide accurate predictions of the formation and strength of these cells.

Research conducted by Angelo Carlucci (University of California, San Diego), suggests that, contrary to earlier concepts of the SSM as a photo-inhibited and biologically inactive region, microbes occur in high densities in the SSM and are generally quite metabolically active. In oligotrophic waters, amino acid utilization rates by surface-film microheterotrophs were greater than that of subsurface (10 cm) populations, whereas in eutrophic waters there was little difference in these rates. Although there were generally fewer metabolizing cells in surface microlayers, populations had a greater activity per cell.

Results of a number of studies by John Hardy (Battelle) conducted over the past 15 years indicate that the SSM frequently contains dense populations of microalgae (phytoneuston). The species populations of these communities are distinct from the phytoplankton below the microlayer. Photosynthetic carbon reduction per unit volume is often 20 to 50 times greater in the SSM than in the bulk water. Greatest densities and activities are found in visible surface slicks.

George Grant, Virginia Institute of Marine Science (VIMS), provided a synopsis of studies conducted by VIMS on the distribution of zooneuston off the mid-Atlantic coast of the United States. Fish eggs and larvae and decapod larvae, including those of commercially important species, comprise a significant portion of the neuston community of the mid-Atlantic shelf area. Neuston communities in offshore waters also warrant consideration. Contamination of the sea surface could impact certain unique species as well as organisms that migrate to the surface at certain times of day to feed.

Concentration of organic contaminants such as PCBs in the SSM was discussed by Philip Meyers (University of Michigan). Hydrophobic organic contaminants fractionate between the SSM and the subsurface water. Atmospheric inputs to the water surface can be important in leading to enrichments. A large portion of PCBs in the microlayer reside in the particulate phase.

Recent studies on the toxicity of SSM contaminants were presented by John Hardy (Battelle). Sea-surface microlayer samples were collected from stations in Puget Sound and returned to the laboratory. Fertilized sole eggs were exposed to these SSM samples during embryonic development and larval hatching. Approximately half of the samples tested showed high concentrations of metal and/or PAH contamination. These same samples caused reductions in the hatching success of the eggs. Current work examined the spatial distribution of surface contamination in Puget Sound.

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Measurements of Biomass and Activity of Neustonic Microorganisms

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Microlayer samples from a coastal marine area near Marseilles (France) collected in 1979 and 1980 have been analysed for POC, PON, chlorophyll *a*, ATP, cell counts, carbon fixation and in some cases for heterotrophic activity. Comparison of microlayer data with those of underlying water showed in most cases enrichment of organic matter and microorganisms in the surface microlayer. Carbon fixation values were comparable to those observed at 0-50 m except in the slicks, where phytoneustonic activity was higher than that of the underlying phytoplankton. Though total heterotrophic activity was higher in the surface film, the turnover time was not significantly different in both microlayer and underlying water. Our data show that enrichment is highly dependent on sea conditions; whenever slicks are present, the surface film seems to function like an eutrophic system, including active living material, although detritus is regularly present in large amounts.

Introduction

Considering the whole marine environment, comparatively little is known about biological processes at the surface microlayer. Manzi *et al.* (1977) pointed out that the surface microlayer must be considered as a biotically important and still unknown component of aquatic ecosystems.

Comparison of the sea surface microlayer with the underlying water has demonstrated higher concentrations of organisms and detrital material in the surface microlayer. Abundant phytoneustonic populations, consisting mainly of the dinoflagellate *Prorocentrum micans* have been reported off La Jolla, California (Harvey, 1966) and in the sea area near the island of Sylt (Brockmann *et al.*, 1976; Wandschneider, 1979). Large number of heterotrophic microneuston (Sieburth, 1963, 1971; Sieburth *et al.*, 1976) and zooneuston organisms (Zaitsev, 1971; Champalbert, 1975) have also been observed in the microlayer surface. Though enrichment at the uppermost layer of aquatic ecosystems has been observed in many studies, this was not the case in a recent bacteriological investigation carried out by Bell & Albright (1982), in the Fraser River estuary, where they observed reduced ATP and neustonic heterotrophic activity.

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Studies carried out in a salt marsh (Gallagher, 1975), in a temperate lagoon (Hardy, 1973) and in a temperate estuary (Manzi *et al.*, 1977) provide much information about the existence of a distinct neustonic community. However, for a better understanding of the metabolic activity in such ecosystems, further studies are required of environmental conditions as well as a description of organisms and their activity. Our study is not an attempt to define processes that lead to the enrichment of organisms at the sea-air interface, but to assess more accurately the relation between microneuston and its autotrophic and heterotrophic activities.

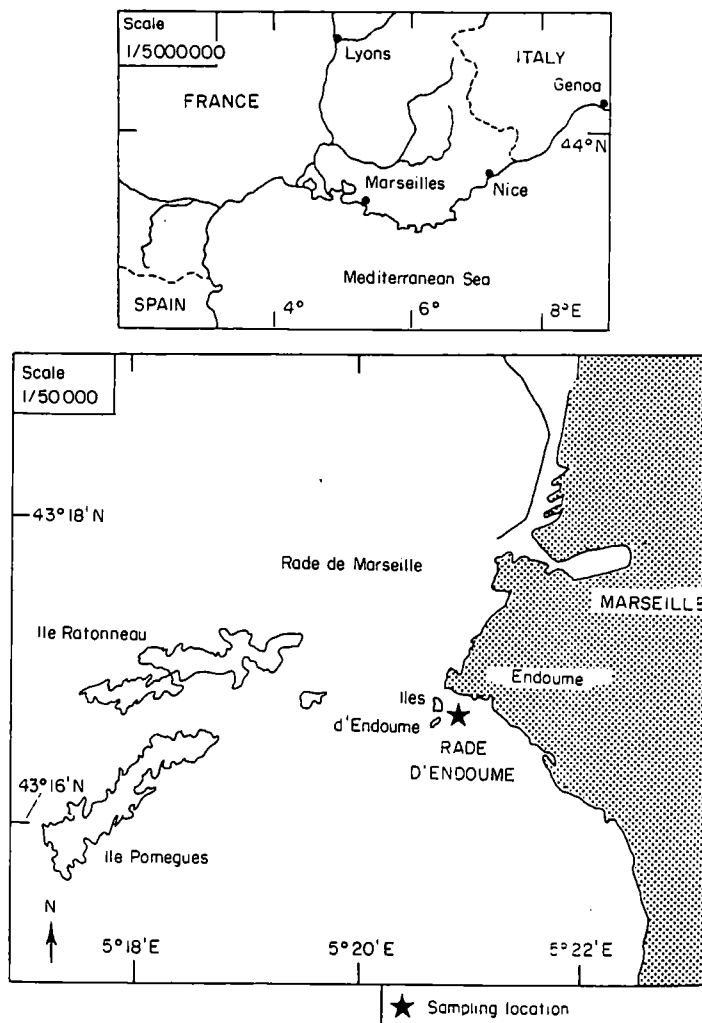


Figure 1. Location of sampling station.

Method

Sampling

The surface microlayer was collected from the shore (Gulf of Genoa) from May 1979 to June 1980. The sampling station was constructed according to the method described in Ta. All samples were filtered through GF/C glass fibre or membrane filters (Nucleopore membrane, (1981).

Analysis

Subsamples for particulate matter were filtered through precombusted glass fibre filters (47 mm) in a vacuum desiccator for 24 h and analysed (model 240). Carbon was analysed using a fluorometer (model 111) as used as a standard.

Subsamples for chlorophyll *a* were filtered through glass fibre filters (47 mm) in a vacuum desiccator for 24 h. Concentrations were determined as modified by Holm-Hansen & Booth (1967), modified by Rostad. For direct examination using a microscope, microneuston counts were determined using Steemann-Nielsen (1956) and 0.50 m two 140 m after addition of 1 ml (their contents filtered through a 0.45 µm filter over fuming HCl, placed in a scintillation counter (In the calculation of ^{14}C fixation). Measurements of the concentration of ^{14}C in the sample, but, when

Methods and material

Sampling

The surface microlayer was sampled by means of a skimmer in a coastal area a few miles from the shore (Gulf of Marseilles, France), in the north-west Mediterranean Sea from May 1979 to June 1980. Station position is shown in Figure 1. The surface film device was constructed according to Harvey's rotating drum principle (Harvey, 1966). Reference samples were collected directly from a depth of 0.50 m by pumping. Sampling was carried out at the surface under various sea conditions, from dead calm with presence or absence of slicks to choppy conditions without slicks. More information about the sampling conditions is given in Table 1.

All samples were filtered directly upon collection through a 200 μm nylon net before analysis in order to remove larger zooplankton and detritus. Microplankton in this paper refers to the material that passes through the 200 μm net and is removed by Whatman GF/C glass fibre or membrane filters (0.45 μm) according to the assays. Nanoplankton refers to organisms less than 20 μm , and bacterioplankton to the filtrate that passes a 3 μm Nucleopore membrane. Physico-chemical conditions are described in De Souza Lima (1981).

Analysis

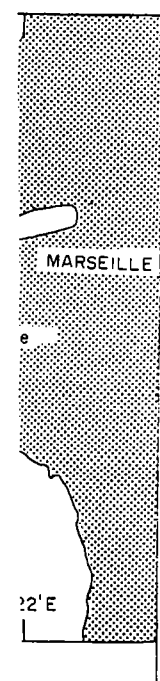
Subsamples for particulate organic carbon (POC) and nitrogen (PON) were filtered through precombusted glass fibre filters (Whatman GF/C 25 mm diameter) and stored in a vacuum desiccator for analysis. POC and PON were measured with a Perkin-Elmer CHN analyser (model 240). Carbohydrates were determined by the phenol-sulphuric acid method of Dubois *et al.* (1956) using glucose as standard. Proteins were analysed with a Turner fluorometer (model 111), using the procedure of Packard & Dortch (1975). Norleucine was used as a standard.

Subsamples for chlorophyll *a* and phaeophytin *a* were filtered through Whatman GF/C glass fibre filters (47 mm diameter) pre-covered with 1 ml of a 1% suspension of MgCO_3 . Concentrations were determined by the fluorometric method of Yentsch & Menzel (1963) as modified by Holm-Hansen *et al.* (1965). Samples for ATP, ADP and AMP were filtered through membrane filters (0.45 μm pore size) and the filters placed immediately in boiling TRIS buffer. Triplicate analysis were made on the extract of each filter as described by Holm-Hansen & Booth (1966). Measurements were carried out using Pradet's technique (1967), modified by Romano & Daumas (1981) for environmental application. Quantification of phytoplankton populations was accomplished in formalin preserved samples by direct examination using the inverted microscope technique of Utermöhl (1958). The microneuston counts were achieved in 5 ml counting chambers, but the organisms of the underlying water were enumerated in large chambers (100 ml). Carbon fixation was determined using Steemann-Nielsen's technique (1952). From each water sample (microlayer and 0.50 m) two 140 ml light bottles and one 140 ml dark bottle were incubated *in situ* after addition of 1 ml (4 μCi) of $\text{NaH}^{14}\text{CO}_3$. After 4 h the bottles were recovered and their contents filtered through membrane filters (0.45 μm pore size). Filters were dried over fuming HCl , placed in scintillation vials and their activity measured using a liquid scintillation counter (Intertechnique). Measurements of dissolved CO_2 required for the calculation of ^{14}C fixation were performed using the method of Van Slyke & Neil (1924).

Measurements of the ^{14}C -glucose uptake were usually made on the whole population in the sample, but, when possible, were also carried out separately on the bacterioneuston

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and/or bacterioplankton after size fractionation. Size fractions were obtained by filtering the sample through a 20 μm mesh Nytex net, and the filtrate through a 3 μm Nucleopore membrane with mild pressure applied to a 50 ml syringe. Care was taken to avoid filter clogging by replacing the membrane when necessary. A kinetic analysis of the ^{14}C -glucose uptake was undertaken with the microneuston and the subsurface water on two occasions (June 1979 and June 1980). The uptake of organic solutes in sea water is regulated by passive and/or active transport. At low concentrations ($< 100 \mu\text{g C l}^{-1}$), the active transport system follows Michaelis-Menten laws. According to Wright and Hobbie (1966), the maximum uptake velocity (V_{max}) is calculated by plotting $C\mu/c$ (ordinate) versus A (abscissa), where $C = \text{cpm from } 1 \mu\text{Ci}$ in the counting apparatus; $\mu = \text{number of } \mu\text{Ci added to the sample}$; $t = \text{incubation time}$; $A = \text{concentration of the added substrate as C equivalent } (\mu\text{g C l}^{-1})$. The slope of the straight line obtained is $1/V_{\text{max}}$, the intercept on the abscissa corresponds to the value $-(K_t + S_n)$ if K_t is the half saturation constant and S_n the natural concentration of the substrate, and the intercept on the ordinate gives the 'turn over time' T_t i.e. the time required for the substrate to be entirely removed by the natural populations. At higher concentrations ($> 100 \mu\text{g C l}^{-1}$), the uptake shows direct dependance on substrate concentration via a passive transport system similar to diffusion through a semi-permeable membrane. The diffusion constant k_d is given by the slope of the straight line obtained by plotting velocity ($\mu\text{g C l}^{-1} \text{ h}^{-1}$) against A , the concentration of the added substrate ($\mu\text{g C l}^{-1} \text{ h}^{-1}$). The turn over time due to uptake by diffusion at the natural concentration is $T_d = 1/k_d$. In a given sample where both T_t and T_d are known, S_n is the same. The relative importance of the two mechanisms in removing the substrate at its natural concentration can be assessed, even though the natural velocities and natural substrate level are not known (Wright & Hobbie, 1966). In both experiments, several concentrations were used to determine the Michaelis-Menten parameters: 8 concentrations were used in June 1979, ranging from 2 to 500 $\mu\text{g C l}^{-1}$, and 22 in June 1980 ranging from 0.3 to 5000 $\mu\text{g C l}^{-1}$. A mixture of labelled and unlabelled glucose was added to the bottles according to the concentration required. Duplicate bottles of 125 ml were filled with the different fractions and incubated after ^{14}C -glucose addition for 3 to 4 h. Incubations were stopped by filtering the bottle contents through 0.45 μm Sartorius filters and radioactivity of the filter was counted by liquid scintillation. In June 1979 the abundance of particulate material did not allow the 3 μm filtration, but only the 20 μm with the microneuston. In June 1980, the 3 μm filtration was carried out on the microneuston and on the underlying microplankton.

Results and discussion

Major phytoneustonic representatives

Cell identification and counts were carried out on microlayer and subsurface samples obtained in June (sample 2), in September (samples 19, 20, 21, 22, 26) and December (from sample 27 to 35). Sea state and presence/absence of slicks concerning these samples are shown in Table 1.

Cell densities in the surface microlayer were generally greater than in the 0.50 m depth samples, the enrichment factor varying from 2 to 284. From the fifteen analysed samples, only three presented no enrichment (samples 2, 32, 35). In June, cell numbers were lower in the microlayer ($7.5 \times 10^5 \text{ cells l}^{-1}$) than in the subsurface water ($8.5 \times 10^5 \text{ cells l}^{-1}$). However, if we take in account the nanoplankton, cell density becomes twice more abundant in the microlayer. In September, cell concentrations show a high variability (from 3.4×10^3 to $226 \times 10^3 \text{ cells l}^{-1}$) in the surface layer. Subsurface values are less variable,

ranging from 0. usually higher c $2.9 \times 10^6 \text{ cells l}^{-1}$ uniformly distrib

Phytoneuston
Prorocentrum oc
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Gonyaulax, *Gym*
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Cryptophyceae a

TABLE 1. Sampling condition data

Sample	Date	Time of day	Temperature (°C)	Sea state	Slick
1	9 May 1979	7.00	13.75	calm	+
2	1 Jun 1979	7.00	19.05	calm	+
3	6 Jun 1979	12.00	21.20	slightly choppy	—
4	7 Jun 1979	7.00	19.70	choppy	—
5	7 Jun 1979	11.00	20.90	slightly choppy	—
6	19 Jun 1979	7.00	16.70	slightly choppy	—
7	19 Jun 1979	12.00	17.20	choppy	—
8	21 Jun 1979	7.00	17.68	calm	+
9	21 Jun 1979	11.00	17.65	choppy	—
10	21 Jun 1979	22.00	17.50	choppy	—
11	5 Jul 1979	7.00	19.50	calm	+
12	5 Jul 1979	11.00	19.60	calm	—
13	5 Jul 1979	16.00	20.10	slightly choppy	—
14	5 Jul 1979	21.00	20.05	slightly choppy	?
15	29 Aug 1979	6.30	18.20	calm	—
16	30 Aug 1979	7.30	16.70	calm	—
17	30 Aug 1979	12.00	17.05	choppy	—
18	5 Sep 1979	6.30	20.00	calm	—
19	5 Sep 1979	7.30	20.00	calm	+
20	7 Sep 1979	7.00	21.42	calm	+
21	12 Sep 1979	7.00	21.15	calm	+
22	12 Sep 1979	11.00	22.30	calm	—
23	12 Sep 1979	16.00	21.50	slightly choppy	—
24	12 Sep 1979	22.00	22.15	calm	—
25	13 Sep 1979	3.00	21.60	calm	—
26	13 Sep 1979	7.00	22.12	calm	+
27	4 Dec 1979	8.00	14.70	calm	—
28	4 Dec 1979	11.00	14.91	calm	—
29	4 Dec 1979	14.00	14.95	calm	—
30	4 Dec 1979	17.00	14.63	calm	—
31	4 Dec 1979	20.00	14.65	calm	?
32	4 Dec 1979	23.00	14.92	calm	?
33	5 Dec 1979	2.00	14.78	calm	?
34	5 Dec 1979	5.00	14.62	calm	?
35	5 Dec 1979	8.00	14.60	choppy	—
36	25 Mar 1980	8.00	12.70	slightly choppy	—
37	26 Mar 1980	8.00	12.45	slightly choppy	—
38	26 Mar 1980	10.00	12.62	slightly choppy	—
39	20 May 1980	7.00	16.90	choppy	—
40	23 Jun 1980	7.00	17.70	calm	—

+ slick present; — slick absent; ? no visible slick during the night.

ranging from 0.2×10^3 to 3.1×10^3 cells l^{-1} . The samples collected in December have usually higher cell concentrations in the microlayer, with values between 5×10^3 and 2.9×10^6 cells l^{-1} . Underlying phytoplankton averaged 6.5×10^3 cells l^{-1} and were more uniformly distributed (s.d. = 2.5×10^3).

Phytoneuston populations mainly consist of Dinophyceae in Summer. The genus *Prorocentrum* occurs at higher frequency, the most common species being *P. lima*, *P. micans*, *P. maximum*, *P. triestinum* and *P. minimum*. Furthermore, in some samples, the following genus are found in greater number in the microlayer than in the underlying water: *Gonyaulax*, *Gymnodinium*, *Glenodinium* and *Protoperdinium*. Nanoplanktonic species may be particularly abundant (10^6 cells l^{-1} in June), the main representatives belonging to the Cryptophyceae and Chlorophyceae. Diatoms are usually dominant in the subsurface layer

but are well represented in winter in the surface film. They generally belong to planktonic forms (*Leptocylindrus danicus* was found in June 1979 in both layers and *Phaeodactylum tricornutum* highly dominated in the surface skin in December 1979); but benthic diatoms may also occur in abundance in the surface layer (*Grammatophora*, *Licmophora*, *Navicula* and *Pleurosigma* were more abundant at the surface on several occasions during the winter). Nevertheless, more than 50% of the species reported here are found to occur in the surface microlayer as well as in the subsurface water and none of them was exclusively found in the surface layer.

Particulate organic matter and biomass

Comparisons between microlayer and references sample data were carried out for particulate organic matter and biomass using Mann-Whitney U non-parametric test (Siegel, 1956; Hollander & Wolfe, 1973). The null hypothesis tested was h_0 : microlayer = underlying water and the alternative hypothesis h_1 : microlayer > underlying water.

The mean and range of POC and PON concentrations in the microlayer surface of the Gulf of Marseilles are given in Table 2. The higher C/N ratio in the microlayer surface with a mean value of 10.4 compared with 7.9 in the underlying water, possibly reflects a greater preponderance of relatively older, and hence nitrogen-poor organic matter.

Values of biochemical constituents (Table 2) show that the carbohydrate content in the skin layer is much greater than the protein content, which gives a remarkably high ratio of carbohydrate to protein. If we take into consideration that the abundance of the protein fraction in POM is associated to living or young matter and the carbohydrate fraction to more or less degraded matter (Handa *et al.*, 1972; Mopper *et al.*, 1978; Delmas, 1980), then the carbohydrate/protein ratio seems to confirm the presence of a detrital component in the microlayer POM.

In accordance with Chl *a* and ATP estimations (Table 3) the surface microlayer is characterized by a high microneustonic biomass, when compared to the underlying water, the mean Chl *a* and ATP concentrations being respectively $1.54 \mu\text{g l}^{-1}$ and $0.98 \mu\text{g l}^{-1}$ in the microlayer compared with $0.74 \mu\text{g l}^{-1}$ and $0.39 \mu\text{g l}^{-1}$ in the bulk water. Though the neustonic detrital fraction as confirmed by C/N and carbohydrate/protein ratios is important, the percentage of living carbon ($250 \times \text{ATP}$) in the POC (Hamilton & Holm-Hansen, 1967) is on the average of 10% for the surface microlayer compared with 20% in the underlying water.

Activity

Adenylic nucleotide ratio. The concept of 'energy charge' (EC) based on the intracellular adenylyate pool ($\text{EC} = \text{ATP} + 0.5\text{ADP} / \text{ATP} + \text{ADP} + \text{AMP}$) has been defined by Atkinson & Walton (1967) and Pradet (1967), in experiments on homogeneous material from cell cultures. This ratio has been used in marine environment during the last few years (Wiebe & Bancroft, 1975; Romano, 1975; Karl *et al.*, 1978) as an indicator of the physiological state in natural populations. However, recent studies show that the three adenylic nucleotide forms are not equally destroyed after cellular death, the AMP form being associated with detritus of biological origin (Romano & Daumas, 1981). Thus, the applications of energy charge in marine ecology (i.e. on heterogeneous material) may be limited. In this study, instead of energy charge (EC) we shall use the term adenylic nucleotide ratio (ANR). In our work, ANR values ranged from 0.30 to 0.62 for the surface microlayer, the mean value being significantly different from the one in the underlying water (Table 4), and also lower than those observed by Romano (1976a, b) in phytoplankton cultures

TABLE 2. Mean, standard deviation and range of POC, PON, carbohydrate and protein concentrations with results of Mann-Whitney non-parametric test (U)

Variable	Surface microlayer				Underlying water				P
	mean	s.d.	range	n	mean	s.d.	range	n	
POC (mg l^{-1})	3.25	2.97	11.51-0.31	30	0.48	0.18	0.83-0.17	30	<0.00003
PON (mg l^{-1})	0.32	0.26	1.10-0.04	30	0.06	0.02	0.13-0.03	30	<0.00003
C/N ratio	10.40	4.10	26.40-2.30	30	7.90	2.90	16.40-4.80	30	0.00090
Carbohydrate-C (mg l^{-1})	0.36	0.41	1.50-0.06	26	0.05	0.03	0.14-0.02	26	<0.00003
Primary amines ($\mu\text{g N-NH}_2 \text{ l}^{-1}$)	8.35	11.10	53.34-0.42	30	2.44	1.71	6.44-0.42	30	<0.00070
Carbohydrate-C amines-N	61.10	59.30	294.40-17.10	26	22.40	14.40	75.00-9.30	26	<0.00003

*Null hypothesis H_0 : microlayer = underlying water rejected (one-tailed test).

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TABLE 3. Range and mean concentrations of chlorophyll pigments ($\mu\text{g l}^{-1}$) and ATP ($\mu\text{g l}^{-1}$) in the surface microlayer and subsurface water for $n=30$ samples

Variable	Surface microlayer			Underlying water			$\frac{U-\bar{U}}{S_U}$	p
	mean	s.d.	range	mean	s.d.	range		
Chlorophyll <i>a</i>	1.53	1.77	7.91-0.14	0.74	0.60	2.21-0.09	2.04*	0.02070
Phaeophytin	0.62	0.70	3.52-0.08	0.18	0.16	0.54-0.00	4.01*	<0.00003
% phaeophytin total pigments	32	14	78-14	21	17	78-0	3.55*	<0.00023
ATP	0.98	1.14	4.64-0.11	0.39	0.25	0.90-0.25	2.31*	0.01040

*Null hypothesis rejected on basis of Mann-Whitney nonparametric test (one-tailed test).

TABLE 4. Mean, standard deviation and range of ^{14}C fixation ($\mu\text{g C l}^{-1} \text{ h}^{-1}$), production/chlorophyll ($\mu\text{g C l}^{-1} \text{ h}^{-1} / \mu\text{g Chl a l}^{-1}$) ratio and adenylic nucleotide ratio (ANR) as M/M

Variable	Surface microlayer				Underlying water				$\frac{U-\bar{U}}{S_U}$	p
	mean	s.d.	range	n	mean	s.d.	range	n		
^{14}C fixation	5.03	5.81	26.68-0.28	25	5.35	3.89	12.34-0.45	25	0.75	
Prod./Chl. <i>a</i>	3.50	1.60	7.70-1.20	25	7.60	4.60	25.40-3.20	25	4.51*	<0.00003
ANR	0.50	0.09	0.70-0.30	30	0.59	0.11	0.81-0.36	30	3.04*	0.00120

*Null hypothesis rejected on basis of Mann-Whitney test (one-tailed test).

where values varied from 0.51 to 0.83. The lowest values are thus found in surface samples associated with important biomass as already reported by Benon *et al.* (1977) in the Gulf of Fos, near Marseilles. Karl & Holm-Hansen (1978) ascribe the lower values of the energy charge observed in natural samples collected at 1 m depth in comparison to 50 m, to a possible photoinhibition or to the influence of ultra-violet rays. Though low EC values in phytoplankton have been associated with stressed cells (Romano, 1975; 1976a, b), low EC values have also been reported in immature ecosystems or in natural populations with a low diversity of species (Romano, 1975; Benon *et al.*, 1977; Amblard, 1981). In our investigation, analysis of structure was performed through a measure of diversity (Shannon & Weaver, 1963). Our results show that phytoplankters in the microlayer exhibit lower informational diversity ($t=2.35^*$; $df=28$) as already reported by Hardy (1973) and Manzi *et al.* (1977) in the surface microlayer of other aquatic ecosystems.

Photosynthetic activity. Though phytoneustonic and microneustonic biomass are higher than in waters below the surface, the carbon fixation values are not significantly different from those observed at 0.50 m (Mann-Whitney test, Table 4), except in the slicks, where production by phytoneuston was higher than that of underlying phytoplankton. The relations between carbon fixation and chlorophyll are given in Figure 2. The regression coefficients differ significantly from zero and there is a consistent difference in the slopes of samples collected at the surface microlayer and subsurface water ($t=2.57^*$; $df=48$) the former presenting a lower slope than the latter. The intercepts do not differ

significantly from origin.

Heterotrophic activity. Heterotrophic activity was found in coastal waters at 0.02 $\mu\text{g C l}^{-1} \text{ h}^{-1}$ (Benon *et al.*, 1975). The results show opposite trends in the concentration of organic matter more than in the turnover time.

($\mu\text{g l}^{-1}$) and ATP ($\mu\text{g l}^{-1}$)

$\frac{U - \bar{U}}{S_U}$	p
2.04*	0.02070
4.01*	<0.00003
3.55*	<0.00023
2.31*	0.01040

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4.51*	<0.00003
3.04*	0.00120

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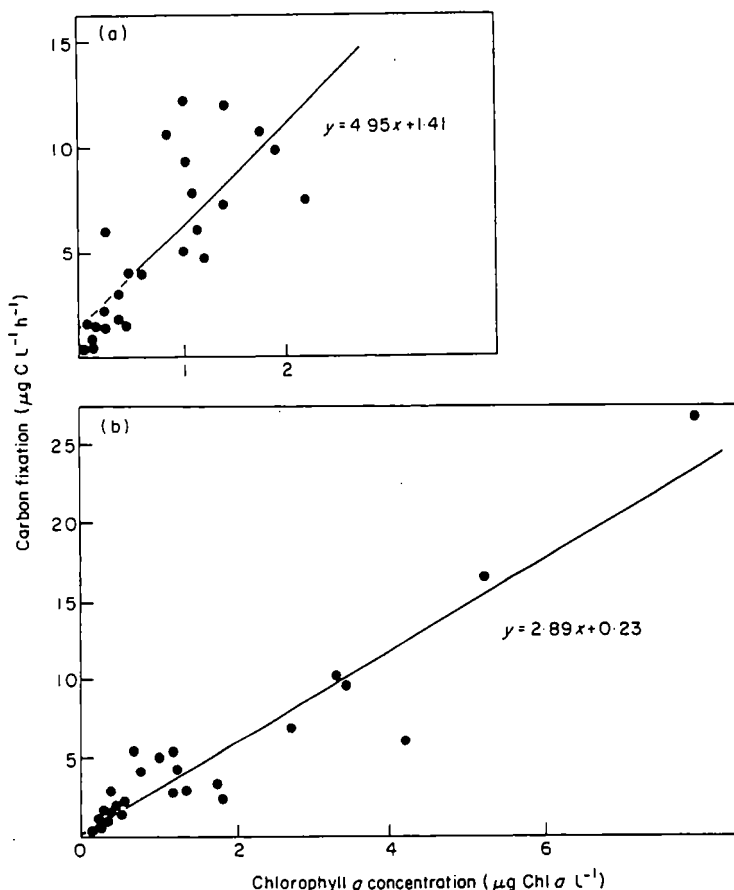


Figure 2. Relationship between carbon fixation ($\mu\text{g Cl}^{-1} \text{ h}^{-1}$) and chlorophyll *a* ($\mu\text{g l}^{-1}$). Standard errors of the regression coefficients (S_b) and intercepts (S_a) in parentheses. (a) Underlying water data: $y = 4.95x + 1.41$ ($S_b = 0.83$, $S_a = 0.83$); $r = 0.77^{**}$; $n = 25$. (b) Surface microlayer data: $y = 2.89x + 0.23$ ($S_b = 0.22$, $S_a = 0.54$); $r = 0.94^{**}$; $n = 25$. Values significant at the 1% level (**).

significantly from zero and the regression lines may be considered to pass through the origin.

Heterotrophic activity. The heterotrophic activity of seawater from 0.50 m is similar to that found in coastal waters (slightly eutrophic), values for V_{max} ranging from 0.008 to 0.02 $\mu\text{g Cl}^{-1} \text{ h}^{-1}$ (Hoppe, 1978; Delattre *et al.*, 1979) and T_i of about one week (Seki *et al.*, 1975). The comparison between the activity of the neustonic film and underlying water shows opposite results in the two kinetic analyses carried out: in June 1979, the concentration of organisms (slicks present) gives rise to a high heterotrophic activity (ten times more than in the subsurface water). Though the total activity is higher in the surface film the turnover time is not significantly different in surface and subsurface seawater (about

TABLE 5. Kinetic parameters of heterotrophy, in presence or absence of slicks, in the surface microlayer and underlying water. Measurements were made on the whole sample (T), the nanoplanktonic fraction (20 μm) and/or on the bacterial fraction (3 μm). V_{max} = maximum uptake velocity ($\mu\text{g C l}^{-1} \text{ h}^{-1}$); K_t = transport constant; S_n = natural substrate concentration; T_t = turn over time due to transport system; k_d = diffusion constant; T_d = turn over time due to diffusion (nd—not determined)

Variable	June 1979—slick present				June 1980—slick absent			
	Surface microlayer		Underlying water		Surface microlayer		Underlying water	
	T	20 μm	T	20 μm	T	3 μm	T	3 μm
$V_{\text{max}} \times 10^{-3}$	972	1006	77	26	11	9.3	21.50	12
$K_t - S_n$	110	112	7	6	0.97	0.6	0.98	1.4
T_t (h)	114	113	92	238	87	63	47	113
$k_d \times 10^{-3}$	499	521	nd	nd	143	103	89	91
T_d (h)	200	192	nd	nd	1122	1094	700	969
Diffusion transport (%)	35	37	nd	nd	7	13	6	10

100 h), values of $K_t + S_n$ being much higher in the neustonic fraction. Diffusion contributes in this case to about 35% to the turnover time of the glucose.

On the other hand, in June 1980, the values for heterotrophy are similar or slightly higher in the subsurface water than in the surface microlayer (Table 5). The turnover time is also similar and diffusion is low. The bacterioplankton activity is not as high as in the whole sample and as $K_t + S_n$ is of the same order. Moreover, the turnover time in the bacterial fraction is more important, suggesting the interference of the phytoplankton in the heterotrophic activity of the sea water. Diffusion, though not very important (=10%) is noticeable in the bacterial fraction.

Influence of sea conditions on the biological aspects of the microlayer surface

Most of the physical and chemical characteristics of the sea-air interface depend upon sea state conditions. When the wind is light, slicks can be easily visualized as streaks or patches of glassy appearance at the sea surface. Our estimate of sea condition refers mainly to the presence (or absence) of these slicks which allow a characterization of the surface microlayer (Lafond & Lafond, 1972).

Calm sea conditions induce a concentration of particulate organic matter at the surface microlayer. This accumulation varies significantly according to sea state (Table 6). On the other hand, photosynthetic activity, if higher on the whole under calm conditions, decreases when referred to biomass units (Chla), the ratio Prod./Chla being higher under choppy sea conditions in the surface microlayer (Table 7). Comparison, under different sea conditions, of these ratio slopes shows for the subsurface waters, a significant difference between calm and choppy states ($t=3.40^{**}$; $\text{df}=22$) (Figure 3).

It is not so for the surface microlayer. Though the slope is less marked under calm conditions, t -test analysis failed to show significant differences, as residual variances of each group are not homogeneous, as verified by the F value (10.36). Nevertheless, the hypothesis of a better productivity under choppy conditions can be put forward. Frechette & Legendre (1978) suggest that on sunny days, the waves would generally have a depressive action on photosynthesis in underlying waters, in inducing repeated variations of the light

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TABLE 6. Mean and standard deviation of POC (mg l^{-1}), Chla ($\mu\text{g l}^{-1}$) and ATP ($\mu\text{g l}^{-1}$) concentrations under calm and choppy sea conditions, in the surface microlayer (sm) and underlying water (0.50 m)

Sea state		Calm			Choppy		
		mean	s.d.	n	mean	s.d.	n
POC:	sm	4.62	3.35	15	1.89	1.74	15
	0.50 m	0.56	0.17	15	0.41	0.19	15
Chla:	sm	2.59	1.99	15	0.47	0.30	15
	0.50 m	0.97	0.68	15	0.50	0.40	15
ATP:	sm	1.54	1.36	15	0.42	0.42	15
	0.50 m	0.43	0.25	15	0.35	0.25	15

TABLE 7. Mean and standard deviation of production/chlorophyll ratio ($\mu\text{g C l}^{-1} \text{ h}^{-1} / \mu\text{g Chla l}^{-1}$) in the microlayer under calm and choppy sea conditions

Sea state		Calm			Choppy		
		mean	s.d.	n	mean	s.d.	n
Surface microlayer		2.61	0.83	13	4.48	1.78	12
Underlying water		6.06	2.63	13	9.22	5.82	12

in the upper half of the photic zone. Near the surface, however, where high light intensities might inhibit photosynthesis, choppy conditions would be more favourable by lowering this photoinhibition. To summarize, water turbulence tends to reduce ecological differences between the neustonic and planktonic biotopes and, under low light intensities, choppy conditions make the microlayer more similar to the underlying water from an ecological point of view. Though it has not been repeatedly observed, the heterotrophic activity is also quite different in the surface microlayer in the presence or absence of slicks (Table 5).

Conclusion

Our study argues for the existence of a surface microlayer enriched with organic matter, which functions like a eutrophic system whenever slicks are present. This enrichment clearly depends on sea state, and accumulation at the surface skin is stronger under calm sea conditions.

Though detrital material is obviously present, high concentrations of POC, Chla, ATP and a general increase in autotrophic and heterotrophic activities tend to prove that this accumulation is the result of a mixing of living as well as dead particles. Cell counts suggest that neustonic populations are able to develop in the microlayer surface. These populations are mainly composed of particular species of dinoflagellates and diatoms. The relatively low productivity (Prod./Chla) at the surface layer (compared with that at the underlying water) may be due to photoinhibition, although the effects of accumulated pollutants such as pesticides and metals cannot be excluded.

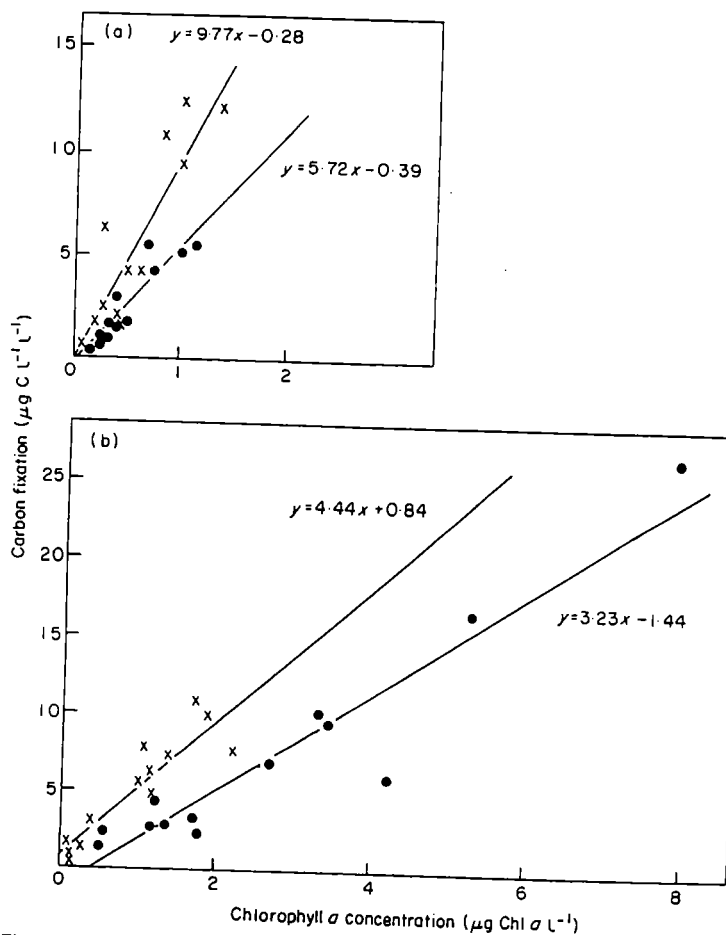


Figure 3. Relationship between carbon fixation ($\mu\text{g C l}^{-1} \text{ h}^{-1}$) and chlorophyll *a* ($\mu\text{g l}^{-1}$) at the microlayer surface (●) and subsurface water (x). Standard errors of the regression coefficients (S_b) and intercepts (S_a) in parentheses. (a) Surface microlayer data: $y = 5.72x - 0.39$ ($S_b = 0.71$, $S_a = 0.42$); $r = 0.93^{***}$; $n = 12$ and subsurface water data: $y = 9.77x - 0.28$ ($S_b = 1.59$, $S_a = 1.12$); $r = 0.89^{***}$; $n = 12$ under choppy sea conditions. (b) Microlayer data: $y = 3.23x - 1.44$ ($S_b = 0.31$, $S_a = 0.89$); $r = 0.92^{**}$; $n = 13$ and subsurface water data: $y = 4.44x + 0.84$ ($S_b = 0.58$, $S_a = 0.70$); $r = 0.95^{***}$; $n = 13$ under calm sea conditions. Values significant at the 0.1% level (***).

Acknowledgements

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The Importance of Surface Microlayer (Neuston) Communities in Estuaries

J. T. HARDY

Batelle Marine Research Laboratory, Sequim, WA

The sea-surface microlayer (upper 50 μm) is an important interface, particularly in estuaries. It serves as a concentration point for many pollutants, including heavy metals, petroleum hydrocarbons, pesticides, and PCB's. It also provides a habitat for a diverse flora and fauna (neuston) often of greater abundance than the underlying water column. Eggs and larval stages of commercial fish and shellfish often depend upon the microlayer for development. We have developed a microcosm system to study the basic biology of microneuston and also to examine the behavior of pollutants entering the microlayer. Initial results using metal-rich atmospheric particulate matter, indicate that neustonic communities may alter transport rates of metals from the atmosphere to the water column.

Comparison of the Structure and Function of Estuarine and Harbor Fish Communities in Southern CaliforniaMICHAEL H. HORN AND LARRY G. ALLEN
California State University, Fullerton, CA

Multiple-gear sampling studies in successive years of fish populations in an estuary (upper Newport Bay) and an artificial harbor environment (Cabrillo Beach area of Los Angeles Harbor) in southern California showed that the two communities were 1) dominated by low trophic level fishes with a large proportion of juveniles, 2) characterized by marked seasonal fluctuations of both juvenile-adult and ichthyoplankton populations, and 3) strongly influenced in occurrence and spatial distribution by temperature and depth. Species composition and the sequence of abundance peaks, however, were considerably different in the two habitats. The shallow waters of both sites were characterized by algal beds that either occurred or were best developed during the summer months. In upper Newport Bay, these beds were distinguished by an atherinid-cyprinodontid-gobiid species group and at Cabrillo Beach by an atherinid-clinid-embiotocid-engraulid association. The unique assemblage of fishes and the distinct chronology of abundance of fish populations in upper Newport Bay do not support the proposition that harbors adequately replace estuaries as inshore fish habitats in southern California.

Feeding Ecology of Juvenile Salmonids at Three Contrasting Habitats at the Fraser River Estuary, B.C.C. D. LEVINGS
West Vancouver Laboratory, West Vancouver, British Columbia, Canada

The study was conducted at 3 low tide refuges at Sturgeon and Roberts Bank, Fraser River estuary. One site, on Roberts Bank, was characterized by tidal channels through an eel grass (*Zostera marina*) bed. The other 2 locations were in sandflats of Sturgeon Bank.

The Steveston site was in a relict river channel, and the Iona location was in a man-made ditch receiving sewage. Chum fry (*Oncorhynchus keta*) used calanoid copepods at Steveston but harpacticoids at Roberts Bank, as did pink fry (*O. gorbuscha*). At Iona pink and chum ate mainly adult insects and calanoid copepods (*Tortanus*, *Metridia*). Chinook diets at Iona were more diverse, and the fish used gammarids, calanoid copepods, adult insects, and mysids. Chinook used several genera of gammarids at Roberts Bank, including *Eogammarus*, *Protomedea*, *Pontogeneia* and *Calliopius*, as well as larval fish including herring. Chinook at Steveston fed on adult dipterans (Chironomids) at the start of an ebb tide, and appeared to change to cumaceans and mysids as water volume decreased and tidal velocities increased. The shift in diet may have been related to increased availability of the crustaceans due to concentration of the prey. Such physical processes leading to accumulation may be as important as features introducing habitat heterogeneity, such as eel grass.

Pioneer Infaunal Communities in the Hayward Salt Marsh Restoration (San Francisco Bay)THOMAS M. NIESEN
San Francisco State University, San Francisco, CAEDWARD B. LYKE
California State University, Hayward, CA

The most extensive salt marsh restoration project on the West Coast involves a 200 acre former salt evaporation pond in Hayward, California on San Francisco Bay. Historically a wetland area, this diked pond was returned to Bay tidal action in May 1980. The site has been graded for restoration to *Spartina-Salicornia* salt marsh habitat; basins, meandering channels and islands for potential development of submerged, intertidal and upland habitat have been created. As part of a coordinated study of marsh development, three permanent transects were sampled monthly to determine the rate and nature of the benthic invertebrate colonization of the site. The composition of the initial benthic assemblage was compared to the faunas of adjacent Bay mud flat and adjoining salt marsh habitats. Colonization of the restoration site was initially slow. Numbers and kinds of benthic organisms decreased with distance from the Bay in both the submerged tidal channels and the intertidal flats. Samples taken from the tidal channels contained a higher abundance and diversity of invertebrates. The earliest colonizers were adult amphipods, which presumably rafted in from the Bay mud flat. Subsequent planktonic recruitment to the site has been dominated by spionid polychaete worms and several species of bivalve molluscs.

Predator Spectra of Microbenthic and Macrobenthic Prey in the Wadden SeaKARSTEN REISE
Zoologisches Institute der Universität, Göttingen, Germany

Tidal flats along the eastern coast of the North Sea are an important nursery ground for demersal fish and

1987.

Most prior work examining the effect of PAHs on algae has been confined to laboratory investigations using freshwater taxa grown in unialgal culture under optimal conditions (Bastian and Toetz 1982; Batterson et al. 1978; Giddings 1979). Since the sea-surface microlayer may contain an inordinately high concentration of PAHs relative to the water column, we decided to investigate the short-term effect of these hydrophobic contaminants on phytoneuston community dynamics under controlled *in situ* conditions during the summer season when bloom conditions can prevail in areas of Puget Sound.

MATERIALS AND METHODS

Three separate experiments were conducted at different times. The first experiment analyzed the effect of 1 mg/L fluoranthene on the rate of growth of phytoneuston during a 96-h period of time. The second experiment examined the effect of 1 mg/L fluoranthene on phytoneuston growth rate immediately following a rainstorm event. The third experiment compared the effects of two concentrations (1 mg/L, 10 mg/L) of fluoranthene and benzantracene on the growth of phytoneuston during a 144-h period of time.

Phytoneuston growth rate is dependent on both recruitment and retention of organisms from the water column below as well as the formation and retention of new organisms by reproduction. The growth rate of phytoneuston populations was determined by the equation:

$$k = \frac{\log_e N - \log_e N_0}{t}$$

where k = exponential growth rate
 N = number of organisms
 t = time interval

All investigations were performed out-of-doors in a Fiberglass tank with a capacity of 1,065 L and a slow flow-through of seawater. The tank was fitted with inlet and outlet plumbing to eliminate surface layer skimming and provided with a constant flow of unfiltered seawater from 10 m below the surface of Puget Sound from Sequim Bay at a rate of 34 L min⁻¹. After several days a microlayer film formed on the surface water within the tank. A previous study has shown that tank microlayers do not differ significantly from the natural phytoneuston community of Puget Sound (Hardy and Valett 1981).

After development of the microlayer, a 1.22-m diameter Plexiglas chamber with six circular portals, each with a diameter of 30.5 cm, was placed on the water surface of the tank. This device served to segregate six microlayer subcommunities, each with a surface area of 730 cm², yet permitted contact with the water column below and the atmosphere above.

Two crystalline PAHs, fluoranthene and benzantracene, were each first dissolved in an organic carrier of methylene chloride. This

solution was mixed with a commercial solvent and heated to 41°C to evaporate the solvent. The formula for the volume of a cylinder was used to calculate that a volume of 3.6 mL of microlayer solution would provide a microlayer depth of 10 µm. In the first and second experiments, of the six portals, three were untreated controls. Unaugmented microlayer was added to the final two portals. The experimental design allowed for duplicate treatments. In only one portal served as an untreated control. A single portal contained unaugmented microlayer. The other four contained 1 mg/L and 10 mg/L of fluoranthene. Portals five and six contained 10 mg/L of fluoranthene, respectively.

Since PAHs have a strong affinity for organic matter, the PAHs remained within the microlayer of the phytoneuston. All microlayers were added in addition of several drops of organic solvent to the surface tension and to allow the microlayer to form on the water surface.

Phytoneuston from each subcommunity was sampled by immersing a 7.62 x 2.54-cm glass slide in the microlayer and withdrawing it, thereby forming a microlayer on the glass. Glass plates are active materials, including microlayer. Immersion of the glass microlayer in the microlayer. Sampling vials were washed off the slide with distilled water, preserved in Lugol's solution, and enumerated by microscope at 400x magnification. Enumeration techniques outlined in Standard Methods for the Examination of Water and Wastewater (American Public Health Association 1975).

RESULTS AND DISCUSSION

Concentrations of 1 mg/L of fluoranthene had a definite impact on the mortality of established phytoneuston after the initial 48-h exposure period. The mortality of established phytoneuston was retarded by the term exposure. A relatively small mortality occurred in the unaugmented microlayer.

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solution was mixed with a commercial brand of mineral oil and heated to 41°C to evaporate the organic carrier. By using the formula for the volume of a cylinder, $V = \pi r^2 h$, it was determined that a volume of 3.6 mL of mineral oil-PAH solution was needed to provide a microlayer depth of 50 μ m in each portal. In the first and second experiments, of the six portals available, two served as untreated controls. Unaugmented mineral oil was added to two of the portals and 1 mg/L fluoranthene dissolved in mineral oil was added to the final two portals. Hence, this experimental design allowed for duplicate treatments. In the third experiment only one portal served as an untreated control. In addition, a single portal contained unaugmented mineral oil. Portals three and four contained 1 mg/L and 10 mg/L fluoranthene, respectively. Portals five and six contained 1 mg/L and 10 mg/L benzanthrane, respectively.

Since PAHs have a strong affinity for lipids, it is likely that the PAHs remained within the hydrophobic microlayer in proximity of the phytoneuston. All mineral oil inoculations required the addition of several drops of the surfactant Tween 80 to reduce surface tension and to allow the oil to spread evenly over the water surface.

Phytoneuston from each subcommunity were collected at 24-h intervals, using the glass plate method which involved vertically immersing a 7.62 x 2.54-cm glass microscope slide into each portal and withdrawing it, thereby allowing the surface film to adhere to the glass. Glass plates are efficient collectors of surface-active materials, including microalgae (Carlson 1982). A single immersion of the glass microscope slide consistently sampled 0.1 mL of microlayer. Sampling variability was determined by dipping 10 replicate glass slides in rapid succession into the tank. The coefficient of variation for total abundance was 17%. Organisms were washed off the slide with a mild detergent-filtered seawater mixture, preserved in Lugol's iodine solution and placed in a settling chamber. Enumeration was performed with an inverted microscope at 400x magnification, according to the counting techniques outlined in Standard Methods (American Public Health Association 1975).

RESULTS AND DISCUSSION

Concentrations of 1 mg/L of the PAH fluoranthene in mineral oil had a definite impact on the growth rate of phytoneuston during the initial 48-h exposure period (Figure 1). It appears that fluoranthene either retarded reproduction and/or contributed to the mortality of established microalgae communities during short-term exposure. A relatively low growth rate of phytoneuston that occurred in the unaugmented mineral oil can perhaps be attributed

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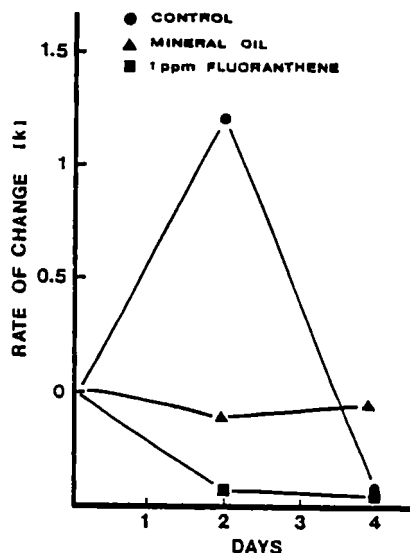


Figure 1. Rate of change in overall phytoneuston abundance.

to PAH impurities present in the liquid paraffin. A more plausible explanation, however, is that the viscous mineral oil acted as a physical barrier that delayed the dispersion of newly formed daughter cells. Even though the surfactant Tween 80 reduced the surface tension to allow the oil to spread, the viscosity may have been high enough to hamper dispersion. After four days the untreated control and 1 mg/L fluoranthene-treated phytoneuston communities showed nearly identical growth rates. Apparently the microflora was able to adapt to the PAH concentration and grow unimpeded to equal the rate of growth of the control community, which slowed after a very rapid initial increase.

A study by Bastian and Toetz (1982) found complete inhibition of growth after 14 days with 0.417 mg/L fluoranthene under laboratory conditions using a freshwater blue-green alga taxon. The interpretation of these results is interesting in the case of the Puget Sound microlayer, since fluoranthene concentrations as high as 0.388 mg/L have been measured in Puget Sound waters (Hardy, personal communication). This may lead one to conclude that some areas of Puget Sound, such as Commencement Bay, would be completely devoid of microalgae because of PAH contamination. This apparently is not the situation. A precursory analysis of samples from the urban bays of Puget Sound have indicated the presence of extensive microlayer communities. There are several explanations for this paradox. One must understand the unique flora that comprises the microlayer. The algae living in this habitat are capable of adapting to widely fluctuating environmental extremes of salinity, light intensity, and temperature, depending on the

season, which in this mari from dry, clear and hot in winter. An analysis of the core throughout the exper: the diatom *Nitzschia* and th comprised the major portion pertaining to *Nitzschia* and these genera have the inher extremes and are very poll probably the major reason dominated by these taxa. U conditions affecting the m these hardy, cosmopolitan others through the process

Another probable cause of even in areas of high PAH organisms to adapt relativ nants (Stockner and Antia only 2 days of inhibition, virtually grew unimpeded, tration of 1 mg/L. It has PAH can be utilized as an of microalgae (Kauss and H therefore feel it imperati isms to measure the effect tures, since results will tions. It would be unwise bioassay to the diverse as system. Other researcher PAHs or crude oil in bioas this fact (Winters et al.

Upon the completion of our fortunate to experience a tation of 1.57 cm. We dec investigate the recruitmen from the natural seed sour mg/L fluoranthene. No add portals as, even after the quite evident. Phytoneust within the untreated contr rainfall, but experienced and growth rate within the h following the rain, ever rapid growth (Figure 2). rate, and presumably reter presence of 1 mg/L fluorar tion during the first 48 h experiment. Prior studies recovery of growth after i unialgal culture (Bastian

season, which in this maritime temperate latitude (48° N) ranges from dry, clear and hot in summer to moist, overcast and cool in winter. An analysis of the species composition, which was monitored throughout the experiment, indicated that several species of the diatom *Nitzschia* and the microflagellate *Exuviaella marina* comprised the major portion of the flora. Ecological data pertaining to *Nitzschia* and many microflagellates indicate that these genera have the inherent ability to adapt to environmental extremes and are very pollution tolerant (Palmer 1969). This is probably the major reason why the microlayer community is dominated by these taxa. Undoubtedly, past extreme environmental conditions affecting the microlayer community have selected for these hardy, cosmopolitan taxa and caused the elimination of others through the process of evolution.

Another probable cause of ubiquity of microlayer phytoneuston, even in areas of high PAH concentration, is the ability of these organisms to adapt relatively quickly to environmental contaminants (Stockner and Antia 1976). Our results indicate that after only 2 days of inhibition, the natural phytoneuston community virtually grew unimpeded, regardless of a fluoranthene concentration of 1 mg/L. It has been postulated that in some instances PAH can be utilized as an organic substrate to enhance the growth of microalgae (Kauss and Hutchinson 1975; Soto et al. 1975). We therefore feel it imperative to use diverse assemblages of organisms to measure the effect of pollution rather than unialgal cultures, since results will be more representative of true conditions. It would be unwise to extend the results of a single taxon bioassay to the diverse assemblage of organisms comprising an ecosystem. Other researchers, using several taxa and a variety of PAHs or crude oil in bioassay experiments, have also emphasized this fact (Winters et al. 1976).

Upon the completion of our first in situ experiment, we were fortunate to experience a rainstorm event resulting in precipitation of 1.57 cm. We decided to utilize this opportunity to investigate the recruitment potential of the microlayer community from the natural seed source in the presence of the residual 1 mg/L fluoranthene. No additional fluoranthene was added to the portals as, even after the rainstorm, a visible slick was still quite evident. Phytoneuston populations increased dramatically within the untreated control portals after severe depletion by rainfall, but experienced a relatively slow initial recruitment and growth rate within the PAH-treated portals during the first 48 h following the rain, even though conditions were adequate for rapid growth (Figure 2). After 48 h, the recruitment rate, growth rate, and presumably retention, increased dramatically in the presence of 1 mg/L fluoranthene. The general pattern of inhibition during the first 48 h of exposure agrees with our first experiment. Prior studies have found similar results of rapid recovery of growth after relatively long exposure to PAH in unialgal culture (Bastian and Toetz 1982; Kauss and Hutchinson

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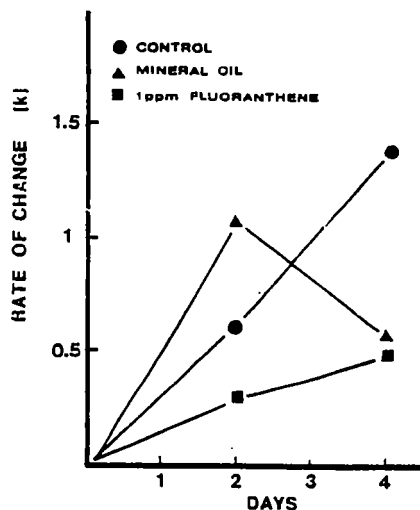


Figure 2. Rate of change in overall phytonuston abundance immediately following rainstorm event.

1975). It has been documented that algae can fully recover from initial exposure to certain chemicals (Soto et al. 1975).

In our third experiment we had the opportunity to follow a population bloom of the dinoflagellate *Exuviaella marina*. In this instance we observed the taxon's growth using different concentrations of two PAHs, fluoranthene and benzanthrane. Our experiment was terminated after 144 h, which coincided with a declining growth rate. The population growth curves did not exhibit the typical 48-h lag period in the PAH-treated portals. Some factor(s) very favorable for growth must have suppressed or overridden the initial inhibitory effect noticed in the previous two experiments. The tremendous rate of growth of this microflagellate was tracked, unimpeded, in both concentrations of fluoranthene and benzanthrane (1 and 10 mg/L). No differences were found in the rates of growth in the untreated control, in the unaugmented mineral oil or in the two concentrations of the PAHs.

From our experiments it appears that the phytonustonic component of the sea-surface microlayer has an inherent adaptive capacity which, under normal conditions, is effectuated after a relatively short exposure period of two days. When conditions, however, are highly favorable for growth, i.e., a bloom situation, PAH toxicants in concentrations up to 10 mg/L do not appear to deter exponential growth of certain taxa. This genetically inherent, adaptive capacity of microalgae to survive and reproduce, unimpeded, in the presence of pollutants, may indeed explain their ubiquitous distribution even in areas with relatively high concentrations of PAH.

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- Received April 21, 1986; accepted October 12, 1986

INTERFACE AIR-MER : ASPECTS ECOLOGIQUES DU MICRONEUSTON DANS LE FILM DE SURFACE

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SUMMARY

AIR WATER INTERFACE : ECOLOGICAL ASPECTS OF MICRONEUSTON DURING
INVESTIGATIONS OF SURFACE FILMS

The sea surface microlayer (upper 100 μ m) was sampled using Harvey's rotating drum collector. Greater amounts of nutrients, particulate organic carbon and living material occurred in the surface film than in samples taken at 0,50m. Neuston displayed a greater level of absolute production, but assimilation numbers were usually lower in the films than at a depth of 0,50m. Algal phytoplankton also occurred in much higher densities in sea-surface films than in subsurface waters. Individual species abundances differed between phytoneuston and underlying phytoplankton. Though surface microlayers with a richer nutrient environment may represent a favorable biotope to microplankton growth, neustonic organisms may be subject to considerable stress due to higher intensities of light and turbulence. These two aspects are discussed in this paper.

INTRODUCTION

L'influence des slicks naturels dans l'interaction entre l'océan et l'atmosphère et l'importance écologique de ce biotope pour les bactéries, algues et protozoaires, ont été mis en évidence par Parker et Barsom (1970). D'autres travaux ont montré une accumulation de bactéries (Sieburth, 1971 ; Tsyban, 1971) et de phytoplancton (Wandschneider, 1979 ; Hardy et Valett, 1981) dans les films de surface par rapport aux eaux sous-jacentes. Tout ceci tend à prouver l'existence d'un véritable écosystème superficiel (Hardy, 1973 ; Champalbert, 1975). Mais du fait de sa nature frontalière, les facteurs abiotiques vont soumettre les organismes neustoniques à de fortes contraintes d'adaptation.

Dans ce travail nous avons tenté d'apporter des informations complémentaires concernant l'écophysiologie du microneuston. Pour ce faire, nous avons confronté des mesures de paramètres chimiques (sels minéraux), pouvant avoir une incidence sur la production de l'échelon primaire, à des paramètres estimatifs de la biomasse ainsi qu'à des mesures d'activité biologique.

MATERIEL ET METHODES

Les prélèvements du film superficiel sur une épaisseur d'eau de l'ordre de 100 μ m ont été effectués au moyen du rouleau de Harvey (1966). Les eaux sous-jacentes (0,50m) ont été récoltées par pompage. L'échantillonnage a été réalisé dans une zone côtière du Golfe de Marseille (Mer Méditerranée), par temps calme, en présence et en absence de slicks. L'eau recueillie a subi une préfiltration sur voile de nylon de 200 μ m de vide de maille, afin d'éliminer la plupart du zooplancton et la fraction détritique grossière. L'aspect chimique du milieu a été évalué par les mesures de phosphates, nitrates et nitrites, selon le protocole de Strickland et Parsons (1972). Le carbone et l'azote organiques particuliers ont été déterminés d'après le protocole de Kerambrun et Szekiélda (1969). La biomasse a été estimée à partir des taux de chlorophylle *a* (Yentsch et Menzel, 1963) et d'ATP (Holm-Hansen et Booth, 1966) et l'activité photosynthétique d'après la méthode de Steeman-Nielsen (1952).

Les échantillons de phytoplancton ont été examinés suivant la méthode de sédimentation d'Utermöhl (1958).

RESULTATS

Sels minéraux.

Les phosphates et nitrates présentent toujours des teneurs moyennes plus élevées dans la microcouche de surface, avec des concentrations plus importantes en présence de slicks (Tableau 1). Les nitrites se caractérisent par un enrichissement plus faible.

Carbone et azote organiques particuliers.

Si l'on analyse la composition du seston des eaux d'extrême surface (Tableau 2), on observe que les teneurs en carbone et azote organiques sont nettement supérieures à celles des eaux sous-jacentes, ce fait étant plus accentué en présence de slicks. Les valeurs du rapport C/N sont légèrement supérieures dans les slicks (10,3) qu'à l'extérieur (9,9), et dans tous les cas, elles sont plus élevées qu'à 0,50m ; ceci est certainement l'indice de la présence en surface d'une matière organique plus dégradée.

Populations phytoplanctoniques.

La détermination du phytoplancton a été réalisée sur six paires d'échantillons (surface de 0,50 m) récoltés en présence et en absence de slicks (Tableau 3). En juin, nous n'avons trouvé dans les films de surface qu'une seule espèce de diatomée, *Leptocylindrus danicus*. La population est surtout constituée de dinoflagellés (90,6%). Numériquement ce sont les Gymnodiniens qui prédominent (56,6 %) suivis de *Prorocentrum triestinum* (34,1%). Par contre, dans les eaux sous-jacentes, 97% de la population est constituée de diatomées. En Septembre, le groupe dominant est, de loin, celui des dinoflagellés, quel que soit le niveau de prélèvement. Plusieurs espèces de *Prorocentrum* sont particulièrement abondantes, en nombre d'individus, en surface comparativement aux eaux sous-jacentes, l'espèce dominante étant *P. lima* suivi par *P. micans* et *P. maximum*. Dans certains prélèvements superficiels, ce sont les dinoflagellés appartenant aux genres *Gonyaulax*, *Gymnodinium* et *Glenodinium*, qui constituent l'essentiel de la population.

Biomasse microplanctonique, chlorophylle a et assimilation photosynthétique.

Les teneurs moyennes en ATP (Tableau 4) observées dans le film de surface correspondent à des biomasses rarement atteintes dans le Golfe de Marseille. Les teneurs en Chl. a sont toujours supérieures à celles des autres prélèvements. On remarque aussi un rapport Chl. a/ATP presque deux fois plus faible dans les slicks qu'en dehors. Il n'est donc pas exclu qu'à côté des biomasses phytoplanctoniques importantes dans les slicks, ceux-ci soient le lieu d'une intense activité bactérienne associée à la charge en particules. En accord avec les fortes teneurs en ATP et Chl. a, les slicks se caractérisent par une production plus importante qu'à 0,50 m ; par contre, en leur absence, la production photosynthétique reste voisine à celle observée à 0,50 m. (Tableau 4).

DISCUSSION

L'accumulation de sels minéraux et matériel organique dans les films de surface, quelle qu'en soit l'origine (allochtone ou autochtone), peut constituer un des facteurs favorables au développement des organismes neustoniques, photoautotrophes et hétérotrophes. Par contre, un certain nombre de contraintes liées à ce biotope sont susceptibles de s'opposer à une croissance des organismes : nous citerons l'éclairement (spectre à peut près complet dans les premiers mm de la colonne d'eau), mais aussi changements rapides et importants de la salinité ou de la turbulence.

A l'appui de l'hypothèse d'une population dans un état déficient sur le plan physiologique comme l'ont déjà signalé d'autres auteurs (Harvey, 1966 ; Marumo et al., 1971), nous citerons quelques éléments. Tout d'abord, l'observation au microscope nous montre, dans les films superficiels, la présence d'une fraction détritique importante (agglomérats jaunâtres, débris de diatomées). Les valeurs élevées du rapport C/N vont également dans ce sens, sans qu'on puisse préciser l'origine de cette matière organique. D'autre part, on remarque que si, en accord avec les fortes biomasses, les productions sont plus élevées dans les slicks, le

rapport P/B est nettement plus faible qu'à 0,50 m (Tableau 4). On pourrait alors postuler que les populations neustoniques sont dans un mauvais état physiologique ou plutôt ne sont pas viables.

D'autres éléments appuient, au contraire, l'hypothèse d'un phytoneuston adapté aux conditions de l'interface. L'observation au microscope met en évidence, à côté de débris cellulaires, la présence de cellules ayant gardé leur intégrité structurale. Mais de plus, les populations du film de surface sont assez particulières par rapport à 0,50 m, avec en général une dominance de dinoflagellés. Par ailleurs, même si nous ne pouvons pas, en toute rigueur, calculer l'indice de diversité spécifique, il semble que le film de surface présente un caractère de paucispécificité.

Pourtant, nous avons pu montrer que les valeurs du rapport P/B, sont plus faibles dans les slicks qu'à 0,50 m. Cependant, il faut signaler que la valeur moyenne de ce rapport est de 3,1, dans le film superficiel, donc comparable à celle que Glover (1980) observe dans des cultures en phase exponentielle de croissance (3,5), et pas très éloignée des valeurs trouvées par Steeman-Nielsen et Hansen (1959) dans les eaux de surface en zone tempérée, où elles varient entre 4,0 et 4,2. Ce rapport peut être faussé par une surévaluation de la biomasse (B) ; celle-ci est en effet estimée par la mesure des pigments actifs qui peuvent être surévalués par la prise en compte des pigments non-fonctionnels (Loftus et Carpenter 1971). Mais la plus faible productivité de l'interface peut aussi être une réalité. En effet, si nous avons vu que les ressources trophiques ne peuvent être considérées comme limitantes, d'autres facteurs peuvent freiner la production, et en premier lieu, l'énergie lumineuse. Une telle photoinhibition ne se traduirait pas forcément par la mort cellulaire, mais par une baisse d'efficacité de la photosynthèse.

En fonction des observations précédentes, il nous est difficile de choisir entre les deux hypothèses formulées, bien que les données de la littérature semblent aller dans le sens d'une population déficiente sur le plan physiologique. Cependant, au vu des résultats obtenus, on pourrait penser que les organismes neustoniques, dans la zone néritique étudiée, correspondraient à des populations paucispécifiques pouvant s'adapter aux conditions sélectives de l'interface.

RESUME

Les prélèvements de surface récoltés selon Harvey (1966) sont comparés à ceux effectués à 0,50 m. Le film superficiel est le siège d'un enrichissement important en sels minéraux en matière organique inerte et en biomasse. Si en accord avec les fortes biomasses, les productions sont plus élevées dans les slicks, l'indice de productivité est nettement plus faible qu'à 0,50 m. Par ailleurs, l'interface se caractérise par des densités cellulaires phytoplanctoniques élevées et une composition spécifique particulière. Vu sa situation, ce biotope présente des conditions favorables au développement du microplancton (sels minéraux et matière organique) mais l'instabilité du milieu et les conditions extrêmes qui y règnent peuvent s'opposer à un développement biologique. Ces deux aspects sont discutés ici.

MOTS CLES

Microneuston ; slicks ; composition spécifique ; productivité ; Golfe de Marseille.

REMERCIEMENTS

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		Présence			Slicks		Absence	
		m	s	max.-min.	m	s	max.-min.	
P-PO ₄	mc	0,66	0,26	1,04-0,33	0,38	0,19	0,68 - 0,13	
	0,50 m	0,21	0,06	0,31-0,13	0,18	0,09	0,35 - 0,06	
N-NO ₃	mc	4,06	3,73	12,58-1,35	1,84	1,50	5,41 - 0,47	
	0,50 m	1,61	1,17	3,53-0,47	0,92	0,58	1,65 - 0,23	
N-NO ₂	mc	0,28	0,33	1,09-0,08	0,22	0,08	0,32 - 0,12	
	0,50 m	0,12	0,06	0,24-0,06	0,13	0,04	0,20 - 0,08	

Tableau 1. Valeurs moyennes (m), maximales et minimales (max.-min.) et écart-type (s) des teneurs en phosphates (P-PO₄), nitrates (N-NO₃) et nitrites (N-NO₂) en µg-at.l⁻¹, dans la microcouche de surface (mc) en présence et en absence de slicks et à 0,50 m.
Les effectifs sont égaux à 8 pour chaque paramètre.

		Présence			Slicks		Absence	
		m	s	max.-min.	m	s	max.-min.	
COP	mc	8,87	6,83	23,88-2,60	2,77	2,05	7,46-0,92	
	0,50 m	0,66	0,14	0,80-0,37	0,46	0,13	0,69-0,32	
NOP	mc	0,83	0,56	2,10-0,38	0,26	0,13	0,48-0,10	
	0,50 m	0,08	0,03	0,13-0,04	0,06	0,02	0,08-0,03	
C/N	mc	10,3	2,8	15,6 -6,1	9,9	6,3	15,6 -7,8	
	0,50 m	8,9	3,3	14,2 -5,1	8,0	2,3	11,6 -5,1	

Tableau 2. Valeurs moyennes (m), maximales et minimales (max.-min.) et écart-type (s) des concentrations en carbone (COP) et azote organiques particuliers (NOP) en mg.l⁻¹, et du rapport C/N, dans la microcouche de surface (mc) en présence et en absence de slicks et dans les eaux sous-jacentes (0,50 m).
Les effectifs étant égaux à 8 pour chaque paramètre.

	01.06.1979		05.09.1979		07.09.1979		12.09.1979		13.09.1979	
Cellules.ml ⁻¹	mc	0,50m	mc	0,50m	mc	0,50m	mc	0,50m	mc	0,50m
BACILLARIOPHYCEES										
<i>Leptocylindrus danicus</i> Cleve	70,0	617,0	-	-	-	-	-	-	-	-
<i>Rhizosolenia</i> sp.	-	110,0	-	-	-	-	-	-	-	-
<i>Nitzschia delicatissima</i> Cleve	-	97,0	-	0,02	-	-	0,1	-	-	-
Autres	-	2,6	6,0	0,3	3,5	0,02	0,7	0,3	13,0	-
DINOPHYCEES										
<i>Glenodinium</i> spp.	-	-	173,7	0,3	-	-	0,8	-	-	-
<i>Gonyaulax</i> spp.	-	-	9,6	-	-	0,1	4,7	0,5	3,6	0,5
<i>Gymnodinium</i> spp.	423,5	-	11,4	0,04	-	-	1,0	-	-	0,1
<i>Prorocentrum lima</i> (Ehr.) Dodge	-	-	17,7	0,08	-	-	0,2	-	-	-
<i>P. micans</i> Ehrenberg	-	-	3,3	0,2	4,5	0,02	-	0,3	15,0	0,7
<i>P. triestinum</i> Schiller	255,0	8,8	1,4	-	-	-	-	-	-	-
Autres	0,2	14,2	2,4	0,2	-	0,06	2,5	0,4	1,1	1,7
Total diatomées plus dinoflagellés.	748,7	849,6	225,5	1,1	8,0	0,2	10,0	1,5	32,7	3,0

Tableau 3. Densités des principales espèces phytoplanctoniques (diatomées et dinoflagellés) dans les films de surface (mc) et dans les eaux sous-jacentes (0,50 m).

		Présence			Slicks			Absence		
		m	s	max.-min.	m	s	max.-min.	m	s	max.-min.
ATP	mc	3,93	4,25	13,90- 0,51	0,70	0,26	1,11 - 0,32			
	0,50 m	0,49	0,23	0,78- 0,07	0,40	0,26	0,84 - 0,08			
Chl. <u>a</u>	mc	4,06	2,33	7,91- 0,57	1,55	0,63	2,71 - 0,52			
	0,50 m	0,99	0,69	1,89- 0,12	0,97	0,67	2,21 - 0,14			
P	mc	13,74	12,13	36,22- 2,31	3,62	1,85	6,90 - 1,48			
	0,50 m	8,61	8,56	27,56- 0,45	4,36	2,65	7,59 - 0,92			
Chl. <u>a</u>	mc	1,4	0,9	3,0 - 0,4	2,3	0,9	4,1 - 1,1			
ATP	0,50	1,9	0,9	3,3 - 0,5	2,6	0,9	5,5 - 1,0			
P/B	mc	3,1	1,5	6,0 - 1,2	2,5	0,6	3,5 - 1,9			
	0,50	9,1	6,9	24,6 - 3,2	5,1	1,4	6,6 - 3,4			

Tableau 4. Valeurs moyennes (m), valeurs maximales et minimales (max.-min.) et écart-type (s) des facteurs estimatifs de la biomasse, adenosine triphosphate (ATP) et chlorophylle a (Chl.a) en $\mu\text{g.l}^{-1}$, de la production photosynthétique (P) en $\mu\text{g.c.l}^{-1}.\text{h}^{-1}$ et des rapports Chl.a/ATP et Production/Chl.a (P/B) en présence et absence de slicks dans la microcouche (mc) et à 0,50 m. Les effectifs (n) sont égaux à 8, à l'exception des valeurs de production en absence de slicks (n=6).

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Walt Reue

nuclear
phosphates
sulfates
CA water.

fil. conf. of all

① water causes river
blindness
contaminants ?

② Speculation - -
DMS - forests / esp.
Rainforests → do not have similar
conveyor belt. clouds??
re. seed

Amazon - presence of forests
increases amt of
conduit of recycling ∴

evapotranspiration
plus catch $\rightarrow$ stays in
canopy.

water stays in basin.

before enough water to
cause rainfall
ex. redwoods in CA.

fresh water
cloud forest

water condenses on
surface $\rightarrow$ trickles down
flows like at

PHOTOCOPY
PRESERVATION

Give back



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Not a membrane -
floating material along
surface of ocean
organic

certain orgs use it as a
place to gather food.

oil can disturb it --
Anything that is suspended -
floating can disturb or
destroy it

org. matter --
if fats & lipids it
might [?] persist & less
soluble organic.



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Phosphorus always there -
essential
Sulfates " " for.
Fibrous & Hyperthermal
vents -
near coastal effects
nonpoint source runoff
eutrophication
Red tides - brown tides.
Acid deposition.

3/28/91

Kirchhoff



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Nanta

gyp v. small orgs -
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"Newton net"

→ this is

not ocean-wide
Gulf of Mexico - kept collecting

Radioactivity

→ The Russians messed up the
oceans.

abt. 10 yrs. ago - on British ships
off UK near radioactive dump.

smuggled to U.S.

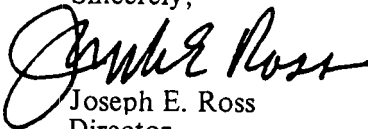
measured → Fe^{55} → radioactive
iron -- only comes from Russians.



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Correlation of ^{210}Po and ^{210}Pb enrichments in the sea-surface microlayer with neuston biomass

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Abstract—Samples of the surface microlayer, of bulk seawater from 20-cm depth and of the neustonic organisms inhabiting the top 5 cm of the sea were collected at regular intervals over a period of 17 months at a site 3 km off Monaco and analysed for the naturally occurring radionuclides ^{210}Po and ^{210}Pb . Enrichment of ^{210}Po in the microlayer compared with the bulk seawater was always observed, and the degree of enrichment was found to be correlated significantly with the neuston biomass per unit volume. Enrichment of ^{210}Pb in the microlayer was also observed, but only under the higher neuston biomass conditions. The $^{210}\text{Po} : ^{210}\text{Pb}$ ratio was always higher in the microlayer than in the bulk seawater. Additional information was obtained from ^{210}Po measurements made on the bulk seawater in which the neuston had been collected and in which it had stood for periods of 2 to 4 h. These showed that the neuston lost ^{210}Po to the water at a rate of about 1 pCi g⁻¹ dry biomass h⁻¹. A significant flux of ^{210}Po from bulk seawater to the surface microlayer, and thence possibly to the atmosphere, is estimated. This flux is mediated by the biota, and will vary seasonally with the planktonic biomass. Under high biomass conditions a similar flux for ^{210}Pb may also be significant. An association of ^{210}Po with the organic cycle at the top of the sea, and with marine bacteria in particular, is suggested.

INTRODUCTION

The nuclide ^{210}Po ($T_{1/2} = 138$ days) is the last radioactive member of the ^{238}U series; it arises from the decay of ^{210}Pb ($T_{1/2} = 22$ y) via the intermediary of ^{210}Bi ($T_{1/2} = 5$ days). The main source of ^{210}Pb in the surface layer of the ocean is natural atmospheric fall-out; there is a small ^{210}Po contribution in this fall-out as well, but this is negligible in comparison with ^{210}Po produced in the surface layer from the decay of ^{210}Pb (SHANNON, CHERRY and ORREN, 1970; BACON, SPENCER and BREWER, 1976). ^{210}Po is heavily concentrated by most marine organisms and is the main contributor to the natural radiation dose received by such organisms (CHERRY and SHANNON, 1974); it is intimately associated with biological processes in the ocean (HEYRAUD and CHERRY, 1979; CHERRY and HEYRAUD, 1981). The association of ^{210}Pb with marine biological processes is less, as is indicated by the changes in the $^{210}\text{Po} : ^{210}\text{Pb}$ activity ratio: about 0.1 in the atmospheric fall-out, 0.5 in surface seawater, 2 in planktonic faecal pellets, 7 in phytoplankton, 30 in zooplankton, and 100 in the crustacean hepatopancreas (TUREKIAN, NOZAKI and BENNINGER, 1977; BISHOP, EDMOND, KETTEN, BACON and SILKERS, 1977; BEASLEY, HEYRAUD, HIGGO, CHERRY and FOWLER, 1978; HEYRAUD and CHERRY, 1979). Both ^{210}Po and ^{210}Pb have become increasingly important as tracers in the study of marine geochemical processes, and both are removed rapidly from the surface layer

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of the ocean. Most investigators agree that this rapid removal results in some way from biological activity (BACON, SPENCER and BREWER, 1980). An association between biological productivity and ^{210}Po : ^{210}Pb distributions is then a logical possibility, and some indications of such an association have been observed (THOMSON and TUREKIAN, 1976). It is probably a consequence of the greater involvement of ^{210}Po in biological activity that the removal time for ^{210}Po from the surface layer (about 0.6 y) is usually shorter than it is for ^{210}Pb , by a factor of up to 8 (BACON *et al.*, 1980; this paper cites the numerous previous residence time estimates). Removal times from the deep sea are also shorter for ^{210}Po than for ^{210}Pb (THOMSON and TUREKIAN, 1976; BACON *et al.*, 1976, 1980), but it is not known if this too reflects association with biological activity. The actual removal process in both the surface layer and in the deep sea is almost certainly on sinking particles. Whether these are fine particulates which have scavenged the two nuclides or whether they are larger aggregates such as zooplankton faecal pellets has been a matter of some debate; insofar as removal from the surface layer is concerned, the present evidence favours the larger aggregates (CHERRY, FOWLER, BEASLEY and HEYRAUD, 1975; BACON *et al.*, 1976; BISHOP *et al.*, 1977; BEASLEY *et al.*, 1978; BACON *et al.*, 1980). How exactly the nuclides become associated with sinking particulates is not clear; since most of the ^{210}Pb in surface waters is of atmospheric origin, a study of the topmost portion of the surface layer of the ocean seemed indicated. At the top of this topmost portion is the surface microlayer, a region which is characterized from the chemical point of view by an enrichment in organic matter and in certain trace elements (DUCE, QUINN, OLNEY, PIOTROWICZ, RAY and WADE, 1972; BARKER and ZEITLIN, 1972; PIOTROWICZ, RAY, HOFFMAN and DUCE, 1972; WALLACE and DUCE, 1975, 1978a, b; HUNTER, 1980). A recent article by BACON and ELZEMAN (1980) reported the enrichment of both ^{210}Po and ^{210}Pb in this microlayer. From the biological point of view the microlayer is known to contain an enrichment in micro-organisms and bacterioneuston (HARVEY, 1966; HARVEY and BURZELL, 1972; SIEBURTH *et al.*, 1976), while the top 5 cm of the ocean has an elevated biomass of living plankton (neuston), dead plankton (particularly crustaceans), and bacteria (ZAITSEV, 1971). For a complete picture it seems important to have data for ^{210}Po and ^{210}Pb in the neuston as well as in the microlayer and in bulk surface seawater. The present paper reports such data.

METHODS

Samples of microlayer water, bulk seawater from a depth of about 20 cm, and neuston were collected concurrently between February 1980 and July 1981 at a site 3 km offshore from Monaco. Collections were scheduled at approximately monthly intervals but were dependent on calm sea conditions with an unbroken sea surface. Unlike BACON and ELZEMAN (1980) we did not collect only when visible surface slicks were present; indeed, we avoided sampling in such areas. In the 17-month period we found satisfactory conditions on 10 occasions; the relative lack of samples during winter months reflects the adverse weather situation at this season. Microlayer samples were collected using the technique of GARRETT (1965): our stainless-steel screen, mesh size 475 μm , samples the upper $150 \pm 30\text{-}\mu\text{m}$ layer. Sample sizes were 1.5 l for both microlayer and bulk seawater samples. Immediately after collection of the water samples, neuston from the top 5 cm of the sea was collected in a 15-min trawl using a neuston net, mesh size 680 μm , constructed from a drawing kindly supplied by R. Vaissiere and based on the design of ZAITSEV (1971, Fig. 17). In both water samples and in the neuston ^{210}Po was measured using standard techniques involving alpha-particle

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detection of ^{210}Po plated onto a silver disc (HALLDEN and HARLEY, 1960; MILLARD, 1963; FLYNN, 1968; SHANNON and ORREN, 1970). A second plating and counting some four or five months later measured ^{210}Po which had grown in from ^{210}Pb subsequent to the first plating, thus determining ^{210}Pb . The measurements on the water samples reflected total, i.e., soluble plus particulate, concentrations of the two nuclides. The measurements on the neuston were made on a sample taken after the neuston had been standing in the water in which it had been collected for between 2 and 4 h. At the end of this time the neuston and any large debris were removed from the water with a strainer. For most collections measurements were also made on the seawater in which the neuston had been standing. This water was filtered through 1.2- μm Millipore filters and ^{210}Po and ^{210}Pb measured in the filter and filtrate.

To complement the *in situ* neuston and seawater data ^{210}Po and ^{210}Pb in total (i.e., rain water plus dry deposition) atmospheric fall-out were measured on a monthly basis over the period April 1980 to March 1981. Collections were made using a Teflon-coated funnel feeding into a pre-acidified polyethylene bottle: the collection site was on a roof in Monaco some 3½ km from the locality where the seawater and neuston samples were collected.

RESULTS

The *in situ* ^{210}Po and ^{210}Pb concentrations in the neuston, in the microlayer, and in the bulk seawater are listed (Table 1). Examination of the table shows: (a) The ^{210}Po concentrations are always higher in the microlayer than in the bulk seawater. This is not always so for ^{210}Pb . (b) The microlayer concentrations vary considerably between collections. The mean values ($\pm 1\sigma$) are $0.098 \pm 0.070 \text{ pCi l}^{-1}$ for ^{210}Po and $0.084 \pm 0.053 \text{ pCi l}^{-1}$ for ^{210}Pb . In the bulk seawater from 20 cm, on the other hand, the variation is remarkably small; means are $0.026 \pm 0.008 \text{ pCi l}^{-1}$ for ^{210}Po and $0.051 \pm 0.016 \text{ pCi l}^{-1}$ for ^{210}Pb . (c) The $^{210}\text{Po} : ^{210}\text{Pb}$ ratio is always higher in the microlayer (mean, 1.2 ± 0.5) than in the bulk seawater (0.6 ± 0.3). (d) The concentrations of the nuclides in the neuston vary with the species present. *Anomalocera patersoni*, blue copepods found in eight out of ten collections, have the highest ^{210}Po concentrations, mean $16 \pm 8 \text{ pCi g}^{-1}$ dry biomass, as compared with $4 \pm 5 \text{ pCi g}^{-1}$ in other samples (insects excluded). Levels of ^{210}Pb are comparable in both the *Anomalocera* (mean $0.5 \pm 0.3 \text{ pCi g}^{-1}$) and the other samples (mean $0.6 \pm 1.3 \text{ pCi g}^{-1}$). (e) The $^{210}\text{Po} : ^{210}\text{Pb}$ ratio is extremely variable in the neuston, ranging from 2 to 77. The lowest value is in an atypical sample composed of insects living on the surface. (f) The highest concentration factor for neuston with respect to bulk seawater, 1.7×10^5 for ^{210}Po , is found in the single sample composed of completely pure *Anomalocera* (wet:dry ratio equal to 9). This sample was selected on an individual animal basis. The other *Anomalocera* samples, less pure, show lower concentration factors, down to 2×10^4 for ^{210}Po . These lower factors probably reflect a degree of contamination of these samples by organisms less rich in ^{210}Po than *Anomalocera*.

The enrichment factors of ^{210}Po and ^{210}Pb in the microlayer with respect to the bulk seawater, calculated from the Table 1 data, are compared with an estimation of the biomass per unit volume in the 5-cm neuston layer (Table 2). This estimation was calculated on the basis of the total biomass collected and the approximate volume of water swept by the neuston net during the trawl. The enrichment factor is always > 1 for ^{210}Po , and is always larger for ^{210}Po than it is for ^{210}Pb . For both nuclides there is a significant correlation between the enrichment factor and the estimated biomass ($r = 0.77$ for ^{210}Po and 0.81 for ^{210}Pb , both significant at the 1% level). For ^{210}Pb , however, the enrichment factors do not differ significantly from unity except for three of the four highest biomass concentrations.

Table 1. In situ concentrations of ^{210}Po and ^{210}Pb in neuston, in the 150- μm surface microlayer and in bulk seawater from 20-cm depth

Collection and date	Neuston composition	Neuston (pCi g^{-1} dry)			Microlayer (pCi l^{-1})			Bulk seawater (pCi l^{-1})		
		^{210}Po	^{210}Pb	$^{210}\text{Po}:^{210}\text{Pb}$	^{210}Po	^{210}Pb	$^{210}\text{Po}:^{210}\text{Pb}$	^{210}Po	^{210}Pb	$^{210}\text{Po}:^{210}\text{Pb}$
P ₁	26.2.80 Copepods, amphipods, eggs, larvae	14.2 ± 0.8	3.2 ± 0.1	4	0.038 ± 0.006	0.074 ± 0.009	0.5	0.019 ± 0.005	0.057 ± 0.009	0.3
P ₂	24.4.80 Copepods, salps, eggs	1.1 ± 0.1	0.03 ± 0.02	37	0.152 ± 0.010	0.156 ± 0.012	1.0	0.025 ± 0.005	0.052 ± 0.008	0.5
P ₃	24.4.80 <i>Anomaloera patersoni</i>	9.7 ± 0.6	0.35 ± 0.07	28	0.152 ± 0.010	0.156 ± 0.012	1.0	0.025 ± 0.005	0.052 ± 0.008	0.5
P ₄	24.4.80 Siphonophores	2.3 ± 0.2	0.03 ± 0.01	77	0.152 ± 0.010	0.156 ± 0.012	1.0	0.025 ± 0.005	0.052 ± 0.008	0.5
P ₅	3.6.80 Eggs, larvae	3.4 ± 0.2	0.33 ± 0.07	10	0.050 ± 0.007	0.042 ± 0.008	1.2	0.030 ± 0.005	0.042 ± 0.008	0.7
P ₆	7.7.80 <i>Anomaloera patersoni</i>	24.4 ± 0.5	0.36 ± 0.04	68	0.225 ± 0.012	0.169 ± 0.013	1.3	0.044 ± 0.008	0.052 ± 0.008	0.8
P ₇	1.8.80 <i>Anomaloera patersoni</i>	12.7 ± 0.4	0.21 ± 0.02	60	0.060 ± 0.005	0.059 ± 0.008	1.0	0.021 ± 0.005	0.075 ± 0.010	0.3
P ₈	28.8.80 <i>Anomaloera patersoni</i>	16.8 ± 0.8	1.1 ± 0.2	15	0.051 ± 0.007	0.043 ± 0.008	1.2	0.019 ± 0.005	0.050 ± 0.010	0.4
P ₉	28.8.80 Insects	6.1 ± 0.9	2.5 ± 1.2	2	0.051 ± 0.007	0.043 ± 0.008	1.2	0.019 ± 0.005	0.050 ± 0.010	0.4
P ₁₀	29.9.80 <i>Anomaloera patersoni</i>	10.5 ± 0.8	0.44 ± 0.18	24	0.039 ± 0.005	0.050 ± 0.008	0.8	0.028 ± 0.005	0.076 ± 0.008	0.4
P ₁₁	6.4.81 <i>Anomaloera patersoni</i> (pure)	28.3 ± 2.4	0.74 ± 0.25	38	0.064 ± 0.007	0.056 ± 0.010	1.1	0.018 ± 0.004	0.047 ± 0.008	0.4
P ₁₂	6.4.81 Remainder of neuston	0.9 ± 0.1	0.04 ± 0.03	23	0.064 ± 0.007	0.056 ± 0.010	1.1	0.018 ± 0.004	0.047 ± 0.008	0.4
P ₁₃	9.6.81 <i>Anomaloera patersoni</i>	6.2 ± 0.4	0.30 ± 0.03	21	0.097 ± 0.007	0.041 ± 0.013	2.3	0.028 ± 0.004	0.026 ± 0.013	1.1
P ₁₄	9.6.81 Remainder of neuston	3.1 ± 0.1	0.22 ± 0.10	14	0.097 ± 0.007	0.041 ± 0.013	2.3	0.028 ± 0.004	0.026 ± 0.013	1.1
P ₁₅	9.7.81 <i>Anomaloera patersoni</i>	15.6 ± 0.6	0.62 ± 0.25	25	0.200 ± 0.020	0.153 ± 0.008	1.3	0.027 ± 0.004	0.032 ± 0.006	0.9

Table 2. Estimated

Collection and date

P ₃	26.2.80
P ₄	24.4.80
P ₅	3.6.80
P ₆	7.7.80
P ₇	1.8.80
P ₈	26.8.80
P ₉	29.9.80
P ₁₀	6.4.81
P ₁₁	9.6.81
P ₁₃	9.7.81

* Concentration

The ^{210}Po data collected are sum statistical errors contents of the w parison with the *in situ* ^{210}Po con correlation exists seawater collecte 0.98, $P < 0.001$ standards, varied from 2 to 4 h. I biomass per unit small considering; between this loss calculates the los 1.2- μm filter), th rate and the bioi single collection. longer significan gives mean loss

Table 3

Collection	Bi (g)
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P ₆	
P ₇	
P ₈	
P ₉	
P ₁₁	
P ₁₃	

* Concentration

Table 2. Estimated in situ neuston biomass in the top 5 cm of the sea and the corresponding enrichment factors for ^{210}Po and ^{210}Pb in the surface microlayer and in bulk seawater

Collection and date	Approximate biomass (mg dry l ⁻¹)	Microlayer enrichment factors*	
		^{210}Po	^{210}Pb
P ₃ 26.2.80	0.027	2.0 ± 0.6	1.3 ± 0.3
P ₄ 24.4.80	0.042	6.1 ± 1.3	3.0 ± 0.5
P ₅ 3.6.80	0.006	1.7 ± 0.4	1.0 ± 0.3
P ₆ 7.7.80	0.069	5.1 ± 1.0	3.3 ± 0.6
P ₇ 1.8.80	0.028	2.9 ± 0.7	0.8 ± 0.2
P ₈ 26.8.80	0.002	2.7 ± 0.8	0.9 ± 0.2
P ₉ 29.9.80	0.002	1.4 ± 0.3	0.7 ± 0.1
P ₁₀ 6.4.81	0.015	3.6 ± 0.9	1.2 ± 0.3
P ₁₁ 9.6.81	0.069	3.5 ± 1.3	1.6 ± 0.9
P ₁₃ 9.7.81	0.077	7.4 ± 1.3	4.8 ± 0.9

* Concentration of nuclide in microlayer divided by concentration in bulk seawater.

The ^{210}Po data from the measurements made on the water in which the neuston had been collected are summarized in Table 3. The corresponding ^{210}Pb data are not cited because the statistical errors were often too large to enable meaningful conclusions to be drawn. The ^{210}Po contents of the water which had been exposed to the neuston are all strikingly high in comparison with the *in situ* levels of Table 1. Clearly, the neuston had lost ^{210}Po to the water. The *in situ* ^{210}Po concentrations in neuston in Table 1 have been corrected for this loss. A strong correlation exists between the ^{210}Po enrichment factor of this water, relative to the bulk seawater collected a few hours earlier, and the biomass per unit volume in the container ($r = 0.98$, $P < 0.001$). These biomasses, measured exactly and artificially high by natural standards, varied from 0.1 to 2.9 g l⁻¹. The time of exposure of the water to the neuston varied from 2 to 4 h. If one calculates the total ^{210}Po lost by the neuston to the water per unit biomass per unit time, one finds a mean of 1.2 ± 0.5 pCi g⁻¹ h⁻¹. The variation is surprisingly small considering the wide range of biomasses involved; there is moreover no correlation between this loss rate and either the biomass or the ^{210}Po concentration in the neuston. If one calculates the loss rate on the basis of the 'soluble' ^{210}Po (i.e., that ^{210}Po not retained on the 1.2- μm filter), the mean rate is 0.7 ± 0.6 pCi g⁻¹ h⁻¹. A significant correlation between this rate and the biomass ($r = 0.84$, $P < 0.01$) does exist, but this correlation is due largely to a single collection, P₆, for which the biomass is the highest observed. The correlation is no longer significant if this collection is excluded. Excluding P₆ from the loss-rate calculations gives mean loss rates for total and 'soluble' ^{210}Po of 1.0 ± 0.6 and 0.5 ± 0.3 pCi g⁻¹ h⁻¹,

Table 3. Enrichment of ^{210}Po in seawater exposed to artificially high neuston biomasses

Collection	Biomass (g dry l ⁻¹)	Exposure time (h)	^{210}Po in neuston seawater (pCi l ⁻¹)	^{210}Po enrichment factor*	% ^{210}Po retained in 1.2- μm filter
P ₃	0.3	2½	0.45 ± 0.04	24 ± 6	74
P ₄	2.9	3	19.0 ± 0.07	432 ± 80	15
P ₇	1.8	3	5.1 ± 0.2	243 ± 59	15
P ₈	0.1	4	0.65 ± 0.04	34 ± 10	54
P ₉	0.1	3	0.37 ± 0.03	13 ± 3	76
P ₁₁	1.1	3	2.7 ± 0.2	96 ± 16	48
P ₁₃	0.8	2	1.42 ± 0.07	53 ± 9	23

* Concentration in seawater exposed to neuston divided by concentration in bulk seawater (Table 1).

respectively. In the Table 3 collections the predominant component of the samples was usually *A. patersoni*, and the animals were mostly alive, even at the end of the 2 to 4-h exposure period. A similar experiment with seawater exposed to dead *Anomalocera* gave similar loss rates, viz. $0.6 \text{ pCi g}^{-1} \text{ h}^{-1}$ and $0.3 \text{ pCi g}^{-1} \text{ h}^{-1}$ for total and 'soluble' ^{210}Po , respectively.

It should be borne in mind that the term 'soluble' is operational. In three cases the $1.2\text{-}\mu\text{m}$ filtrate was subsequently refiltered on a $0.22\text{-}\mu\text{m}$ Millipore, and evidence of some association of ^{210}Po with bacterial-size particles was obtained. In the first case (collection P₇) the water had been exposed to living *Anomalocera* and the proportion of the total ^{210}Po associated with particles between 0.22 and $1.2 \mu\text{m}$ was found to be 11%. In the second case the water had been exposed to dead *Anomalocera*, and the proportion of ^{210}Po associated with such particles was 35%. In the third case (collection P₉) the $1.2\text{-}\mu\text{m}$ filtrate was allowed to stand, covered, at room temperature for 24 h before filtering again through $1.2 \mu\text{m}$ and then through $0.22\text{-}\mu\text{m}$ filters. Nearly all (95%) of the ^{210}Po which had passed through the $1.2\text{-}\mu\text{m}$ filter 24 h previously was found to be associated with 'particles', 74% of it on the $1.2\text{-}\mu\text{m}$ filter and 21% on the $0.22\text{-}\mu\text{m}$ filter. Moreover, 90% of the ^{210}Po in the final filtrate was found to be non-dialysable (Visking membrane, nominal molecular weight limit 6000 to 8000).

The results of the fall-out measurements showed that over the year in question the ^{210}Pb atmospheric deposition averaged $245 \text{ pCi m}^{-2} \text{ month}^{-1}$, or $0.65 \text{ dpm cm}^{-2} \text{ y}^{-1}$ in the units in which such fluxes are usually cited. The ^{210}Po deposition averaged $0.04 \text{ dpm cm}^{-2} \text{ y}^{-1}$, or about 6% of that for ^{210}Pb . These fluxes are unexceptional in comparison with previously published values from other locations; the ^{210}Pb deposition flux is in good agreement with theoretical model predictions for our geographic location (TUREKIAN *et al.*, 1977).

DISCUSSION

The fact that ^{210}Po and ^{210}Pb can be enriched in the surface microlayer, observed previously by BACON and ELZEMAN (1980), is confirmed by the results reported in this paper. Our data were obtained over a longer time-scale and under less selective conditions than those of Bacon and Elzerman and they show two additional features of particular importance. Firstly, the ^{210}Po enrichment in the microlayer relative to bulk seawater is consistently higher than that for ^{210}Pb ; secondly, the degree of enrichment of both nuclides is higher at high neuston biomasses. It is clear that one is dealing with a seasonally varying situation, a fact which must be borne in mind in the discussion which follows. The nuclide fluxes we shall calculate must be regarded as rough estimates of quantities which are in reality dependent on time as well as location.

An excess of an element in the oceanic surface can arise either by downward deposition from the atmosphere or by upward concentration from within the sea (PIOTROWICZ *et al.*, 1972; PEIRSON, CAWSE and CAMBRAY, 1974), and it is of interest to estimate the upward concentration fluxes for ^{210}Po and ^{210}Pb so as to compare them with the measured atmospheric deposition fluxes. Before doing so it is worth emphasizing the situation insofar as the $^{210}\text{Po} : ^{210}\text{Pb}$ activity ratio is concerned. We find this to be 0.06 in the atmospheric fall-out, about 0.6 in bulk seawater and always higher, at about 1.2, in the surface microlayer. It is difficult to imagine a mechanism whereby atmospheric deposition, with its low $^{210}\text{Po} : ^{210}\text{Pb}$ ratio, could result in such a preferential enrichment of ^{210}Po relative to ^{210}Pb in the microlayer. (Simple preferential retention of atmospherically deposited ^{210}Po in the microlayer would require the existence in the removal process from this layer of a material with a

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$^{210}\text{Po} : ^{210}\text{Pb}$ ratio even lower than that in atmospheric fall-out, and no such material is known.) On the other hand, the fact that a significant correlation exists between the ^{210}Po enrichment in the microlayer and the neuston biomass, plus the fact that this biomass comprises material with a $^{210}\text{Po} : ^{210}\text{Pb}$ ratio substantially larger than unity, suggest strongly that for ^{210}Po the enrichment in the microlayer is due largely to an upward concentration flux which is mediated by the biota. Our data indicate further that ^{210}Po is lost from both living and dead neustonic organisms to the surrounding seawater. It is likely that at least the particulate fraction of this released ^{210}Po is transferred subsequently to the surface microlayer, probably via a bubble flotation mechanism of the type which has been proposed to account for the transport of particulate trace metals from within the sea to the ocean surface (WALLACE and DUCE, 1975, 1978a, b; HUNTER, 1980).

Assuming that bubble flotation is indeed the mechanism giving rise to the upward concentration flux, we can estimate this flux by using the WALLACE and DUCE (1975) estimate for the bubble flotation flux of particulate organic carbon (POC) in coastal waters, viz. $4.4 \mu\text{g m}^{-2} \text{ s}^{-1}$. If we assume further (WALLACE and DUCE, 1975; HUNTER, 1980) that the ^{210}Po to organic carbon ratio in marine microplankton is the same as that in organic detrital matter capable of bubble flotation, then we can use published data for Mediterranean microzooplankton, plus an assumption that dry microzooplankton contains 25% organic carbon, to calculate the ^{210}Po bubble flotation flux. Taking ^{210}Po as 13 pCi g^{-1} dry microzooplankton (HEYRAUD and CHERRY, 1979) results in a ^{210}Po bubble flotation flux of $2.3 (10^{-4}) \text{ pCi m}^{-2} \text{ s}^{-1}$ or $1.6 \text{ dpm cm}^{-2} \text{ y}^{-1}$. This is 40 times larger than the measured ^{210}Po atmospheric deposition flux. In coastal regions it thus seems likely that the upward concentration flux of ^{210}Po to the microlayer is substantially larger than the downward atmospheric flux. In the open ocean, where the POC bubble flotation flux is about two orders of magnitude lower than in a coastal region because of the lower POC content (WALLACE and DUCE, 1975), the two fluxes might well be competitive. Our microlayer data and these flux estimates support the postulate that the sea surface is a potential source of aerosols enriched in ^{210}Po and that there may as a result be an excess ^{210}Po flux from the sea surface to the atmosphere (TUREKIAN, KHARKAR and THOMSON, 1974; LAMBERT, SANAK and ARDOUIN, 1974). The enrichment of trace metals in marine aerosols has been investigated by several authors (HOFFMAN, DUCE and HOFFMAN, 1972; BARKER and ZEITLIN, 1972; PEIRSON *et al.*, 1974), and the general problem of the global cycles of atmospheric trace metals has been considered by LANTZY and MACKENZIE (1979). These latter authors suggested that for Hg, As, and Se, and perhaps for other 'atmophile' metals, there are significant fluxes from the sea surface to the atmosphere. They suggest that such fluxes may be the result of "low-temperature volatilization, probably as a result of biological activity". Perhaps ^{210}Po falls into this category of elements as well.

For ^{210}Pb the relative importance of the upward flux is less clear. In microzooplankton ^{210}Pb is at about 0.4 pCi g^{-1} dry biomass (HEYRAUD and CHERRY, 1979); using this low concentration and the coastal POC bubble flotation flux already cited (WALLACE and DUCE, 1975) implies that the upward ^{210}Pb flux in our coastal situation is about $0.05 \text{ dpm cm}^{-2} \text{ y}^{-1}$, or <10% of the atmospheric deposition flux. Our Table 1 data show that ^{210}Pb enrichment of the microlayer is not the general rule, as is the case for ^{210}Po , but that it does usually occur when the neuston biomass is elevated. This suggests that the upward flux of ^{210}Pb to the microlayer is not generally dominant, even in a coastal region, but that it cannot be ignored at those times of the year when the plankton biomass is at its maximum.

The ^{210}Po loss-rates from neuston (mostly copepods) which we measured are also worthy

of comment. The average neuston biomass during the period covered by the investigation was about 0.03 mg dry biomass l^{-1} ; the average zooplankton biomass over the whole 100-m surface column would have been less than this, probably about 0.01 mg dry biomass l^{-1} (NIVAL, NIVAL and THIRIOT, 1975). If we assume that half the particulate ^{210}Po lost by the zooplankton participates in the upward concentration flux (WALLACE and DUCE, 1978b) then a particulate ^{210}Po loss rate of about 0.5 pCi $g^{-1} h^{-1}$ implies that the ^{210}Po concentration flux above 1 cm^2 in a 100-m column will be about 0.5 dpm $cm^{-2} y^{-1}$. Although no more than a crude estimate, the fact that this flux is the same order of magnitude as the estimated ^{210}Po bubble flotation flux suggests that the ^{210}Po loss rate we observed in an artificially high biomass situation may be a reasonable approximation to that which occurs under natural conditions.

The size of the samples we collected was not large enough to enable us to investigate directly the form of ^{210}Po in the microlayer. For certain other trace elements, however, enrichments in this layer are observed in the particulate and organic fractions rather than in the inorganic fraction (BARKER and ZEITLIN, 1972; PIOTROWICZ *et al.*, 1972).

Our data from the measurements in the water which had been exposed to neustonic copepods suggest that the same is likely to be the case for ^{210}Po as well. More hypothetically, these data hint at a possible association of ^{210}Po with marine bacteria, since (a) the proportion of ^{210}Po associated with particles between 1.2 and 0.22 μm was substantially higher when the copepods were dead than when they were living (35 as compared with 11%) and (b) 95% of the 'soluble' ^{210}Po was found to be converted to the 'particulate' form after 24 h (74% being retained on a 1.2- μm filter and 21% on a 0.22- μm filter). The dialysis experiment, where some 90% of the ^{210}Po in the final filtrate was found to be non-dialysable, suggests further that even the 'soluble' ^{210}Po might be associated with large organic molecules (molecular weight >6000). A recent paper by EPPLEY *et al.* (1981) evaluated the role of microzooplankton in the flux of carbon to bacteria and dissolved organic matter, and the conceptual model proposed involved carbon flows from plankton to dissolved organic carbon to bacteria and then back into plankton. A similar cycle for ^{210}Po , well-known to be associated with biological processes in the sea, seems to be a strong possibility, particularly in the neuston layer and the microlayer which are rich in dead organisms and marine bacteria (ZAITSEV, 1971; BEZDEK and CARLUCCI, 1972). Marine bacteria are major users of dissolved organic matter in the euphotic zone and are implicated in the formation of particulate organic matter (WANGERSKY, 1976): at the top of the ocean it seems plausible that they play an important role in the transformation of ^{210}Po from the soluble to the particulate form.

CONCLUSION

Enrichment of ^{210}Po in the microlayer compared with bulk seawater is observed in all of our samples, and the fact that this enrichment is correlated significantly with the neuston biomass is probably the most important result which emerges from our data. For the average neuston biomass of about 0.03 mg dry biomass l^{-1} , a least squares fit to our data shows that the ^{210}Po concentration in the microlayer is about three times higher than the mean of 0.026 pCi l^{-1} observed in the bulk seawater. The ^{210}Po fluxes which we can calculate or estimate are worth summarizing (Table 4). In this table the radioactive ingrowth, radioactive decay, and removal fluxes are all calculated directly from our experimental data. The zooplankton loss and the bubble flotation fluxes are, on the other hand, rough estimates only, but the fact that they are of the same order of magnitude as the removal flux suggests that the

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Table 4. Measured, calculated, and estimated ^{210}Po fluxes in $\text{dpm cm}^{-2} \text{y}^{-1}$

Atmospheric deposition to the surface of the UML*	0.04
Radioactive ingrowth from ^{210}Pb in the UML†	2.08
Radioactive decay of ^{210}Po in the UML‡	1.06
Removal flux from the UML§	1.06
Loss from zooplankton inside the UML	0.5
Upward bubble flotation to the microlayer	1.6

* Measured flux (see Results). UML = upper mixed layer, comprising a 0 to 100-m box including the microlayer.

† Calculated using mean bulk seawater ^{210}Pb concentration of 0.051 pCi l^{-1} from Table 1.

‡ Calculated using mean bulk seawater ^{210}Po concentration of 0.026 pCi l^{-1} from Table 1.

§ Removal by all processes other than radioactive decay. Calculated from UML steady-state balance.

|| Estimates (see Discussion).

processes which they represent play a non-negligible role in ^{210}Po dynamics near the ocean surface. More detailed flux balance calculations cannot be performed at present, because we lack essential data. We do not know what fraction of the upward bubble flotation flux to the microlayer appears subsequently as an upward flux of ^{210}Po from the microlayer to the atmosphere, nor do we know to what extent the ^{210}Po enrichment of the microlayer is recycled downwards into the bulk seawater. The details of the mechanisms involved are, moreover, not yet clear, although the inference, from our laboratory experiment data, that bacteria may play an important role in the ^{210}Po cycle seems worthy of further investigation.

Insofar as ^{210}Pb is concerned, the microlayer enrichment factors are always less than they are for ^{210}Po , and they do not differ significantly from unity except at high neuston biomass concentrations. The biologically mediated processes we have discussed for ^{210}Po are likely to be less important for ^{210}Pb , although they may become significant under high biomass conditions and/or in regions of particularly high biological productivity.

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A comparative survey of neuston: geographical and temporal distribution patterns

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Abstract

Neuston samples were collected from 149 stations during a voyage west from Fiji to the Bay of Biscay from August 1979 through November 1980. The neustonic fauna was counted and assigned to 50 species groups, chosen to represent the most numerous animals in the hauls. Analyses of neustonic concentration and population structure showed regional and temporal differences in the fauna. Permanent inhabitants of the surface waters, the euneuston, were most numerous in the open tropical waters of the Central Indian Ocean. In contrast, the temporary neuston, which was composed of juveniles, vertical migrants and the uppermost individuals from deeper populations, attained its greatest concentration in the upwelling region of the Somali Current and at inshore stations around the Indonesian archipelago and in the Gulf of Aden and Red Sea. Heavy rains adversely affected the neuston, possibly by diluting the surface waters. Both neustonic groups were sparsely represented in the cooler waters of the Mediterranean Sea and the eastern Atlantic Ocean. At night considerable immigration occurred into the neustonic zone, and the mean faunal density at dusk was 21 times greater than was found at mid-day. Surface waters were inhabited by the developmental stages of many species, and eggs and juveniles of both vertebrates and invertebrates were consistently present in the hauls.

Introduction

A classification scheme of marine neuston, the biota of the ocean surface, was adopted by David (1967) and Zaitsev (1970) and subsequently condensed by Weikert (1972). Organisms which permanently inhabit the sea surface as adults are termed "euneuston". The euneuston includes the

epineuston which is represented solely by the insect genus *Halobates* (Cheng, 1973) living on top of the surface film; and the pleuston, e.g. *Physalia physalis* and *Velella velella*, which have submerged bodies and aerial flotation devices. Submerged organisms which inhabit the surface waters of the pelagic zone, the hyponeuston, may be euneustonic e.g. some pontellid copepod species, or members of the temporary neuston which is composed of facultative and pseudoneustonic species. Animals which concentrate at the surface only during certain hours, generally at night, and the neustonic larval and juvenile stages of planktonic, nektonic or benthic species, together comprise the facultative neuston. The third neustonic group, the pseudoneuston, consists of stray individuals of species which have their maximum concentration deeper in the water column.

Zaitsev (1970), basing his data largely on studies undertaken in the Black and Caspian Seas, described the neustonic zone as a nursery for many vertebrate and invertebrate species. The majority of neuston research has been limited to investigations into the taxonomy and distribution of epineuston (Herring, 1958; Cheng, 1973) and pleuston (Laursen, 1953; Savilov, 1968; Cheng, 1975). Although the distribution of euneustonic pontellid copepods has been examined in the Atlantic (Weikert, 1973, 1975), Pacific (Heinrich, 1960, 1964, 1969, 1971; Sherman, 1963, 1964; Voronina, 1964) and Indian (Voronina, 1962) Oceans, studies on the temporary hyponeuston have been confined to the relatively small areas of the Black and Caspian Seas (Zaitsev, 1961, 1963, 1970), the Gulf of Marseilles (Champalbert, 1969, 1970, 1971a, b), and the north east Atlantic Ocean (Hempel and Weikert, 1972; Weikert, 1972). In contrast to Zaitsev's (1970) observations in Soviet waters, Hempel and Weikert (1972) found that embryonic and larval invertebrates were sparse in the hyponeuston of the north-east Atlantic; however, large numbers of juvenile fish were noted by all these authors. The current study was undertaken to examine the structure of neustonic populations in neritic and oceanic environments by day and night.

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Materials and methods

Neuston samples were collected from the brigantine "Eye of the Wind". The sampling programme extended from August 1979 to November 1980, during which time neuston was collected from 149 stations (Fig. 1) between Fiji and the Bay of Biscay.

Initially, neuston was collected using a net of the David design (David, 1965a), but the bulk and weight of the catamaran net frame made the apparatus unsuitable for use on a small ship. A system was then devised which was used throughout the sampling programme, in which the mouth (10×30 cm) of a neuston net measuring 200 cm in length was mounted on a tubular stainless steel frame. The frame was weighted with 4 kg of lead and a towing bridle was attached to each corner. The net was towed at up to 6 knots, 10 m away from the hull, clear of the ship's bow wave, from a boom mounted forward on the vessel. It was possible for one person to launch and retrieve the neuston net. The net was constructed of 335 μ m aperture mesh, with a 20 cm deep band of 2 mm mesh around the mouth. Samples were taken over a time period of 30 min at an average speed of 4.5 knots, so, assuming total efficiency, the net sampled to a depth of 5 cm and filtered 62.5 m³ of water at each station. Morris (1980) ascribed an efficiency rating of 25 to 50% to the David net. The net assemblage used in this survey followed wave contours, and from visual observation, maintained a high fishing efficiency in all but the rough seas with short wave intervals which were encountered in the Atlantic. Neuston were always captured from the windward side of the ship to avoid the barren leeward zone caused by the shadowing effect of the hull (Zaitsev, 1970).

In addition to local time and geographical coordinates, data on sea state, sea and air temperature, cloud cover and

wind speed were noted for each sample. The samples were preserved in 10% neutral formalin and subsequently counted in Bogorov trays. Individual animals were assigned to 50 taxa chosen to represent the most numerous animals in the hauls. All other animals were classified in a single miscellaneous group. Some animals, especially euneustonic types, were classified to genus.

Results

Geographical distribution of neuston

The voyage (Fig. 1) was divided into 9 geographical areas (Table 1). Locations of surface currents are described by Sverdrup *et al.* (1942) and Cotter (1965). Between Fiji and Mombassa (Areas 1–5; Fig. 1a) the stations were situated mainly in the South Equatorial Current. A station near the African coast between the Seychelles and Mombassa (Area 5) was also influenced by the Somali Current. Stations off the east coast of Africa and the west coasts of Portugal and Spain (Areas 7–9) were influenced by the Somali and Portuguese Currents, respectively. The majority of stations throughout the voyage were within 200 km of land and the only oceanic samples were taken in the west Pacific and Indian Oceans (Fig. 1a).

The neuston caught varied in concentration and diversity from one part of the voyage to another (see Table 1). The greatest mean neuston concentrations were found in Areas 6 and 7 along the east and north-east coasts of Africa. Oceanic samples yielded low neuston concentrations of relatively great species diversity. Neuston from the 3 oceanic stations in the western Pacific (Fig. 1a) were less concentrated and more diverse than the mean population values obtained for Area 1 (Table 1). These 3 oceanic stations were similar in neuston concentration (1 400 ani-

Table 1. Collection data on neuston populations and surface-water temperatures (*T*) at stations in the 9 areas between Fiji and the Bay of Biscay. Temperature data are means plus (standard deviation); other values are means ($\pm$ standard errors)

Area (date)	Route traversed	No. stns	Animals per haul	Taxa per haul	T (°C)
Area 1 (Aug.–Sept. 1979)	Fiji–Papua New Guinea (Pacific Ocean, Solomon Sea)	14	5 600 (2 949)	13 (1.6)	28.1 (2.1)
Area 2 (Jan.–March 1980)	Papua New Guinea–Sulawesi (Banda Sea)	7	3 300 (1 537)	15 (0.9)	29.2 (0.4)
Area 3 (April 1980)	Sulawesi–Jakarta (Banda, Flores, and Java Seas)	13	8 600 (2 218)	19 (1.2)	25.9 (0.2)
Area 4 (May–June 1980)	Jakarta–Seychelles (Indian Ocean)	33	1 700 (263)	20 (0.8)	28.1 (0.6)
Area 5 (July 1980)	Seychelles–Mombassa (Indian Ocean)	7	5 700 (2 270)	22 (1.1)	26.3 (0.4)
Area 6 (August 1980)	Mombassa–Cap Guardafui (Indian Ocean)	6	16 100 (5 879)	26 (2.5)	28.4 (2.9)
Area 7 (Aug.–Sept. 1980)	Cap Guardafui–Port Suez (Gulf of Aden, Red Sea)	18	21 100 (6 402)	19 (1.6)	31.2 (2.1)
Area 8 (Sept.–Oct. 1980)	Port Said–Gibraltar (Mediterranean Sea)	44	2 900 (571)	14 (0.8)	21.2 (3.2)
Area 9 (Nov. 1980)	Gibraltar–Bay of Biscay (Atlantic Ocean)	7	1 100 (489)	9 (1.7)	17.6 (1.3)

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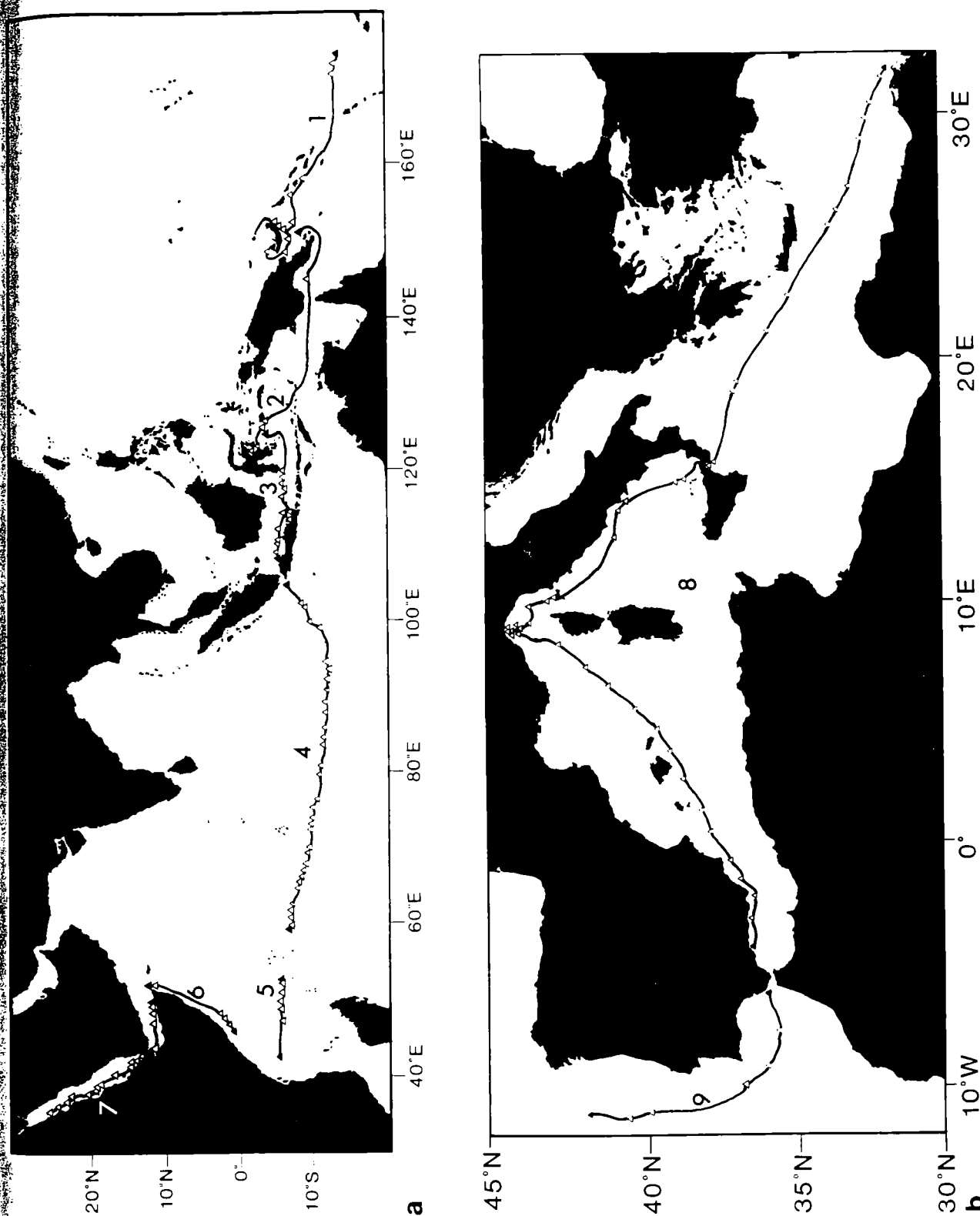


Fig. 1. Neuston sampling stations (triangles) and areas between (a) Fiji and Port Suez (Areas 1–7), and (b) between Port Said and the Bay of Biscay (Areas 8 and 9) from August 1979 through November 1980

imals from 21 taxa per haul) to the Indian Ocean stations (1 700 animals from 20 taxa per haul – Area 4). Between the Seychelles and Mombassa (Area 5), the concentration and diversity of neuston were intermediate between the levels noted in the central Indian Ocean (Area 4) and the Somali Current (Area 6). In Indonesian waters, neuston was found in lower numbers in the Banda Sea, to the east

of Sulawesi, than in the Flores and Java Seas to the north east and north of Java.

Stations between Fiji and Sulawesi (Areas 1 and 2) were sampled when torrential rains promoted terrestrial run-off from the many islands in the area. High numbers of phytoplankton (*Rhizosolenia alata* and *Chaetoceros* spp.) were prominent in the surface waters. However, the con-

centration and diversity of the neuston was lower here than in the coastal waters of Indonesia and north-east Africa (Areas 3 and 6). Samples from the cooler waters of the Mediterranean and Atlantic also contained few individuals and species groups (Areas 8 and 9).

The percentage composition of neuston varied geographically (Table 2). Copepods were the dominant taxa in every area, forming over 50% of the neuston in all but Area 3. Gastropod larvae were the most common component of

the molluscan neuston except in Areas 3 and 8 (pteropods) and 7 (bivalves). Cephalopods and the nudibranch *Glaucus* spp. were sparsely represented in the hauls. *Glaucus* spp. was always observed associated with chondrophores. Cephalopods were caught mainly at night, although 2 argonauts were captured in daylight.

Copepods and siphonophores formed the most consistent components of the neuston throughout the cruise (see Table 2). Chaetognaths formed 9.3% of the neustonic

Table 2. Percentage composition of neuston populations in different geographical areas (see Table 1)

Taxa	% composition of neustonic fauna of Area No.:									
	1-9	1	2	3	4	5	6	7	8	9
Siphonophores										
(excluding <i>Physalia physalis</i>)	2.3	2.5	1.9	3.1	1.9	1.3	2.9	1.8	3.3	0.9
<i>Physalia physalis</i>	0.1	0.1	0	0	0.2	0.1	0.1	0.1	0	0
<i>Porpita</i> spp.	0.1	0	0	0.1	0.4	0.1	0.1	0.1	0.1	0
<i>Veilella</i> spp.	0.1	0.1	0.2	0.1	0.7	0.1	0.1	0.1	0.1	0.3
Medusae	0.4	0.2	0.5	2.0	0.2	0.1	0.3	0.2	0.1	0
Ctenophores	0.1	0.1	0	0	0.1	0	0	0	0	0
Nematodes	0.1	0.1	0	0	0	0	0	0	0	0
Platyhelminthes	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.5	0
Polychaeta larvae	0.1	0.2	0.1	0.1	0.1	0	0.1	0.1	0.1	0
Polychaete adults	0.1	0.3	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0
Trochophore larvae	0.3	0	0	0	0.1	0	2.7	0.1	0	0
Brachiopod larvae	0.1	0	0	0	0.1	0	0.1	0.1	0	0
Cyphonautes larvae	0.2	0	0	0	2.4	0.1	0.1	0.1	0	0.9
Cladocerans	0.5	0.1	0.2	0.4	0.1	0.1	0.1	0.2	2.8	0.2
Ostracods	1.5	0.1	5.4	3.3	0.7	0.1	0.1	2.0	0.8	0.1
Cirripede nauplii	0.1	0.1	0.2	0	0.1	0	0.1	0.1	0.2	0
Cirripede cyprids	0.1	0.1	0.1	0	0.2	0.1	0.1	0.1	0.2	0
Copepods	64.5	82.0	82.5	47.0	68.5	83.4	66.9	58.9	71.5	86.1
Isopods	0.3	0	0	0	0.1	0	0	0.1	1.6	3.3
Amphipods	0.9	0.7	0.2	1.2	0.9	0.5	1.6	0.8	0.5	1.1
Mysids	1.5	0.5	0.3	0.8	6.4	1.1	3.3	0.3	3.4	1.0
Euphausiid calyptopis	0.3	0.1	0.1	0.1	0.1	0.1	1.6	0.1	0.6	0.4
Euphausiid furcilia	0.2	0.1	0.1	0.3	0.2	0.1	0.1	0.3	0.3	0.4
Euphausiid adults	0.1	0.1	0.2	0.2	0.1	0	0.1	0.2	0.2	0.1
Penaeids	0.1	0	0	0.1	0.1	0.1	0.1	0.1	0.1	0
Sergestid larvae	0.2	0.4	0	0	0.1	0.2	0.3	0.1	0.3	0
<i>Lucifer</i> spp.	1.7	0.1	0.2	1.9	0.2	0.9	0.3	3.3	0.3	0
Caridean larvae	0.2	0.2	0.1	0.3	0.2	0	0.4	0.2	0.2	0
Brachyuran zoeae	0.4	0.1	0.1	0.4	1.6	0	0.2	0.4	0.5	0
Brachyuran megalopa	0.3	0.4	0.2	0.1	1.0	1.0	0.1	0.3	0.3	0.4
Anomuran larvae	0.1	0.3	0.1	0.1	0.1	0	0.1	0.1	0.1	0
Stomatopod larvae	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.1
Phyllosoma larvae	0.1	0.1	0	0.1	0.1	0	0	0	0	0
<i>Halobates</i> spp. eggs	0.1	0.1	0.2	0.1	0.7	0.1	0.1	0.1	0	0
<i>Halobates</i> spp. juveniles	0.2	0.1	0.1	0.4	1.1	0.5	0.2	0.1	0	0
<i>Halobates</i> spp. adults	0.1	0.1	0	0.1	0.5	0.2	0.1	0.1	0	0
Gastropod larvae	1.3	1.3	2.6	1.9	2.8	0.5	1.5	1.0	1.2	0
Bivalve larvae	0.9	0.1	0	0.1	0.2	0.2	0.2	2.1	0	0
<i>Ianthina</i> spp.	0.1	0.1	0	0.1	0.1	0	0.1	0.1	0.2	0
Pteropods	0.9	0.2	0.8	2.8	0.4	0.5	0.5	0.4	2.0	0.1
Heteropods	0.5	0.1	1.1	0.1	0.8	0.3	0.1	0.8	0.5	0
Cephalopods	0.1	0.1	0.1	0	0.1	0	0.1	0	0	0
<i>Glaucus</i> spp.	0.1	0	0	0	0.1	0	0.1	0.1	0	0
Echinoderm larvae	1.5	0.1	0.1	10.6	1.7	0.1	0.1	0.1	0.7	0
Chaetognaths	3.0	5.2	0.4	1.3	2.3	2.7	9.3	1.5	3.7	1.0
Salps	1.1	1.8	0.9	5.2	0.7	2.8	0.3	0.1	0.3	0.1
Doliolids	0.3	0.2	0.1	0.3	0.1	0.2	0.1	0.1	1.5	0.2
Larvaceans	0.9	1.8	0.1	0	0.1	2.0	5.2	0.2	0.3	0.2
Fish eggs	12.0	0.3	0.3	14.0	1.1	0.4	0.5	24.3	0.6	2.9
Fish	0.5	0.6	0.4	1.6	0.6	0.5	0.3	0.2	0.3	0.4
Miscellaneous	0.2	0.1	0.5	0.2	0.1	0.1	0.1	0.1	1.0	0.2

population represented constituted on a very much more concentrated Java Sea area. Larvaceans, which were found in 10 samples, are also present in the Atlantic (see Table 1) where doliolids and larvaceans were found in 10 samples. The current, though, was not in the same direction. Most of the numbers were of low density in the neustonic air. Frequently, north-western Trochophore larvae from the stations in the South Atlantic were noted. Less than 1% of the stations, however, (Areas 3 and 4) were noted. 3 cm deep, they were represented in the adult and adult. Many or juvenile composed of trochophore carideans and echinoderms. In the Atlantic, they were more common. The relative area, but the neustonic. Euneu the centre, represented in the Atlantic tropical. *Physalia* not found spp. and in low numbers in species open tropical. Champs

population in the Somali Current (Area 6), but were poorly represented in the Banda Sea (Area 2), where they constituted only 0.4% of the total population. Salps were relatively more numerous in the southern stations, and large concentrations occurred frequently in hauls made in the Java Sea and the east Indian Ocean. The doliolids and larvaceans, which were less numerous than salps in southern samples, also displayed regional differences in abundance (see Table 2). The Mediterranean Sea was the only area where doliolids formed more than 1% of the neuston. Larvaceans, which were otherwise a minor neustonic constituent, amounted to 5.2% of the total population in the Somali Current. The Pyrosomidae was found throughout the tropics, but in low numbers.

Most taxa formed less than 0.5% of total neustonic numbers. Some, such as platyhelminthes and polychaetes were of low but widespread abundance. Others, especially the neustonic juvenile stages of benthic, planktonic or nektonic animals, occurred sporadically. Echinoderm larvae frequently blocked the net at stations situated around the north-western coast of Java in Area 3 (Table 2). Trochophore and cyphonautes larvae, which were absent from the neuston in most hauls, were relatively numerous in the Somali Current (trochophores), and in Area 4 stations between the Chagos Ridge and the Seychelles (cyphonautes).

Less than 50 fish eggs were found per sample at most stations, but at some stations in the Java and Red Seas (Areas 3 and 7; see Table 2) 10^4 to 10^5 eggs per sample were noted. These concentrations formed surface slicks 2 to 5 cm deep, visible from the ship's deck. Fish were represented in the neuston by eggs and juveniles; yolk sac larvae and adults were rarely captured.

Many species were present in the neuston only as eggs or juvenile stages. Twenty-one of the taxa were entirely composed of juvenile animals, 10 of which (larval trochophores, brachiopods, cyphonautes, sergestids, carideans, stomatopods, phyllosomas, gastropods, bivalves and echinoderms) were absent from the surface waters as adults. In penaeids and cephalopods, the juvenile stages were more numerous at the sea surface than the adults. The relative numbers of juveniles differed from area to area, but they were a numerically important constituent of the neuston in all areas studied.

Euneuston were found in the greatest concentrations in the central Indian ocean (Area 4) and were poorly represented in the cooler waters of the Mediterranean Sea and Atlantic Ocean (see Table 2). *Veleva* spp. was the only tropical euneuston found during the Atlantic passage. *Physalia physalis*, *Halobates* spp. and *Glaucus* spp. were not found north of Suez, although chondrophores, *Ianthina* spp. and cirripede cyprids were noted in the Mediterranean in low numbers. The temporary surface fauna were diverse in species groups but relatively sparsely represented in open tropical water. Tropical forms of euneuston have pigimentary (Herring, 1967) and structural (Savilov, 1968; Champalbert, 1981) adaptations to withstand the con-

ditions of high UV radiation, heat, and fluctuations in salinity caused by evaporation and precipitation.

Siphonophores (excluding *Physalia physalis*), cladocerans and isopods were most abundant in the Mediterranean sea (Table 2). Floating tar, plastic and wood provided habitats in the Mediterranean and Atlantic for *Idotea metallica* and *I. baltica*, the most numerous isopod species in the samples.

Diel occurrence

Neuston concentrations and species diversity were greater by night than by day (Fig. 2). Species diversity reached a maximum between 03.00 and 04.00 hrs. There was a lag period at dawn before many nocturnal groups departed from the surface waters; diversity increased again between 17.00 and 18.00 hrs.

Eleven species groups demonstrated pronounced differences between the day and night populations. The mean numerical night:day ratios of these groups are shown in Table 3 together with probability values derived from the Mann-Whitney *U* statistic for differences between day and

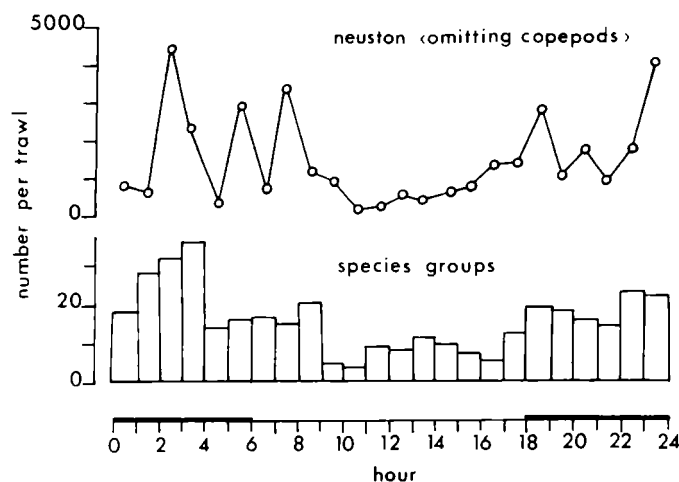


Fig. 2. Neuston concentrations and species diversities during the day/night cycle (abscissa)

Table 3. Mean night:day concentration ratios and probability values (*P*) for differences between night and day populations derived from Mann-Whitney *U* statistic for taxa exhibiting pronounced diel variations in surface numbers

Taxa	Night:day	<i>U</i> test (<i>P</i>)
Cyphonautes larvae	24:1	< 0.01
Ostracods	41:1	< 0.01
Isopods	15:1	< 0.02
Amphipods	11:1	< 0.05
Mysids	25:1	< 0.01
Euphausiid furcilia	11:1	< 0.05
Euphausiid adults	7:1	< 0.05
Sergestid larvae	9:1	< 0.05
Caridean larvae	13:1	< 0.02
Brachyuran megalopa	11:1	< 0.02
Heteropods	9:1	< 0.05

night. Stations in the Mediterranean and the Atlantic were visited during the autumn when the day/night periods were similar to those in the tropics. Hours from 06.00 to 18.00 and from 18.00 to 06.00 were thus regarded as day and night, respectively for all the stations. The diel rhythms of the 3 most numerous species exhibiting great differences in day and night concentrations are shown in Fig. 3. Most taxa were taken in greatest numbers before 21.00 hrs or after 03.00 hrs; only 4 groups peaked between these times.

Pteropods, medusae and *Lucifer* spp. (Fig. 4), together with 3 less numerous taxa (salps, euphausiid calyptoses and echinoderm larvae), also exhibited diel variations. They differed from the groups in Fig. 3, in that maximal numbers were noted just before dusk or after dawn.

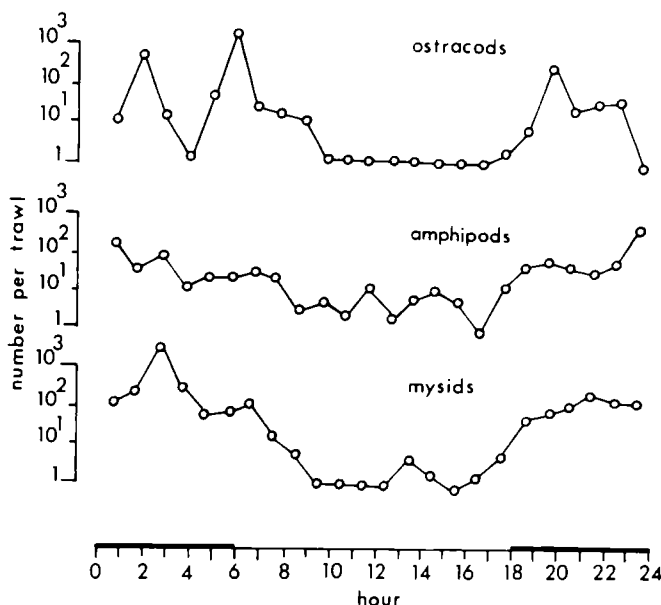


Fig. 3. Diel rhythms of 3 most numerous taxa exhibiting pronounced variations

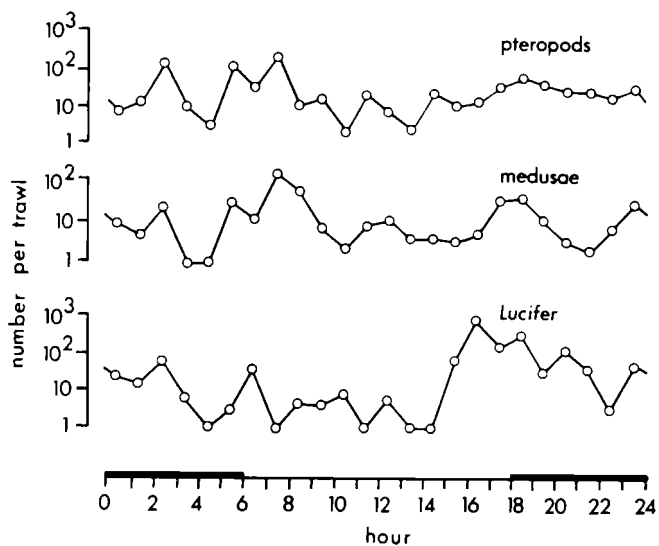


Fig. 4. Diel rhythms of 3 taxa entering the neuston in pre- or post-crepuscular hours

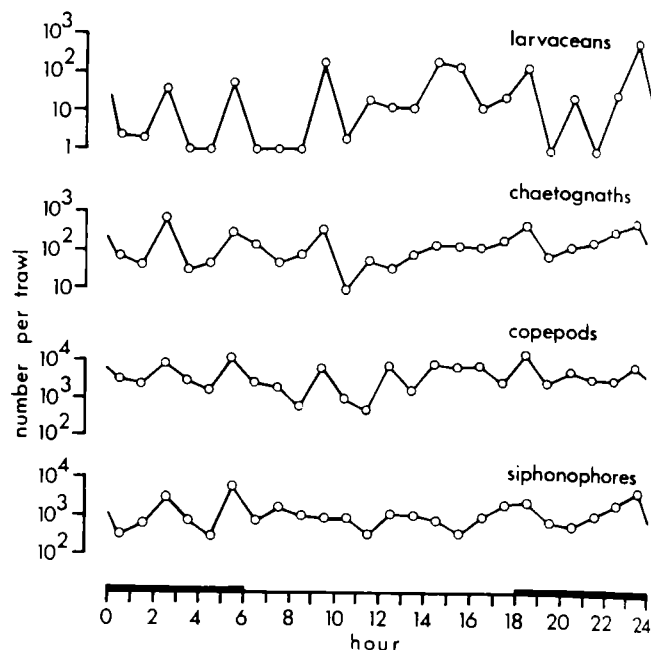


Fig. 5. Diel rhythms of the 4 most numerous taxa

Four of the most numerous taxa showed little diel variation (Fig. 5), and high numbers were frequently caught during daylight. Individual genera and species within these taxa had different diel rhythms: e.g. some pontellid copepod species are euneustonic, whereas other copepods are members of the temporary neuston (Heinrich, 1960).

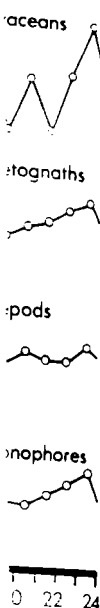
In contrast to the 17 groups which were more common by night, cladocerans, brachyuran zoaea, gastropod larvae, doliolids and fish showed no diurnal variation in abundance. However, myctophids were dominant by night and exocoetids by day. The mean night:day ratio of the most numerous euneustons, *Physalia physalis*, *Porpita* spp., *Veella* spp. and *Halobates* spp., was 1.01:1. Individuals of 13 species groups were caught in insufficient numbers to draw conclusions on diurnal variations.

Discussion and conclusions

The euneuston had a characteristic geographical distribution in the current survey, the greatest concentrations occurring in the central Indian Ocean. Temporary neuston, which do not possess structural (Savilov, 1968; Champalbert, 1981) and pigmentary (Herring, 1967) adaptations, were relatively sparse in open tropical waters. The lack of phytoplankton in oceanic tropical waters also imposes limitations on the surface fauna, since low nutrient levels limit phytoplankton growth and intense radiation precludes phytoplankton from the surface layers (Albright, 1980). Therefore, as Bieri (1966) demonstrated, euneuston are carnivores or omnivores, and herbivorous animals (with the exception of stray pseudoneustonic individuals) will be poorly represented in the neustonic zone.

Large concentrations of temporary neuston were found in samples taken from the Somali Current on the eastern coast of Africa, and from stations proximal to land around

tion pattern.



diel variability caught in these lid copepods are common larvae, in abundance and the most common species, diatoms of others to

1 distribution neuston. Champ-tations. lack of imposes levels in pre-bright. neuston animals (individuals)

found eastern around

the Indonesian archipelago and in the Gulf of Aden and Red Sea. In upwelling and coastal areas, the growth of temporary neuston is encouraged by the proliferation of phytoplankton supported by nutrient-rich waters (Hempel and Weikert, 1972). Numbers of temporary neuston were low in Areas 1 and 2, where dilution of surface waters by rain may have inhibited the neuston.

In Mediterranean and north-east Atlantic waters, large quantities of floating tar, plastic, and other debris frequently blocked the net. These materials provided a habitat for a category of euneuston which was rarely evident in unpolluted waters. The epifauna on tar and other materials has been described by David (1965 b); the isopods *Idotea metallica* and *I. baltica* were dominant, and hydroids, *Eepas* spp., polychaete worms and egg masses were also present. Facultative and pseudoneustonic animals were sparse in the Mediterranean and Atlantic (see Table 1).

With the exception of floating eggs, which are ontogenetic members of the facultative neuston, it is generally not possible to differentiate between facultative and pseudoneustonic species in the absence of a series of nets fishing at different depths. Champalbert (1969) estimated that, globally, 27% of fish eggs occurred in surface waters; however, few neustonic fish eggs or yolk-sac larvae were found by Hempel and Weikert (1972) in their investigations in boreal and sub-tropical waters. Yolk-sac larvae were also absent during the voyage of "Eye of the Wind", although post-larval stages of many species were found. This indicates that after hatching, the larval fish descend in the water column, rising to the surface again as young juveniles.

Hempel and Weikert (1972) calculated that crustaceans constituted 94% and molluscs 5.4% of the total invertebrate neuston in the north east Atlantic, Norwegian and North Seas. Crustacea were also dominant in the 9 areas examined during the current survey. However, they composed over 90% of the total population only in Atlantic samples. At low latitudes, coelenterates and tunicates, in addition to molluscs, formed numerically important components of the neuston fauna.

The majority of taxa were sparsely represented. Individual samples, however, were often dominated by one of the minor species groups. Successive hauls taken within short time-intervals would frequently furnish different faunal assemblages, as noted by David (1965 b) and Craddock (1969). This was especially evident with the capture of bioluminescent ostracods at night, when the animals formed discrete visible patches 1 to 5 m in diameter. Discontinuous distributions also occurred amongst euneustonic organisms. Larger pleustal forms were arranged in Langmuirian windrows (Langmuir, 1938), particularly in the calm waters of the Red Sea, and the catch rate was dependent on the ship's track across these windrows. Faunal sensitivity to vibrations of the net may have caused avoidance, influencing the catch rate. The most highly motile euneustont, *Halobates* spp., did not demonstrate any day/night differences in catch numbers, showing no evidence of visual net avoidance (Cheng and Holdway, 1983).

Diel variability patterns were determined on an hourly basis at all the sampling stations. Roe (1974) points out that combining observations from stations separated by time and distance results in defects in migratory analyses, since faunal responses may change seasonally and geographically. These inaccuracies could be corrected only if the same body of water was sampled over 24 h, which is a rare occurrence even in on-station analyses.

Neuston animals have been shown to migrate into the surface layers at night in the Gulf of Marseilles (Champalbert, 1971 b), the Black and Caspian Seas (Zaitsev, 1961, 1970), the western Indian Ocean (David, 1965 b) and the sub-tropical north-east Atlantic Ocean (Weikert, 1972). Similar increases in nocturnal neustonic concentration and diversity were also evident in the current survey, indicating that migratory activity may occur in many taxa. However, conclusive evidence of vertical migration requires sampling through the water column.

The greater faunal concentrations were found at dusk and dawn, and the least at mid-day. At dusk (18.00 to 19.00 hrs), a mean concentration of 21 300 animals/100 m³ was noted, and at dawn (05.00 to 06.00 hrs), 19 700 animals/100 m³ were found, whereas between 11.00 to 12.00 hrs only 1 000 animals/100 m³ resided in the neuston.

Weikert (1972) studied diel variability in the eastern Atlantic. He also found greater concentrations at twilight than at mid-day, but the concentrations were an order of magnitude lower than those found in the current survey, which refers mainly to tropical neuston.

Maximal species diversity (03.00 to 04.00 hrs) did not coincide with the greatest concentration of organisms. This suggests that there was a change over period when animals that had migrated to the surface early in the evening descended and later migrants ascended in the water column. The majority of the taxa demonstrating pronounced diel variations were juveniles, e.g. euphausiid furcilia, sergestid larvae and caridean larvae. Isolated individuals of these groups remained at the surface during the day after the main population had descended, showing that an animal can be pseudoneustonic in addition to being an ontogenetic and diel member of the facultative neuston.

Individual species within each group showed variations in behaviour: although *Idotea metallica* and *I. baltica* were euneustonic, isopods, as a species group, demonstrated strong diel variations with a night:day numerical ratio of 15:1. Some pontellid species and *Candacia ethiopica* were also euneustonic members of a taxa that was otherwise composed of facultative or pseudoneustonic species. Juvenile flying fish were the most numerous fish caught in morning samples. Although Zaitsev (1970) describes the Exocoetidae as euneustonic, their capture was infrequent when the sun was at its zenith. It was not determined whether increased net avoidance or a downwards migratory reaction caused the decrease in catch numbers during the hours of maximum daylight.

In all sampling areas the temporary neuston, composed of facultative and pseudoneustonic species, outnumbered the euneuston, both by day and, more markedly, by night.

The majority of temporary neuston residing in the surface waters during daylight were juvenile forms. At night the population was augmented by adults and additional juveniles which had ascended from deeper in the water column. In addition to larval and juvenile stages, solitary eggs and egg masses were a constant feature in the neuston hauls, indicating that the surface waters provide a habitat for the early developmental stages of many species.

Although patterns of neustonic geographical and temporal distribution have been determined, the factors controlling distribution warrant further investigation. Cloud cover and lunar radiation may influence the extent of immigration of temporary neuston into the surface waters, since in the tropics low radiation levels appeared to be associated with large neuston populations. The relationships between temporary and euneustonic species also require evaluation, to observe whether large populations of temporary neuston limit euneuston in coastal and upwelling areas. In contrast, carnivorous euneustonic species may influence temporary neustons by preying upon them. For example, pontellid copepods are predators of larval fish (Lillelund and Lasker, 1971) and the omnivorous or carnivorous feeding habits of other euneustonic species (Bieri, 1966) could have a significant effect on the numbers of the temporary inhabitants of the surface waters.

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L'HYPONEUSTON PERMANENT. APPROCHE ECOPHYSIOLOGIQUE DE LA RÉPARTITION DES PONTELLIDAE (CRUSTACEA, COPEPODA).

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Summary. — *The permanent hyponeuston. An ecophysiological approach to the distribution of the Pontellidae (Crustacea, Copepoda).* Neustonic populations and especially Pontellid copepods have a typical distribution near the surface in spite of possible rapid and large changes in environmental factors.

This paper summarizes observations and experimental studies carried out *in situ* and *in vitro*. They concern the effects of some environmental factors on the physiology and the behaviour of a few species of Pontellidae. The factors considered, light, pressure, temperature, salinity, trophic resources, were chosen according to their influence on planktonic animals on the one hand and to the importance of their variations in the superficial layer on the other hand.

It appears that Pontellidae have developed some characteristic morphological, physiological and behavioral adaptations. They are photosensitive and sensitive to pressure which increase their swimming and metabolic activity but delays egg hatching; furthermore, temperature diminution appears to induce upward movements. Changes in respiration in response to changes in temperature and salinity, and the distribution observed in the sea show that most Pontellidae are relatively stenothermic and stenohaline; they avoid polluted or turbid waters and waters of low salinity. Eventually, most of them disappear from the sea surface during the unfavorable season, and lay resting eggs that provide for repopulation.

Résumé. — Les populations neustoniques et notamment les copépodes Pontellidae présentent une distribution caractéristique à proximité de l'interface où les conditions ambiantes sont très particulières et susceptibles de changements rapides et importants.

Cette note résume plusieurs séries d'observations et expériences effectuées *in situ* et *in vitro*, qui concernent les effets de quelques facteurs du milieu sur la physiologie et le comportement des Pontellidae, les facteurs considérés, lumière, pression, température, salinité, et ressources trophiques ayant été choisis du fait de leur importance sur les organismes planctoniques d'une part, et de l'amplitude de leurs variations dans le biotope superficiel d'autre part.

Il apparaît que les Pontellidae sont sensibles à la lumière et à la pression, laquelle augmente leur activité natale et métabolique mais retarde l'éclosion de leurs œufs. Les Pontellidae sont également sensibles à la température dont les fluctuations provoquent des variations d'activité natale ainsi que des modifications de leur métabolisme respiratoire; relativement sténothermes, la plupart disparaissent pendant la mauvaise saison et pondent des œufs de repos qui éclosent quand les conditions redeviennent favorables. Enfin, les variations de répartition des espèces neustoniques qui ont été observées en milieu dessalé et/ou turbide ainsi que les variations de consommation d'oxygène consécutives à une diminution de salinité montrent que les Pontellidae sont relativement sténohalins.

Le biotope ultrasuperficiel est une fraction du pélagos d'une importance majeure dont les éléments vivants et non vivants constituent un écosystème bien individualisé, l'écosystème neustonique.

En raison de l'hydrodynamisme et des variations d'éclairement, de température et parfois même de salinité, ce milieu instable peut sembler peu favorable au développement et à la multiplication d'espèces non adaptées à ces conditions particulières. Toutefois, c'est un milieu où les ressources trophiques — ressources organiques non vivantes et vivantes, substances oligodynamiques (Daumas, 1974; Goering et Menzel, 1965; Zaitsev, 1968) — sont particulièrement abondantes et variées, certaines étant propres à l'interface, d'autres provenant des eaux sous-jacentes et d'autres enfin des terres émergées. Il est probable que cette richesse au plan trophique explique en partie l'abondance et la diversité de l'hyponeuston animal; celui-ci comprend une faune temporaire ainsi qu'une faune permanente caractéristique dont les espèces les plus typiques sont pour la plupart des copépodes Pontellidae qui appartiennent aux genres *Pontella*, *Anomalocera*, *Pontellopsis* et *Labidocera*.

Une des particularités des Pontellidae est leur répartition au voisinage de l'interface. En effet, leurs densités, pouvant atteindre 500/m³, sont maximales entre 0 et 10 cm et diminuent jusqu'à un mètre; par calme plat, il n'est pas rare de récolter dans les dix premiers centimètres jusqu'à 95 % des individus présents dans le premier mètre (Champalbert, 1969); il est évident que ce pourcentage est susceptible de varier légèrement en fonction des conditions météorologiques ainsi que des caractéristiques physico-chimiques des eaux (Champalbert, 1977).

La stratification particulière des espèces hyponeustoniques à proximité de la surface et leur maintien dans le biotope ultrasuperficiel sont assurés par des adaptations variées. Certaines concernent la pigmentation en bleu ou bleu-vert, fréquente chez de nombreuses espèces neustoniques (Wada, 1953; David, 1965, 1967; Zaitsev, 1964, 1968, 1970; Herring, 1967). Chez les Pontellidae, cette couleur est particulièrement intense; une caroténoprotéine bleue et cinq chromoprotéines, dont quatre vertes et une jaune (laquelle a des propriétés photosensibili-

satrice) ont été mises en évidence chez *Anomalocera patersoni* et *Pontella mediterranea* (cf. Momzikoff et Santus, 1981).

Le mode de locomotion constitue aussi une caractéristique des espèces superficielles (Lowndes, 1935; Lochhead, 1962). Les Pontellidae très actifs, maintiennent souvent leur côté dorsal ou leurs antennes au contact de la surface et sont capables d'éviter les prédateurs en effectuant des bonds de plus de 15 cm hors de l'eau (Wada, 1953; Zaitsev, 1971; Champalbert, 1981; Pérès, 1982). Cette aptitude au saut apparaît aussi chez de jeunes alevins (Zaitsev, 1971).

D'autres adaptations, qui concernent la physiologie et le comportement des Pontellidae, ont été étudiées chez quelques espèces de l'Atlantique (Anraku, 1964), du Pacifique (Ikeda, 1974; Omori, 1969) et de Méditerranée (Champalbert, 1975) où les deux espèces les plus abondantes du golfe de Marseille (*Anomalocera patersoni* et *Pontella mediterranea*) ont fait l'objet de recherches *in situ* et *in vitro* : une analyse de l'impact de quelques facteurs ambiants sur la répartition, la physiologie et les réactions comportementales des animaux a été envisagée, les facteurs considérés, lumière, pression, température, salinité, ressources trophiques ayant été choisis en raison de leur importance sur la physiologie et la répartition des organismes marins d'une part, et, d'autre part, en raison de l'importance de leurs variations à proximité de la surface.

INFLUENCE DES FACTEURS DU MILIEU SUR LA DISTRIBUTION, LA PHYSIOLOGIE ET LE COMPORTEMENT DES PONTELLIDAE.

LUMIÈRE

Les observations recueillies non seulement en différents secteurs de Méditerranée (Champalbert, 1971, 1975) mais encore en mer Noire (Zaitsev, 1962, 1971), dans l'océan Atlantique (Weikert, 1975) et dans l'océan Pacifique (Sherman, 1963; Guérédrat, 1970) montrent que l'étagement caractéristique des Pontellidae dans le premier mètre persiste jour et nuit. Toutefois, il y a des variations nycthémérales d'abondance et certains Pontellidae sont plus nombreux entre 0 et 10 cm pendant la nuit que pendant la journée. Ceci permet de penser que les espèces hyponeustoniques, comme la plupart des espèces planctoniques, peuvent effectuer des migrations verticales plus ou moins liées à des variations de lumière; le problème des fluctuations de la réparti-

tion verticale des Pontellidae en fonction des conditions d'éclairement a donc été appréhendé, en laboratoire, par une étude expérimentale de l'activité natatoire et des réactions d'orientation de quelques espèces (Champalbert, 1973b, 1975, 1976b, c, 1978, 1979a).

Influence de la lumière sur les réactions d'orientation

Des expériences faites à température constante sur les deux Pontellidae *Anomalocera patersoni* et *Pontella mediterranea*, étudiés isolément ou par lot d'individus avec une lumière horizontale blanche parallèle (intensités : 4000, 400, 40, 4 lux) ou colorée (violet, vert, bleu-vert, orange) ont montré d'une part, que ces espèces sont sensibles à la lumière et d'autre part, que leur orientation par rapport à la source est susceptible de changer à certaines intensités et/ou à certaines longueurs d'onde, pouvant être différentes selon le sexe et l'espèce (Champalbert, 1973b, 1975). Par ailleurs, le sens de l'orientation des individus est susceptible de changer sans changement apparent d'intensité lumineuse, ce qui permet de supposer qu'il existe un rythme endogène d'activité. De plus, les vitesses de déplacement les plus élevées ont généralement été observées chez les individus exposés aux plus fortes intensités expérimentales et chez *A. patersoni*, le nombre de réactions photopositives augmente quand la température diminue.

Influence de la lumière sur l'activité natatoire

Elle a été faite dans des cuves cylindriques de 15 cm de diamètre et de 30 à 80 cm de hauteur, sur des animaux pouvant se déplacer librement et détectés soit par des barrages photoélectriques soit par des sondes à scintillation ou des compteurs Geiger lorsqu'il s'agissait d'individus marqués à l'iode radioactif.

A la lumière naturelle, *Anomalocera patersoni* présente une activité natatoire rythmique différente de celle qui apparaît chez les individus gardés à l'obscurité totale. Les heures d'activité intense varient en fonction des conditions expérimentales et du sexe. Chez *Pontella mediterranea* et à l'obscurité, on a observé au cours de plusieurs expériences deux phases d'activité intense (l'une en fin d'après-midi et en début de nuit, l'autre peu après minuit) et deux phases d'activité plus réduite (l'une en fin de nuit, l'autre en fin de matinée). Au laboratoire et en présence d'un éclairage naturel, deux types de rythmes ont été décelés chez cette espèce : l'un, paradoxalement, est peu différent de celui des animaux gardés à l'obscurité, l'autre est marqué par une phase d'activité très intense qui commence en début de nuit, dure 5 à 6 h, puis cesse brusquement (Champalbert, 1976b, 1978, 1979a).

Influence de la lumière sur l'éclosion des œufs

La lumière est susceptible d'intervenir sur l'éclosion des œufs de repos. En effet, les résultats de Marcus (1980) sur *Labidocera aestiva* montrent que la production d'œufs à éclosion rapide et celle des œufs de repos sont notablement différentes selon les photopériodes. Exposés à une photopériode de 18 h de lumière — 6 h d'obscurité, 89,9 % des œufs produits sont des œufs à éclosion rapide survenant 4 à 5 jours après la ponte; exposés à une photopériode de 8 heures de lumière — 16 h d'obscurité, seulement 13,2 % des œufs produits sont des œufs à éclosion rapide. De plus, l'auteur a constaté que parmi les œufs non éclos rapidement et gardés un certain temps à 5°C, 85,9 % ont éclos : ce sont des œufs de repos. *L. aestiva* présente une période diapause facultative qui est induite par une photopériode à période d'éclairement court; selon Marcus (1982a, b), il est possible que dans le milieu les femelles produisent un type d'œufs ou un autre après perception des changements de la durée de l'éclairement naturel journalier. Au contraire, les travaux de Uyé et al. (1979) semblent montrer que l'éclosion des œufs de repos est relativement indépendante des conditions d'éclairement.

PRESSION

Influence de la pression sur le comportement

Les recherches concernant l'influence de la pression hydrostatique sur les rythmes d'activité et la physiologie des animaux marins en général et des organismes neustoniques en particulier, sont assez peu nombreux malgré l'importance évidente de ce facteur sur les manifestations d'ordre physiologique, biologique et motrice.

Korringa (1947), Hardy et Paton (1947), ont été les premiers à penser que certains copépodes effectuant des migrations verticales possèdent un sens de la profondeur (« barosens ») les rendant sensibles à la pression. Depuis plusieurs années, les travaux effectués dans le but de préciser la sensibilité des divers groupes d'animaux aquatiques aux variations de pression se sont multipliés (Hardy et Bainbridge, 1951; Knight Jones et Qasim, 1955; Rice, 1961, 1962; Morgan, 1965). Plus récemment, MacDonald, Gilchrist et Teal (1972a, b) ont observé l'activité de divers crustacés dont les copépodes *Megacalanus longicornis*, *Euaugaptilus magna*, *Paraeuchaeta gracilis*, *Pleuromamma robusta* et le Pontellidae hyponeustonique *Anomalocera patersoni*. Parmi les copépodes, c'est ce dernier qui est le plus sensible : à 7°5 C, sous 50 atmosphères, et durant 5 min. son activité natatoire est accrue, mais elle s'arrête à 100 atmosphères.

D'une façon assez générale, il semble que la sensibilité à la pression des différentes espèces dépende beaucoup de leur répartition verticale et de leurs exigences et tolérances écologiques.

La synthèse des résultats concernant le rôle de la pression sur les déplacements verticaux de Pontellidae marqués à l'Iode 131 montre qu'une augmentation de pression de 2 bars provoque une augmentation rapide de l'activité natatoire. Dans les cuves expérimentales, les déplacements verticaux des individus maintenus pendant plusieurs jours sous une pression constante modérée (2 bars) semblent dépendre des conditions d'éclairement : à l'obscurité totale, le rythme d'activité des animaux soumis à une surpression est moins net que celui des animaux témoins; à la lumière naturelle, le rythme d'activité des animaux soumis à une surpression semble plus net que celui des animaux témoins. Les résultats sont plus spectaculaires chez *Anomalocera patersoni* que chez *Pontella mediterranea* et chez *Pontella* que chez *Labidocera wollastoni*. Des variations cycliques de pression de courte période imposées à des Pontellidae maintenus sous un éclairement artificiel constant se traduisent généralement par des variations cycliques de l'activité natatoire (Champalbert, 1976c, 1978).

Influence de la pression sur la physiologie.

Les travaux concernant l'influence de la pression hydrostatique sur la physiologie des espèces planctoniques sont peu nombreux; quelques-uns font état des effets de la pression sur les activités enzymatiques (Champalbert et Kerambrun, sous presse), mais la plupart portent sur les effets de la pression sur la consommation d'oxygène d'espèces effectuant des migrations verticales importantes (Cattel, 1936; Napora, 1964; Morita, 1967; Teal et Carey, 1967; Schlieper, 1968; Teal, 1971; MacDonald et al., 1972; Ikeda, 1974).

Les expériences effectuées *in situ* en Méditerranée (golfe de Marseille) sur la respiration des Pontellidae montrent que la consommation d'oxygène d'*Anomalocera patersoni* et de *Pontella mediterranea* augmente avec la profondeur d'immersion de 0 à 60 m, alors que chez d'autres crustacés, les différences sont moins apparentes (Champalbert et Gaudy, en préparation).

Par ailleurs, la pression peut intervenir sur l'éclosion des œufs de Pontellidae. chez *Labidocera aestiva*, à l'obscurité, une pression de 6 à 7 bars semble retarder l'éclosion des œufs aussi bien à la température correspondant à celle du milieu naturel qu'à une température inférieure à celle de l'habitat. De plus, la pression ne semble pas léser les œufs : des œufs ayant été soumis à une surpression puis placés dans des conditions normales éclosent envi-

ron 24 h plus tard. Il est cependant à noter que sous des pressions relativement élevées pour des espèces superficielles (50 bars), les œufs peuvent éclore, mais les nauplii meurent presque instantanément.

TEMPÉRATURE

Influence de la température sur la répartition

Les Pontellidae sont, pour la plupart, thermophiles. En effet, la diversité spécifique est maximale dans la zone intertropicale des océans Pacifique, Indien, Atlantique (Heinrich, 1960, 1971, 1974; Voronina, 1962; Sherman, 1963, 1964; Hempel et Weikert, 1972, 1975). Toutefois, quelles que soient leurs exigences, les Pontellidae semblent relativement sténothermes dans une aire géographique déterminée. Par exemple, dans le golfe de Marseille, leur présence dans le biotope ultrasuperficiel, est limitée à quelques mois : *Anomalocera patersoni* est une espèce à tendance psychrophile qui apparaît approximativement en novembre et disparaît en mai ou juin; son maximum d'abondance est hivernal; au contraire, *Pontella mediterranea*, à tendance thermophile apparaît vers la fin de l'automne. *Labidocera wollastoni* semble plus eurytherme que les deux espèces précédentes: on la rencontre plus ou moins toute l'année, parfois en petit nombre, avec les maxima en début d'été, en début d'automne et en début d'hiver (Champalbert, 1975).

Influence de la température sur le comportement

Des expériences effectuées sur des lots d'*Anomalocera patersoni* ont montré que l'activité natatoire des Pontellidae ne semble pas indépendante de la température. Des variations cycliques de température (période de 8 h environ) peuvent être à l'origine de déplacements verticaux cycliques: quand la température est faible (8°C) les *Anomalocera* nagent au voisinage de la surface alors qu'à 17°C ils tendent à s'accumuler au fond des cuves.

Influence de la température sur la physiologie

La répartition saisonnière limitée des Pontellidae traduit une certaine sténothermie qui se manifeste au niveau du métabolisme respiratoire dont les variations en fonction de la température traduisent la plus ou moins grande capacité d'adaptation des individus aux variations thermiques du milieu.

Bien que relativement peu nombreuses et limitées à quelques espèces (*Pontella mediterranea*, *Pontellopsis villosa*, *Anomalocera patersoni*, *Labidocera aestiva*, *L. wollastoni*, *Pontella lobiancoi*), les études consacrées à la respiration des Pontellidae tendent à montrer que leurs besoins en oxygène sont relativement élevés (Champalbert, 1973a, 1975; Shushkina et al., 1971; Ikeda, 1974), ce qui résulte vraisem-

blablement en partie de leur régime essentiellement carnivore et de leur activité particulièrement intense. Ainsi, Muravskaya et al. (1980), comparant la consommation d'oxygène de *Pontella mediterranea* et de *Calanus helgandicus*, ont trouvé une consommation d'oxygène une fois et demi plus élevée chez *Pontella* que chez *Calanus*. L'intensité de la respiration ainsi que la dispersion forte des mesures qui est observée fréquemment semblent constituer une caractéristique générale des copépodes prédateurs (Conover et Corner, 1968).

Par ailleurs, les différentes modalités d'adaptation des Pontellidae dépendent de l'habitat d'origine: en effet, Anraku (1964) a trouvé que les courbes R/T de *Labidocera aestiva* sont étroitement corrélées aux conditions hydrologiques de l'habitat. Des résultats analogues ont été obtenus par Champalbert (1973a, 1975) sur les Pontellidae du golfe de Marseille; dans la relation liant la respiration et le poids, le coefficient de régression, qui varie avec la température, est généralement maximum à des températures proches de celles du biotope: il est élevé entre 10 et 14°C chez les adultes de l'espèce psychrophile *Anomalocera patersoni* et fort entre 20 et 22°C chez les adultes de l'espèce thermophile *Pontella mediterranea*; au contraire, dans l'Atlantique subtropical, Champalbert et Gaudy (1972), mesurant la respiration de Pontellidae (dont *Anomalocera patersoni*) ainsi que d'autres copépodes, ont trouvé un coefficient de régression maximum à 18°C, température de l'habitat au moment de l'expérimentation.

L'intensité de la respiration des Pontellidae peut varier au cours des saisons:

— Chez l'espèce psychrophile *Anomalocera patersoni*, la consommation d'oxygène par unité de poids est assez peu élevée chez les individus des premières générations (fin de l'automne, début de l'hiver), malgré leur taille relativement petite comparativement à celle des individus du milieu de l'hiver et du début du printemps dont la respiration est plus intense. Ces individus, plus robustes et vraisemblablement mieux adaptés que ceux des premières et dernières générations annuelles ont, dans la gamme du préférence (10-14°C) un métabolisme assez stable, que l'on peut considérer comme relativement eurytherme dans cet intervalle. Au contraire, chez les individus des premières et dernières générations annuelles, les différences de consommation d'oxygène à 10° et 14°C sont plus marquées. Aux températures supérieures à celles du biotope, les variations de la consommation d'oxygène sont souvent irrégulières et donc celles des Q10 le sont aussi. Aux températures beaucoup plus élevées que celles de l'habitat, la respiration peut diminuer.

— Chez l'espèce thermophile *Pontella mediterranea*, on note aussi des variations saisonnières. En mai, la température des eaux est souvent voisine de 15°C lorsqu'apparaissent les premières générations dont le métabolisme n'est pas très intense à la température du biotope; il augmente légèrement à la mi-juin, davantage en été et rediminue chez les individus des dernières générations annuelles. Les individus des premières et dernières générations paraissent plus sténothermes que les individus des populations estivales qui semblent pouvoir ainsi mieux supporter les éventuelles variations thermiques brusques survenant pendant la période chaude.

Chez *Anomalocera patersoni*, psychrophile, les Q10 tendent à augmenter quand la température

augmente; ils sont donc plus élevés chez les individus des premières et dernières générations qui semblent les moins bien adaptées. Chez *Pontella mediterranea*, thermophile, les Q10 tendent à diminuer quand la température augmente; ce sont donc les premières et les dernières générations annuelles qui ont les Q10 les plus forts et qui semblent les moins bien adaptées. Les Q10 les moins élevés correspondent ainsi aux individus des populations hivernales d'*A. patersoni* et estivales de *Pontella mediterranea*, les uns et les autres paraissent les mieux adaptés. Au contraire, les individus des premières et dernières générations d'*Anomalocera* et de *Pontella* semblent avoir un métabolisme plus sténotherme sans doute moins bien adapté à une régulation difficile. Enfin, il est à noter que les Q10 des espèces n'effectuant pas de migrations sont généralement plus élevés que ceux des espèces migrantes (Champalbert et Gaudy, 1972).

Enfin, chez les Pontellidae comme chez la plupart des organismes marins, la consommation d'oxygène est inversement liée au poids et *Pontella mediterranea* consomme plus d'O₂ par unité de poids qu'*Anomalocera patersoni* dont la taille est plus grande.

Somme toute, dans le golfe de Marseille, *A. patersoni* et *P. mediterranea* sont deux espèces relativement sténothermes comme en témoigne le déséquilibre physiologique apparaissant dès que la température devient trop élevée ou trop faible pour que l'adaptation optimale puisse se faire; la régulation métabolique devient alors suboptimale avant que les mécanismes de résistance entrent en jeu et que la mortalité augmente considérablement.

Influence de la température sur la croissance

L'impact de la température sur la croissance et le développement de tous les organismes marins, surtout très important, a une action particulièrement marquée chez les Pontellidae qui, d'une génération à l'autre, ont des tailles, et des poids, parfois très différents. Par exemple, dans le golfe de Marseille, une étude suivie des variations pondérales saisonnières (Champalbert, 1975), fait apparaître des différences extrêmement importantes chez des individus des générations successives, différences pouvant aller, chez les mâles de *Pontella mediterranea*, de 0,044 à 0,087 mg et chez les femelles de 0,050 à 0,094 mg; pour *Anomalocera patersoni* les variations vont de 0,050 à 0,205 mg chez les mâles et de 0,105 à 0,330 mg chez les femelles.

Des différences pondérales apparaissent également entre les individus d'une même espèce mais de secteurs géographiques différents. Ceci a été observé entre des *P. mediterranea* de divers secteurs de Méditerranée et entre des *A. patersoni* de Méditerranée et d'Atlantique subtropical (Champalbert, 1975).

Outre ces différences pondérales, les différences d'ordre biométrique peuvent affecter des copépodes de régions différentes. Ainsi, une étude préliminaire de la morphologie de *P. mediterranea* et des *A. patersoni* de Méditerranée et de mer Noire (Champalbert et al., 1978; Zaitsev et al., 1979) a permis de mettre en évidence une augmentation de la longueur de l'abdomen des individus de mer Noire et parallèlement, un raccourcissement de leur céphalothorax, qui peut correspondre à une adaptation des populations pontiques aux faibles salinités.

En raison des variations de température saisonnières importantes des eaux superficielles et de leur relative sténothermie, les Pontellidae ont à subir des conditions thermiques défavorables au cours de l'année. Pour traverser la mauvaise saison, la plupart d'entre eux, produisent des œufs de repos, différents des œufs à éclosion rapide (Grice et Gibson 1975). Ces œufs ont été décrits chez *Pontella meadi* (cf. Grice et Gibson, 1977), *Labidocera aestiva* (cf. Grice et Gibson, 1975; Grice et Lawson, 1976; Marcus, 1979, 1980, 1982; Grice et Marcus 1981), *L. wollastoni* (cf. Grice et Gibson, 1982), *L. bipinnata* (cf. Uyé et al., 1979), *Pontella mediterranea* (cf. Grice, 1981; Grice et Gibson, 1981).

En général, les œufs de repos diffèrent des œufs normaux par leur morphologie et leurs caractéristiques d'éclosion. Uyé et al. (1979), étudiant les conditions d'éclosion des œufs de repos de 6 copépodes de la mer du Japon (*Calanopia thompsoni*, *Labidocera bipinnata*, *Acartia erythrea*, *A. clausi*, *Centropages abdominalis* et *C. yamadaï*) constatent que la température, ainsi que la teneur en oxygène ont un rôle important.

SALINITÉ

La relative sténothermie des Pontellidae s'accompagne aussi d'une certaine sténohalinité. Dans le milieu naturel, la distribution de l'hyponeuston ne semble pas modifiée par des variations de salinité faibles, résultant de l'action directe des précipitations atmosphériques; au contraire, ces précipitations ont souvent une action indirecte sur le plancton superficiel néritique car elles augmentent le débit des effluents côtiers et donc la turbidité et la dessalure (Champalbert, 1977). Or, turbidité et dessalure modifient la répartition et l'abondance des populations neustoniques. Des récoltes de plancton effectuées tous les 10 cm entre 0 et un mètre en plusieurs points situés à plus ou moins grande distance de l'embouchure du Rhône ont montré que les Pontellidae étaient des espèces sténohalines sensibles à la turbidité (Champalbert, 1976a, 1979b): leur abondance est maximale dans la zone marine typique où leur stratification est particuliè-

rement nette et où les individus se maintiennent pour la plupart dans les dix premiers centimètres; au niveau de la zone de transition, où la salinité est de 17 ‰ entre 0 et 10 cm, de 25 à 30 ‰ entre 30 et 40 cm, la densité des copépodes hyponeustoniques décroît; elle devient minimale dans la zone où la salinité est la plus faible (12 ‰ entre 0 et 10 cm) et la turbidité la plus forte; dans ce secteur, les Pontellidae, très rares, sont dispersés dans le premier mètre.

Les zones de rejet d'effluents constituent des milieux où les conditions écologiques sont extrêmes et se répercutent non seulement sur les populations hyponeustoniques mais encore sur l'ensemble des populations zooplanctoniques, phytoplanctoniques et bactériennes : les recherches effectuées dans l'aire de rejet de l'émissaire urbain de Marseille-Cortiou (Epope, 1978, 1979; Arfi et al., 1980) ont montré que dans la zone la plus polluée ne subsistent que des espèces extrêmement eurybiotiques; dans toute la zone polluée les Pontellidae sont toujours totalement absents mais ils réapparaissent dans l'aire marine typique voisine, ce qui permet de penser qu'ils peuvent être des indicateurs d'eaux non polluées (Champalbert, 1979).

Ainsi dans une aire géographique donnée, les Pontellidae semblent donc relativement sténohalins, caractère qui apparaît au niveau du métabolisme respiratoire (Champalbert, 1975). Cependant, la synthèse des travaux concernant leur répartition mondiale montre que certaines espèces ont des exigences moins strictes que d'autres : dans le Pacifique comme dans l'océan Indien, bon nombre d'entre elles vivent dans des eaux dont la teneur en sels est comprise entre 34,5 et 36,5 ‰, alors que d'autres sont plus abondantes dans les masses d'eaux de salinité inférieure à 34,5 ‰ (*Pontella fera*).

Par ailleurs, certaines espèces, dont les exigences paraissent assez strictes ont, paradoxalement, une répartition géographique très étendue, recouvrant des aires où les caractéristiques physiques et chimiques sont extrêmement différentes. C'est le cas par exemple, de *Pontella mediterranea* et d'*Anomalocera patersoni* dont les limites de répartition sont particulièrement vastes et dont l'adaptation en mer Noire semble constituer un cas extrême du fait même des faibles salinités (16 à 22 ‰) et de la large gamme de température tolérées; en effet, bien qu'à tendance psychrophile, *A. patersoni* peut vivre entre 1°C et 28°C, tandis que *P. mediterranea* est plus thermophile : rare entre 8 et 12°C, sa densité augmente régulièrement avec la température et atteint son maximum entre 24 et 28°C. Il est intéressant de souligner aussi que l'abondance d'*Anomalocera* et de *Pontella* diminue près des côtes où la salinité est de 16 ‰.

Enfin, il est à noter que l'éclosion des œufs de repos peut avoir lieu dans une large gamme de salinités (Uyê et al., 1979).

RESSOURCES TROPHIQUES

La répartition des Pontellidae ne semble pas indépendante des ressources trophiques. Il existe des différences numériques et spécifiques entre l'hyponeuston néritique et l'hyponeuston océanique; celles-ci résultent probablement de l'importance plus grande, dans la province néritique, des apports terrigènes qui s'accumulent au niveau de l'interface où certaines substances peuvent être utilisées par des unicellulaires ou même par des animaux.

La productivité locale semble pouvoir affecter la distribution des espèces hyponeustoniques. Dans l'Atlantique sud, Weikert (1975) suppose que les plus grandes concentrations de Pontellidae sont associées à des eaux à moyenne productivité tandis que dans l'océan Pacifique, Sherman (1963, 1964) a relevé de fortes densités le long d'un gradient latitudinal de productivité croissante. En fait, les relations entre fertilité des eaux et abondance de l'hyponeuston sont encore imprécises, de même que la production secondaire du biotope superficiel ainsi que les exigences trophiques des espèces neustoniques.

Les observations de Zelezinskaya (1962), confirmées par la suite, ont montré que les Pontellidae peuvent être omnivores mais qu'ils sont fréquemment prédateurs. En effet, Anraku et Omori (1963) ont constaté que *Labidocera aestiva* peut être nourrie avec des cultures de *Thalassiosira* bien que les pièces buccales de cette espèce, comme celles de la plupart des Pontellidae soient plutôt adaptées à un régime carnivore (Fleminger, 1967; Itoh, 1970; Turner, 1978; Greenwood et Othman, 1979; Grice et Gibson, 1982). De son côté, Marcus (1979, 1980) a entrepris des élevages de *Labidocera aestiva* avec des cellules de *Gymnodinium nelsoni*, *Gonyaulax polyedra*, *Procentrum micans* et *Peredinium trochoideum*. Landry (1978), quant à lui, a étudié en laboratoire, la prédation de *Labidocera trispinosa* sur des nauplii et des copépodites de 5 espèces de copépodes. La quantité de proies capturées ne semble pas dépendre de leur densité mais de leur taille : les taux de prédation maximum sont observés sur les nauplii âgés bien que ces derniers évitent plus facilement la capture que les jeunes; la prédation sur les copépodites diminue nettement. Observant les réactions trophiques de *Labidocera jollae*, *L. trispinosa*, *Pontellopsis occidentalis*, Lillelund et Lasker (1971) ont constaté que ces espèces se nourrissaient de larves d'*Artemia* mais étaient également capables de capturer de jeunes larves de poissons. Enfin Weikert

(1975) a remarqué, dans l'Atlantique nord, que *Pontella atlantica* constitue un prédateur de la communauté neustonique pendant les heures d'insolation maximum.

Les Pontellidae ainsi que d'autres espèces hypo-neustoniques peuvent à leur tour faire partie de la nourriture de certains jeunes poissons tels *Atherina* et *Belone* (Hempel et Weikert, 1972; Weikert, 1972) et constituer ainsi une ressource trophique importante. De ce fait l'étude de leur composition élémentaire en carbone, hydrogène, azote et de leur teneur protéique, a fait l'objet de plusieurs séries de travaux montrant une certaine homogénéité de la composition en C et N. En effet, étudiant les variations de composition élémentaire des quatre Pontellidae *Anomalocera patersoni*, *Pontella mediterranea*, *P. lobiancoi* et *Labidocera wollastoni* en fonction du sexe et des stades de développement, Champalbert et Kerambrun (1978) ont trouvé des taux de carbone minimum (32,4) chez les femelles de *L. wollastoni* et des taux maximum (43,3) chez les femelles de *P. lobiancoi*, tandis que les teneurs en azote sont comprises entre 9,3 % chez les femelles de *L. wollastoni* et 11,5 % chez les femelles de *P. lobiancoi* et les mâles d'*A. patersoni*. Chez *Labidocera acuta*, *L. detruncata*, et *Pontella danae*, Ikeda (1974) a observé des variations comprises entre 41,2 et 44,3 pour le carbone et entre 11,4 et 12,6 pour l'azote. Par ailleurs, comparant les valeurs des rapports C/N des quatre espèces *Pontella mediterranea*, *P. lobiancoi*, *Anomalocera patersoni* et *Labidocera wollastoni*, Champalbert et Kerambrun (1978) ont trouvé des variations interspécifiques assez faibles, comprises entre 3,5 et 3,8. Certaines différences apparaissant entre ces résultats et ceux de Omori (1969) peuvent procéder de différences latitudinales ou de répartition verticale (Childress et Nygaard, 1974). Une autre particularité des Pontellidae concerne les différences entre mâles et femelles, les premiers paraissant avoir des teneurs élémentaires plus élevées que les femelles alors que l'inverse est souvent vrai chez d'autres crustacés (Kerambrun, 1972; Guérin et Gaudy, 1977).

La teneur protéique d'*Anomalocera patersoni* et *Pontella mediterranea* est particulièrement élevée puisqu'elle se situe chez les adultes entre 70 % et 80 % du poids sec. Ces valeurs qui sont du même ordre que celles signalées par Omori (1969) et Childress et Nygaard (1974) placent ces espèces parmi les copépodes les plus riches en protéines.

CONCLUSIONS

La synthèse des recherches effectuées sur les Pontellidae montre que les populations neustoni-

ques prospèrent dans le biotope superficiel où l'intensité et la rapidité des variations des facteurs ambiants sont souvent plus importantes que dans les zones plus profondes. De ce fait, ces espèces ont développé des adaptations dont certaines correspondent à la manifestation exacerbée des adaptations à la vie pélagique alors que d'autres sont ou semblent être la conséquence directe d'un ajustement aux conditions exceptionnelles du milieu ultrasuperficiel. Par exemple, la couleur et les propriétés des pigments des espèces neustoniques, leur photosensibilité ainsi que leur sensibilité aux variations de pression, de température, de salinité, semblent être des manifestations particulières de l'adaptation à la vie en surface.

Compte tenu des variations de répartition dans le milieu naturel et des observations effectuées *in vitro* sur les changements de comportement, il est permis de penser que les Pontellidae effectuent des déplacements verticaux vraisemblablement limités dans leur amplitude et dans leur durée par leur sensibilité à la température ainsi qu'à la lumière et à la pression, laquelle en particulier, pourrait limiter l'extension des migrations en profondeur où la dépense métabolique est élevée. Toutefois, il convient de rappeler que le comportement et les réactions métaboliques (qui sont la résultante des actions cumulatives, antagonistes ou interférentes de nombreux facteurs internes et externes parfois difficilement contrôlables) peuvent être modifiées par les conditions expérimentales : en particulier, Digby (1967) a constaté que les conditions de laboratoire influent sur la réponse à la pression et l'on comprend l'avantage d'une expérimentation *in situ*, lorsqu'elle est réalisable.

Par ailleurs, il faut tenir compte des fluctuations saisonnières de sensibilité à la température, à la lumière et à la pression : ainsi, des variations saisonnières du métabolisme respiratoire ont été observées chez les Pontellidae (Champalbert, 1975), tandis que des variations saisonnières de sensibilité à la pression ont été observées chez des copépodes Calanidae (Lincoln, 1971).

Il faut remarquer l'importance que semble avoir la pression sur l'éclosion des œufs de Pontellidae et l'impact de ce facteur au plan écologique. En effet, de nombreuses espèces produisent des œufs de repos qui sédimentent sur le fond puis éclosent lorsque la saison critique est terminée. Selon Marcus (1982b), photopériode et température sont les deux principaux facteurs du contrôle de l'éclosion œufs de repos chez *Labidocera aestiva*; chez cette espèce l'éclosion des œufs normaux étant retardée par une augmentation de pression, la connaissance des effets de la pression sur l'éclosion des œufs de repos présenterait un intérêt évident.

Par ailleurs, les copépodes pélagiques dont on connaît les œufs de repos sont pour la plupart des espèces thermophiles et les recherches sur les modalités de la reproduction et de la ponte de Pontellidae psychrophiles tels *Anomalocera patersoni* méritent d'être développées.

En définitive, malgré l'instabilité relativement importante du milieu où ils vivent, les Pontellidae sont, dans une aire géographique déterminée, des organismes relativement sténotopes et sensibles aux variations des facteurs ambiants (température, salinité, lumière, pression). Toutefois, certaines espèces semblent faire preuve d'un remarquable potentiel d'adaptation qui se traduit par une distribution géographique très vaste, recouvrant des aires hétérogènes au plan hydrologique.

En effet, dans le domaine de l'hyponeuston la connaissance de l'échelon secondaire s'élargit progressivement mais la production et les relations entre les différents échelons et les processus biochimiques propres à l'interface restent encore à préciser.

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The sea-surface microlayer: phytoneuston productivity and effects of atmospheric particulate matter

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Abstract

The sea-surface microlayer, the upper 50 μm of the ocean surface, provides a habitat for an important biota (the neuston), an interface for exchange of gases between the atmosphere and oceans and a site for deposition of anthropogenic metals and other materials from the atmosphere. Several recent studies have suggested that biochemical processes, including photosynthesis, in the microlayer are inhibited relative to the bulk seawater. We compared the biomass, species composition and productivity of phytoneuston to that of phytoplankton in Sequim Bay, Washington State, USA. Mean enrichment ratios (microlayer:bulk water concentrations) for bacteria, microalgae, chlorophyll pigments and photosynthesis (estimated gross) were 2 444, 380, 12 and 40, respectively. Compared to the bulk water, the microlayer had a unique assemblage of microalgae with a higher concentration of chlorophyll *c*. When exposed to high light intensities (summer) or metal-rich urban atmospheric particulate matter, radiocarbon-measured photosynthesis was lower in phytoneuston than in phytoplankton. Deposition of atmospheric particulate matter at rates similar to those occurring in urban coastal areas resulted in a significant ($P < 0.01$) reduction in radiocarbon-measured photosynthesis in the sea-surface microlayer. These apparent decreases in photosynthesis are believed to result from the extracellular release of ^{14}C as glycolate or other soluble compounds and may not reflect a true decrease in gross primary productivity in the microlayer. Further measurements of the degree of extracellular carbon release will be necessary to quantify gross photosynthetic rates in the microlayer.

Introduction

The sea-surface microlayer (upper 50 μm or less) covers 71% of the Earth's surface, and biological and chemical

processes in the microlayer could affect the exchange of gases as well as anthropogenic materials between the atmosphere and oceans (MacIntyre, 1974; Wangersky, 1976). Of the 5 billion metric tons of carbon released to the atmosphere annually from the burning of fossil fuel, about 1 billion metric tons diffuse across the air-sea interface into the dissolved CO_2 pool of surface ocean water (Smith, 1981). In addition, a major portion of metals (Settle and Patterson, 1982) and hydrocarbons (Hunter and Liss, 1977; Atlas and Giam, 1981) released from the combustion of fossil fuels deposits on the sea surface.

Neuston (microorganisms which inhabit the aquatic microlayer) could affect the exchange rates of gases and materials at the interface. Any negative impact on the health or physiology of neuston, then, could have important implications for the global cycling of materials (Hardy, 1982).

Previous comparisons of phytoneuston and phytoplankton differ in their results. Many reports indicate an enrichment of biological activity in the microlayer with, for example, phytoneuston (microalgae) densities 10 to 10 000 times greater than phytoplankton densities only a few centimeters below (Harvey, 1966; Bursa, 1968; Maynard, 1968; Hardy, 1973; Manzi *et al.*, 1977; Wandschneider, 1979; Nesterova, 1980; Hardy and Valett, 1981). Several studies of chlorophyll pigments in the microlayer compared to the bulk water have found high surface enrichments at least in natural slick areas (Nishizawa, 1971; Harvey and Burzell, 1972; Hardy, 1973; Gallagher, 1975). Likewise, studies of photosynthetic productivity indicate that the microlayer is about ten times as productive as the subsurface water (Hardy, 1973; Gallagher, 1975).

Other studies have found depletions or only occasional enrichments in the microlayer biota. For example, Taguchi and Nakajima (1971) reported enrichments of chlorophyll pigments in only 9 of 22 samples and Daumas *et al.* (1976) found a drum-collected sample from a clean area depleted while a polluted area was enriched. Also, several reports

suggest that neuston are stressed in some way and not as physiologically active as plankton (Marumo *et al.*, 1971; Dietz *et al.*, 1976). Depletions in microlayer chlorophyll *a* (Albright, 1980; Carlson, 1982) and photosynthetic carbon fixation (Albright, 1980) compared to bulk water have been attributed to inhibitory factors such as high light intensities in the sea-surface microlayer.

Metals, primarily of atmospheric and anthropogenic origin (Patterson and Settle, 1974; Duce *et al.*, 1976; Dehairs *et al.*, 1982), frequently occur in high concentrations in sea-surface microlayers relative to the bulk seawater (Dehairs *et al.*, 1982; Hardy *et al.*, in press, a, b). We suggested that biologically active metals might inhibit the photosynthetic productivity of phytoneuston (Hardy and Crecelius, 1981). Others have suggested that anthropogenic contaminants, collecting at the air-sea interface, could lead to a decrease in worldwide productivity beginning with a suppression of the photosynthetic activity of phytoneuston (Mileikovskii, 1981).

We conducted microcosm and field studies to test the hypothesis that the sea-surface microlayer is typically depleted in species, chlorophyll pigments and photosynthetic productivity compared to the subsurface water. In addition, we examined sea-surface deposition of urban atmospheric particulate matter as a potential inhibitor of photosynthesis in natural phytoneuston and phytoplankton populations.

Materials and methods

Bacterial density

Densities of bacterioneuston and bacterioplankton present during the photosynthetic experiments were determined. Samples were collected from the microlayer (upper 20 μm) using the polycarbonate filter technique (Sewell *et al.*, 1981) and from 10 cm depth in the water through a syringe. Acridine orange was added to the samples and stained individuals were enumerated by epifluorescence microscopy (Watson *et al.*, 1977).

Species abundance of microalgae

Samples were collected from the microlayer (upper 50 μm) by the glass plate technique (Hardy *et al.*, in press, b) and from the bulk water (20 cm depth) by subsurface opening of 250 ml polyethylene bottles. Samples were preserved in Lugol's iodine solution, concentrated by settling and enumerated at 400 $\times$ magnification by the Utermohl technique to a 10% confidence level for the total counts (Venrick, 1978). Our purpose was to obtain an estimate of total abundance and numbers within major taxonomic groups; consequently, no attempt was made at detailed species identifications. In all samples, occasional dead cells were found. These were rare, and only visibly viable (chloroplast-containing) cells were enumerated.

Chlorophyll pigments

Samples were collected from Sequim Bay (Washington State, USA) near the laboratory in July. To derive mean values for the entire bay, a random sampling method was employed. The bay was divided into 250 numbered quadrats and the 7 stations to be sampled in the middle of each quadrat were drawn from a random number generator. Samples for chlorophyll were also collected during the photosynthetic experiment of 21 July 1983. Samples were collected from the microlayer (upper 50 μm) with a glass plate sampler (Hardy *et al.*, in press, b) and from the subsurface water (0.5 m depth) by subsurface opening of 2-liter polyethylene bottles. Samples were filtered, frozen at -70°C , later extracted with a tissue grinder in 90% acetone and then analyzed for pigments using the spectrophotometric equations of Strickland and Parsons (1972).

Photosynthetic productivity

Photosynthetic rates of phytoneuston and phytoplankton and the effects of atmospheric particulate matter (APM) were determined by both incubator and *in situ* experiments. Seawater was collected at outgoing to slack tide near the entrance to Sequim Bay. In six experiments conducted between January and May, 1983, water was collected in 1-liter polyethylene beakers. Duplicate treated beakers were placed in an incubator at ambient seawater temperature either in the light ($85 \mu\text{E m}^{-2} \text{s}^{-1}$ cool-white fluorescent) or in the dark. In the July experiment, seawater was collected in 7.6-liter clear polycarbonate tanks (Cambro[®] Co.) modified to contain a drain near the bottom. Tanks, with lids on, were lowered below the surface, the lids were removed and the tanks were raised slowly to the surface (with the drain open) to trap the surface microlayer and 6 liters of subsurface water. The drains were closed and duplicate tanks without lids were placed in an outdoor sea table, cooled with flowing ambient-temperature seawater and exposed to natural daylight (mean $1\,230 \mu\text{E m}^{-2} \text{s}^{-1}$). Dark tanks or beakers were placed in an incubator at the same temperature. $\text{NaH}^{14}\text{CO}_3$ (0.1 to 0.5 ml; 200 to 1 000 $\mu\text{Ci l}^{-1}$ of seawater) was added below the water surface of all experimental tanks. Salinity was measured with a refractometer and light energy, in the photosynthetically active wavelength range (400 to 700 nm), with a Li-Cor Inc.[®] photometer (LI-185A, with 190-S probe).

Urban APM (NBS Standard 1648) contains high levels of potentially toxic metals, especially Pb (Hardy and Crecelius, 1981). Between 0 (control) and 256 $\mu\text{g m}^{-2}$ of APM was sprinkled onto the water surface of each container. The APM dust dispersed within 1 to 2 min to form an almost uniform layer on the water surface.

After 4 h incubation (10.00 to 14.00 hrs), we collected samples of microlayer and subsurface water. Microlayer samples were collected on 47 mm diam 0.45 μm polycarbonate filters (Unipore[®], Bio Rad Laboratories). The

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filters were floated on the surface for 1 min and then lifted off with forceps (Kjelleberg *et al.*, 1979; Van Vleet and Williams, 1980; Sewell *et al.*, 1981; Syzdek, 1982). The quantity of sample removed from the microlayer was determined gravimetrically and indicated a volume of $32.6 \pm 7.6 \mu\text{l}$ (SD) or a sample depth of $20 \mu\text{m}$. The samples were placed, sample side up, on a filter holder and rinsed at less than 1 atm vacuum with 100 ml of clean prefiltered seawater. For collection of subsurface water, 50 ml samples were taken by syringe, filtered onto polycarbonate filters (as above) and rinsed. Filters were fumed over concentrated HCl to remove inorganic carbon (Lean and Burnison, 1979) and counted by liquid scintillation. Counts were corrected for background and efficiency (external standards ratio) and converted to mg carbon using appropriate pH, salinity and carbonate alkalinity (Strickland and Parsons, 1972).

Results

Ambient seawater and incubation temperatures ranged from 8.3°C in January to 13.0°C in July. Salinity was 30‰ from January to 4 May, and 31‰ on 24 May and 21 July. Daylight conditions from January through 4 May were mostly cloudy before and on the day of sample collection, with light energy (similar to the incubator) of $85 \mu\text{E m}^{-2} \text{s}^{-1}$ or less. The week previous to and on the day of 24 May and 21 July experiments, the weather was clear with bright sun.

On the average over the sampling seasons, concentrations of bacteria, microalgae, total chlorophyll pigments and rates of photosynthetic carbon fixation were all highly enriched in the surface microlayer compared to the bulk seawater (Fig. 1).

Bacteria

Bacteria were abundant in both the microlayer and subsurface water during the photosynthetic experiments (Table 1). Densities of total bacterioneuston were significantly greater than those of bacterioplankton. Ratios of neuston to plankton density (N:P) were 133 in February, 23 to 34 in April through May, and reached over 12 000 in July when a dense, visible, surface-slick was present.

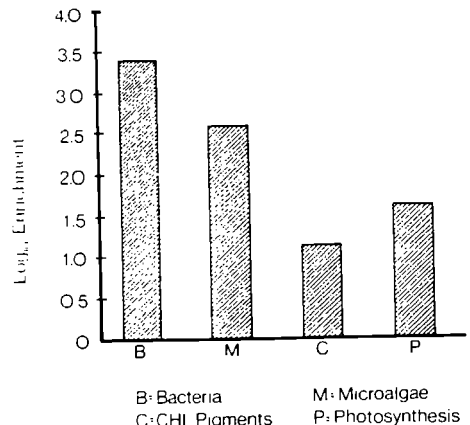


Fig. 1. Mean biological enrichments over the 5 sampling months (microlayer concentration divided by bulk water concentration)

Microalgae

We found major differences in abundance and taxonomic composition between the phytoneuston and phytoplankton (Table 2). Phytoneuston were consistently more abundant than phytoplankton. Ratios of density (N:P) for total individuals were 4 to 9 in April and May and reached over 1 500 in July. Some taxa (*Cocconeis* sp., *Cylindrotheca* sp., small pennate diatoms, *Tropidoneis* sp., *Cyclotrichium* sp., *Cryptomonas* sp., small microflagellates and *Ebria tripartita*) occurred preferentially as part of the neuston community. Other taxa (*Chaetoceros* sp., *Skeletonema* sp. and *Amphidinium* sp.) were typically or exclusively planktonic (Table 2).

Chlorophyll pigments

In July, the microlayer enrichment of photosynthetic pigments differed according to the pigment type. Throughout Sequim Bay, chlorophyll *a* concentrations in the microlayer compared to the bulk water were enriched at some stations and depleted at others. A similar pattern for chlorophyll *a* has been reported elsewhere (Carlson, 1982). Considering the mean and variance over all seven stations sampled in Sequim Bay on 11 July, there was no significant difference between chlorophyll *a* concentrations in the microlayer (upper $50 \mu\text{m}$) and bulk water (30 cm) depth (Table 3). Chlorophylls *b* and *c*, on the other hand,

Table 1. Total number of bacteria per ml in neuston and in plankton of Sequim Bay, Washington State, USA, in 1983. Values are means ($\pm$ SD)

Sample	25 February	6 April	4 May	24 May	21 July
Bacterioneuston (N) (microlayer)	4.60×10^8 (4.83×10^8)	1.41×10^7 (0.69×10^7)	1.96×10^7 (5.00×10^6)	2.58×10^7 (6.46×10^6)	30.5×10^9 (6.7×10^9)
Bacterioplankton (P) (bulk water)	3.45×10^6 (2.77×10^6)	4.67×10^5 (3.51×10^5)	8.6×10^5 (1.8×10^5)	7.7×10^5 (1.8×10^5)	2.46×10^6 (4.5×10^5)
Ratio N:P	133	30	23	34	12.3×10^3

Table 2. Abundance of microalgae (individuals ml⁻¹) in neuston and plankton of Sequim Bay, Washington State, USA

Taxon	6 April 1983		4 May 1983		24 May 1983		21 July 1983	
	Neuston	Plankton	Neuston	Plankton	Neuston	Plankton	Neuston	Plankton
Centric diatoms								
<i>Chaetoceros</i> sp.	0.00	0.00	0.00	0.00	0.00	260.00	0.00	0.00
<i>Coscinodiscus</i> sp.	0.00	0.00	0.00	30.00	0.00	0.00	0.00	0.00
<i>Leptocylindrus</i> sp.	0.00	0.00	100.00	79.00	0.00	15.00	0.00	0.00
<i>Rhizosolenia</i> spp.	23.00	0.00	0.00	3.00	1 990.00	182.00	0.00	0.00
<i>Skeletonema</i> sp.	0.00	0.00	0.00	0.00	0.00	130.00	0.00	0.00
<i>Melosira</i> sp.	0.00	0.00	100.00	0.00	100.00	0.00	0.00	0.00
Pennate diatoms								
<i>Cocconeis</i> sp.	0.00	0.00	40.00	3.00	300.00	0.00	7 576.00	0.00
<i>Cylindrotheca</i> sp.	13.00	5.00	100.00	30.00	50.00	33.00	8 250.00	20.00
<i>Navicula</i> sp.	0.00	0.00	0.00	41.00	0.00	0.00	0.00	59.00
<i>Nitzschia</i> sp.	0.00	0.00	540.00	330.00	400.00	200.00	0.00	0.00
Small pennates	81.00	29.00	610.00	20.00	2 180.00	28.00	39 904.00	60.00
<i>Tropidoneis</i> sp.	0.00	0.00	0.00	0.00	50.00	0.00	82 500.00	0.00
Ciliates								
<i>Cyclotrichium</i> sp.	6.40	5.80	20.00	0.00	50.00	10.00	0.00	0.00
Dinoflagellates								
<i>Amphidinium</i> sp.	0.00	14.85	0.00	0.00	0.00	0.00	0.00	0.00
<i>Dinophysis</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.00
<i>Gymnodinium</i> sp.	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00
<i>Peridinium</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.00
Unidentified spp.	89.00	14.00	20.00	3.00	0.00	0.00	31.00	0.00
Euglenoids								
<i>Eutreptiella marina</i>	6.40	1.70	50.00	0.00	0.00	2.60	0.00	0.00
Microflagellates								
<i>Cryptomonas</i> sp.	170.00	67.00	100.00	30.00	400.00	150.00	0.00	19.70
Unidentified spp.	174.00	8.40	6 070.00	290.00	1 850.00	270.00	4 260 000.00	59.00
Silicoflagellates								
<i>Dictyocha</i> sp.	0.00	0.00	0.00	0.00	0.00	2.60	0.00	0.00
<i>Ebria tripartita</i>	0.00	7.30	100.00	0.00	1 850.00	5.10	96 000.00	0.00
Total	562.80	153.05	7 750.00	862.00	9 220.00	1 319.30	4 494 230.01	2 957.70
Ratio neuston:plankton	3.7		9.0		7.0		1 519	

Table 3. Chlorophyll pigments (mg m⁻³) in the microlayer (neuston) and bulk seawater (plankton) of Sequim Bay

		Chl <i>a</i>	Chl <i>b</i>	Chl <i>c</i>	Total chl	Phaeo- pigment
July 11 (7 stations throughout bay) <i>n</i> = 7	Neuston	23 ± 28	6 ± 16	61 ± 20	94 ± 41	21 ± 23
	Plankton	13 ± 10	0	8 ± 3	21 ± 13	1 ± 1
	Enrichment ^a	—	+	+	+	—
July 21 (experiment) <i>n</i> = 2	Neuston	1 213 ± 24	5 ± 8	556 ± 166	1 775 ± 150	177 ± 54
	Plankton	7 ± 1	0	10 ± 2	17 ± 3	0
	Enrichment ^a	+	—	+	+	—

^a Significantly elevated in the microlayer compared to subsurface water ($P < 0.05$); Student's *t*-test

were highly enriched in the microlayer compared to the bulk water, resulting in an average total chlorophyll concentration 4.5 times greater in the microlayer than in the bulk water. Phaeopigments, chlorophyll degradation products, were generally higher in the microlayer at the

seven stations (11 July), but their enrichment was not significant, due to the variability between sampling stations.

During the photosynthetic experiment of 21 July, the concentration of total active pigments was 100 times greater in the microlayer than in the bulk water; phaeo-

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igments were high in the neuston, but absent in the plankton (Table 3). Samples for the experiment were from a thick, visible, surface-slick. Such natural slicks cover much of the area of the bay during mid-to-late summer.

Photosynthetic productivity

The difference between carbon fixation in the light and the dark normally yields a rate of particulate carbon fixation believed to be somewhere between gross and net photosynthesis (Harris, 1978; Peterson, 1980). We found that radiocarbon-measured photosynthetic rates were much greater in the microlayer than in the bulk water during the winter and spring. From January to early May, phytonuston productivity (light minus dark values) without additions of APM was between 8 and 227 mg C m⁻³ h⁻¹ compared to rates of 0.25 to 6.5 mg m⁻³ h⁻¹ in the bulk phytoplankton (Table 4). Productivity of the phytoplankton was low in winter, increased during the typical spring bloom (Chester *et al.*, 1979), and then decreased in mid-summer (21 July). In contrast, particulate carbon fixation (light minus dark) in the phytonuston was highest during the winter and early spring (21 January–4 May), but decreased to negative rates during summer (Table 4). The negative summer values in the phytonuston result from low rates of carbon fixation in the light compared to the dark. However, when carbon fixation in the light only is compared, that in the neuston was about 14 times greater than that in the plankton even in summer.

Photosynthetic efficiency ($\mu\text{g C h}^{-1} \text{ cell}^{-1}$) ranged between 2 and 8 for the phytoplankton, but in the phytonuston decreased from 15 in April to 0.05 in July, probably reflecting increasing photoinhibition in the sur-

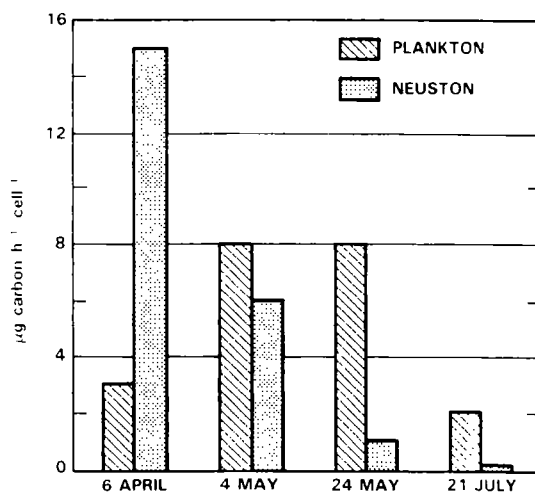


Fig. 2. Photosynthetic efficiency in the sea-surface microlayer

face layer (Fig. 2). Also, on 21 July, photosynthesis per unit chlorophyll in phytonuston was only 34% of that in phytoplankton.

In January, we also measured the increase in dissolved carbon possibly released by photorespiration. Over a period of 7 h of light, followed by 17 h of dark there was 46 mg C m⁻³ h⁻¹ more dissolved carbon (activity passing through a 0.45 μm membrane filter) released during the light/dark cycle than in the continuous dark exposure.

Our data (Table 4) indicate that addition of atmospheric particulate matter rich in metals inhibited photosynthesis in the neuston as measured by light minus dark radiocarbon uptake. Photosynthesis as a percentage of the control (no APM addition) decreased exponentially with increasing APM deposition rates (Fig. 3). APM additions as low as 1 mg m⁻² h⁻¹ resulted in a significant ($P < 0.01$)

Table 4. Influence of atmospheric particulate matter (APM) on photosynthetic productivity (mg C m⁻³ h⁻¹ $\pm$ SD). N: no. of replicates for each condition

Date	APM (mg m ⁻² h ⁻¹)	N	Neuston (N)				Plankton (P)			Ratio N:P
			Light	Dark	Light minus dark	% change from control	Light	Dark	Light minus dark	
21 Jan	0	4	455 $\pm$ 249	228 $\pm$ 84	227 $\pm$ 148	— ^a	1.89 $\pm$ 0.38	0.30 $\pm$ 0.29	1.6	143
	3	3	209 $\pm$ 251	225 $\pm$ 187	-16 $\pm$ 103	-116 $\pm$ 31	2.98 $\pm$ 0.95	0.33 $\pm$ 0.31	2.7	0
	16	4	104 $\pm$ 62	231 $\pm$ 213	-128 $\pm$ 133	-134 $\pm$ 49	2.52 $\pm$ 0.35	0.41 $\pm$ 0.24	2.1	0
25 Feb	0	4	15.0 $\pm$ 1.0	7.0 $\pm$ 1.2	8.0 $\pm$ 0.6	— ^a	0.27 $\pm$ 0.06	0.02 $\pm$ 0.00	0.25	27
	0.5	4	10.5 $\pm$ 1.0	4.4 $\pm$ 0.5	6.1 $\pm$ 0.5	-21 $\pm$ 8	0.32 $\pm$ 0.08	0.03 $\pm$ 0.01	0.29	21
	1.7	3	15.4 $\pm$ 2.7	9.2 $\pm$ 4.5	6.2 $\pm$ 1.9	-22 $\pm$ 27	0.30 $\pm$ 0.08	0.04 $\pm$ 0.01	0.26	23
6 April	0	4	18.9 $\pm$ 2.5	10.6 $\pm$ 3.7	8.3 $\pm$ 2.2	— ^a	0.45 $\pm$ 0.19	0.05 $\pm$ 0.02	0.4	20
4 May	0	4	62.0 $\pm$ 5.1	18.9 $\pm$ 6.9	43.1 $\pm$ 2.0	— ^a	6.73 $\pm$ 5.79	0.20 $\pm$ 0.11	6.5	7
	16	4	81.1 $\pm$ 45.0	114.5 $\pm$ 58.1	-33 $\pm$ 30	-180 $\pm$ 73	9.79 $\pm$ 5.84	0.31 $\pm$ 0.14	9.5	0
	64	4	65.0 $\pm$ 27.0	105 $\pm$ 83	-40 $\pm$ 59	-201 $\pm$ 150	11.73 $\pm$ 0.68	0.33 $\pm$ 0.09	11.4	0
24 May	0	3	59 $\pm$ 12	140 $\pm$ 12	-81 $\pm$ 1	— ^a	10.35 $\pm$ 5.14	0.27 $\pm$ 0.11	10.1	1 ^b
21 July	0	5	177 $\pm$ 53	236 $\pm$ 50	-59 $\pm$ 16	— ^a	6.14 $\pm$ 0.25	0.18 $\pm$ 0.04	5.96	34 ^b

^a Control value, i.e., no added APM

^b Estimate based on 60% extracellular ¹⁴C release from photoinhibition

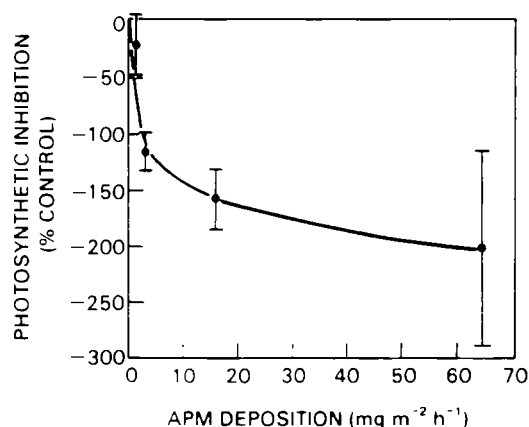


Fig. 3. Inhibition (percentage change from control) of radiocarbon-measured primary productivity in the sea-surface microlayer (upper 20 μm) with increasing additions of metal-rich atmospheric particulate matter (APM)

reduction in the light minus dark photosynthetic rate of phytoneuston.

Discussion and conclusions

Our results support those of Albright (1980) and Carlson (1982) and indicate no consistent enrichment of chlorophyll *a* in the microlayer. However, we find that concentrations of total active chlorophylls (chlorophylls *a* + *b* + *c*), on the average, are 12 times greater in the microlayer than in the bulk water. Unpublished studies by us confirm that such microlayer pigment enrichments are typical in Puget Sound. Chlorophylls *b* and *c* are believed to transfer energy to chlorophyll *a*, especially under conditions of high light intensity (Jeffrey, 1980) typical of the surface microlayer. The higher concentrations of accessory pigments in the microlayer probably reflect the abundance of cryptomonads and diatoms at the surface. Because of high variability in concentrations between field stations (July 11), we found no significant difference in phaeopigment concentrations, although enrichment of these pigments in the microlayer was strongly suggested (Table 3). High phaeopigment concentrations in the microlayer could result from: (1) photo-oxidation of chlorophyll under high surface light intensities, (2) a higher grazing rate and pigment digestion by zooneuston compared to zooplankton, or (3) simply collection of less active or dead phytoplankton at the surface. The last possibility seems unlikely since we found a unique species composition and no apparent increase in the percentage of dead cells in the phytoneuston compared to the phytoplankton. Thus, our results do not support the hypothesis that the microlayer is typically depleted in chlorophyll pigments compared to the subsurface water.

We found that during the summer, or in winter and spring when exposed to levels of urban atmospheric particulate matter $> 2 \text{ mg m}^{-2} \text{ h}^{-1}$, carbon fixation rates of neuston appeared lower in the light than in the dark

(Table 4). Ultraviolet radiation can reduce carbon-14 measured photosynthesis in surface waters (Lorenzen, 1979; Smith and Baker, 1980; Worrest *et al.*, 1980, 1981). However, the ^{14}C technique underestimates total photosynthesis in proportion to the release of ^{14}C -labelled soluble products of photosynthesis from cells. Such apparent photoinhibition is a common occurrence in *in situ* ^{14}C experiments, especially in the presence of high levels of ultraviolet irradiance (Harris, 1980), when marine diatoms are exposed to elevated levels of lead (Rivkin, 1979) or during nutrient depletion (Harris, 1978). Thus, subtraction of dark ^{14}C fixation from light ^{14}C fixation can lead to serious underestimates of primary production (Legendre *et al.*, 1983).

Rapid formation of glycolate and other soluble organics appears to occur when cells are metabolically stressed (Sharp, 1977) and increases with increasing photoinhibition (Fogg, 1966). These compounds are released as soluble extracellular products or metabolized by the glycolate pathway to CO_2 (photorespiration). The percentage of ^{14}C released in this way increases with light intensity and can exceed 50% of the total fixed carbon in the presence of very high light intensities (Watt, 1966). Even in our January experiment, we found a significantly higher release of dissolved ^{14}C in the light over that in the dark. Light-saturated rates of photosynthesis often occur in phytoplankton above about $100 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Harris, 1978). At the natural light intensity of our July experiment ($1\,230 \mu\text{E m}^{-2} \text{ s}^{-1}$), photoinhibition probably exceeds 60% (Harris, 1980). Applying a 60% correction to our neuston rates in the light, light minus dark carbon fixation on 24 May becomes: $59 \text{ mg m}^{-3} \text{ h}^{-1}$ [in light] $\times 2.5$ [correction factor for photoinhibition] $= 140 \text{ mg m}^{-3} \text{ h}^{-1}$ [in dark] $= 7.5 \text{ mg m}^{-3} \text{ h}^{-1}$, a value slightly less than that of the plankton. Similarly, on 21 July, productivity would be 34 times greater in the neuston than in the plankton. Such corrections provide, at best, only an estimate of the actual productivity. Future studies on neuston productivity should include measurements of extracellular carbon release and/or a correction using the inhibitor 3-(3,4-dichlorophenyl)-1,1-dimethyl urea (DCMU) to replace the dark bottle (Legendre *et al.*, 1983).

Albright (1980) found that the photosynthetic activity of phytoneuston in coastal British Columbia was inhibited compared to the plankton. However, data for light-dark bottles only were reported. Thus, identification of possible photorespiration or extracellular release of carbon is not possible. In addition, Albright's samples were preserved in formalin which can cause marked losses of ^{14}C from the particulate fraction (Peterson, 1980), especially from delicate flagellates which often dominate neuston populations. Our results suggest that photoinhibition, higher metal levels in the microlayer, or some other form of stress probably leads to release of significant quantities of labelled extracellular products. This can lead to erroneously low estimates of productivity in phytoneuston using the ^{14}C radiocarbon technique. Indeed, our data, corrected for extracellular carbon release, indicate that the productivity per unit volume without atmospheric particle addi-

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ons is 10 to 100 times greater in the phytoneuston than in the phytoplankton, an enrichment which agrees with that measured previously by the oxygen-production technique (Gallagher, 1975).

APM is highly enriched in metals, such as Pb (Hardy and Crecelius, 1981), which are potentially toxic to marine phytoplankton (Rivkin, 1979). Sea surface deposition of Pb over northern hemisphere ocean areas alone amounts to about 31 000 metric tons annually (Servant, 1982), of which 40 to 60% may solubilize in seawater (Hardy and Crecelius, 1981). We reported previously (Hardy and Crecelius, 1981) that deposition rates of APM greater than $50 \text{ mg m}^{-2} \text{ d}^{-1}$ could inhibit phytoplankton productivity. Natural deposition levels do not normally reach this level, but we suggested that because APM metals have long residence times and remain at high concentrations in the sea-surface microlayer (Hardy *et al.*, in press. a), they might inhibit phytoneuston productivity.

Our previous data (Hardy *et al.*, in press. a) indicate that during a 4 h exposure of the microlayer to atmospheric particulate matter (APM) most of the lead remains in the microlayer. Therefore, in the present study, deposition of $16 \text{ mg m}^{-2} \text{ h}^{-1}$ (Table 4) would represent a total Pb concentration in the microlayer of 22 mg l^{-1} and a soluble Pb concentration in the microlayer of about $4.3 \mu\text{g l}^{-1}$ (Hardy *et al.*, in press. a). Rivkin (1979) has shown that soluble Pb between 1 and $10 \mu\text{g l}^{-1}$ decreases net photosynthetic production by increasing the excretion of labelled organics to between 27 and 61% of the total carbon fixed by photosynthesis.

Our results indicate that APM depositions greater than about $1 \text{ mg m}^{-2} \text{ h}^{-1}$ ($157 \mu\text{g Pb m}^{-2} \text{ d}^{-1}$) inhibit primary productivity at the sea surface when light minus dark particulate ^{14}C values are used. This probably results from an increased release of ^{14}C -labelled extracellular products when the microalgae are exposed to high levels of lead (Rivkin, 1979). Natural deposition rates in coastal areas often reach $40 \text{ mg APM m}^{-2} \text{ d}^{-1}$ or $150 \mu\text{g Pb m}^{-2} \text{ d}^{-1}$ (Hodge *et al.*, 1978; Rohbock *et al.*, 1981). Such levels would be expected to reduce particulate carbon fixation in the sea-surface microlayer.

Acknowledgements. This research was supported by U.S. Department of Energy Contract DE-AC06-76RLO 1830. The manuscript was improved by the helpful comments of Drs. G. Roesijadi, L. Small and D. J. Carlson. The Marine Research Laboratory is part of the Pacific Northwest Laboratory, which is operated for the Department of Energy by Battelle Memorial Institute under Contract DE-AC06-76RLO 1830. The registered trademarks are referenced for reader convenience in replicating experiments and do not represent endorsement by the Pacific Northwest Laboratory.

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Date of final manuscript acceptance: April 24, 1984.
Communicated by N. D. Holland, La Jolla

Abundance of Car

K. A. Hou

Department
St. John's.

Abstract

The abundance in the 48°40'W latitudinal In contrast to outside (m⁻²), biomass was 0.03 g in with depth type had at the e. Larger a depend

Introduction

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News



PHOTO BY KENNY BENNETT FOR WILDER

once again.

young red-backed squirrel monkey from the Boston home of a Costa Rican national, who was illegally keeping it as a pet. One of only 2,000-3,000 surviving members of this endangered species, the little male was sent to the Phoenix Zoo in December,

when it was believed to be eight or nine months old. There it was joined by the only other two red-backed squirrel monkeys in the U.S., a father and daughter that came from the Santa Ana Zoo, in California. The Phoenix Zoo is developing a captive-breeding program for the species. Reg Hoyt, the zoo's curator of mammals, hopes to acquire more captive animals, possibly from a private breeder in Costa Rica.

In the wild, the red-backed squirrel monkey lives only in the southwestern corner of Costa Rica and northwestern Panama. Deforestation of its rainforest habitat has caused its

numbers to plummet. Human exploitation has also taken a heavy toll: The monkeys are considered prestigious pets and, typically, hunters shoot the mothers to capture their infants.

Sources: U. S. Fish and Wildlife Service; Reg Hoyt, Phoenix Zoo

EARTH: MORE POISONS IN THE SEAS

CHEMICAL PRESERVATIVES for wood and paint, along with a bevy of other toxic chemicals, pose a growing threat to marine life.

Researchers from the Plymouth Marine Laboratory, in England, have discovered that poisonous chemicals are accumulating in the "microlayer" (the top one millimeter of water) of open sea in far greater concentrations than expected. In the North Sea, they found highly toxic levels of tributyltin (TBT), an ingredient of marine paints, as far as 125 miles offshore. Lead and copper were also present in disturbingly high concentrations. Many fish feed on the microscopic organisms that live in the surface layer, and the eggs of some fish species mature there.

A scientist at Western Washington University has found high concentrations of carcinogens in the microlayer. The compounds, products of burning oil and gas, are deposited from the atmosphere.

From the Benedict Estuarine Research Laboratory, in Maryland, comes a report that pressure-treated lumber—wood impregnated with a preservative to

guard against rot and insect damage and widely used to build decks and piers—appears to be releasing substantial amounts of arsenic and other metals into many bodies of water. In recent years the preservative of choice has been a compound known as CCA, a mixture of chromium, copper, and arsenic. The Benedict researchers found that sensitive species of algae would not grow in water exposed to CCA-treated wood, and they suggested that the possibility that CCA is harming other aquatic life forms is very strong.

Sources: Peter Leonard, Philadelphia; U. S. Fish and Wildlife Service

HAWAII: THE END NEARS FOR ISLAND'S CROW

THE ALALA, OR HAWAIIAN crow, is down to fewer than 10 birds. The 10 living in a state breeding center are dangerously inbred, so



U.S. FISH AND WILDLIFE SERVICE

Hawaiian crow

biologists are eager to add some wild birds to the captive flock. But aside from one seen on state land and another spotted in a military area, all the remaining wild crows are on private property. Although, after lengthy negotiations, the owner agreed to let biologists enter her land to do

LETTING IT PILE UP

JUNK IS WASTED. It doesn't have a place in anyone's life, but it's still around today's junkies. It's not until it's gone away, it's gone.

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Sources: The Zoo hortiv

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U.S. FWS inspector Timothy J. Santel readies red-backed squirrel monkey for transport to Phoenix Zoo.



The Cousteau Society

930 West 21st Street
Norfolk, Virginia 23517

PHOTOCOPY
PRESERVATION

TELEFAX TRANSMITTAL

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Message:

Re. neutron, the enclosed seems
pertinent - especially since it's not
concerned with depositional pollution.
From Wildlife Conservation, May -
June, 1991. CCM

P.S. The fine-print credit goes
New Scientist, Philadelphia Academy
of Sciences.

AUTHORS, CONTINUED

Christine Padoch (page 48) has been part of an interdisciplinary study of native fruits of the Peruvian Amazon since 1981. "When we realized that most agricultural production came from the floodplains," says Padoch, "we turned our attention to such areas. The floods and how people adapted to them became the focus of our research." An associate scientist at the Institute of Economic Botany at the New York Botanical Garden, Padoch is now doing research on traditional forest management in West

Kalimantan, Indonesia. Born and raised in a small village along the Ucayali River in Peru, coauthor Miguel Pinedo-Vasquez has observed floods, and how people contend with them, all his life. A student at the Yale School of Forestry, Pinedo-Vasquez is also adviser to the Small Farmer's Federation of Loreto, in Iquitos, Peru. For further information, the authors recommend Mario Hiroka's article "Mestizo Subsistence in Riparian Amazonia" (*National Geographic Research*, vol. 1, no. 2, pp. 236-46, 1985).



When in the field, William E. Ferguson (page 88) rarely misses the opportunity to photograph interesting insect behavior. In addition to the image of the honey ants that are the subject of this month's "Natural Moment," two of his photographs of desert-dwelling tiger beetles appear in this issue. As an entomologist, Ferguson's fieldwork has taken him to temperate and tropical areas of the world, but his focus has been insect life in North American deserts. Ferguson received his undergraduate and graduate degrees from the University of California at Berkeley. He is currently a professor emeritus of entomology at San Jose State University and is studying a group of parasitic wasps, known as velvet ants, that thrive in the deserts of the Southwest. The "Natural Moment" photograph was taken with a Nikon F camera, a 55mm Micro-Nikkor lens, and a hand-held electronic flash.



A few weeks after he read Jacques Cousteau's book *The Silent World* at the age of fourteen, John ("Jack") Hardy (page 58) donned scuba gear and began to explore the underwater world of his native southern California. From these early firsthand observations of ocean life, Hardy's boyhood interest eventually led to a doctorate in marine botany and aquatic ecology from the University of Washington. For his thesis, he studied a group of tiny, obscure algae that live on the water's surface. Fascinated with this unique habitat, he has since pioneered the study of the seotopmost layer and how it is affected by pollution. This research has led him around the world, from the Pacific lands to the Mediterranean, the North Sea, and the Atlantic Ocean. Now an associate professor at Huxley Environmental College, Western Washington University, Hardy heads a research group examining the effects of climatic change on the marine environment and continues research on the aquatic surfmicrolayer. He is a coauthor (with Phyllis W. Basson et al.) of *Biotores of Western Arabian Gulf* (Aramco Department of Loss Prevention and Environmental Affairs, Dhahran, 1977), the first comprehensive study of the marine ecology of the Persian Gulf. For further reading on pollution and the sea, he recommends the special issue of the journal *Marine Environmental Research* (vol. 23, no. 4, 1987).

Attacked on the open seas, a Portuguese man-of-war is helpless as it floats partly submerged. The voracious snail Janthina gets about by attaching its bubble raft to the underside of the surface film. It is impervious to the jellyfish's stinging tentacles, upon which it feeds. Minute scraps from the meal may go to the goose barnacles hitchhiking on the snail's shell.

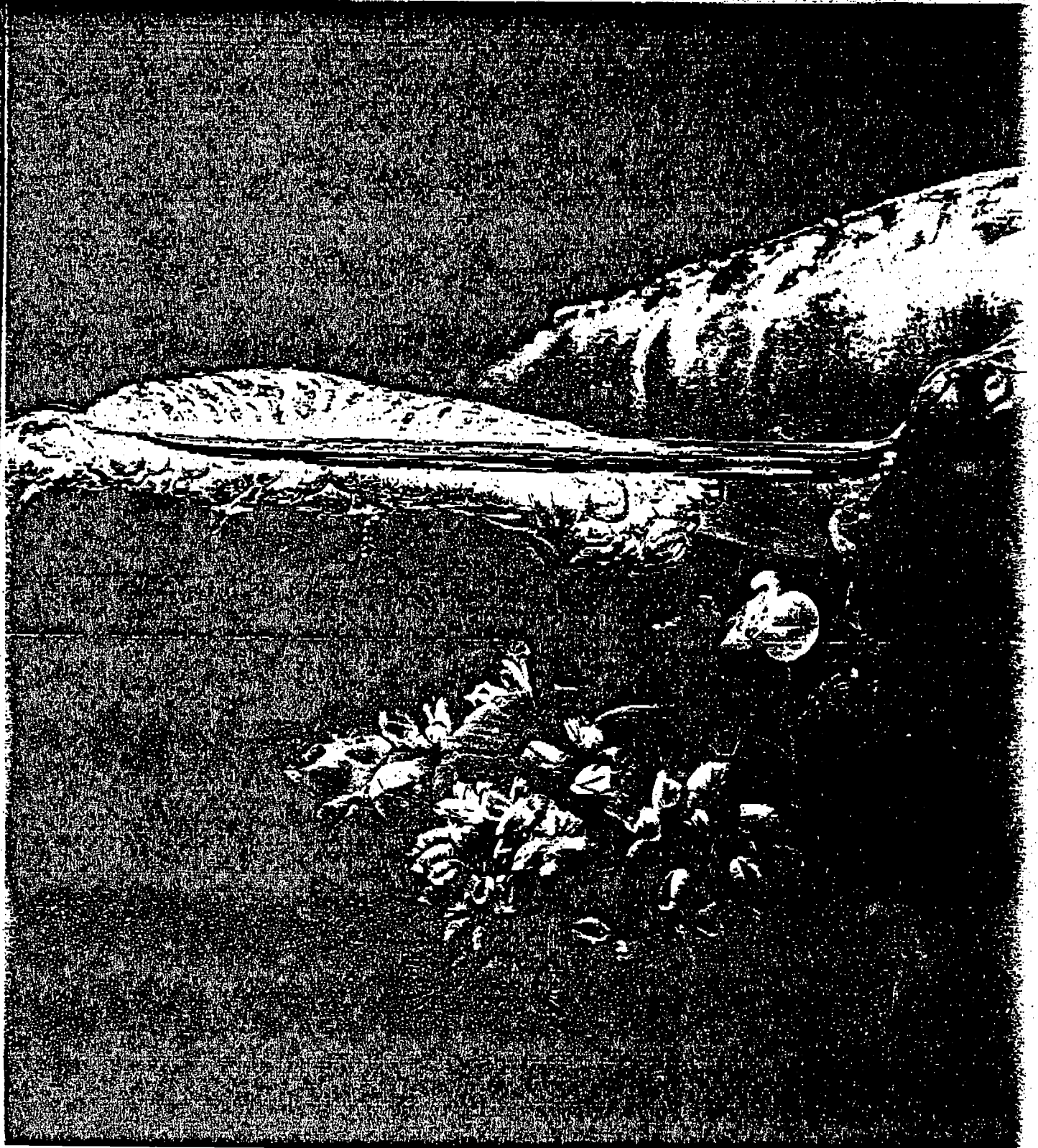


though others may disintegrate and dissolve harmlessly.

Dense populations of microbes and small animals inhabiting the aquatic surface layer form the base of an extensive food chain. While seabirds and other creatures feast on the microlayer's bounty from above, many larger organisms from the deep sea migrate upward to feed at the surface. A polluted surface microlayer has the potential to poison much of the complex marine food web, including fish, crustaceans, whales, and seabirds.

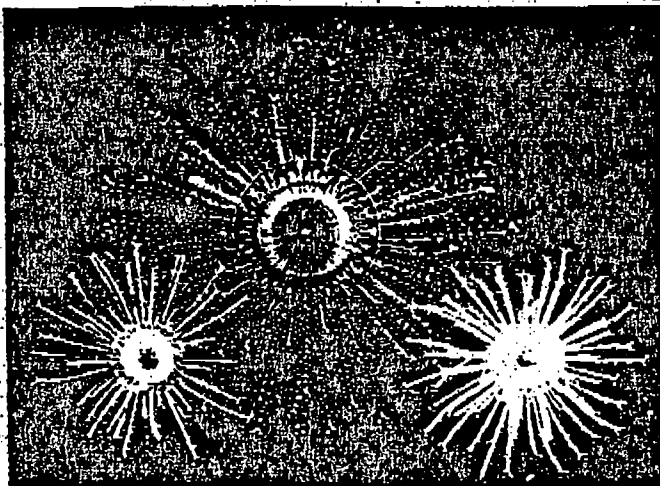
Destruction of the microlayer may even alter the exchange of materials between the atmosphere and the ocean, thereby affecting global climate. According to Robert J. Charlson, an atmospheric chemist at the University of Washington, microscopic plants (phytoplankton) from the ocean's upper layers may be part of a thermostatic system that regulates the amount of solar energy that warms the earth. A complex chain begins when the plankton produce a sulfide gas that carries particles of sulfur into the atmosphere. Cloud droplets form around them, and their density determines how much solar heat reaches the earth. According to the theories of Charlson and others, recently backed up by studies in Australia, these natural emissions are the world's main source of the nuclei for cloud condensation and a major source of sulfur. Where the layer is polluted, as in the North Sea, more sulfide gases flow into the atmosphere, producing denser clouds that cool the air. This in turn may cause a decrease in phytoplankton and a seesaw warming of the region.

Studying the sea's remarkable "skin" has confirmed our worst suspicions about the global dimensions of the poisoning of our oceans. This surface habitat is becoming as endangered as the dwindling homelands of the mountain gorilla, but its destruction may affect many more life forms. It is a vast trough for pollutants to enter into the web of life, a juncture for understanding the complexities of marine ecology, a sensitive diagnostic indicator of environmental problems, and quite possibly the key to a thermostatic system regulating global climates. □

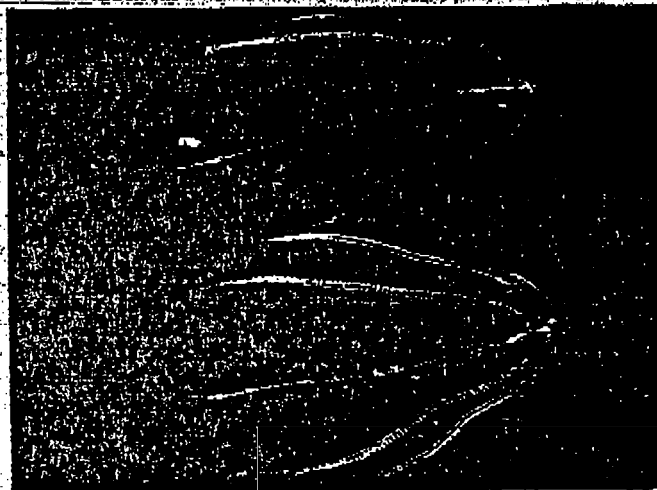


Jellyfish, which as adults feed on plankton, are themselves part of the planktonic mix when young. In extreme close-up, Potpita jellyfish larvae, top, reveal their variable colors. Newly hatched shrimp, such as this diaphanous larva from Pacific coast waters, center, are abundant near the ocean's surface. They feed on diatoms, such as the single-celled algae, bottom, colored by light passing through their transparent bodies.

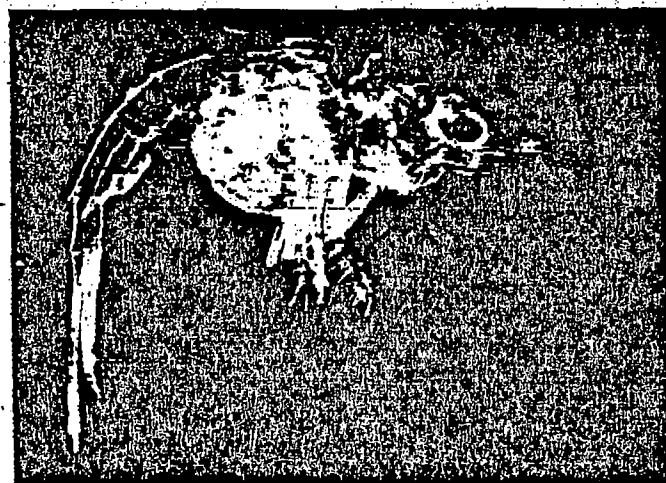
Early colored comb jellies, armed with stinging cells that explode and ensnare their microscopic prey, top, are aggressive predators of arctic seas. The growth and development of healthy marine fish eggs, such as those from Australia's Great Barrier Reef, center, provide a good baseline for measuring the effects of toxic pollutants. Bottom: Another tiny predator of the surface layer, the copepod, is the most numerous animal not only in the plankton but also in the world.



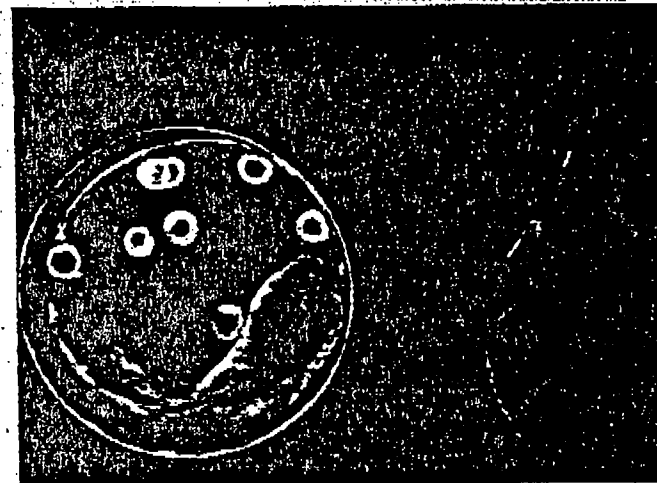
Peter Parks; Oxford Scientific Films



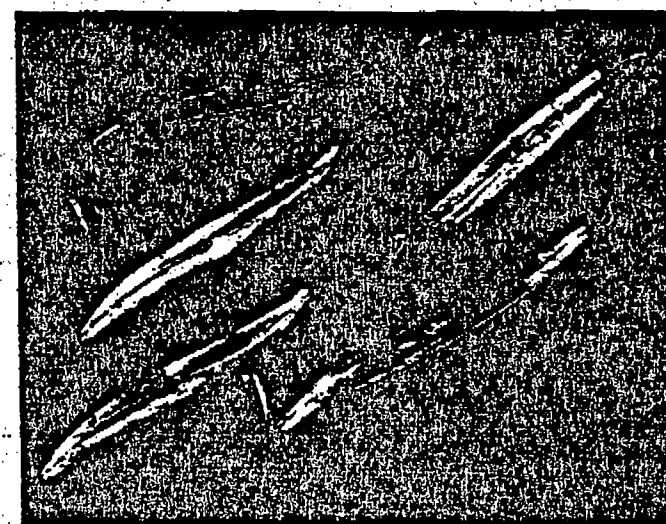
Norbert Wu



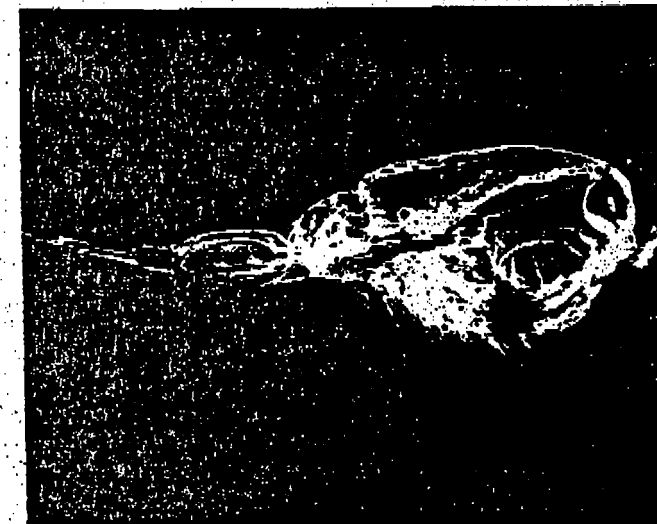
David Downing; Earth Images



Peter Parks; Oxford Scientific Films



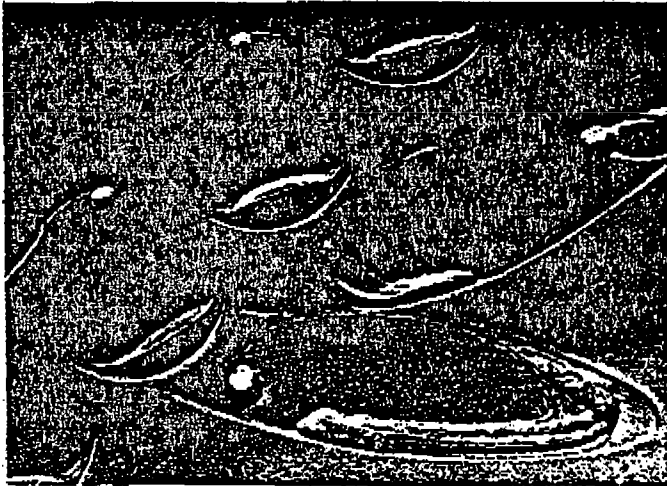
Peter Parks; Oxford Scientific Films



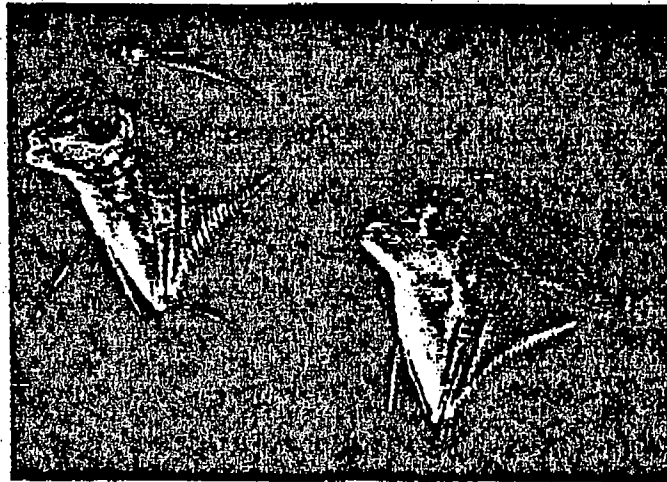
Peter Parks; Oxford Scientific Films

Fish eggs of many species, top, float at the ocean's surface, buoyed by their own fat globules. Larvae of reef-dwelling fish, such as tang, center, congregate near the surface to feed on tiny plants and animals, as do juvenile swordfish, bottom.

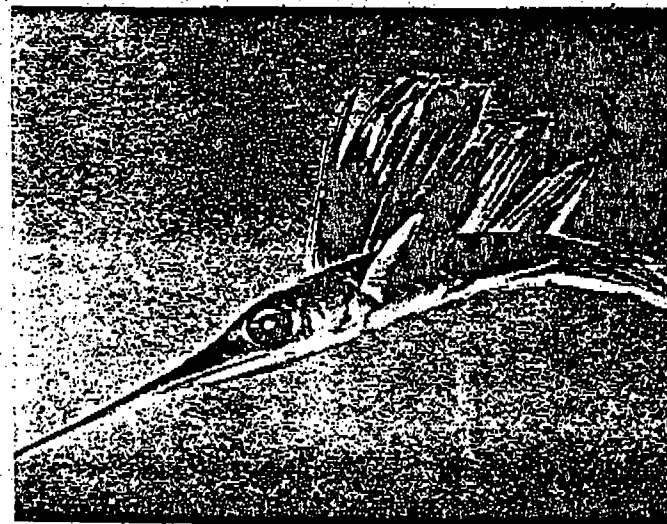
A glass jellyfish, top, moves through the upper layers of arctic waters, feeding on the various small organisms known as plankton, the same microscopic life that nourishes the great baleen whales. Bottom: A mixture of one-celled plankton, including radiolarians, diatoms, and dinoflagellates, swim in the waters off Bermuda.



Peter Parks: Oxford Scientific Films



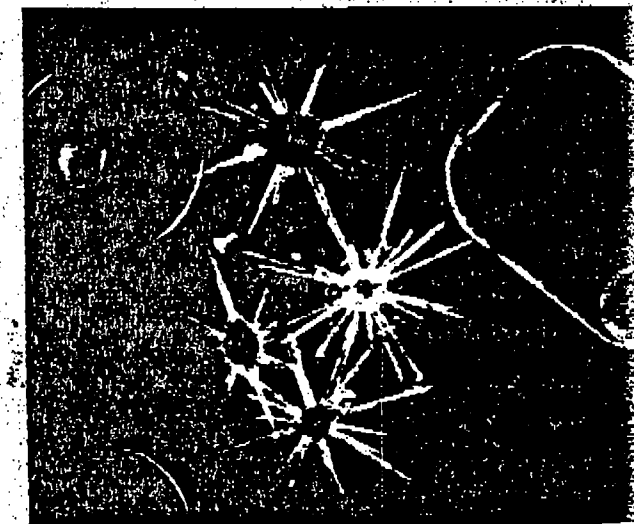
Norbert Wu



Norbert Wu



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Peter Parks: Oxford Scientific Films



ticles easily become more concentrated on the surface than in the waters below.

We are all familiar with the dramatic destructiveness of large petroleum spills, although most television images are of cuddly otters and birds suffering fouled fur and feathers. However, the less visible—but much more pervasive—chronic contamination of the microlayer may present an even greater threat to many species. Oil, spreading over the water's surface at the same time that fish are releasing their floating eggs, can devastate a population's reproductive success.

Our research team and a few others have been trying to assess this less obvious danger to animals and plants that depend on the microsurface habitat for food and

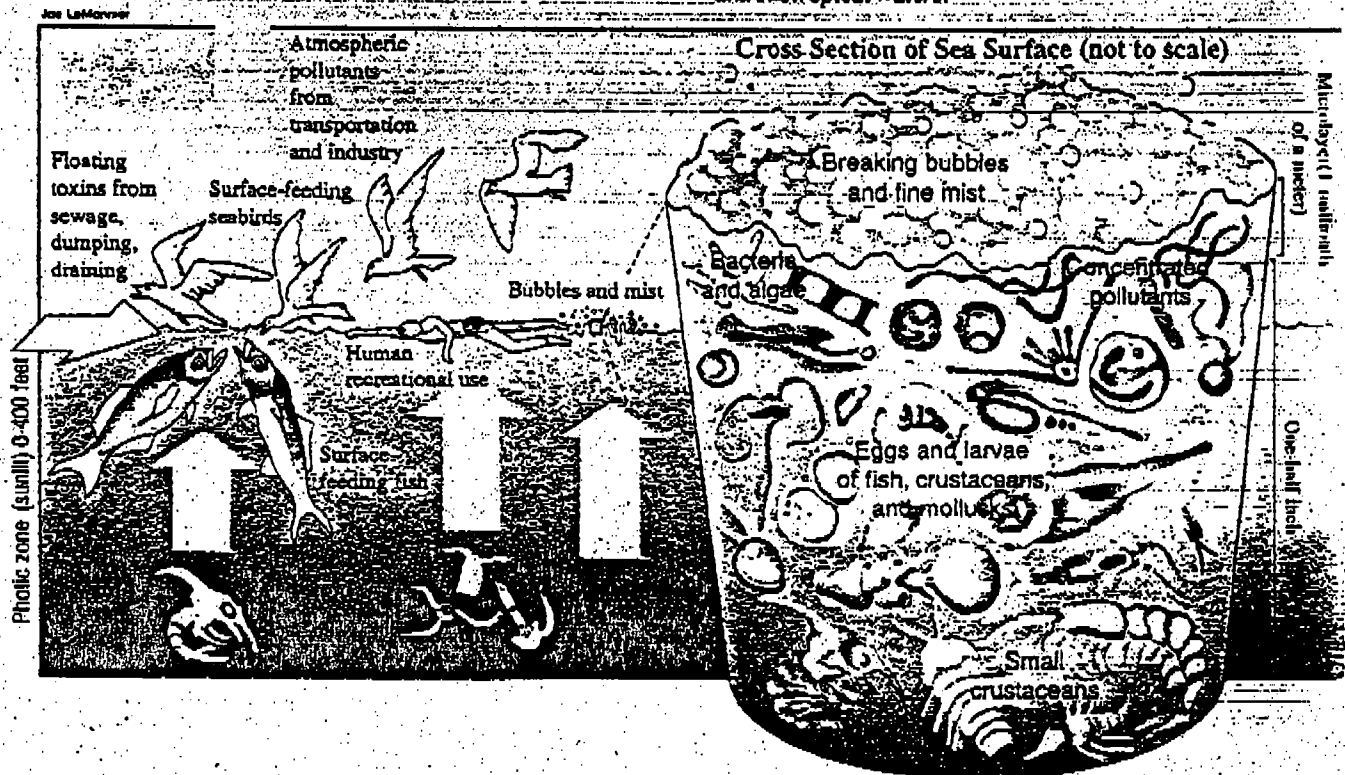
reproduction. In the more than 200 microlayer samples we have collected from rivers, estuaries, bays, and oceans (including Puget Sound, Chesapeake Bay, the North Sea, and the waters off Southern California and Florida), there is a sadly consistent picture: the surface microlayer is becoming a soup of toxic metals, organic pollutants, bacteria, pesticide residues, and the byproducts of combustion-derived hydrocarbons from cars, trucks, airplanes, refuse incinerators, and power plants. Coastal sewage, waste-water discharges, runoff from municipal and agricultural drainage systems, and direct industrial discharges into rivers contribute to the contamination.

We assess the effects of pollution by

observing the development of healthy fish eggs placed both in containers attached to moored buoys and in lab dishes filled with samples collected from polluted microlayers. Using the known data on the healthy development of fish eggs in clean water as a baseline, we have repeatedly observed that larvae hatched in polluted microlayers either die, develop slowly, or emerge malformed. We have often seen this result in some widely scattered locations throughout the world.

The same physical stability that enables the microlayer to support so much life also fosters the persistence of pollutants in high concentrations. In the presence of sunlight, some contaminants break down into even more harmful chemicals, al-

The ocean's uppermost layer concentrates nutrients and toxins alike; below. Pollutants enter from sewage, drainage systems, or the atmosphere and are ingested by skimming birds, top-feeding fish, and sometimes, by human swimmers. Right: A whale shark, the world's largest fish, scoops up tons of plankton from the surface layer. With gill arches modified to act as a sieve, it filters food from tropical and subtropical waters.



waters contain complex mixtures of chemicals that are often absent or greatly diluted at lower levels. Yet most of these natural compounds are derived from deeper-dwelling organisms. The billions of tiny plants and animals known as plankton occupy the sunlit photic zone, which may extend downward as far as 400 feet in the open ocean. The plankton excrete many organic compounds, such as amino acids, proteins, and fatty acids, that serve as nutrients for bacterial growth. Rising air bubbles capture these rich materials and carry them to the surface, where they become concentrated. When plankton die and disintegrate, some debris sinks to the bottom, but tons of cellular particles, along with oils, fats, and proteins, float to the surface.

Accumulation of these natural organic chemicals modifies the physical and optical properties of the sea surface. Thin organic films, invisible to the naked eye, are ubiquitous in lakes, oceans, and rivers. Where currents converge, these films merge and thicken; wave action some-

times makes them visible as "surface slicks." Strong surface tension acts on the slicks, resulting in a layer of sandwiched molecules, about as thick as a human hair, that resists turbulent mixing. This unique surface layer habitat even extends into the atmosphere. Just above the surface film, millions of bursting bubbles contribute to an aerosol blanket containing dense concentrations of both natural chemicals and man-made pollutants.

Metal ions, common in seawater, bind to the organic molecules and concentrate within the surface film, creating an environment that is very different from the subsurface waters. Some metal ions, such as iron, are necessary and useful to marine life; others, from human pollution, are poisonous. Such toxins as copper, lead, zinc, and cadmium, for instance, have been found in the microlayer in concentrations of 10 to 100 or more times greater than in the water below. Pesticides have been found in concentrations up to millions of times greater than in the rest of the water.

This complex aquatic surface is surpris-

ingly stable and can hold together despite buffeting by sixteen-knot winds and four-foot waves. According to Soviet biologist Yuri Zaitsev, fish eggs, larvae, and fry cling tenaciously to the surface layer even in waves three to six feet high. General winds strong enough to whip up whitecaps and cause surface mixing are not as widespread as often imagined, occurring less than 5 percent of the earth's surface any given time. Even when disturbed and mixed, visible surface slicks can reform less than an hour after the strong wind calms down.

Because of its unique tendency to collect and condense chemicals, this resilient surface habitat is increasingly threatened by a variety of human activities, particularly the dumping of industrial wastes and widespread atmospheric pollution. Soluble pollutants bind to buoyant particles and wind up concentrated within the surface microlayer. Contaminants that fall from a fouled atmosphere collect in the natural organic films. Like nutmeg powder sprinkled on an eggnog, such

...ake Passage near Antarctica, a giant petrel flies low over the water, seeking crab and fish larvae that live in the ocean's nutrient-rich surface layer.

Vol de Roy: Hedgesburg House

Where the Sea Meets the Sky

The ocean's skin is the richest, most extensive habitat of all

by John T. Hardy

Charles Darwin was fascinated by an explorer's account of an American black bear "swimming for hours with widely open mouth, thus catching, like a whale," thousands of insects, fish, and crustacean larvae that cluster near the water's surface. The bear that captured Darwin's imagination was exploiting an ecological niche that has only recently been studied: an immense, paper-thin habitat that blankets more than 71 percent of the earth.

Known as the sea surface microlayer, it is a remarkable "skin" that separates bodies of water from the surrounding atmosphere—the familiar dividing line between ocean and sky. Within this complex skin of the seas dwell thousands of species of plants, animals, and microbes, all attracted there by its special ability to nurture life.

Since 1989, I have been working with a team of marine biologists, chemists, and toxicologists at the Huxley College of Environmental Studies at Western Washington University investigating the biology and chemistry of the surface layer. On clear, relatively calm days, we have sampled waters as near as Puget Sound or as far away as the North Sea. Our collecting device is a barrel-sized, teflon-coated rotating drum towed alongside our research boat. Organic film from the water's surface adheres to this revolving cylinder and is continuously scraped by a squeegee into a large glass jar. Several quarts of the surface layer habitat can be collected by this method in just a few minutes. We also skim the surface with a special plankton net attached to pontoons, to collect samples of surface-dwelling crustaceans, fish eggs, and larvae.

Scientists have known for years that the thin aquatic surface layer teems with life. In 1917, a Swedish researcher of freshwater habitats, Ernst Naumann, coined the

term *neuston* to describe certain protozoans that use the surface film for support. His coinage was taken from the Greek *neustos*, which means "floating" but refers to many inhabitants of the upper few inches of oceans and lakes. Since Naumann's time, biologists have discovered scores of plants and animals, ranging from tiny bacteria and algae to large jellyfish and seaweeds, that live, reproduce, or feed within a few inches of the surface.

Bacteria adhere to the underside of the surface film, as do some unicellular protozoans that attach themselves with a special appendage. Fish eggs are packed with fat globules, which cause them to float in contact with the surface. Other organisms, such as snails and some jellyfish and seaweeds, entrap air bubbles and float on the film. Sargassum seaweed clusters in floating mats that nurture many small creatures, including baby sea turtles.

Along with the protozoans, a dense blanket of microalgae lives at the surface layer, attracted by both sunlight and the concentration of nutrients found there. Some microalgae actually migrate to the surface at midday and then descend many feet during the night.

Capitalizing on this concentration of biota, many seabirds make their living by skimming food from the water's surface (some are even called skimmers). One of the surface layer's main attractions for shearwaters, auklets, and petrels is that it provides an important nursery ground for numerous fish species: cod, sole, flounder, hake, menhaden, anchovy, mullet, flying fish, greenling, saury, rockfish, and halibut. The tremendous risk for so many fish larvae and eggs being so near the surface appears to be balanced by the abundance of food found there and perhaps the lack of predators that live in deeper waters.

The northeast Pacific, the U. S. conti-

ental shelf, and the North Sea are typical of rich fishery areas where dozens of fish species produce eggs or larvae that concentrate at the sea surface. In Puget Sound, English sole and sand sole spawn between January and April, releasing billions of eggs that float at the surface until they hatch, generally about a week after fertilization. Because of the buoyancy of their large yolk sacs, newly hatched larvae of these flatfish often float upside down near the surface.

The ocean's skin is also a vital habitat for many commercially important shellfish at certain stages of their life cycles. Crab and lobster larvae, for instance, seek the sunlight of the near-surface, where they feed on concentrations of minuscule life forms: the microalgae and protozoans. In Chesapeake Bay, 99 percent of blue crab larvae migrate to the surface layer and spend several days feeding there. After increasing in size, the larvae return to deeper waters, where they feed upon larger foods.

The extraordinary vitality of the sea's microlayer depends on special physical and chemical properties that are very different from those of the waters just below. The topmost three feet of water contains a whole series of sublayers, each with its own distinctive biological and chemical features. Within the surface layer (upper few feet), the first two-thousandths of an inch contains an especially dense concentration of minerals, chemicals, protozoans, and microorganisms. The upper few inches contain a greater density of larger organisms: fish eggs, fish larvae, and crustaceans. Larger, floating jellyfish and seaweeds may occupy the upper foot. The surface layer includes many transients, with plants and animals constantly migrating up and down.

The surfaces of both fresh and marine

