ISSN 0240-8759

Vie et Milieu

Life and Environment

Vol. 48 nº 4 – Déc. 1998

Périodique d'écologie - Publication trimestrielle

VIE ET MILIEU

Life and Environment

PÉRIODIQUE D'ÉCOLOGIE GÉNÉRALE
JOURNAL OF GENERAL ECOLOGY

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Publié avec le concours financier/Published with the support
du Conseil Régional du Languedoc-Roussillon
de l'Association Naturalia et Biologia

ABONNEMENTS/SUBSCRIPTIONS 1998

	FRANCE	AUTRES PAYS
Un an (4 numéros) / *Annual subscription (4 issues)*..	820 F	970 FF

Adresser le paiement à l'ordre de / *Address payment to the order of :*

Vie et Milieu, Laboratoire Arago, BP 44, 66651 BANYULS-SUR-MER CEDEX, FRANCE

Les abonnements partent du premier numéro de l'année / *subscriptions begin with the first calendar year*

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VIE MILIEU, 1998, 48 (4) : 229-241

BURIAL PATTERN OF CARBON, NITROGEN AND PHOSPHORUS IN THE SOFT BOTTOM SEDIMENTS OF THE BALTIC SEA

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BALTIC SEA
SEDIMENT
CARBON
NITROGEN
PHOSPHORUS
BURIAL

ABSTRACT. – The burial pattern of carbon, nitrogen and phosphorus in soft bottom sediments from all sub-basins of the Baltic Sea has been investigated. The highest total concentrations of carbon and nitrogen are found in the central deep part of the Baltic proper. The inorganic concentration of carbon is normally far below 1 % in the entire Baltic Sea except for some localities with anoxic conditions where authigenic precipitation of mixed manganese carbonates occurs, for example, the eastern Gotland deep. Manganese seems to be of essential importance for such precipitation. As in the case for carbon, a dominant proportion of the nitrogen found in the sediments is organically bound. For phosphorus, on the other hand, a dominant proportion is inorganically bound. The highest total concentrations are found in the eastern part of Gulf of Finland and in the well-oxidized sediments of the Bothnian Bay and Bothnia Sea. The organic C/N ratio is very stable vertically through the sediment very stable at each location indicating that the degradation of the organic matter in the sediment proceeds in a C/N proportion. The organic C/P ratio within the sediment departs considerably from the Redfield ratio, mainly due to more or less instantaneous releases of easily hydrolyzable organic phosphorus molecules.

MER BALTIQUE
SÉDIMENT
CARBONE
AZOTE
PHOSPHORE
ENFOUISSEMENT

RÉSUMÉ. – L'enfouissement du carbone, de l'azote et du phosphore dans les sédiments meubles de l'ensemble des bassins de la Mer Baltique a été étudié. Les concentrations les plus élevées en carbone et en azote se trouvent dans la partie centrale profonde de la Baltique proprement dite. La concentration de carbone inorganique est normalement très inférieure à 1 % dans toute la Baltique, à l'exception de quelques sites aux conditions anoxiques où une précipitation authigène des carbonates de manganèse se produit, par ex. dans l'Est Gotland profond. Le manganèse semble avoir une importance essentielle lors d'une telle précipitation. Comme pour le carbone, une proportion dominante d'azote dans les sédiments est liée organiquement. Par contre, une proportion dominante de phosphore est liée inorganiquement. Les concentrations totales les plus élevées se trouvent dans la partie est du Golfe de Finlande et dans les sédiments bien oxygénés de la Baie de Bothnia et de la Mer de Bothnia. Le rapport C/N organique est pratiquement constant suivant la verticale dans les sédiments très stables et à chaque site, ce qui suggère que la dégradation de la matière organique dans les sédiments concerne le carbone et l'azote dans une même proportion. Le rapport C/P organique dans les sédiments s'écarte considérablement du rapport de Redfield, principalement en raison du relargage plus ou moins instantané de molécules de phosphore organique facilement hydrolysables.

1. INTRODUCTION

The Baltic Sea, which is one of the largest bodies of brackish water in the world, represents a unique environment both in terms of its impoverished fauna and flora and its hydrography and biogeochemistry (see e.g., Voipio 1981, Elmgren 1984, Larsson *et al.* 1985, Emelyanov 1988). The Baltic Sea can be divided in three distinct main basins (the Baltic proper, Bothnian Sea and Bothnian Bay; Fig. 1) which are separated by shallow sills. The southernmost main basin (the Baltic proper) could in turn be divided in additionally two smaller basins (the Gulf of Riga and Gulf of Finland). These two latter basins make up a comparatively small area of the total Baltic proper and have comparably shallower water depth. Further, these two basins are also considered to be the most polluted areas of the Baltic

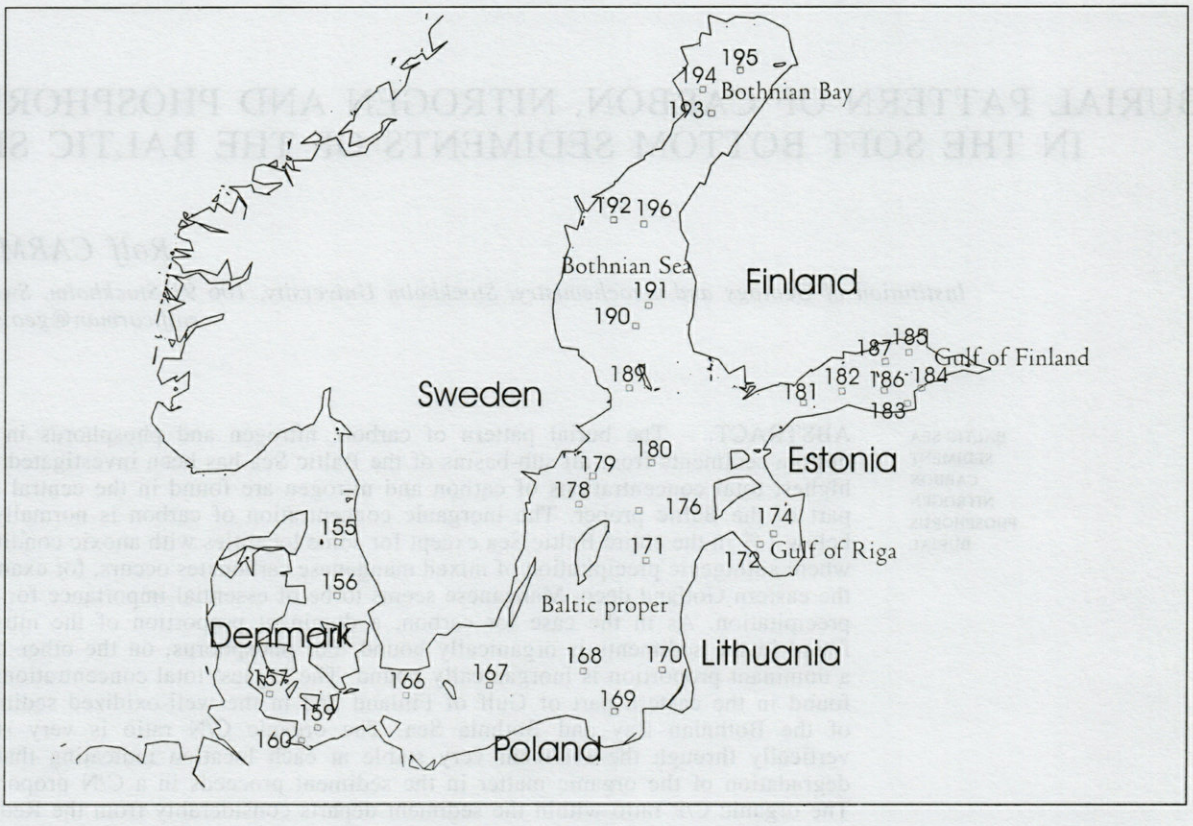

Fig. 1. – Map showing the location of the sampling sites in the Baltic Sea.

Sea (HELCOM 1990; Andrushaitis *et al.* 1992). The two northernmost basins of the Baltic Sea have the lowest salinity values (1-3 and 3-7 PSU for the Bothnian Bay and Bothnian Sea, respectively) and a weak salinity stratification. The Baltic proper (excluding the Gulf of Finland and Gulf of Riga) has a strong halocline located at 60-80 m deep (Kullenberg 1981) which separate the surface water with a salinity between of 7-8 PSU from the deep water with a salinity of 9-20 PSU. Renewal of the deep water in the Baltic proper, through the Belts of Denmark and the Sound, is virtually continuous. However, inflow of highly saline water is mainly the result of certain storm events and large-scale atmospheric disturbance and therefore occurs less frequently. The Gulf of Finland has a weaker salinity stratification (Perttilä *et al.* 1995) whereas the Gulf of Riga normally exhibits a lack of such stratification. The salinity stratification in the Baltic proper and Gulf of Finland sometimes result in more or less complete oxygen depletion, which in some areas of the Baltic proper is permanent (Jonsson *et al.* 1990). In these environments microorganisms will preferably use sulfate instead of oxygen in the oxidation of supplied dead organic matter. The subsequent production of hydrogen sulfide eliminates all benthic macrofauna which, in turn, entails the formation of laminated sediments. Such lamination has described as covering large areas in the Baltic proper (Jonsson *et al.* 1990) as well as restricted areas in the Gulf of Finland (Morris *et al.* 1988). Changes in oxygen-redox conditions in the water and within the sediment will greatly alter the biogeochemical processes. Hence, the fate of supplied carbon and nutrients to the sediment surface will change to different degrees as a result of altered diagenetic processes.

The main aim of this study is to characterize the carbon, nitrogen and phosphorus chemistry with respect to spatial and vertical distribution patterns at the deep accumulation bottoms in the Baltic Sea, and also to determine if there are any relationships between the concentration trends and certain transitions and trace metals.

2. MATERIALS AND METHODS

Thirty-two soft bottom sediment samples were collected from all sub-basins of the Baltic Sea (Fig. 1 and Table I). The sediments were collected by the use of a Gemini gravity corer, which is equipped with two parallel acrylic liners with an inner diameter of 80 mm. The sediment cores were sliced on board the ship in centimeter slices normally down to at least 25 cm below the sea floor. The sediment slices were immediately put

Table I. – Study site description and some water and sediment characteristics. The redox potentials originate from the uppermost centimetre of the sediment. The salinity and oxygen measurements originate from the water just above (≈ 1 m) the sediment surface.

Site	Position (Lat; Long)	Water depth (m)	Redox potential (mV)	Oxygen (ml/l)	Salinity (PSU)
155	56 26,57; 11 38,02	28	493	6.96	32.84
156	57 17,57; 11 28,59	75	518	5.58	34.72
157	54 44,30; 10 10,54	23	478		20.19
159	54 19,03; 11 32,57	27			
160	54 04,59; 11 10,00	22	464		17.25
166	54 59,57; 13 45,01	45	398	4.65	15.11
167	55 15,29; 15 57,56	90	396	3.65	16.53
168	55 32,53; 18 23,48	89		4.47	10.94
169	54 55,00; 19 14,44	107	36	0.71	12.26
170	55 34,59; 20 29,47	68		2.85	7.82
171	57 18,28; 20 03,33	240	-111	0.44	11.64
172	57 31,14; 23 13,14	45	-26	3.50	
174	57 28,58; 23 13,18	62		3.83	6.34
176	58 05,44; 19 59,57	183		8.14	6.31
178	58 10,59; 18 09,11	145	190	2.22	8.49
179	58 37,50; 18 31,59	215			
180	58 50,57; 20 13,03	200	-149	0.20	9.80
181	59 42,29; 24 41,12	84	61	4.25	7.83
182	59 50,30; 25 51,59	84	250	4.87	7.58
183	59 32,57; 27 46,09	35	95	6.70	6.15
184	59 45,51; 28 14,21	24	118	6.78	5.24
185	60 20,29; 28 00,29	44	10	6.88	6.23
186	59 47,21; 27 07,39	67	419	7.16	6.78
187	60 14,16; 27 15,29	61	-39	6.27	6.48
189	60 01,18; 19 32,48	214	172	7.65	6.72
190	60 59,21; 19 43,59	130	469	7.97	6.33
191	61 18,51; 20 07,31	130			
192	62 39,02; 18 59,56	200	474	6.13	5.98
193	64 18,50; 22 19,14	110	453	8.61	3.98
194	64 41,26; 22 02,57	137		8.46	3.88
195	64 54,29; 23 23,20	100	470	8.75	3.59
196	62 35,13; 19 58,28	210		6.05	6.04

into a deep-freezer and then freeze dried to measure the water content (WC %). Before starting chemical analyses, the sediment was ground to a fine powder in an agate mortar.

Sub-samples were taken for total C, N and P analyses and for different subfractions of these elements. Total carbon (TOT-C) and nitrogen (TOT-N) were measured on a Leco element analyser with a precision of ± 0.5 %. Organic carbon (ORG-C) was determinated on sediment samples pretreated with 1 M HCl in the same element analyser (Hedges & Stern 1984). Inorganic carbon (IN-C) was obtained from the difference between the total and organic carbon values. Fixed nitrogen (FIX-N) and exchangeable nitrogen (EX-N) were measured only on selective sites down to a maximum depth of 5 cm below sea floor according to the method described by Silva & Bremner (1966) and Mackin & Aller (1984), respectively. Organic nitrogen (ORG-N) was obtained from differences between the TOT-N and the sum of FIX-N and EX-N. All wet extracts of N were measured according to Parson *et al.* (1984). Total phosphorus (TOT-P) and inorganic phosphorus (IN-P) were measured according to Froelich *et al.* (1988). Mobile phosphorus (MOB-P) was measured according to Carman & Jonsson (1991) without pretreatment with other chemicals. Apatite phosphorus (AP-P) was obtained from the difference between IN-P and MOB-P whereas the amount of organic phosphorus (ORG-P) in the sediment was obtained from the difference between TOT-P and IN-P. All wet extracts of P were measured using standard spectrophotometric technique (e.g. Murphy & Riley 1962). Transition and trace metals in the sediments have been analyzed by using the ICP-AES technique.

3. RESULTS AND DISCUSSION

3.1. Carbon

The spatial distribution of total carbon in the Baltic Sea is shown in Fig. 2. Most of the carbon in the sediments of the entire Baltic Sea is in organic form. This is mainly due to the fact that inorganic carbonates (e.g. calcium carbonates) are unstable in the water mass (e.g. Carman & Rahm 1996) which results in the dissolution of sedimented biogenic as well as abiogenic carbonates. Nor-

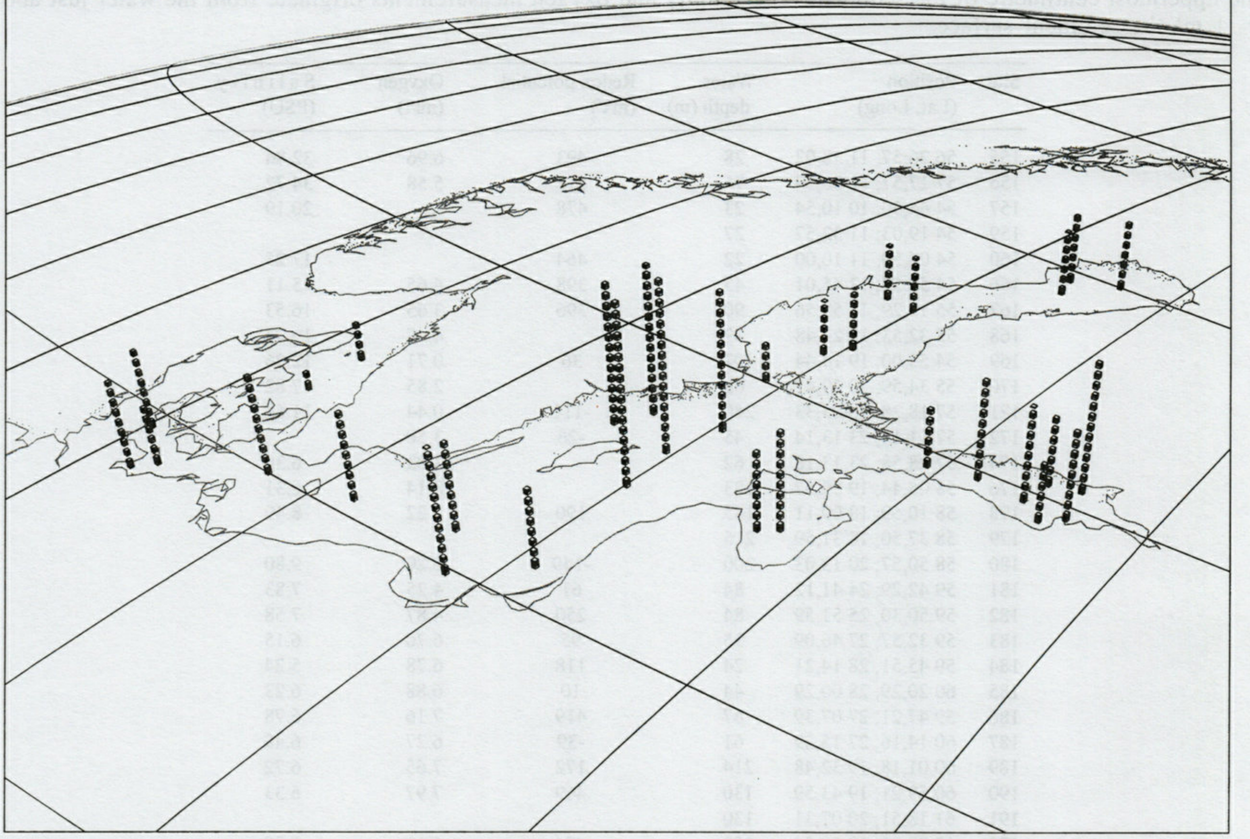

Fig. 2. – Spatial sediment distribution (0-1 cm) of total carbon in the Baltic Sea. Each unit of scale = 0.5 % C d.w.

mally inorganic carbon constitutes less than 0.5 mmol/g (< 1 % d.w). In the adjacent Kattegatt (e.g., sites 155 and 156; Fig. 1) and Skagerrak the concentration of inorganic carbonates often exceeds % d.w. and represents often a significant proportion of the total carbon content (> 30 %). Authigenic precipitation of mixed carbonates in the sediments under the euxinic conditions of the Baltic proper (eastern Gotland Basin) is a frequently described process (Manheim 1961, Suess 1979, Jakobsen & Postma 1989, Carman & Rahm 1997). Such authigenic precipitation can also be found in this study at site 171 (Gotland deep). The precipitation seems to start below 9 cm depths beneath the sea floor (Fig. 3). The molar ratio Mn/IN-C of the precipitate is 0.64 (Fig. 4) with a very high coefficient of determination ($R^2 = 0.97$). Thus, manganese is an important cation for the mixed authigenic precipitate in this environment. The ratio found in this study is very close to that reported by Jakobsen & Postma (1989) who suggested that the precipitate is a Ca-rhodochrosite in which calcium constitutes almost the entire remainder of the precipitate. Hence, the prolonged euxinic conditions of the eastern Gotland basin with continuous reduction of manganese oxides together with the microbial breakdowns of organic matter using sulfate, with resulting increases in alkalinity, maintains a perfect environment for authigenic precipitation of mixed manganese carbonates. Relatively high manganese concentrations are also found in the sediments at sites 167 and 180. However, even though Jakobsen & Postma (1989) found small amounts of Ca-rhodochrosite in the Bornholm basin (site 167), there is no such excellent correlation between manganese and inorganic carbons as that found at site 171.

3.2. Nitrogen

As in the case of carbon most of the nitrogen in the sediments of the Baltic Sea is organically bound although Müller (1977) shows that the concentration of inorganic nitrogen (fixed and exchangeable; FIX-N and EX-N, respectively) in some areas of the Baltic Sea is much higher than in most other marine areas. Hence, the spatial distribution pattern of total and organic nitrogen follows very closely the distribution pattern of carbon (Fig. 2). Inorganic nitrogen is reported as adsorbed on minerogenic particles (preferably on clay minerals) and organic matter in two different

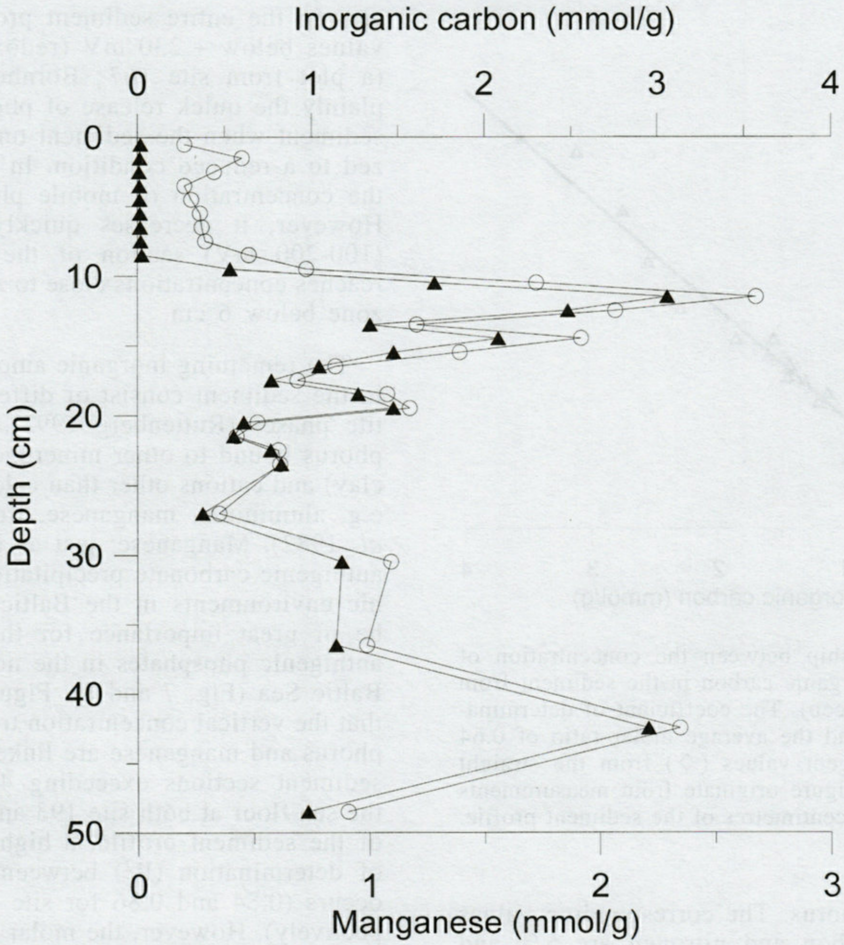

Fig. 3. – Vertical trends of manganese and inorganic carbon in the sediments of site 171 (Gotland deep).

ways (e.g. Rosenfeld 1979), namely as exchangeable ammonium (EX-N) and as fixed ammonium (FIX-N). While EX-N is adsorbed through an ion-exchange reaction on the surface of certain organic or mineral surfaces, FIX-N is incorporated in the sediments through adsorption into the clay structure and is not easily replaced by other cations. In soft bottom sediments the sum of these two inorganic phases seldom constitutes more than 10 % of the total nitrogen content of which FIX-N is the dominant component. However, even though they often represent a minor fraction their concentrations cannot be disregarded when, for instance, investigations of alterations in organic C/N ratios within and between different sediment environments of the Baltic Sea are investigated.

3.3. Phosphorus

In contrast to carbon and nitrogen, a substantial proportion of the phosphorus in the sediment is inorganically bound. Therefore, the spatial distribution pattern (sediments 0-1 cm deep) of total phosphorus does not entirely follow that of the carbon and nitrogen (compare Fig. 2 and Fig. 5). The most obvious difference is that the total concentration of phosphorus in the central Baltic proper is about the same as or lower than in the Bothnian Sea, whereas the concentrations of both carbon and nitrogen are much lower in the Bothnian Sea than in the central part of the Baltic proper. Further, the high coefficient of determination between both the total and the organic content (Fig. 10) of carbon and nitrogen at each site in the Baltic Sea does not exist for carbon/nitrogen as opposed to phosphorus. The main reason for such a distribution pattern is that the degradation of the organic matter with respect to carbon/nitrogen versus phosphorus occurs in different ways, that is, the utilization of phosphorus during decomposition of organic matter is independent of the concentration of carbon. Further, phosphorus is probably, unlike carbon, unaffected by variations in sedimentation rates (Froelich *et al.* 1982, Ingall & van Cappellen 1990).

Inorganic phosphorus rarely constitutes less than 50 % of the total phosphorus and the percentage of inorganic phosphorus at certain deposition bottoms could be as high as 90 % of the total

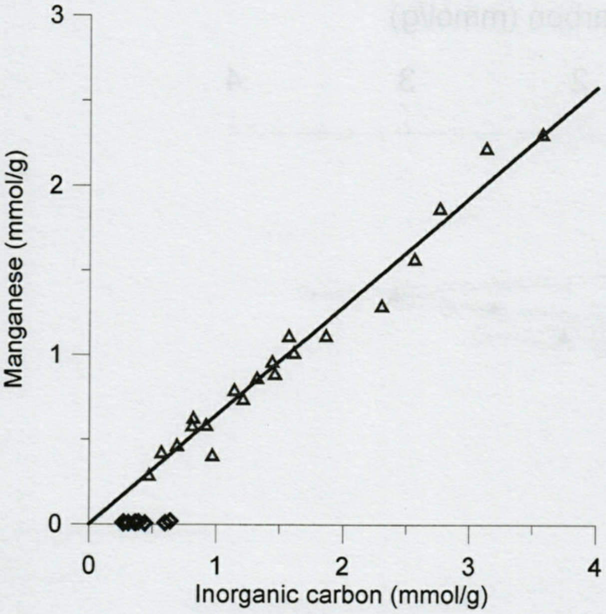

Fig. 4. – Relationship between the concentration of manganese and inorganic carbon in the sediment from site 171 (Gotland deep). The coefficient of determination (R^2) is 0.97 and the average molar ratio of 0.64 (Mn/C). The divergent values (◇) from the straight line shown in the figure originate from measurements in the uppermost 9 centimetres of the sediment profile.

amount of phosphorus. The corresponding values for inorganic carbon and nitrogen are 5 % and 10 % of the total amounts, respectively.

The nature of the sedimentary matrix (grain size, chemistry etc.), combined with the redox conditions, depends on how the burial of P occurs and to what extent. Low concentrations and often x-ray amorph phases preclude to a large extent direct identification of pure mineral phases. Therefore, a common, and in many cases the only way, to interpret the possible and dominant incorporation mechanisms and to quantify the buried amount of different more or less exclusive phosphorus fractions in the sediments is the use of different sequential leaching procedures (e.g. Williams *et al.* 1967, Balzer 1986, Carman & Jonsson 1991, Ruttenberg 1992).

The iron cycle is well known as being important for the redox-dependant sequestering/release of phosphorus. In the oxic zone, large amounts of phosphorus adsorb onto solid ferric complexes. When those complexes dissolve in the reduced zone, the adsorbed amount of P will consequently also be released together with an almost simultaneous release of phosphorus from other sources, (e.g., from bacteria) (Gächter *et al.* 1989, Gächter & Meyer 1993). This can be seen clearly in some sites in the central part of the Baltic proper (e.g. sites 171, 176, 179 and 180). At these sites, low concentration of redox-dependent phosphorus occurs in the entire sediment profile due to redox values below + 230 mV (redox cline). Figure 6 (a plot from site 167; Bornholm deep) reveals plainly the quick release of phosphorus from the sediment when the sediment turns from an oxidized to a reduced condition. In the oxidized zone the concentration of mobile phosphorus is high. However, it decreases quickly in the hypoxic (100-200 mV) section of the sediment profile reaches concentrations close to zero in the reduced zone below 6 cm.

The remaining inorganic amount of phosphorus in the sediment consist of different kinds of apatite phases (Ruttenberg 1992), as well as phosphorus bound to other minerogenic particles (e.g. clay) and cations other than calcium and iron(III), e.g. aluminium, manganese, iron(II) (Froelich *et al.* 1982). Manganese, just as it obviously is for authigenic carbonate precipitation in certain euxinic environments in the Baltic proper, seems to be of great importance for the precipitation of authigenic phosphates in the northern part of the Baltic Sea (Fig. 7 and 8). Figure 7 shows nicely that the vertical concentration trends of total phosphorus and manganese are linked to each other in sediment sections exceeding 4 cm depth below the sea floor at both site 193 and 195. In that part of the sediment profile, a high linear coefficient of determination (R^2) between these parameters occurs (0.84 and 0.86 for site 193 and 195, respectively). However, the molar ratios of phosphorus and manganese differ between these two sites (Fig. 8). Similar trends between manganese and phosphorus can be noticed in sites in the Bothnian Sea (190 and 192), even though the coefficients of determination between phosphorus and manganese are lower at these sites. In the sediments from the Baltic proper (including the Gulf of Finland and Gulf of Riga) there is no such pronounced correlation between phosphorus and manganese, although the main common trend is that their concentrations, roughly at the same rate. The sediments from the bights in the entrance to the Baltic (site 157,159 and 160) differ completely from the general trends found in the other areas of the Baltic Sea. At these sites the concentration trends of manganese and phosphorus exhibit a slight inversely proportional relation to each other (Fig. 9). Obviously, the differences in the biogeochemical environment between the northern part (Bothnian Sea and Bothnian Bay) and the middle and the southern areas of the Baltic Sea affect the burial of phosphorus, carbon and manganese. That the redox potential in the sediments of the Bothnian Bay and the Bothnian Sea are normally higher is common in most soft bottom sediments in the Baltic proper indicates that both manganese and iron oxides and hydroxides are preserved deep down in the sediment column. This situation with high abundance of metal oxides (mostly as nodu-

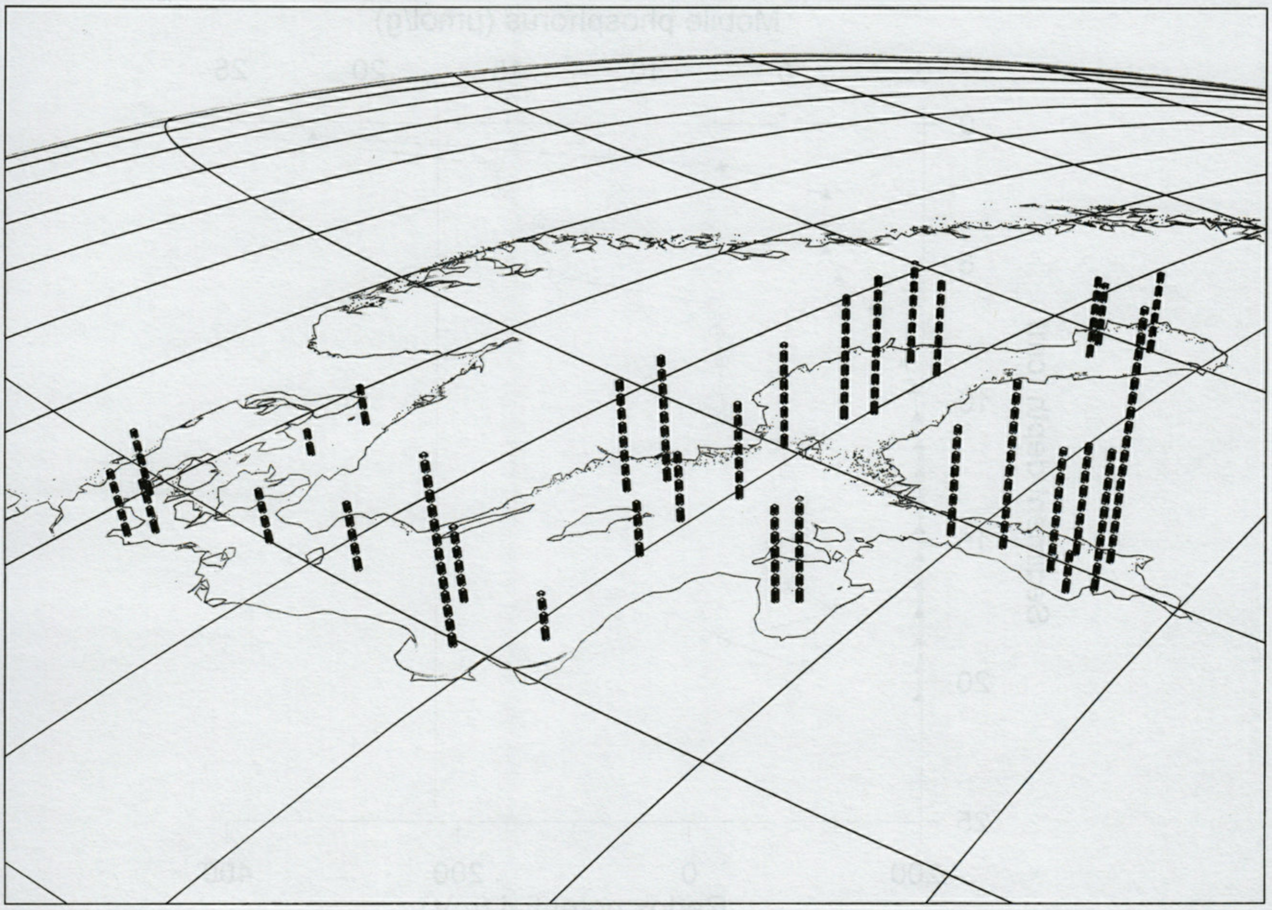

Fig. 5. – Spatial sediment distribution (0-1 cm) of total phosphorus in the Baltic Sea. Each unit of scale = 10 µmol/g P d.w.

les with high content of manganese; Ingri 1985) may explain the close connection between phosphorus and manganese as shown in Fig. 7 and 8. In the Baltic proper, in contrast, where anoxic or suboxic conditions prevail even in the uppermost part of the sediment, a dissolution of iron and manganese oxide-hydroxides is generated. The resulting increase in the concentrations of these elements in the pore water combined with increasing alkalinity, due to a microbial breakdown of the organic matter using sulfate instead of oxygen as electron acceptor, demonstrably results in the authigenic precipitation of mixed manganese carbonates (see previous discussion; and e.g., Jakobsen & Postma 1989) and iron sulfides (Bågander & Carman 1994) rather than the precipitation of iron and manganese phosphates and/or the adsorption of phosphate on redox-dependent metal oxides.

3.4. *Redfield ratios*

The C_{org}:N_{org}:P_{org} ratio of marine particulate organic matter is quite consistent (Redfield *et al.* 1963, Copin-Montegut & Copin-Montegut 1983). Since the middle of this century, the C:N:P ratio of 106:16:1 has been accepted as the average organic molar ratio in marine organic matter. However, in the Baltic Sea deviation from Redfield ratio have been reported with C_{org}/N_{org} ratio higher than Redfield (i.e., between 7 and 10 instead of 6.625 (Hendrikson 1975, Iturriaga 1979, Shaffer 1987). The N_{org}/P_{org} ratio is, on the other hand, commonly lower, between 12 and 14 (Sen-Gupta & Koroleff 1973), whereas the ratio between carbon and phosphorus usually is higher ratios than Redfield. Shaffer (1987) suggests that the most likely or "best" average value for this ratio in the Baltic Sea and adjacent areas should be around 130. In the interpretation of the C_{org}:N_{org}:P_{org} ratio in sediments it should be remembered that the sediments contain a range of ages (from 10 000 – 100 ^{14}C years) of allochthonous matter (e.g., precipitated humus, particulate land-delivered organic remnants) with high C/N ratios. However, measured ratios in sedimenting material and in stable sediments are important as a base for characterizing the organic matter with respect to the degree of fractionation during de-

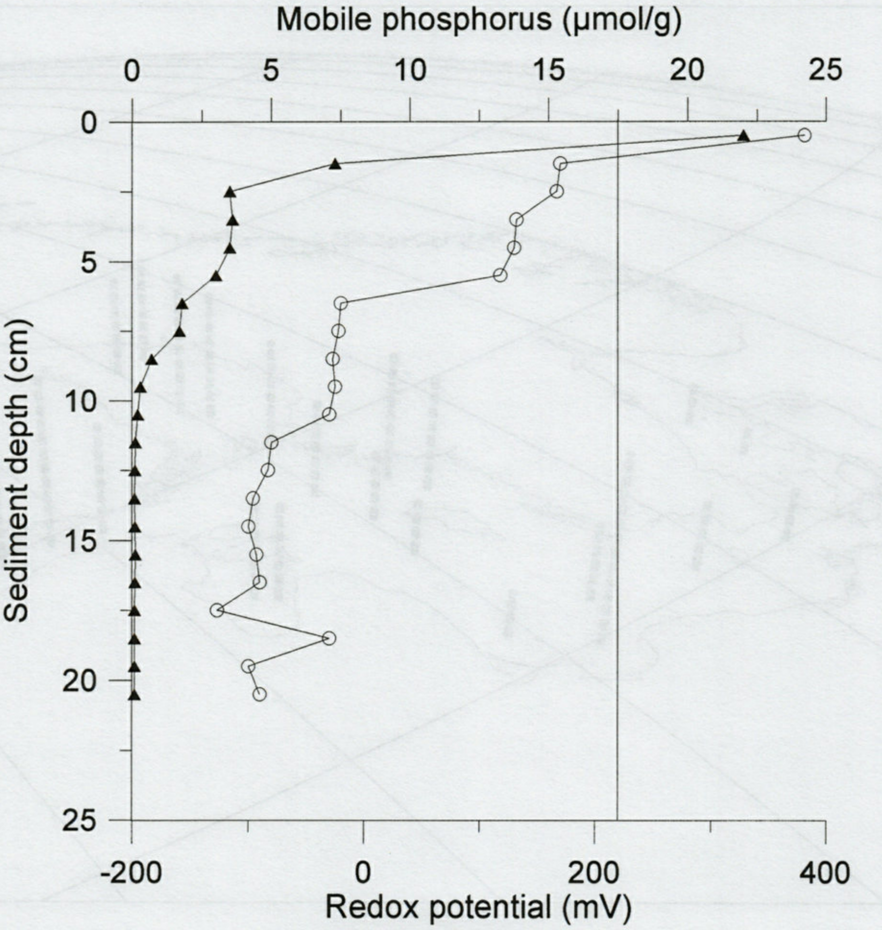

Fig. 6. – Vertical sediment profiles of mobile phosphorus (Δ) and redox potential (○) from site 167 (Bornholm deep).

composition. Fractionation processes during settling and during benthic degradation usually increases the C_{org}/N_{org} and the C_{org}/P_{org} ratios, as well as the N_{org}/P_{org} ratio. This is caused by different degree of preferential N and P use (e.g. Froelich *et al.* 1988).

Figure 10 presents data from all sites in this study as well as some additional sediment data from similar deposition bottoms sampled in connection with other projects. The average organic C/N ratios from the different sub-basins are given in Table II. The data represent measurements from the five uppermost centimeters (centimeter sections) of the sediment. As can be seen from Fig. 10 the organic C/N ratios from all sub-basins of the Baltic Sea exhibit high linear coefficient of determination, although with different slopes. The C/N ratio in the Baltic proper, Gulf of Riga and Gulf of Finland, exhibits almost the same value while the ratios in the Bothnian Sea and Bay are considerably higher (Table II). The large supply of freshwater with an abundance of terrestrial organic material (e.g. humus) provided by the many streams in that area may explain why the C/N ratios in that area are higher than in the southern part of the Baltic Sea. The ratios seem almost independent of water depth, depth below the sea floor, carbon content, sediment characteristics and extent of diagenesis within the different basins. Even the topmost section exhibits the same ratio, which suggests that all preferential fractionation (departing from the Redfield ratio) mainly occurs prior to settling at the sediment surface or during an early diagenetic stage.

The average organic C/P ratio deviates considerably from the Redfield ratio (106 :1) in all basins (Table II). This is mainly a result of preferential instantaneous autolytic release of easily hydrolyzable P compounds (e.g. Froelich *et al.* 1988). Furthermore, in addition to the C/P ratios deviating considerably from Redfields, they also exhibit large vertical as well as spatial variations. From the data presented it is hard to find a clear explanation for the observed trends. However, a combination of differences in sedimentation rates, variations in the amount of supplied

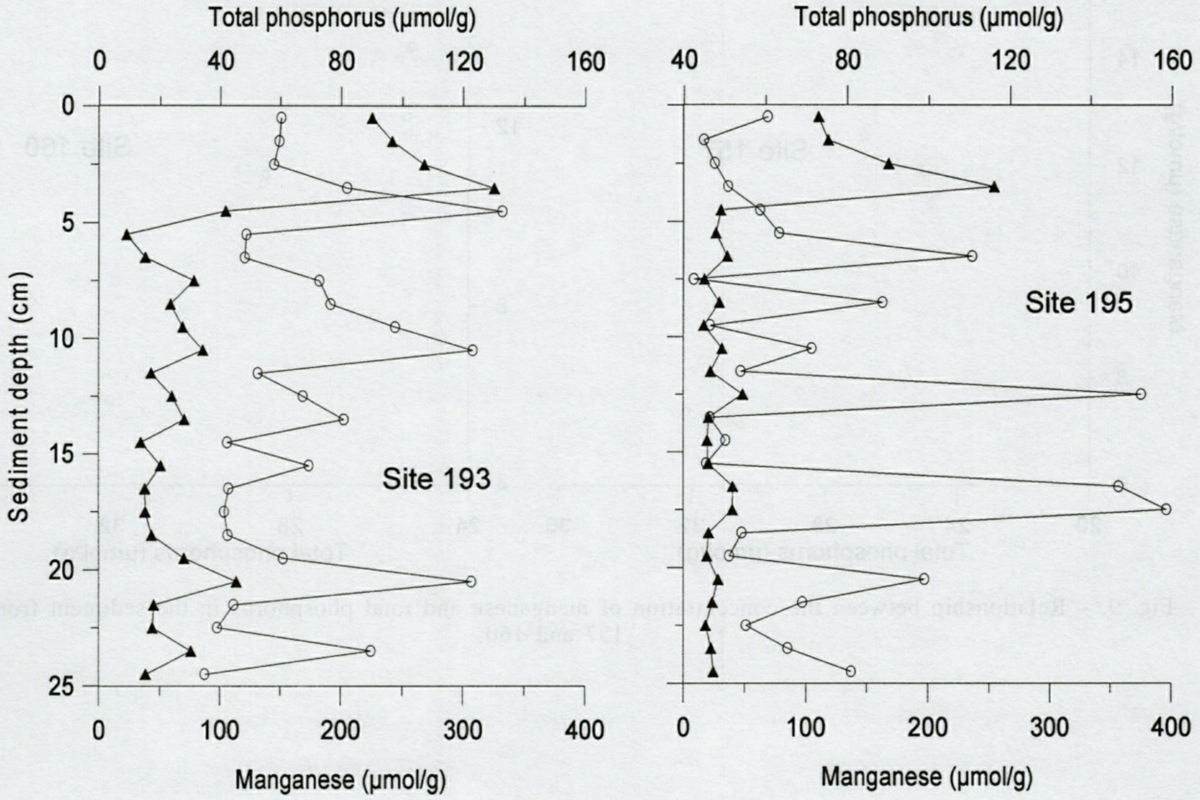

Fig. 7. – Vertical concentration profiles of total phosphorus (○) and manganese (Δ) at site 193 and 195 (Bothnian Sea, northern Baltic Sea).

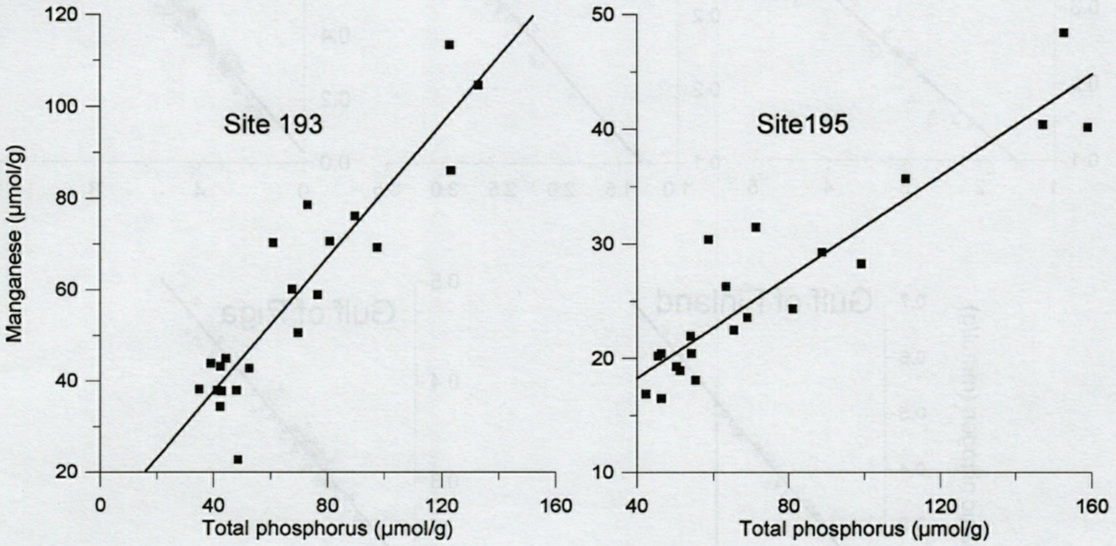

Fig. 8. – Relationship between the concentration of manganese and total phosphorus in the sediment from sites 193 and 195. The linear coefficients of determination (R^2) from sediment sections deeper than 4 cm depth below sea floor are 0.84 and 0.86 for site 193 and 195, respectively. The average molar ratios (Mn/P) are 0.88 and 0.364 with a standard deviation of 0.17 and 0.066 for site 193 and 195, respectively.

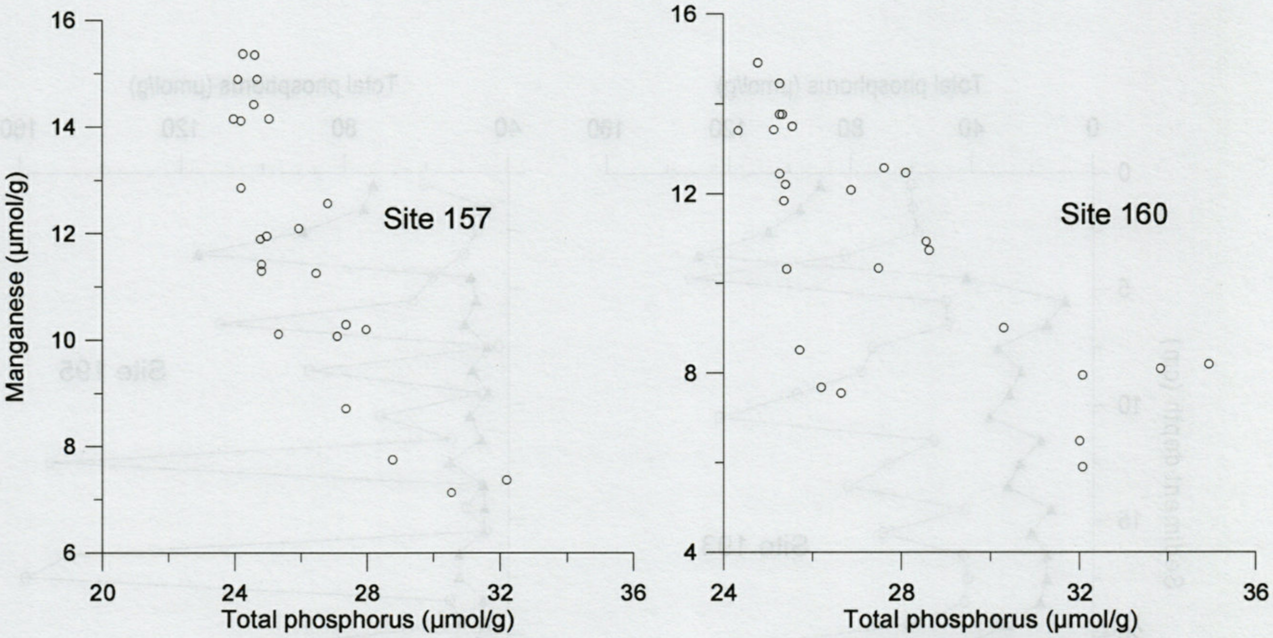

Fig. 9. – Relationship between the concentration of manganese and total phosphorus in the sediment from sites 157 and 160.

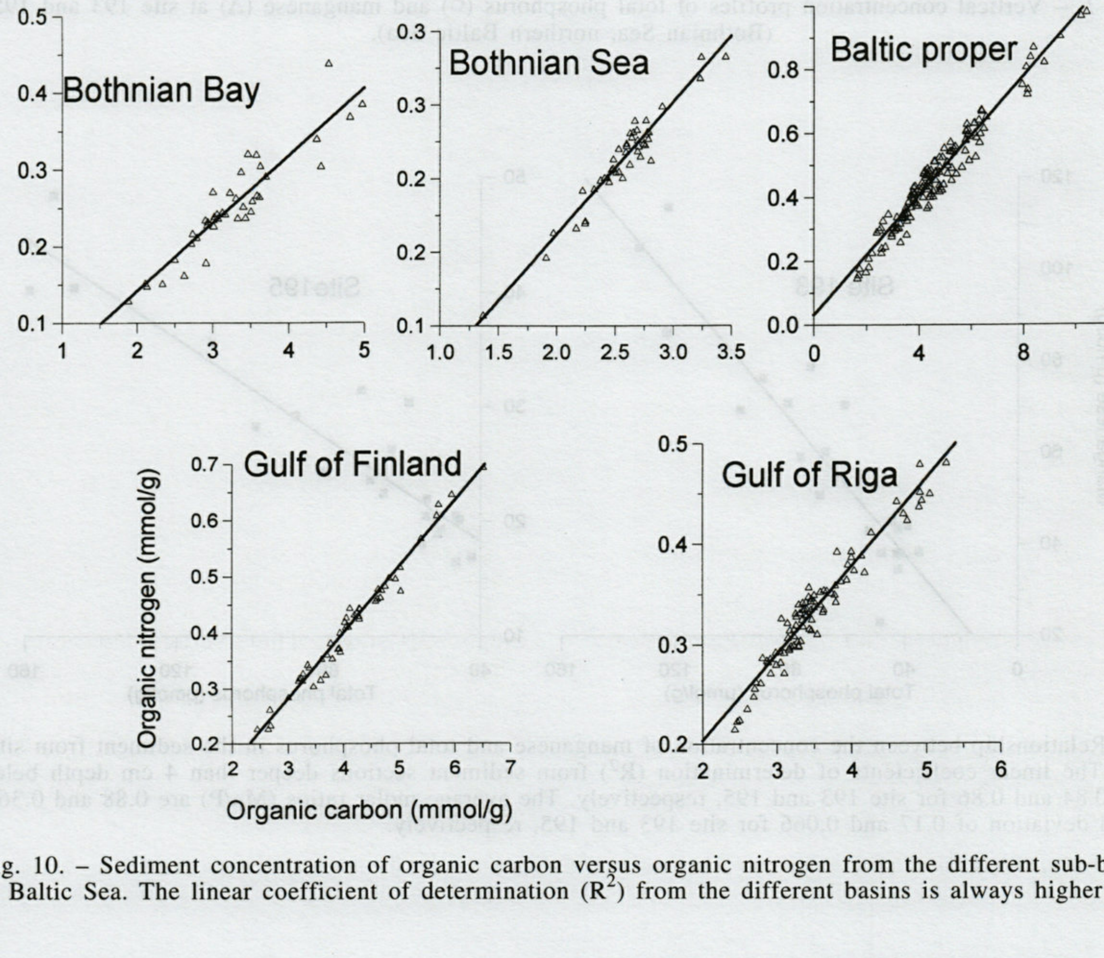

Fig. 10. – Sediment concentration of organic carbon versus organic nitrogen from the different sub-basins of the Baltic Sea. The linear coefficient of determination (R^2) from the different basins is always higher than 0.9.

Table II. – Average and range of organic C/N and C/P ratios from the different main sub-basins of the Baltic Sea. SD= standard deviation.

Basin	**C/N**	**Low**	**High**	**SD**	**C/P**	**Low**	**High**	**SD**	**Counts**
Baltic proper	10.0	8.0	12.6	0.89	343	115	611	88	142
Gulf of Finland	10.1	9.1	11.6	0.59	266	195	389	37	50
Gulf of Riga	10.5	9.4	11.4	0.46	266	106	384	106	90
Bothnian Sea	12.1	11.1	13.2	0.52	213	138	325	45	45
Bothnian Bay	13.1	10.3	16.3	1.3	249	108	492	102	40

terrestrial organic matter, and variations in redox conditions may explain the large variation in the organic C/P ratios (Froelich *et al.* 1982, Ingall & van Cappellen 1990, Jahnke 1990). The average ratios found in the sediment of this study diverge from similar ratios in other marine environments (see e.g., Mach *et al.* 1987, Ingall & van Cappellen 1990, deLange 1992). However, the data are in close agreement with the investigation done by Balzer (1984) in Kiel Bight in the southern Baltic proper. It thus, that the fractionation and preservation of carbon and phosphorus in the Baltic Sea differ from the general pattern found in more pelagic marine environments. One probable explanation for the observed pattern may be that the settling time for organic matter in the Baltic Sea is short compared to that in deep-sea sediments, so that fractionated decomposition has not been completed to the same degree when the organic matter finally settles on the sediment surface.

4. SUMMARY AND CONCLUSIONS

Differences in primary production, water depths, salinity and biogeochemical conditions in the bottom and pore water of the Baltic Sea result in completely different diagenetic and burial patterns of supplied organic and inorganic substances of carbon, nitrogen and phosphorus. Commonly, most of the carbon and nitrogen found in the sediments are in the organic form. For carbon the main explanation is that both organic and inorganic produced carbonates under most circumstances are thermodynamically unstable. However, in the euxinic parts of the Baltic proper (e.g. the eastern Gotland Basin), with succeeding prolonged anoxic conditions in the pore waters, it is quite common to observe authigenic precipitation of mixed manganese carbonates. Manganese is of essential importance for such precipitation. Though a comparatively high concentration of inorganic nitrogen is reported from the Baltic Sea as compared to other marine areas the percentage amount at examined deposition bottoms seldom exceeds 10 % of the total amount of nitrogen. However, the inorganic amount of nitrogen cannot be neglected in, for instance, burial calculations and in the interpretation of alterations of Redfield ratios within and between different localities in the Baltic Sea.

On the other hand, most of the phosphorus in the sediment is inorganically bound. The main reason for this is that phosphorus under most natural conditions only exists as orthophosphate, a molecule with a high reactivity to solid particles either through adsorption or precipitation. Iron adsorbs a large amount of phosphorus during oxidized conditions, whereas precipitation of different kinds of phosphorus minerals are common during reduced conditions. Manganese plays an important role in the burial of phosphorus in the Bothnian Bay and in some other restricted anoxic areas of the Baltic proper. In these areas of the Baltic Sea it is common to find a high coefficient of determination between phosphorus and manganese. Ferric manganese nodule formations in the Bothnian Bay together with authigenic manganese-calcium phosphate and apatite precipitation in the Baltic proper, is the most likely explanation for the high coefficients of determination between manganese and phosphorus found at these sites.

The constant vertical organic C/N ratio in the sediments of the Baltic Sea suggests most likely that the preferential release of nitrogen most likely occurs during halmyrolysis or during a very early diagenetic stage. The average C/N ratio in the southern part of the Baltic Sea is close to 10. The corresponding ratio values in the Bothnian Bay and Sea are 12.1 and 13.1, respectively. The most likely explanation for higher organic C/N ratios in the northern part of the Baltic Sea is a high terrestrial organic material supply through the streams in that area of the Baltic Sea.

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Reçu le 25 juin 1998 ; received June 25, 1998
Accepté le 22 octobre 1998 ; accepted October 22, 1998

VIE MILIEU, 1998, 48 (4) : 243-257

IRRIGATION AND DEPOSIT FEEDING BY THE LUGWORM *ARENICOLA MARINA*, CHARACTERISTICS AND SECONDARY EFFECTS ON THE ENVIRONMENT. A REVIEW OF CURRENT KNOWLEDGE

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WATER PUMPING
IRRIGATION
DEPOSIT FEEDING
ENERGETICS
REWORKING
BIOTURBATION
NUTRIENT FLUXES

ABSTRACT. – The present review gives a short presentation of current knowledge with main emphasis on recent advances in the understanding of the lugworm *Arenicola marina*'s irrigation pump, food energy requirements and feeding biology as related to bioturbation, nutrient fluxes and other secondary effects on the environment. The lugworm uses little energy (< 5 % of total metabolic output) to pump water through its burrow into the sediment, but it is unlikely that the worm significantly enhances its nutritional intake by filter feeding as it does not filter sufficient water to gain enough nutritional benefit. While *A. marina* is found in a wide range of habitats, its mode of life sets limits on the types of sediments it can inhabit. It is critical for the lugworm to be able to pump water into the feeding pocket to adequately ventilate its burrow and to loosen and feed on sediment particles. There appears to be ample food in most sediments to support the nutritional needs of *A. marina*. These food sources may be dead organic matter and living organisms such as bacteria, microalgae, micro- and meiofauna, but there seems to be an unnecessary dichotomy between microbial and detrital food sources in the ongoing discussion of deposit feeder nutrition. Several food sources are probably utilised by *A. marina*, the balance being shifted depending on what is available in a given environment. *A. marina* is a good example of a "ecosystem engineer" as it profoundly affects both the structure and chemical nature of as well as processes occurring within the sediment. As such *A. marina* plays an important role in affecting both energetics and material fluxes at the sediment-water interface of the habitats in which it lives.

EAU POMPÉE
IRRIGATION
MANGEUR DE DÉPÔTS
FLUX ÉNERGÉTIQUES
BIOTURBATION
FLUX DE NUTRIENTS

RÉSUMÉ. – Les connaissances actuelles sont résumées en présentant plus particulièrement les progrès récents concernant notre compréhension de la pompe d'irrigation, des besoins énergétiques et de la biologie de la nutrition en relation avec la bioturbation, du flux de nutriments et des autres effets secondaires sur l'environnement. L'Arénicole utilise très peu d'énergie (< 5 % de la production métabolique totale) pour pomper l'eau à travers sa galerie creusée dans le sédiment, mais il est peu probable que la filtration contribue beaucoup au budget alimentaire de l'Arénicole. Bien que *A. marina* occupe une grande diversité d'habitats, son mode de vie limite les types de sédiments qu'elle peut occuper. L'Arénicole doit être capable de pomper l'eau dans sa cavité alimentaire pour pouvoir ventiler sa galerie correctement et pouvoir séparer et ingérer les particules sédimentaires. Il existe suffisamment de nourriture dans la plupart des sédiments pour assurer les besoins nutritifs de *A. marina*. Elle peut provenir de débris organiques et d'organismes vivants comme les bactéries, les microalgues, la micro et la méiofaune. Il semble exister une dichotomie non fondée entre une origine microbienne et une origine détritique dans la discussion actuelle sur la nutrition par ingestion de dépôts sédimentaires. Plusieurs sources sont sûrement utilisées par *A. marina*, l'importance de chacune variant suivant la disponibilité dans un environnement donné. *A. marina* est un bon exemple d'« ingénieur de l'écosystème » puisqu'elle modifie profondément non seulement la structure et la nature chimique du sédiment, mais aussi les processus se déroulant dans ce sédiment. Comme tel, *A. marina* joue un rôle important en affectant à la fois les flux énergétiques et les flux de matériel à l'interface sédiment-eau des habitats qu'elle occupe.

INTRODUCTION

The lugworm *Arenicola marina* (L.) is a dominant member of the macrobenthos on lower shore in clean to muddy sand throughout much of its geographic range on North west European coasts from the Arctic to the Mediterranean. The lugworm is found almost everywhere on the tidal flats in the Dutch Wadden Sea where it accounts for about 20 % of the benthic biomass. Here the density of adult lugworms is about 20 ind. m^{-2}, and their numbers usually do not surpass 50 m^{-2} (Beukema 1976, Cadée 1976, Dankers & Beukema 1983, Flach 1992). In the sandy parts of the German Wadden sea the density is about 40 lugworms m^{-2} (Reise 1985).

Arenicola marina lives in 20 to 40 cm deep J-shaped burrows in the sediment. With its head down the worm ingests sediment, and as a result the sand above sinks downwards forming a funnel. For defecation, the worm moves backwards in the burrow until its tail reaches the surface where it ejects its castings which form a characteristic sand-pile. The burrowing and feeding activities of the worm thus physically stir the sediment causing 'bioturbation' which increases the penetration of oxygen into the otherwise anoxic world below the sediment water-interface (Cadée 1976).

The principal food source of the lugworm is still a point of contention, but generally, the lugworm is regarded as a non-selective subsurface deposit-feeder which is nourished by swallowing relatively large amounts of sediments with low nutritive value.

The pumping activity of the lugworm causes a tail-to-head directed ventilatory water flow through its tube, resulting in an in upward flow of oxygenated water in the sediment in front of the head (Wells 1966, Foster-Smith 1978, Toulmond & Dejours 1994). The irrigation of the burrow by the lugworm, combined with the bioturbation activity, may exert a profound effect on the chemistry (Hüttel 1990) and microbiology (Reichardt 1988) of the sediment, and by this also the nutrient fluxes across the sediment-water interface (Davey *et al.* 1990, Retraubun *et al.* 1996 a & b).

A short presentation of recent advances in the understanding of the lugworm irrigation pump and, the worm's food energy requirement and feeding biology as related to bioturbation, nutrient fluxes and other secondary effects on the environment is the subject of this review of current knowledge.

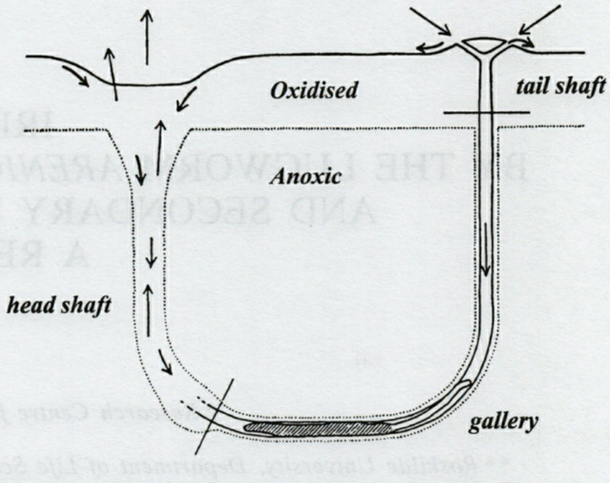

Fig. 1. – Sketch of lugworm in its burrow. The cross lines indicate the boundaries between : head shaft, gallery, and tail shaft. The dotted line indicates the boundary between oxidised yellow sand and anoxic black sand. Long thin arrows indicate direction of water pumped by the worm ; short thick arrows show movement of sand ingested by the worm. From Wells (1966).

HOW *ARENICOLA MARINA* MAKES A LIVING

The older literature on the lugworm way of life was reviewed by Wells (1949 a & b, 1950, 1951, 1961, 1966) and will not be repeated here. In this section a short examination of how *Arenicola marina* makes a living is presented. Normally *A. marina* stays in its burrow, eating the sand and ejecting the familiar sand castings. This is done in a cyclic pattern characterised by the ejection of the faecal cylinders at regular intervals of time. This "normal cyclical pattern (NCP)" may continue uninterrupted for many hours, and the faecal cylinders may gradually build a pile on the sediment surface. The intervals between castings may be about 40 min in large worms and about 15 min in smaller worms. The lugworm feeds in short bursts, each of a few minutes' duration, and each burst is accompanied by a partial inhibition of pumping activity. The pattern of pumping activity has been repeatedly monitored by different workers, most recently by Davey *et al.* (1990) who used thermistors to detect the venting of irrigation water from the lugworm burrow. There is no doubt that the NCP is the worm's regular activity pattern, although it may easily be disturbed in laboratory studies (Wells 1950, Jacobsen 1967).

The lugworm burrow consists of two main parts, the gallery and the head shaft (Fig. 1). The gallery descends from below the pile of faeces. Its walls are impregnated with the worm's secretions, which makes them firm. The worm moves backwards and forwards in the gallery, keeping

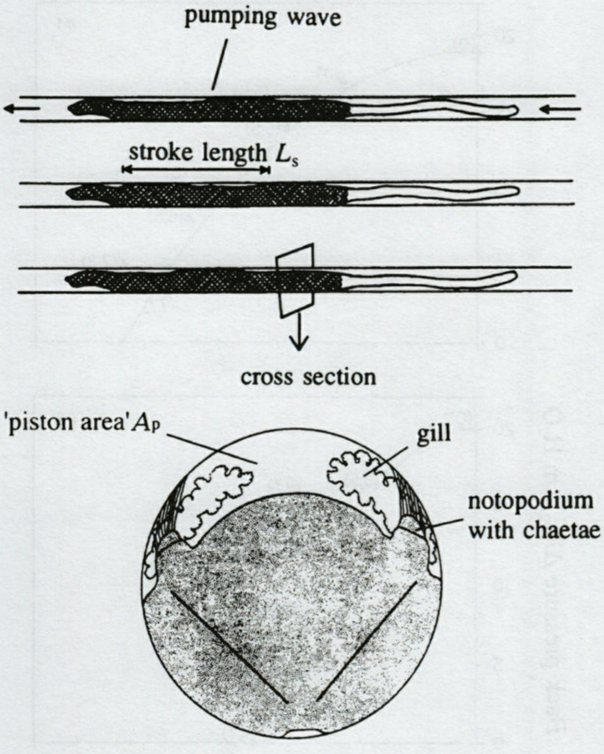

Fig. 2. – *Arenicola marina.* Sketch illustrating the peristaltic waves of contraction and relaxation causing a tail-to-head pumping wave with a stroke length *(Ls)* defined by the distance between the front of two synchronous 'piston' waves. The 'piston' area *(Ap)* is defined by the percentage (estimated to 25 %) of cross sectional area of the tube not filled up by the worm body. From Riisgård *et al.* (1996).

its head downwards. At the top of the gallery, the burrow narrows to become the tail shaft through which the tail is advanced at the time of defaecation. The head shaft, which is not sealed off by secretions, is a descending column of sand resembling the oxidised surface sand. The worm feeds at the lower end, and here accumulates rejected shell fragments and small stones.

The feeding biology of *Arenicola marina* has been studied and debated for many years (Newell 1948, Krüger 1959, 1962, 1964, Jacobsen 1967, Hobson 1967, Seymour 1971, Hylleberg 1975, De Wilde & Berghuis 1979, Rijken 1979, Pollack 1979, Retraubun *et al.* 1996 a & b), but knowing what the lugworm ingests is not the same as knowing what the worm actually digests and assimilates. The nutritional possibilities seem to be numerous and may be realized in any combination of dead organic matter (detritus) digested directly, bacteria at normal sediment densities or enhanced in abundance externally by 'gardening' in the head shaft which is oxygenated by the worm's irrigation current (Hylleberg 1975) or bacteria may be enhanced in abundance internally (in the hindgut) by microbial fermentation as in ruminants (Plante *et al.* 1989). Furthermore, diatoms, other microphytobenthos and living micro- and meiofauna (ciliates, flagellates, nematodes etc.) small and slow enough to be ingested may serve as food (Hylleberg 1975, Retraubun *et al.* 1996 a & b). According to Krüger (1959) the sediment in front of the worm's head may also be enriched by suspended organic matter 'filtered' from the ventilatory water pumped through the burrow. A precise knowledge of the main nutritional source of the lugworm is still lacking, however, and is a major limitation for a better understanding of this important worm as a subsurface deposit feeder.

The lugworm pumps water through its burrow, in a tail-to-head direction, by means of piston-like waves that run along its dorsal surface (Fig. 2). Most of the water so pumped returns to the surface along the head shaft, although some of it mixes with the surrounding porewater because of porous nature of the sediment in which it lives. The irrigation stream transports oxygen, flushes away soluble excretory products, and may also bring suspended particles that get trapped in the sand at the lower end of the shaft. The pumping of water cause the sand in the head shaft to be more loose and soaked with seawater than the general sand. Because of the oxygenated water stream the walls of the burrow are yellow/brown, in contrast to most of the surrounding black and anoxic sediment. The energy cost of pumping water through a burrow and head shaft into a thick layer of sand that offers a considerable frictional resistance to water flow is dealt with in the following section.

THE LUGWORM PUMP

Referring to Van Dam (1938), Foster-Smith (1978), Baumfalk (1979) and Toulmond & Dejours (1994), the performance of the lugworm pump may decisively deviate from the high-pumping-rate, low-pressure and low-energy pumps which are characteristic of filter-feeding invertebrates (Riisgård & Larsen 1995). This doubt lead Riisgård *et al.* (1996) to make a thorough analysis of the *Arenicola* pump, including an estimate of the energetic costs of pumping. The main findings are presented in the following.

The *Arenicola marina* pump can be considered to be a closed positive displacement pump yielding a constant volume flow *(Q)* = displacement volume (D_v) multiplied by strokes per unit time *(f)*, or because D_v = stroke length (L_s) multiplied by the 'piston' area (A_p) : $Q = D_v f = A_p L_s f$ (Fig. 2). *A. marina* was studied by Riisgård *et al.* (1996) in an observation aquarium and the typical

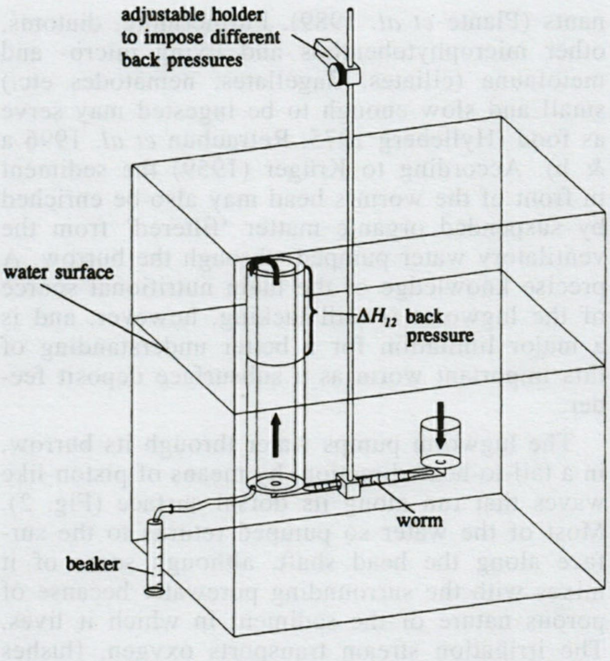

Fig. 3. – Experimental set-up for measurement of pumping rate (= volume flow) at different imposed back pressures for *Arenicola marina*. The arrows indicate direction of water flow caused by the pumping activity of the worm. The collecting device ensured drainage and quantitative collection of the pumped water. From Riisgård *et al*. (1996)

undisturbed stroke frequency of the muscular piston pump was $f_{max} = 7$ strokes min^{-1}. Afterwards, a new experimental set-up was used for direct measurement of volume flow at zero and different imposed back-pressures (Fig. 3). The volume flow at zero back pressure ($\Delta H_{12} = 0$) as a function of stroke frequency (f, strokes min^{-1}) was linear as expected from a positive displacement pump, complying with the expression :

$$Q = Q_{op}(f/f_{max}), \qquad (1)$$

where Q_{op} = resulting volume flow at the normal operating pressure head (ΔH_{op}). The back pressure characteristic was empirically found to be a non-linear function, the stroke frequency being reduced with increasing imposed back pressure, attaining a maximal pressure head $\Delta H^0_{12} = 20$ χμ H$_2$O (Fig. 4). Referring to eq.(1), the back pressure-volume flow characteristic may be modelled by the expression :

$$\Delta H_{12} = \Delta H^0_{12}[1-(Q/Q_{op})^2], \qquad (2)$$

Curve fits, based on experimental data and eq.(2), show that it is the stroke frequency that controls the volume flow. Thus, the displacement volume (D_v) of the lugworm pump is constant and unaffected by internal leakage flow when the back pressure is increased.

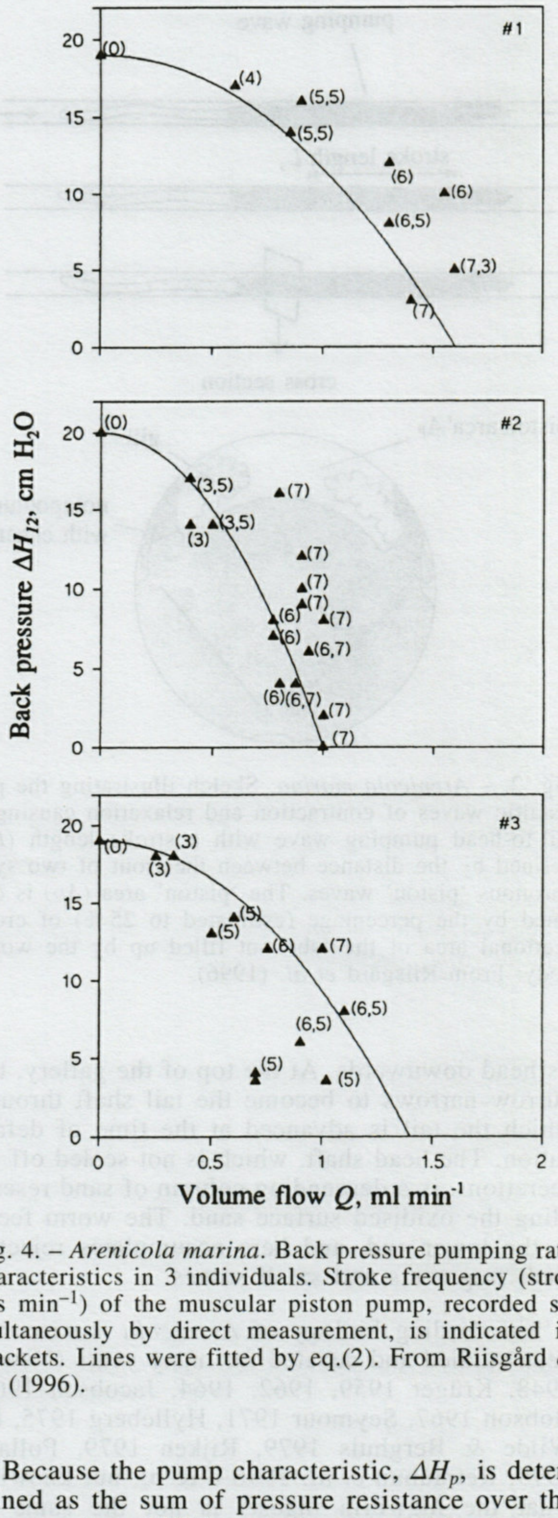

Fig. 4. – *Arenicola marina*. Back pressure pumping rate characteristics in 3 individuals. Stroke frequency (strokes min^{-1}) of the muscular piston pump, recorded simultaneously by direct measurement, is indicated in brackets. Lines were fitted by eq.(2). From Riisgård *et al*. (1996).

Because the pump characteristic, ΔH_p, is determined as the sum of pressure resistance over the pump-system (ΔH_s), and the imposed back pressure (ΔH_{12}), the following expression applies (*cf.* Riisgård & Larsen 1995) :

$$\Delta H_p = \Delta H_s + \Delta H_{12}, \qquad (3)$$

or referring to eq.(2)

$$\Delta H_p = \Delta H_s + \Delta H^0_{12}\,[1-(Q/Q_{op})^2]. \qquad (4)$$

Table I. – Parameters and performance of 'standard' *Arenicola marina* at 15 °C. From Riisgård *et al*. (1996).

Wet weight (W_w, wet wt): 3.5 g
Dry weight (W_d, dry wt): 0.5 g
Stroke frequency (f_{max}): 7 strokes min^{-1}
Volume flow = normal pumping rate ($Q_{op} = D_v f_{max}$): 1.5 ml min^{-1}
Maximal pressure rise ($\Delta H_{12}^0 = \Delta H_p^0$): 20 cm H_2O
Stroke length (L_s): 4 cm
Tube diameter (D): 5 mm
Piston area (A_p): 0.05 cm^2
Displacement volume: $D_v = L_s A_p = 0.20$ ml stroke^{-1}
Normal operating pressure (ΔH_{op}): 5 cm H_2O
System resistance (ΔH_s): 5 cm H_2O
Power output (P_p): 12.6 µW
Metabolic rate (R_{tot}): 232 µl O_2 h^{-1} = 1281 µW
Overall pump efficiency (η): 0.01

The system resistance, which is due to frictional resistance to flow through tube and sediment, is a linear function of flow :

$$\Delta H_s = QC_f, \tag{5}$$

where C_f is a constant. Thus, eq. (3) may be expressed as :

$$\Delta H_p = QC_f + \Delta H_{12}^0\,[(1-(Q/Q_{op})^2]. \tag{6}$$

From eq. (6), the pumping power-volume flow characteristic of the pump, *Pp*, may now be obtained as pump pressure ($\rho g \Delta H_p$) multiplied by volume flow *(Q)* :

$$P_p = \rho g \Delta H_p Q, \tag{7}$$

where ρ = density of seawater and g = acceleration due to gravity.

The total resistance offered by the system (ΔH_s) of the normal active worm pump is due to frictional resistance derived from flow in the tube and through the space between worm body and tube wall, and pressure drop across the sediment in the head shaft. It was calculated by Riisgård *et al*. (1996) that the total head loss of frictional resistance constitute only 0.01 cm H_2O in a 'standard' *Arenicola marina* pumping 1.5 ml min^{-1} (Table I). Thus, the resistance offered by the sediment dominates the total system resistance.

RESISTANCE OF SEDIMENT TO WATER FLOW

The frictional resistance to water flow through the sediment above a pumping lugworm can be estimated by means of Darcy's law. This empirical law states that the volume flow *(Q)* is inversely proportional to the thickness (or length *(ΔL)* of a core of sediment and directly proportional to the applied pressure *(ΔH)* and the cross-sectional area of *(A)* of the core (Riedl 1971, Fetter 1994) :

$$Q = AK\Delta H/\Delta L, \tag{8}$$

where the constant of proportionality *(K)* is known as the permeability or hydraulic conductivity. The friction caused by water flow in the pore system depends upon the permeability of the sediment and has constant values for each type of deposit. The hydraulic conductivity of rather clean sand from a lugworm habitat was experimentally determined by Riisgård *et al*. (1996) in core samples of different length and diameter to be about 5 × 10^{-4} m s^{-1}.

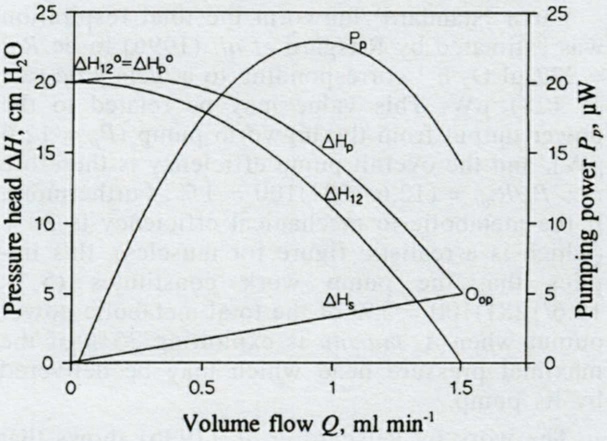

Fig. 5. – *Arenicola marina.* Pressure head-pumping rate characteristics for pump pressure *(ΔH_p)*, system resistance (ΔH_s) and back pressure (ΔH_{12}). P_p : pumping power-pumping rate characteristic of the pump. O_{op} : normal operating point. The calculations are based on a 'standard' lug worm, cf. Table I. From Riisgård *et al*. (1996).

ENERGY COST OF PUMPING

When the following parameters apply for a 'standard' *Arenicola marina* : ΔL = 20 cm, A = 5.5 cm^2, and $K = 5 \times 10^{-4}$ m s^{-1} then the 'system' resistance of the sediment can be calculated using eq.(8) to be $\Delta H_s \approx 2$ cm H_2O or 10 % of the maximum pressure rise that the lugworm pump may deliver. A realistic upper figure to be experienced by a normal active lugworm in nature may probably be up to 5 cm H_2O or 25 % of its maximum pressure rise. Therefore, a maximum system resistance of ΔH_s = 5 cm H_2O may be adopted for further calculations. The curves for the different equations are shown in Fig. 5. At the specified operation pressure ($\Delta H_p = \Delta H_s$ = 5 cm H_2O), the power output (P_p) from the 'standard' lugworm pump is calculated to be 12.6 µW.

For a 'standard' lugworm the total respiration was estimated by Riisgård *et al.* (1996) to be R_{tot} = 232 µl O_2 h^{-1} corresponding to a metabolic rate of 1281 µW. This value may be related to the power output from the lugworm pump (P_p = 12.6 µW), and the overall pump efficiency is therefore $\eta = P_p/R_{tot} = (12.6/1281)100 = 1\,\%$. Furthermore, if the metabolic to mechanical efficiency is 20 % (which is a realistic figure for muscles), this implies that the pump work constitutes $(5 \times 12.6/1281)100 = 5\,\%$ of the total metabolic power output when *A. marina* is exploiting 25 % of the maximal pressure head which may be delivered by its pump.

The work by Riisgård *et al.* (1996) shows that the energy cost of pumping by *Arenicola marina* is modest (< 5 %), especially in a loose sediment. On the other hand the powerful pump may at times (presumably over shorter periods) be used for loosening a compact sediment. In this way a high initial system resistance may be reduced to a relatively low value during the normal ventilatory state which is characterized by a steady and continuous stroke frequency of about 7 strokes min^{-1}.

BIOIRRIGATION

Ventilatory pumping by *Arenicola marina* leads to 'bioirrigation' of the sediments it inhabits. Rates of exchange of water (and solutes) between sediment porewaters and the overlying water are enhanced 10- to 20-fold due to irrigation by *A. marina* over what they would be due to diffusive exchange alone (Rasmussen *et al.* 1998). This is a moderate enhancement of water movement typical of bioturbating infauna. In contrast to most other infauna, however, bioirrigation by *A. marina* occurs deep within the sediments and is advective in nature, leading to non-local mixing (*sensu* Boudreau 1984) of overlying water with porewaters surrounding the feeding gallery. The effects of bioirrigation by *A. marina* can be observed as 'flat' porewater profiles flushed of metabolites to depths corresponding to the feeding depths or deeper (Hüttel 1990). In addition, bioirrigation by *A. marina* flushes and oxidizes the sediments to significant depths, thus altering the biogeochemical nature of the environments it inhabits (Nielsen 1997, Banta *et al.* 1998).

BURROWING AND FEEDING

Arenicola marina is an effective burrower, capable of digging several centimetre per minute and establishing its burrow quite quickly in a new area. *A. marina* usually lives at depths of 10 to 40 cm, depending on the size of the individual. Once established, *A. marina* typically remains in its burrow for long periods of time, moving only if forced to do so because of disturbance or to search for better food resources (Wells 1966, Rijken 1979). Adult *A. marina* change positions occasionally, however, by moving short distances laterally through the sediments (Brey 1991, Flach & Beukema 1994). Both its feeding mode (see below) and how often *A. marina* move depend on the sediment type and food resources available (Rijken 1979, Brey 1991). In contrast to adults, juvenile *A. marina* occasionally migrate over longer distances by swimming, usually during winter (Flach & Beukema 1994).

Arenicola marina is characterized as a head-down, subsurface deposit feeder (Wells 1966). Its most common feeding mode is as a conveyor-belt feeder (*sensu* Rhoads 1974) where sediment is ingested in the feeding gallery at depth and deposited on the sediment surface in faecal cast shortly afterwards. A single worm ingests approximately 1 to 2 ml sediment per hour (see case study below) and has relatively short gut passage times of approximately 1 h (Plante & Mayer 1994). Sediment removed from the feeding gallery is rapidly replaced by sediment above leading to the formation of the feeding funnel. In this way, *A. marina* may ingest sediment and associated materials originating from the sediment surface. While this is the classic feeding pattern, the exact mode of feeding for *A. marina* and the characteristics of the feeding funnel depend on the sediment characteristics, including the sediment structure and organic content (Cadée 1976, Rijken 1979). In some cases there is no identifiable feeding funnel and it appears that *A. marina* feeds on subsurface sediment (Rijken 1979, Brey 1991).

Arenicola marina is not considered a selective feeder in the classic sense (e.g. Lopez & Levinton 1987) of particle selection, although the maximum size particle that can be ingested is ca. 2 mm (Baumfalk 1979). *A. marina* thus preferentially feeds on particles smaller than 2 mm, although below 1 mm it feeds non-selectively (Jones & Jago 1993). This inadvertent selection against larger particles by *A. marina* leads to the establishment of a layer of large particles, often shell fragments, which accumulates at or just below the feeding zone. This 'shell layer' is well know in sediments inhabited by populations of *A. marina* (Van Straaten 1952).

SEDIMENT REWORKING – A CASE STUDY

Recent work by Berntsen & Tarp (unpublished) may serve as a case study for the subject of this section : sediment reworking. The aim of the work

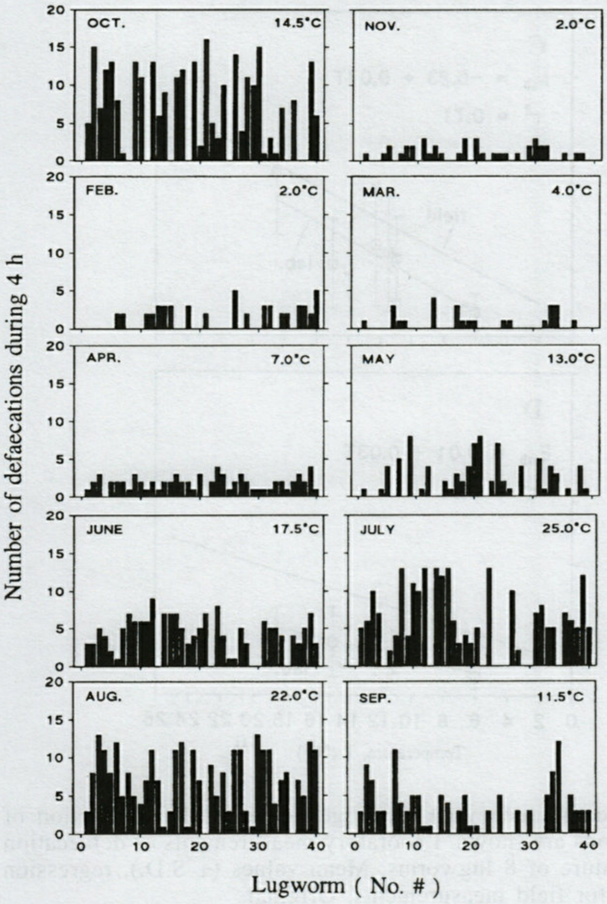

Fig. 6. – *Arenicola marina.* Total number of defaecations during 4 h periods measured on 40 randomly numbered lugworms measured in the field on 10 different times from October 1993 to September 1994. Each bar represents one lugworm. Original.

was to gather field data for the undisturbed feeding activity of *Arenicola marina* because such data are important reference values for prospective studies on feeding and growth of lugworms, and likewise for studies dealing with sediment decomposition processes which may be highly influenced by water pumping and bioturbation.

Population density and defaecation frequency of *Arenicola marina* were measured in Bregnór Bugt, Odense Fjord, Denmark. At low tide an extensive mud flat in the south eastern part of the bay is often laid bare and the sediment surface is seen to be marked by innumerable faecal piles of *A. marina*. Studies on the tidal mud flat were carried out 10 times during the period October 1993 to September 1994. The volume/dry weight ratio of sediment from Bregnór Bugt was measured to be $V = 0.67$ cm^3 g^{-1} dry wt.

The egestion rate was quantified on the basis of the total amount of faeces delivered at the sediment surface during 4 h by the lugworms, and the defaecation frequency was estimated as the number of deliveries per unit of time. At low tide (usually 20 to 50 cm water depth) on calm days without disturbing waves, 40 fresh lugworm faecal piles were marked with numbered sticks before the piles were gently blotted out. During the following 4 h the number of faecal deliveries were measured by counting the number of new faecal strings every 15 min. The faecal strings were sucked up by means of a syringe and transferred to a beaker for determination of dry wt in the laboratory. The population density of lugworms was estimated by counting the number of faecal piles within 10 randomly chosen squares of 1 m^2.

Corresponding to the field studies the defaecation frequency was measured in the laboratory with lugworms (2 to 4 g wet wt) collected at the field study locality. Individual lugworms were collected by digging up with a spade. The worms were brought to the nearby laboratory where 8 to 10 individuals were placed in an aquarium with sediment and running seawater. Measurements of egestion and defaecation frequency were performed within 1 to 2 days after the worms had established their burrows and started to make faecal piles on the sediment surface.

The frequency of defaecation for the 40 numbered *Arenicola marina* in 10 different months of the year is shown on Fig. 6 with water temperatures measured on the day of examination. There was a pronounced individual variation in the number of defaecations, but it is clear that the activity of the lugworms was highly dependent on season with very low values in the winter months.

The individual defaecation frequency (*f*, castings h^{-1}) and egestion rate (*E*, g dry wt h^{-1}) as a function of water temperature measured during low tide in the different months are shown on Fig. 7 A & B. The regression lines illustrate that both parameters increase with increasing temperature. Correspondingly, the defaecation frequency and egestion rate are shown on Fig. 7 C & D as a function of temperature for lugworms established in sediment in the laboratory. In order to compare the field- and laboratory results the regression lines from the field studies are also indicated. It is seen that the activity was generally reduced in the laboratory.

Fig. 8 shows the population density (estimated by counting casts, *cf.* Flach & Bruin 1993) during the year. From October to April the population density was approximately 25 lugworms m^{-2}. In May and June the density increased due to the establishment of a new lugworm generation, but later the population density decreased again due to mortality caused by predation and/or competition for food and space.

The following calculations are based on the assumption that the lugworm population consists of uniformly distributed 'standard' 3.5 g- wet-

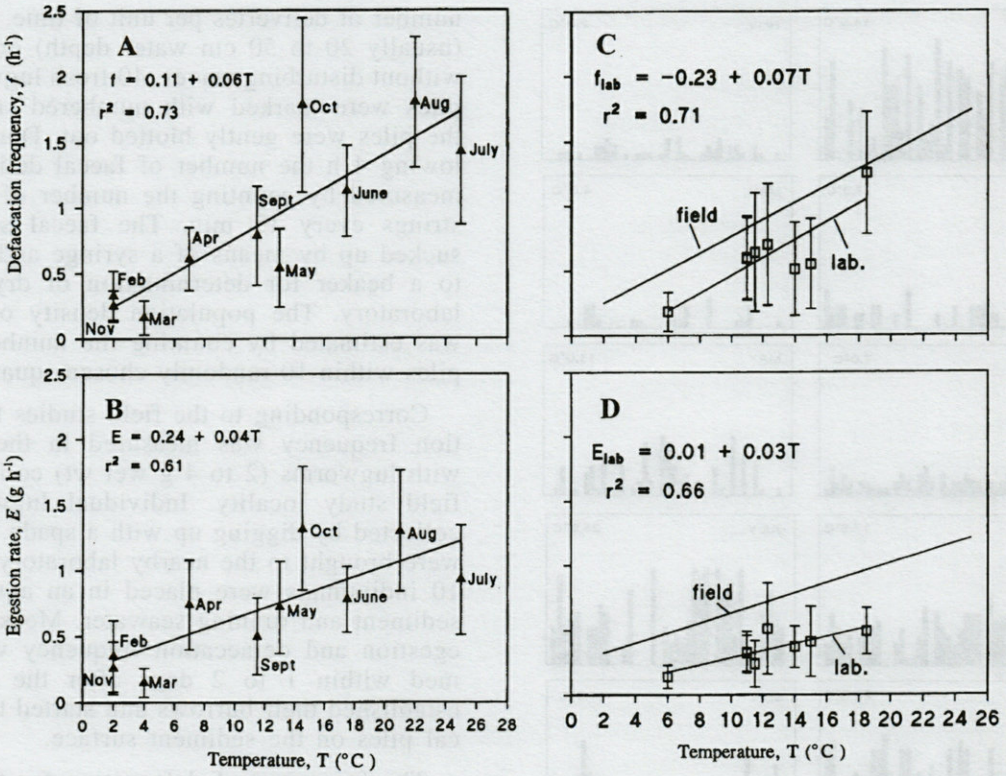

Fig. 7. – *Arenicola marina.* Field measurements of defaecation frequency (A) and egestion rate (B) as function of temperature. Mean values (± S.D.), regression lines and equations are shown. Laboratory measurements of defaecation frequency (C) and egestion rate (D) as a function of temperature of 8 lugworms. Mean values (± S.D.), regression lines and equations are shown together with the lines found for field measurements. Original.

weight individuals with at density D = 25 worms m^{-2} (which is a fairly reasonable assumption in the present case, *cf.* Fig. 8). The individual egestion at 15 °C may be found from the regression equation shown on Fig. 7 A & B to be : $E = 0.24 + 0.04 \times 15 = 0.84$ g h^{-1}. Now, the reworking of sediment may be estimated as : $Rw = (E \times D \times V)/\text{cm}^2 = (0.84 \times 25 \times 0.67 \times 720\ \text{cm}^3/\text{month})/10^4\ \text{cm}^2 = 1$ cm month^{-1} = 12 cm yr^{-1}.

PARTICLE BIOTURBATION

The results of burrowing and sub-surface deposit feeding by *Arenicola marina* is a circular, conveyor belt-like movement of sediment particles. When feeding, sediment particles in the feeding funnel are rapidly drawn (in minutes to hours, Jacobson 1967, Rijken 1979) down to the feeding chamber where they are ingested and returned shortly afterwards to the sediment surface, at a location several cm's away, as faecal casts. This results in burial or subduction of surface sediments (top 10 to 20 cm, depending on the feeding depth) at rates significantly higher than natural sedimentation rates in the environments inhabited by *A. marina.* The rates of sediment reworking in the case study above yielded sediment burial rates of 12 cm yr^{-1} assuming a standard worm density of 25 m^{-2} (Fig. 8) and an average

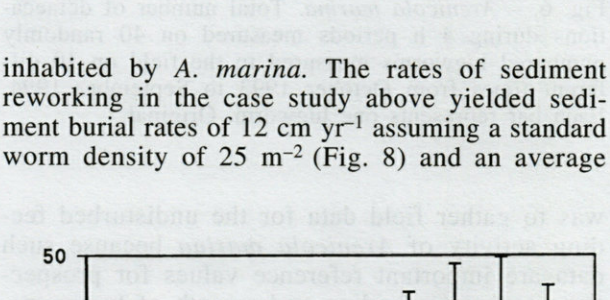

Fig. 8. – *Arenicola marina*. Population density of lugworms at Bregnór Bugt from October 1993 to September 1994. Mean values (± S.D.) are indicated. The standard density (25 lugworms m^{-2}) is indicated by the dashed line. The hatched area illustrates a new generation of lugworms. Original.

feeding rate corresponding to 15 °C. Others have estimated rates of subduction due to bioturbation by *A. marina* to be 4 to 40 cm yr^{-1} (see Table II in Cadée 1976). In contrast, sedimentation rates for most coastal environments are in the range of 0.01 to 1 cm yr^{-1} (e.g., Berner 1980). Note that these subduction rates are only true for the upper, bioturbated layer where *A. marina* affects particle movement via its feeding and burrowing. True rates of sedimentation, leading to permanent burial under the bioturbated layer, cannot be estimated from feeding rates by *A. marina,* but are probably not significantly affected by the worm. An exception would be in the cases where *A. marina* burrows function as sediment traps (Rijken 1979, Hüttel 1990).

In conclusion, bioturbation by *Arenicola marina* leads to much faster rates (4 to 400 times) of particle movement in the upper layers of sediments they inhabit. This particle bioturbation will be observed first as enhanced rates of burial of surface sediments and ultimately as a homogeneously mixed upper, bioturbated zone of the sediment. At the highest rates of bioturbation, sediment particles in the bioturbated zone will be cycled from the sediment surface, buried and resurface again several times per year. This represents a significant deviation from the normal mode of particle movement in sedimentary environments, namely unidirectional, slow burial.

FOOD SOURCES AND ENERGY DEMAND

Lack of precise knowledge of the nutritional source is still a major limitation for understanding how *Arenicola marina* makes energetic profit from eating nutritionally-poor sediment despite the fact that it has been a point of discussion for many years (e.g., Krüger 1959, 1971, Jacobson 1967, Longbottom 1970, DeWilde & Berghuis 1979, Rijken 1979, Retraubun *et al.* 1996a). *A. marina* usually lives and feeds in sandy, relatively organic-poor sediments (0.3-3 % organic matter, e.g., Cadée 1976, Beukema *et al.* 1983, Brey 1991) where presumably only a fraction of the ingested sediment is digestible (Lopez & Levinton 1987) suggesting that the worm may be organic matter limited. In addition, the worm may be limited in growth by the quality of the food as by its quantity as these low organic matter sediments are of poor nutritional value (high C/N ratio). *A. marina* appears to spend nearly all its time ingesting sediment suggesting that extracting nutrition is a 'full time job'. This is a common characteristic for true deposit-feeders (Lopez & Levinton 1987).

There are several possibilities of food sources for *A. marina*, which may be utilised alone or in combinations : 1) nonliving detrital organic matter (sediment organic matter), 2) bacteria at normal sediment densities, 3) bacteria enhanced in abundance externally by 'gardening' activities, 4) bacteria enhanced in abundance internally by microbial fermentation, 5) bacterial exudates and products, 6) microphytobenthos, 7) living animal matter, 8) dissolved organic material, and 9) suspended organic matter originating from the water column but 'filtered' by *A. marina* (i.e. trapped in the sediment during irrigation).

In the following sections, we attempt to evaluate the importance of most of these potential nutritional sources for *A. marina* based on current knowledge. We use energetic calculations of food demand based on data for metabolic requirement and sediment ingestion rate of a 'standard' *A. marina* as a tool for contributing to this decade-long discussion. The respiration rate of a 'standard' lugworm (3.5 g wet wt) is R_{tot} = 232 µl O_2 h^{-1} (Table I). If it is suggested that 1 ml O_2 is used for combustion of 1 mg dry organic matter then the worm demands 0.232 mg assimilated organic matter h^{-1}.

Utilization of sediment detritus

Assuming a feeding rate of 0.84 g sediment dry wt h^{-1} as observed in our case study, the percentage of total ingested sediment *(I)* which must be digestible organic matter available for the lugworm is : $I/E = (0.232 \times 10^{-3}/0.84)100 = 0.03\,\%$. This value may be compared to measured concentrations of organic matter in sediments where *A. marina* lives. *A. marina* inhabits sediments ranging widely in organic matter contents, including quite organic-poor sediment. In most cases the sediment organic content is greater than 0.03 % suggesting that it is possible for the worm to live as a true deposit feeder, depending on assimilation efficiencies.

There is current discussion of the effectiveness of deposit feeders for extracting dead sediment organic matter (detritus). Part of the difficulty with addressing the use of sediment detritus is that it is difficult to estimate the assimilation of dead organic matter alone, independent of associated microbes. Deposit feeders have been shown to be quite efficient at assimilating sediment microorganisms (Lopez & Levinton 1987). In their review, Lopez & Levinton (1987) argue based on the fact that sediment microbial populations are too small an organic pool for many deposit feeders that some portion of sediment detritus must be utilised by deposit feeders. Furthermore, recent work by Mayer *et al.* (1997) characterising the digestive capabilities of deposit feeders suggests that *A. marina* is effective at extracting some portion of detrital organic matter. Most deposit feeders assimilate 5 to 15 % of the total sediment organic matter (including microbial pools) (Lopez & Levinton 1987). If we apply such assimilation efficiencies to our standard lugworm, then the sediments would have to have an organic content dry weight of 0.2 to 0.6 % to support the worm's nutritional needs. This required organic content corresponds quite well with most of the sediments in which *A. marina* lives, suggesting that it could live as a 'pure' deposit feeder in most cases.

Microbial food sources – is 'gardening' necessary?

There is good evidence that *A. marina* is capable of assimilating sediment associated bacteria (Plante & Mayer 1994, Retraubun *et al.* 1996a). In general, deposit feeders assimilate bacteria with high efficiency (40 to 90 %, Lopez & Levinton 1987) indicating that they utilize sediment microbes as a food source. But there is not enough microbial biomass to support the nutritional needs of the deposit feeder. For our standard lugworm to live off of 'microbial stripping' alone, sediment microbes would have to have a concentration of 0.03 to 0.1 % (as dry wt organic matter) to be a sufficient food source. Bacterial biomass typically is 0.2 to 2 % of the total sediment organic matter (measured as C, Rublee 1982, Cammen 1982). Sediments inhabited by *A. marina* would thus have bacterial biomasses (as dry wt organic matter) in the range of 0.001 to 0.1 %, which suggests that the lugworm may live by microbial stripping only in the more organic rich (> 1.5 % dry wt) sediments. In less organic rich sediments, the standing bacterial biomass is probably not a sufficient food source alone for *A. marina*.

'Gardening', introduced by Hylleberg (1975) has been suggested as a way that lugworms can enhance the availability of microorganisms as a food resource. Briefly, gardening refers to the stimulation of microbial growth due to effects of the lugworm's irrigation and bioturbation on the sediment environment. While this has been a rather controversial subject, there is good evidence that microbial biomass and production is enhanced in the feeding pocket of *Arenicola marina* burrows (Reichardt 1988, Grossmann & Reichardt 1991, Retraubun *et al.* 1996a). Compared to surrounding sediments, bacterial biomass and productivities can be several-fold higher (Reichardt 1988, Retraubun *et al.* 1996a). This process helps expand the range of sediments in which *A. marina* can live exclusively on microbial sources. Microbial gardening would be advantageous for *A. marina* living in organic poor sediments, but has not been shown.

In addition to the classical type microbial gardening, there is evidence that the growth of the bacteria that survive passage through the gut is stimulated in the hind gut of *Arenicola marina* (Plante *et al.* 1989). This mechanism may also play a role in stimulating microbial populations in sediments consumed by *A. marina*. The net effect on the bacterial population depends on the balance between digestion and stimulation, which has not been studied. Several investigators (Grossmann & Reichardt 1991, Retraubun *et al.* 1996a) have measured significant reductions in bacterial numbers upon gut passage indicating bacterial grazing. The surviving bacteria may have very high growth rates (Plante *et al.* 1989), however, leading to a rapid reestablishment of the microbial population. This would be a good example of the kind of renewable resource hypothesized for deposit feeders by Levinton & Lopez (1977). It should be noted, however, that bacteria egested by *A. marina* are deposited on the sediment surface, far away from the feeding zone, so this mechanism of microbial stimulation is probably of little immediate benefit to the lugworm.

Benthic microphytobenthos

Another food source that can be utilised by *Arenicola marina* is benthic microphytobenthos. Similar to sediment microbes, they are readily assimilated by lugworms (Retraubun *et al.* 1996a) and thus a potential food source. Obviously benthic microalgae do not grow at the typical feeding depths of *A. marina,* so a rapid subduction of surface sediments containing microalgae is the only mechanism that would supply this food source in significant numbers. Both correlative (Cadée 1976) and observational (Retraubun *et al.* 1996a) evidence suggests that this occurs. On the other hand, many benthic diatoms are motile, capable of moving several cm per hour (MacIntyre *et al.* 1996) and such motility might allow benthic diatoms to escape feeding by *A. marina.* Retraubun *et al.* (1996a) observed similar concentrations of benthic diatoms in the feeding funnel and head shaft as in the sediment surface suggesting that diatoms were drawn down by lugworms. Furthermore, they observed significant preferential selection of diatoms as a food source. More work is needed to determine to what extent *A. marina* feeds on benthic microphytobenthos and thus functions to some extent as surface deposit feeder.

The nutritional requirements for our standard lugworm living on benthic microalgae would be similar to that of sediment microbes as a sole food source, namely 0.03 to 0.1 % dry wt organic matter. Benthic microalgal concentrations of surface sediments ranging between 0.1 and 50 µg chlorophyll *a* g^{-1} sediment are reported by MacIntyre *et al.* (1996). This corresponds to 4 to 2000 µg

C g^{-1} sediment or 0.0004-0.2 % (ca.0.0008 – 0.4 % dry wt organic matter) assuming a C/chlorophyll *a* ratio of 40 (Valiela 1995), suggesting that only the highest benthic microalgal biomasses could serve as a sole food source for the standard lugworm. But undoubtedly, the benthic microalgae that are present in the sediments ingested by *A. marina* contribute to its diet (Rijken 1979, Retraubun *et al.* 1996).

Micro- and meiofauna consumption

Microfauna and meiofauna both potentially represent high quality sources of nutrition for *A. marina,* although it is unclear to what extent they may be utilised. Hylleberg (1975) observed ciliates and flagellates in the foregut of *Abarenicola pacifica,* a closely related lugworm species, but not in the hindgut and therefore concluded that these organisms were digested. Furthermore, ciliates and flagellate abundances were enhanced in the feeding pocket of this lugworm leading Hylleberg to conclude that this food resource was stimulated as part of the gardening by the lugworm. In contrast, Retraubun *et al.* (1996a) observed only low numbers of meiofauna in the head shaft of *A. marina* and concluded that they could not be an adequate food source. Reise (1985) contends that meiofauna in the feeding pocket are unavailable to the lugworm because they live among the courser particles which cannot be ingested.

While it is unclear to what extent *A. marina* may feed on micro- and meiofauna, we can again consider how much must be consumed by our standard lugworm to be sufficient as a sole food source. Being animals, these are highly digestible food sources, as is corroborated by the absence of such organisms in the posterior sections of lugworm digestive tracts (e.g., Hylleberg 1975). We can thus assume an utilisation efficiency of near 100 %. Thus micro- or meiofauna biomasses must be greater than 0.03 % (dry wt) to satisfy the needs of the lugworm. Gerlach (1978) estimated that the biomass of ciliates and flagellates, the most important microfauna, to be approximately 1 µg ml^{-1} sediment, that is, less than 0.0001 %. On the other hand, meiofauna (including Foraminifera) biomass was estimated as 70 µg ml^{-1} or approximately 0.01 %. In neither case, are these animals likely to be sufficient as a sole food source for *A. marina*, although meiofauna may contribute significantly to the lugworm's diet.

Filter feeding excluded

It is unknown if or when *Arenicola marina* exploits the full capacity of its pump. The maximal pressure head which can be delivered by the lugworm pump is $\Delta H_p^0 = \Delta H_{12}^0 = 20$ cm H_2O (Table I, Figs. 4 & 5) which is 30 to 150 times higher than found in filter-feeding macro-invertebrate pumps (Riisgård & Larsen 1995). The latter group is characterized by pumping large amounts of water per ml of oxygen consumed. Thus, the filter-feeding polychaetes *Sabella penicillus, Chaetopterus variopedatus* and *Nereis diversicolor* pump 354, 50 and 40 litres of water per ml of oxygen consumed, respectively (Riisgård & Larsen 1995). These values may be compared with $(1.5 \times 60 \times 10^{-3})/0.232 = 0.4$ l ml^{-1} O2 in the 'standard' *A. marina*. This very low value excludes that the lugworm can make a living as a true filter feeder, using the sand immediately in front of the head as a particle retaining filter for restraining suspended food particles in the ventilatory water, as proposed by Krüger (1959, 1962, 1964).

While we can rule out the likelihood of *A. marina* living as a true filter feeder, we do not exclude the possibility that some fraction its nutrition may come from suspended material drawn down into the sediment while irrigating. Especially resuspended material from the sediment surface may represent a potential food source given the high concentration of organic material in such a benthic nepheloid layer, if pumped into and retained within the sediments by *A. marina.* This mechanism has not been investigated to our knowledge.

Summing up, there appears to be ample food in most sediments, from a number of sources, to support the nutritional needs of *Arenicola marina* living as a deposit feeder. These food sources may be dead, detrital organic matter and living organisms such as bacteria, microalgae, micro- and meiofauna. There is an unnecessary dichotomy between microbial and detrital food sources in the ongoing discussion of deposit feeder nutrition (Lopez & Levinton 1987). Several sources are probably utilised by *A. marina*, the balance being shifted depending on what is available in a given environment.

EFFECTS OF *ARENICOLA MARINA* ON THE ENVIRONMENT

Irrigation and oxidation

The irrigation of burrows by benthic polychaete worms exerts a profound effect on the chemistry and microbiology of shallow-water sediments because the burrows extend the sediment-water interface (Fenchel 1996 a & b). Without actively burrowing and irrigating worms, most sediments in estuaries and coastal regions would be anoxic within a depth of a few mm. The infauna worms irrigate their tubes with overlying seawater rich in oxygen, not only for obtaining oxygen for respiration purposes, but also for producing surrounding oxidised zones which can protect themselves against poisonous sulphide that develops in the anoxic sediment. During irrigation events dissolved nutrients that accumulate in the burrows due to porewater diffusion are transported up into the overlying water. This irrigational transport of dissolved components is much more efficient than the diffusive flux driven by porewater concentration gradients because it is faster than molecular diffusion and because it by-passes the oxidised surface layer of the sediment which acts as a chemical barrier to the upward flux of nutrients. The burrowing worms also physically stir the sediment (bioturbation) which increases the penetration of oxygen so that the upper 2 to 10 cm of the sediment becomes a mosaic of oxic and anoxic microhabitats which enable that anaerobic and aerobic microbial processes may take place at the same depths. The apparent vertical zonation of microbial and chemical processes over a scale of several cm just reflect a diminishing fraction of oxic habitats with depth. The activity of worms has a profound effect on the chemistry of the sediment by extending the surface area of the oxic-anoxic boundary and by importing oxidants (O_2, NO_3^-, SO_4^{2-}) to deeper layers in the sediment. Irrigation of burrows by benthic worms and increased surface of the oxic/anoxic boundary caused by bioturbation enhances the microbial process rates and thus the nutrient fluxes at the sediment-water interface.

Particle reworking and sediment structure

In addition to affecting sediment chemistry and redox, infauna have profound effects on the physical characteristics of the sediments they inhabit. With *Arenicola marina,* via it's intense bioturbation, there is rapid mixing of sediment particles in the layers above the feeding zone. Here sediment particles will be advectively subducted (i.e., buried) due to feeding by *A. marina*. Once a sediment particle reaches the feeding depth it will be returned to the sediment surface, due in the feeding process, if it is small enough. Coarse particles move down wards only (Van Straaten 1952). Depending on the feeding depth, feeding rate and mode of feeding, the upper sediment layer may be turned over several times per year. In this sense, *A. marina* can be considered one of the many infauna organisms functioning as earthworms of coastal areas.

In the area surrounding the feeding gallery, the sediments water content (porosity) is enhanced by *A. marina*'s irrigation (Jones & Jago 1993). Just below the feeding zone, the sediment consists of much larger particles due the accumulation of rejected large (> 2 mm) particles (Jones & Jago 1993). This leads to the establishment of a 'shell layer' (Van Straaten 1952) if an *A. marina* population has been established for some time.

Effects on other benthic organisms

Macrofauna

The influence of *Arenicola marina* on the abundance of other benthic animals has been studied by Flach (1992) and Flach & Bruin (1993). The lugworm was found to have a strongly negative effect on the densities of the tube-building amphipod *Corophium volutator* and densities of juveniles of various polychaete and bivalve species. This negative effect of adult *A. marina* on juveniles is true for juvenile *A. marina* as well (Flach & Beukema 1994). Similarly, Brey (1991) observed both positive and negative effects of *A. marina* on other macrofauna, although the specific effects varied among habitats. Therefore, the structure of the macrozoobenthic community can be strongly influenced by the density of *A. marina* which is relatively stable in place and time as compared to other infauna species (Beukema *et al.* 1983, Flach & Beukema 1994). The controlling effect of *A. marina* does appear to be dependent on its feeding mode and the stability of the environment (Brey 1991).

Meiofauna

The effects of *A. marina* on meiofauna have been well described by Reise (1981, 1985), among others. Some groups of meiofauna are stimulated by the activities and structures of lugworms while others are inhibited. For example, nematodes numbers are reduced in both the feeding funnel and faecal mounds, while Foraminifera are enhanced in the funnels. The various parts of the lugworm burrow also represent different environmental conditions which enhance meiofaunal populations to various extents, although there is some disagreement at to whether there are distinct groups of meiofauna in lugworm burrows (Reise 1985, Wetzel *et al.* 1995).

Microorganisms

Arenicola marina has both positive and negative effects on sediment microbes. The positive effects can be characterized as the indirect effects of *A. marina*'s burrow structure, mode of feeding and bioturbation which stimulate bacterial growth. In addition, microbes surviving the passage through the gut of a lugworm may also be stimulated (Plante *et al.* 1989). These effects have been seen with other macrofauna (see reviews of Andersen & Kristensen 1991, Krantzberg 1985), although they are strongly evident with lugworms.

The negative effects of *A. marina* are direct, grazing effects. Many researchers (e.g. Grossmann & Reichardt 1991, Plante & Mayer 1994, Retraubun *et al.* 1996) have demonstrated that sediment microbes are consumed by *A. marina*, reducing their biomass, at least immediately. The ultimate effect *A. marina* on sediment microbes is thus a balance of these opposite effects. The general perception is that the overall effect of lugworms is a local stimulation of sediment microbes, despite significant consumption of many.

Effects on material pools and nutrient fluxes

Organic matter decomposition

Macrofauna organisms generally enhance rates of organic matter decomposition (Kristensen & Blackburn 1987). This effect has been poorly studied for *Arenicola marina*. Recent work by Banta *et al.* (1998) confirms the general trend for other macrofauna, that *A. marina* also enhances organic matter decomposition. Organic matter decomposition was enhanced in laboratory microcosms by *A. marina* by 40-125 %, depending on the organic matter content of the sediments.

In contrast, *A. marina* had a negative effect on anaerobic decomposition in the study by Banta *et al.* (1998). Thus, while *A. marina* enhances overall organic matter decomposition, it helps favour aerobic processes. This is ecologically important as much of the decomposition ($\geq 50\,\%$) in marine sediments usually is by anaerobic processes (Mackin & Swider 1989, Jørgensen 1996). Aerobic decomposition thus plays a larger role in organic matter cycling in sediments inhabited by *A. marina* than in other sediments without or with smaller macrofauna. This means that there is a lower production and storage of reduced metabolites than there would be in sediments dominated by anaerobic processes.

Nutrient fluxes and cycling

As an active bioirrigator, *A. marina* enhances the exchange of dissolved materials between sediments and the overlying water. This effect is true for all bioturbating macrofauna, but *A. marina* is especially effective in enhancing the flux of dissolved materials due the mode it irrigates the sediment, namely by advectively pumping water from its burrow out into the porous sediment surrounding the burrow. This pumped water returns to the sediment surface via the feeding funnel in an upwards, advective flow. It is this advective irrigation process that leads to the 'flushed out' porewater nutrient profiles observed in sediments inhabited by *A. marina* (Hüttel 1990, Banta *et al.* 1998). This active irrigation means that the cycling of dissolved materials is greatly enhanced by *A. marina*, particularly the removal of reduced metabolites (e.g., NH_4^+, sulfides) from sediments to the overlying water.

In addition to enhancing the exchange of dissolved materials, *A. marina* profoundly affects biogeochemical cycles that are redox dependent. *A. marina* affects the sediment N cycle by stimulating nitrification and subsequently stimulating denitrification which is coupled to nitrification (Hüttel 1990). Similarly, *A. marina* affects sediment S cycling by inhibiting sulfate reduction and rapidly oxidizing reduced S compounds such as dissolved sulfides or pyrite (Banta *et al.* 1998). Thus two of the most important sedimentary element cycles are influenced significantly by the presence of *A. marina.*

CONCLUSIONS

The lugworm *Arenicola marina* is a true subsurface deposit feeder in organic-poor sediments. *A. marina* lives in tidal and sub-tidal areas consuming sediment organic matter, microorganisms and possibly benthic microalgae. It uses little energy to pump water through its burrow into the sediment, but it is unlikely that the worm significantly enhances its nutritional intake by filter feeding. While *A. marina* is found in a wide range of habitats, its mode of life undoubtedly sets limits on the types of sediments it can inhabit. It is critical for the lugworm to be able to pump water into the feeding pocket to adequately ventilate its burrow and to loosen and feed on sediment particles, and as such it is not found in sediments that are too cohesive. *A. marina* is a good example of a 'ecosystem engineer' as described by Levinton (1995) as it profoundly affects both the structure and chemical nature of as well as processes occurring within the sediment. As such *A. marina* plays an important role in affecting both energetics and material fluxes at the sediment-water interface of the habitats in which it lives.

ACKNOWLEDGEMENTS. – Thanks are due to I. Berntsen and B. Tarp for placing their data ('case study' project supervised by H.U.R.) at our disposal, and to Dr. J. Beukema and Prof. R. Rosenberg for their comments on the manuscript. G. Desportes made the French translation of the English abstract.

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Reçu le 18 juillet 1998 ; received July 18, 1998
Accepté le 31 août 1998 ; accepted August 31, 1998

VIE MILIEU, 1998, 48 (4) : 259-269

SULFATE REDUCTION AND TOTAL BENTHIC METABOLISM IN SHELF AND SLOPE SEDIMENTS OFF NOVA SCOTIA

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BENTHIC METABOLISM
SULFATE REDUCTION
CONTINENTAL SHELF
CARBON MINERALIZATION
SEDIMENTS
SCOTIAN SHELF

ABSTRACT. – Studies of sediment oxygen consumption, carbon dioxide efflux, and sulfate reduction were carried out in muddy sediments on the Nova Scotia continental margin to examine seasonal and spatial variation in carbon mineralization. Differences in sediment texture were predominantly caused by variation in the size and abundance of faunal fecal pellets, and carbon and nitrogen content were lower on the Slope than on the Shelf. Fluxes derived from shipboard incubations of subcores obtained from boxcores were compared to published values from the same cruises obtained from microelectrode and porewater profiles, and multicorer incubations. Carbon mineralization measured by either oxygen consumption or CO_2 release was generally not significantly different within stations. Oxygen consumption was highest at the shallowest station (Emerald Basin, 230 m) and least on the Slope (800 m), with intermediate values in the Laurentian Trough (500 m), but temporal differences in fluxes were not consistent between stations. Shipboard oxygen consumption rates obtained with subcore incubations from boxcores were usually similar to rates from incubations of multicorer samples. Rates of oxygen uptake determined from microelectrodes and carbon dioxide flux from porewater samples were lower than rates from core incubations, likely due to exclusion of bioturbation from profile calculations. Total benthic metabolism was dominated by sulfate reduction at all stations to at least 35 cm sediment depth, with again higher rates on the Shelf than on the Slope. Despite the greater depth of the Slope compared to Emerald Basin, the relative decline in carbon mineralization is slight, suggesting the significance of lateral input to the Slope from the Scotian Shelf. Compared to sandy banks that comprise most of the shelf, the relative importance of fine shelf sediments is accentuated, because mineralization processes in these sediments (particularly sulfate reduction) involve a greater length of sediment column than in organic-poor sands. Moreover, the relatively high mineralization that occurs on the Slope must be included in carbon budgets of the continental margin, especially in the event of significant offshelf transport.

MÉTABOLISME BENTHIQUE
RÉDUCTION DES SULFATES
PLATEAU CONTINENTAL
MINÉRALISATION DU CARBONE
SÉDIMENTS
NOUVELLE-ÉCOSSE

RÉSUMÉ. – Des recherches sur la consommation d'oxygène des sédiments, les productions de dioxyde de carbone et la réduction des sulfates ont été menées dans les sédiments vaseux de la marge continentale de Nouvelle Ecosse, afin d'examiner les variations saisonnières et temporelles de la minéralisation du carbone. Les différences dans la texture des sédiments sont causées principalement par les variations de taille et d'abondance des pelotes fécales, et les contenus en carbone et en azote sont plus bas au niveau du talus que sur le plateau continental. Les flux mesurés sur un navire à partir d'incubations de sous-échantillons provenant d'un carottier-boîte sont comparés aux valeurs déjà publiées obtenues au cours des mêmes campagnes mais avec des microélectrodes, par analyses de profiles verticaux réalisés sur l'eau interstitielle et par incubations d'échantillons provenant d'un carottier multitubes. La minéralisation du carbone mesurée soit par la consommation d'oxygène soit par la production de CO_2 n'est généralement pas significativement différente pour une même station. La consommation d'oxygène est plus élevée à la station la moins profonde (Emerald Basin, 230 m) et moindre sur le talus (800 m), avec des valeurs intermédiaires dans la Laurentia Trough (500 m), mais les différences temporelles dans les flux ne sont pas les mêmes à toutes les stations. Les taux de consommation d'oxygène mesurés à bord à partir d'incubations de sous-échantillons d'un carottier-boîte sont généralement identiques à ceux obtenus par incubations d'échantillons provenant d'un carottier multitubes. Les taux de consommation d'oxygène déterminés par microélectrodes et les flux de CO_2 obtenus pour l'eau interstitielle sont plus bas que ceux issus d'incubations, probablement en raison de la non prise en compte de la bioturbation dans les calculs réalisés sur les incubations. Le métabolisme benthique total est dominé par la réduction des sulfates à toutes les stations jusqu'à au moins 35 cm au-dessous de la surface du sédiment, avec à nouveau des taux plus importants sur le plateau que sur le talus. Malgré une plus grande profondeur au niveau du talus, comparée à Emerald Basin, la diminution de la minéralisation du carbone est faible, ce qui suggère un apport latéral significatif au talus en provenance du plateau de Nouvelle Ecosse. En comparaison avec les sables qui recouvrent la plus grande partie du plateau, l'importance relative des sédiments fins de celui-ci est accentuée car les processus de minéralisation dans ces substrats (particulièrement la réduction des sulfates) impliquent une plus grande hauteur de la colonne de sédiment que dans les sables, pauvres en matière organique. En outre, la minéralisation relativement élevée sur le talus doit être prise en compte dans les budgets de carbone de la marge continentale, en particulier dans le cas d'un transfert significatif en dehors du plateau continental.

INTRODUCTION

Continental shelves are areas of enhanced primary production and important fishery resources compared to open ocean. As a result of a relatively shallow water column, significant amounts of organic matter derived from primary production may be delivered to the shelf benthos and even beyond to the continental slope (Rowe *et al.* 1994). Studies of carbon fluxes on continental margins must therefore include benthic pathways. In the northwestern Atlantic, bottom topography reflects glacial history, and there are large banks of coarse relict sediment that are not obviously depositional. Interspersed with the banks are deeper muddy basins. The relative significance of banks and basins in energy flow is important because banks are often the sites of both benthic and pelagic fisheries (Lough *et al.* 1989; Thouzeau *et al.* 1991), despite their ostensibly organic-poor sediments. Basins make up a smaller proportion of the shelf area, but are relatively more important in benthic carbon cycling (Grant *et al.* 1991).

The increased organic input to basins compared to banks results in oxygen depletion in the sediments, and a shift to anaerobic mineralization through processes such as sulfate reduction (Buckley 1991). There are relatively few measurements of anaerobic metabolism in shelf sediments, although surveys of these data indicate that as much as 50 % of the carbon oxidation may proceed through sulfate reduction (Jørgensen 1982, Canfield 1989). Other electron acceptors such as nitrate, iron, and manganese are of variable importance in carbon cycling (Canfield *et al.* 1993).

Despite the necessity of documenting these processes in shelf sediments, their measurement is not straightforward for several reasons. Direct measurement of solute fluxes with shipboard core incubations is subject to disturbance artefacts from sample collection and subcoring, although benthic landers surmount some of these problems (Miller-Way *et al.* 1994). Enclosed samples also alter the near-bottom flow environment compared to the natural seabed (Buchholtz-ten Brink *et al.* 1989). Furthermore, various non-biological reactions impact the dynamics of sulfur, oxygen and carbon. For example, sulfides arising from sulfate reduction are chemically oxidized in oxic waters, accounting for some of the observed oxygen consumption in cores (e.g. Rowe *et al.* 1988, Canfield *et al.* 1993). In addition, carbon dioxide efflux as a measure of total carbon mineralization is affected by carbonate dissolution and precipitation reactions (Berelson *et al.* 1996, Mucci *et al.* in press).

Despite these potential problems, there are several flux measurements that can hypothetically constrain the benthic carbon cycle. These include oxygen consumption as a measure of aerobic metabolism (confounded by oxidation of reduced substrates), carbon dioxide release as a measure of total carbon mineralization, and sulfate reduction as a measure of the primary form of anaerobic carbon consumption. Although this suite of measurements provides complementary measures of system metabolism, they are not often determined concurrently. In the Canadian Joint Global Ocean Flux Study (CJGOFS), a series of studies on benthic processes sought to quantify carbon sequestration in sediments of the Scotian Shelf and Gulf of St. Lawrence. In the present study, we couple sediment-water exchange of oxygen and carbon dioxide with radiotracer measurements of sulfate reduction to quantify seasonal and regional differences in carbon mineralization at the CJGOFS study sites. In addition, drawing on companion CJGOFS studies (Mucci *et al.* in press, Silverberg *et al.* in press), we compare various methods of estimating these fluxes.

Table I. – Sampling locations and site characteristics of Laurentian Channel and Scotian Shelf and Slope stations. Cabot Strait was not sampled in May, and the Slope was not sampled in December. Median diameter refers to sediment grain size (see text).

Site	Location	Depth (m)	Bottom temperature (°C)			Median diameter (μm)		
			May	Dec	June	May	Dec	June
Cabot Strait	47°50'N, 60°05'W	494-531	-	5.4	5.3	-	47	44
Emerald Basin	43°50'N. 62°49'W	229-244	9.4	9.9	10.2	60	44	48
Scotian Slope	42°88'N. 61°75'W	779-847	6	-	5	94	-	66

MATERIALS AND METHODS

Sediments were sampled at 3 sites off Nova Scotia on cruises in May and December 1993 and June 1994 (Fig. 1, Table I). All sites discussed herein were muddy sediments with depths > 200 m. Cabot Strait is at the head of the Laurentian Channel at the outflow of the Gulf of St. Lawrence. Emerald Basin is one of a series of deep muddy basins interspersed on the Scotian Shelf, which contrasts the coarse sediment of shallow banks (Grant *et al.* 1991). The final site is on the mid-continental slope at ~ 800 m depth. Oxygen penetration in the sediment at these sites ranges from 4-17 mm (Silverberg *et al.*, in press).

Sediments were sampled with a 0.12 m^2 boxcorer (Ocean Instruments Mark II) and subcored to ~15 cm depth with acrylic core liners (12 cm id, 30 cm length). Incubation of cores was conducted as in Hatcher *et al.* (1994). Caps sealed with o-rings were fitted to core liner bottoms and overlying water was slowly topped off with unfiltered bottom water from the same site. Cores were sealed with o-ringed lids containing magnetic stirrers and incubated in the dark in a temperature-controlled bath, corresponding to on-site bottom temperature (Table I). Stirring was maintained at a level just below the resuspension threshold of the surface sediment. Control cores with bottom water only were also incubated. Samples were taken by opening a valve in the core and depressing the lid until water was purged into a BOD bottle. Incubations were carried out for periods ranging from 16-38 h depending on site and temperature. Water was sampled for various dissolved species although emphasis in the present paper is on fluxes of carbon dioxide and oxygen.

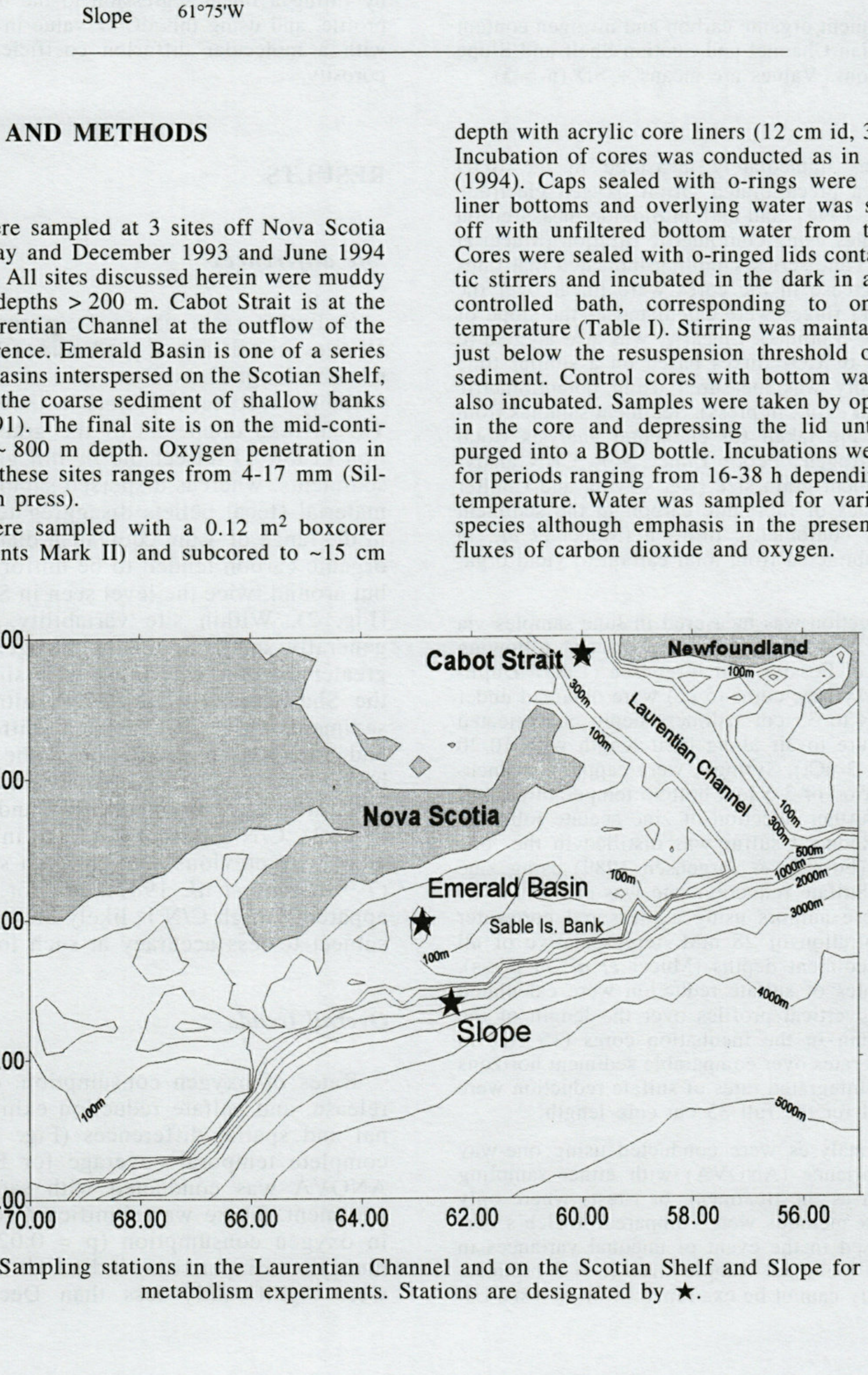

Fig. 1. – Sampling stations in the Laurentian Channel and on the Scotian Shelf and Slope for benthic metabolism experiments. Stations are designated by ★.

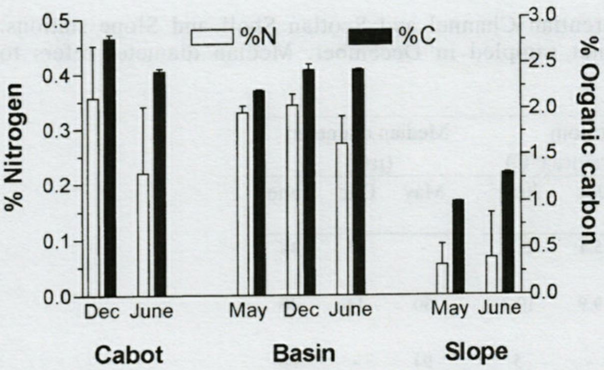

Fig. 2. – Sediment organic carbon and nitrogen content at the Laurentian Channel and Scotian Shelf and Slope sampling stations. Values are means + SD (n = 5).

Oxygen was immediately measured in the BOD sample using a precalibrated Orion oxygen electrode (Hatcher *et al.* 1994), and carbon dioxide measured on acidified samples using coulometric titration (Mucci *et al.*, in press). Time series sampling indicated that rates of oxygen decrease in the cores were linear over the incubations and fluxes were calculated as the slope of the decreases (~5 points). Linearity was also applied to the estimation of CO_2 fluxes based on a similar time series. Alkalinity was measured using potentiometric titration (Mucci *et al.*, in press). Sediment samples from the boxcore were taken for elemental analysis (total carbon and nitrogen; Perkin-Elmer 2400 CHN analyzer), and sediment grain size (wet sieving and Coulter Counter). Values of inorganic carbon in the sediment determined by coulometric titration (Mucci *et al.*, in press) were subtracted from total carbon to yield organic carbon.

Sulfate reduction was measured in June samples via injection of $^{35}SO_4$ into sediment horizons following the procedure of Fossing and Jørgensen (1989). Duplicate truncated syringe cores (5 cc) were obtained under N_2 at intervals to 35 cm sediment depth and injected without exposure to air along their length with 10-20 µl of $^{35}SO_4$ (~ 2 µCi). Syringes were capped and incubated for a period of 3-5 h at bottom temperature, until fixed with a further injection of zinc acetate followed by freezing. Reduced sulfur was distilled in the 'one step method' (Fossing & Jørgensen 1989) using zinc acetate traps. Sulfate reduction rate was calculated according to these authors using a measured porewater sulfate concentration of 28 mM, representative of all stations and sediment depths (Mucci *et al.* in press). Whole core rates of sulfate reduction were calculated by integrating vertical profiles over the length of the sediment column in the incubation cores (15 cm) in order to assess rates over comparable sediment horizons for all fluxes. Integrated rates of sulfate reduction were also calculated for the full 35 cm core length.

Statistical analyses were conducted using one-way analysis of variance (ANOVA) with either sampling date or station as the treatment, or t-tests where only 2 dates or flux methods were compared. Welch's correction was used in the event of unequal variances in t-tests. Due to the small sample sizes (n = 3 replicate cores) normality cannot be examined in these tests, but non-parametric tests (e.g. Wilcoxon rank sum) were not used because for n = 3, the probability of a Type II error is 1.0.

In order to facilitate comparisons with measurements of Silverberg *et al.* (in press) and Mucci *et al.* (in press), basic details of these studies are provided. Multicorer incubations were conducted in 10 cm i.d. core liners (10-15 cm sediment column; 3 replicates), stirred with magnetic lids. Samples were taken in time series and analyzed for oxygen with Winkler titration.

Microelectrode profiles were made at 0.5 mm intervals in a single multicorer sample (3 replicate profiles) using Diamond 737 electrodes. Fluxes were calculated by fitting a linear regression to the upper part of the profile, and using this dC/dz value in Fick's first law, with a molecular diffusion coefficient corrected for porosity.

RESULTS

Site differences

Sediment grain sizes were generally uniform at all sites, consisting of predominantly silt-clay. Variations in grain size are due to the presence of variably sized fecal pellets in the sieve fractions. The median diameters of the grain size distribution (Table I) reflect the *in situ* grain size of the sediments, whereas dispersed samples of the same material (fecal pellets disaggregated) show peaks in the range of 4 µm equivalent diameter. Sediment organic carbon tended to be uniform on the shelf, but around twice the level seen in Slope sediments (Fig. 2). Within site variability in carbon was generally small. Sediment nitrogen showed even greater intersite variability with similar values on the Shelf, but 4-7 times less nitrogen in Slope sediments (Fig. 2). Sediment nitrogen generally had little seasonal variation at the times sampled herein, but considerable small-scale variability in replicate values at Cabot Strait and Slope stations (Fig. 2). C/N ratios of 7-11 are in general agreement with previous Scotian Shelf sediment values (7-9; Grant *et al.* 1987), but for the Slope, the apparently high C/N is likely due to the N values, subject to less accuracy at such low levels.

Overall trends

Rates of oxygen consumption, carbon dioxide release, and sulfate reduction exhibit both seasonal and spatial differences (Fig. 3). Due to the complete temporal coverage for Emerald Basin, ANOVA was conducted with sampling date as treatment. There was significant seasonal change in oxygen consumption (p = 0.022). Bonferroni multiple comparisons indicated that May rates were significantly less than December oxygen

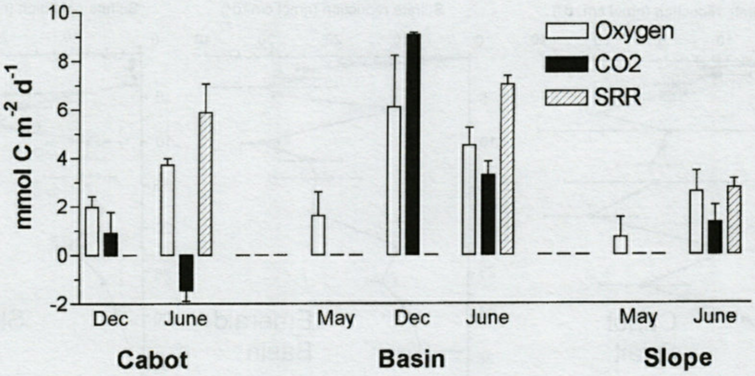

Fig. 3. – Measurements of benthic metabolism in the Laurentian Channel and on the Scotian Shelf and Slope expressed as carbon equivalents : oxygen consumption (RQ = 1), carbon dioxide production, and sulfate reduction (CO_2/SO_4 = 2). All values are means + SD. Oxygen consumption and carbon dioxide flux are based on means of 3 incubation cores obtained from a boxcore. For sulfate reduction rates (SRR), values are the mean of two integrated vertical profiles.

consumption ($p < 0.05$), and June values were intermediate. CO_2 production in Emerald Basin was also high in December, and greater than June values. In December the ratio of CO_2/O_2 was 1.5, while in June the value was < 1, however in both cases, variability at this site was such that mean values of carbon consumption measured by either O_2 consumption or CO_2 production were not significantly different from each other (t-test, $p > 0.14$).

For a similar comparison at Cabot Strait, temporal differences were reversed, with significantly higher oxygen consumption in June than December (t-test, $p = 0.004$). There was no significant difference between December carbon consumption measured by CO_2 versus O_2 flux ($p = 0.35$), but an obvious difference in June with CO_2 influx. The continental slope site showed higher oxygen consumption in June compared to May, but the difference is only marginally significant (t-test, $p = 0.052$). June CO_2/O_2 for the Slope is < 1 (Fig. 3), but again these means are not significantly different from each other (t-test, $p = 0.24$).

Statistical comparisons between stations were conducted for June using a one-way ANOVA, when complete data sets exist for both CO_2 and O_2 fluxes. Oxygen consumption was significantly different between stations in June ($p = 0.036$), when rates in Emerald Basin sediments were greater than those from the Slope (Bonferroni test, $p < 0.05$), and Cabot Strait was intermediate. One-way ANOVA of CO_2 fluxes also revealed a significant difference between stations in June ($p = 0.002$). A Bonferroni test showed that CO_2 influx at Cabot Strait was significantly different than the efflux measured at both the Basin ($p < 0.01$) and the Slope ($p < 0.05$), and that there was no significant difference between the latter two stations (Fig. 3). Thus for spatial comparisons of oxygen uptake, the continental slope is similar to Cabot Strait and different from Emerald Basin, but for carbon dioxide, the CO_2 uptake of sediments at Cabot Strait is clearly different than both Emerald Basin and the Slope.

The value of sulfate reduction in June at all 3 sites (expressed as carbon equivalents ; CO_2 produced/SO_4 reduced = 2) was greater than either oxygen or carbon dioxide fluxes, suggesting the dominance of anaerobic respiration at these sites (Fig. 3). Although these data suggest that all organic carbon mineralization is anaerobic, this conclusion is unlikely as discussed below. Sulfate reduction profiles indicated the typical pattern of low values at the sediment surface and subsurface peaks at 6 cm (Cabot Strait), 3.5 cm (Emerald Basin), and 8 cm (continental slope) (Fig. 4). Both Cabot Strait and Emerald Basin displayed deeper subsurface peaks equal in magnitude to peak values in the upper sediment. In every case, sulfate reduction trailed off at the bottom of the profile, especially at Cabot Strait and the Slope. There is considerable variation between replicate values in the profile (Fig. 4), particularly at Cabot Strait. Each replicate set of samples was used to calculate integrated rates, providing an estimate of the error involved in rates derived from individual cores (Fig. 3). The errors on the integrated rates tended to be small (Fig. 3), with coefficients of variation (CV = SD/mean) of 7 % (Emerald Basin), 9 % (Slope), & Cabot Strait (29 %).

Comparison of methods

Multicorer incubations produced similar or slightly higher values of oxygen consumption than boxcore incubations in most comparisons (Fig. 5). In the multicorer incubations, no controls were conducted for the unfiltered water overlying the cores (sometimes a substantial part of respiration

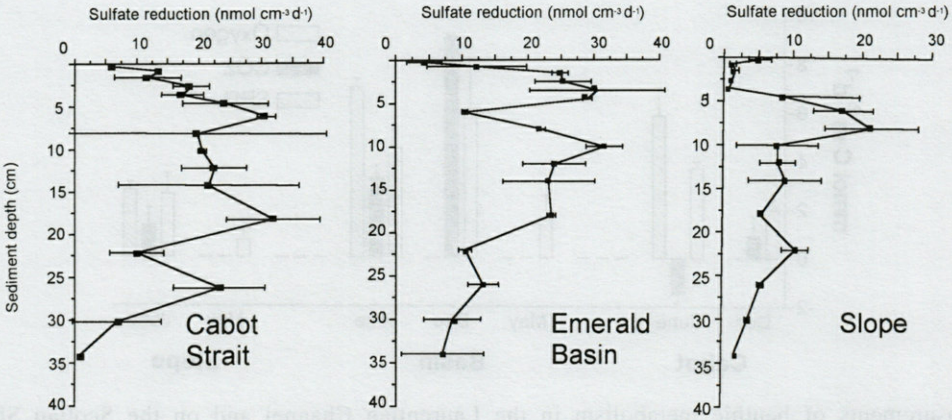

Fig. 4. – Sulfate reduction profiles in the Laurentian Channel and in Scotian Shelf and Slope sediments. Error bars are SD (n = 2).

in boxcore incubations), potentially accounting for higher values. In December at Emerald Basin, the two methods yield apparently disparate rates, although this difference in O_2 consumption did not prove significant (t-test, $p = 0.073$). Oxygen uptake measured by incubation of boxcore subcores was consistently greater than rates calculated from microelectrode profiles (Fig. 5). As pointed out by Silverberg *et al.* (in press), consumption in supernatant water would not impact the slope of the profile seen by microelectrodes, making microelectrode O_2 uptake free of this effect.

Comparison of carbon dioxide incubation fluxes with calculated fluxes based on profiles (Fig. 6) showed greater discrepancies than a similar comparison for oxygen (Fig. 5). In the sediments of Emerald Basin, values derived from incubations were always greater than those derived from vertical profiles. The opposite was true at Cabot Strait and the Slope. In only 2 of the 5 station/time cases (Cabot Strait, December; Slope, June), were the values between the two methods comparable. These discrepancies may be related to several factors as detailed below. Sulfate reduction rates derived from different methods may also be compared, since Mucci *et al.* (in press) provided integrated rates based on ammonia flux and C:N:S stochiometry. In general, these calculated values were an order of magnitude less than rates we measured with ^{35}S. However, no attempt was made to correct ammonia profiles in their study for removal processes such as adsorption and nitrification, making them a suboptimal measure of nitrogen flux resulting from organic matter mineralized by sulfate reduction (Canfield *et al.* 1993).

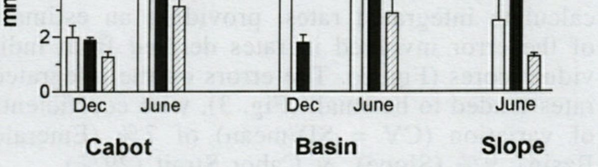

Fig. 5. – Methodological comparisons of oxygen consumption in Laurentian Channel and Scotian Shelf and Slope sediments including incubations of subcores obtained from a boxcore (incubation – boxcore), incubation of cores from a multicorer (incubation – multicorer; Silverberg *et al.*, in press), and calculations based on microelectrode profiles (profile; Silverberg *et al.*, in press). All values are means + SD. The SD of core incubations is based on replicate cores (n = 3), whereas the microelectrodes involve replicate profiles within a single core (n = 2).

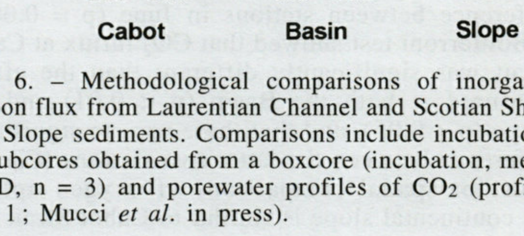

Fig. 6. – Methodological comparisons of inorganic carbon flux from Laurentian Channel and Scotian Shelf and Slope sediments. Comparisons include incubations of subcores obtained from a boxcore (incubation, mean + SD, n = 3) and porewater profiles of CO_2 (profile, n = 1; Mucci *et al.* in press).

DISCUSSION

Relative importance of electron acceptors

Sulfate reduction is an important if not the major pathway of carbon mineralization at our Scotian Shelf and Slope sampling sites. This finding agrees with the suggestion of Canfield *et al.* (1993) of the dominance of sulfate reduction for shelf sites off Denmark. It is clear however that other modes of anaerobic metabolism including nitrate, iron and manganese reduction may also be important at shelf sites (Canfield *et al.* 1993, Hines *et al.* 1993). Other studies of sulfate reduction in adjacent waters provide a regional comparison for our values. Our estimates of sulfate reduction are similar to those measured in shallower muddy basins of the Gulf of Maine (Hines *et al.* 1993). However, their values for Wilkinson Basin, a site of similar depth to Emerald Basin are considerably lower (Hines *et al.* 1993). Edenborn *et al.* (1987) found generally much lower sulfate reduction rates than ours in the Gulf of St. Lawrence, even at comparable water depths. As pointed out by both of these authors, exclusion of chromium-reducible sulfur (e.g. pyrite) from their extraction may have contributed to decreased rates. Edenborn *et al.* (1987) observed subsurface spikes in their profiles of sulfate reduction, and associated decreased rates with a clay deposit and lower organic matter at depth.

The high rates of integrated sulfate reduction make it difficult to partition sediment metabolism with respect to oxic and anoxic processes. Thamdrup & Canfield (1996) reiterate that there is no measure of aerobic consumption that can be dissociated from chemical oxidation of reduced compounds. In the past, addition of poisons has been used to inhibit aerobic respiration and separately measure chemical oxygen demand (COD) of sediments, but the poisons also kill anaerobes, altering the production of reduced products (Hargrave & Phillips 1981). In addition, the limited water bath space of shipboard incubations creates potential for contamination of live cores with poisons. Based on measured pyrite profiles and estimated sedimentation rate, Mucci *et al.* (in press) suggest that accumulation of reduced products at our sites is small relative to their oxidation, making oxygen consumption a reasonable measure of total (aerobic and anaerobic) benthic metabolism (Howes *et al.* 1984, Rowe *et al.* 1988, Canfield *et al.* 1993). Some verification of the magnitude of these rates is provided by independent incubations of sediment cores from our sites using a multicorer (Silverberg *et al.* in press), producing reasonably similar values of oxygen consumption (Fig. 5) to those based on subcores from the boxcore.

Under these circumstances, oxygen consumption, if reflecting total benthic metabolism, should be similar to carbon dioxide efflux, a result borne out in our measurements from Emerald Basin and the Slope, but not at Cabot Strait in June (Fig. 3). Carbonate release (total CO_2 efflux) is not an exclusive measure of respiration because alkalinity changes cause CO_2 release in carbonate dissolution that is non-metabolic (Mucci *et al.* in press). Sulfate reduction also influences alkalinity, so our June measurements which included sulfate reduction rates provide the best opportunity to partition organic from total carbon dioxide release. June alkalinity fluxes at both Cabot Strait and Emerald Basin were negative in June, implying carbonate precipitation. At Cabot Strait, this is matched by CO_2 flux into the sediment (Fig. 3). Based on CO_2 profiles at this site however, Mucci *et al.* (in press) found carbonate precipitation only at depth in the sediment column. At the Slope station, we measured a drop in alkalinity in cores of 5.4 meq m^{-2} d^{-1}. Applying Berelson *et al.*'s (1996) calculation of carbonate dissolution based on Slope sulfate reduction and this change in alkalinity during our incubations suggests that carbonate dissolution was ~ 32 % of total carbon dioxide flux. Mucci *et al.* (in press) estimated that calcium carbonate dissolution was ~ 41 % of total carbon dioxide flux in June at this station, and 45 % at Cabot Strait. Berelson *et al.* (1996) reported that carbonate dissolution accounted for 10-27 % of total CO_2 flux at sites off California ranging from 231-1010 m. These types of corrections would further reduce our estimates of total benthic metabolism based on CO_2 release, as would CO_2 uptake due to processes such as chemoautotrophy. For these reasons, Hargrave & Phillips (1981) refer to CO_2 release as a "conservative estimate of production" (see also Therkildsen & Lomstein (1993)).

When comparisons are made of organic carbon mineralization (Fig. 3), sulfate reduction can account for all of the sediment respiration. It is unlikely that sediments at these 3 sites are entirely anoxic, since simultaneous oxygen microelectrode studies indicated that all of the surface sediments were oxic (Silverberg *et al.* in press). In addition, there are substantial macrofauna communities at all of the sites (Grehan *et al.* 1994). The potential error in estimation of sulfate reduction is not problematic despite considerable spatial variation at single sediment horizons in replicate cores (Fig. 4), because integrated rates calculated from single profiles due not show excessive variability (Fig. 3). The high rates of sulfate reduction may instead be related to methodology wherein small aliquots of sediment are subsampled and isolated for the ^{35}S incubations. Although the sediments are not intentionally mixed during incubations, they are no doubt disturbed relative to the intact core. Previous studies of slurry techniques for uptake of labelled organic substrates indicate that mixing homogenizes substrate and disrupts microgradients leading to increased rates (Osinga *et al.* 1996). Canfield *et al.* (1993) suggested that anoxic conditions used in incubations killed aerobic organisms present causing additional organic supplement to the system. They applied a factor of 2 to account for this enhancement. If 2 is a reasonable correction factor which includes all of these potential artifacts, then sulfate reduction would account for 76, 76, and 55 % of total system carbon consumption (based on oxygen demand) at Cabot Strait, Emerald Basin, and the Slope respectively. The model of Boudreau *et al.* (in press) estimated values of only 53, 9, and 26 % for these sites respectively. We interpret our measurements to indicate that sulfate reduction is an under-appreciated process on the shelf and slope. Canfield *et al.* (1993) found anaerobic metabolism to be the primary pathway of carbon degradation in the Skaggerak at depths from 190-695 m. Analagous to our sites, this region is known as a repository for fine sediments from the North Sea (Lohse *et al.* 1995). Our work and that of Canfield *et al.* (1993) suggest that the paradigm of decreasing importance of sulfate reduction in an offshore direction (Jørgensen 1982) must be reconsidered.

Season and site differences

Fine sediments on the Scotian Shelf comprise only 34 % of its area, whereas their oxygen consumption is greater by a factor of 2.7 compared to coarse sediments (Grant *et al.* 1991). This underscores the importance of depositional shelf basins as sinks for shelf production (see also Lohse *et al.* 1995), and indicates the extent to which sediment texture must be accommodated in these types of budgets. Recent studies of the North Sea also stress this contrast in granulometry and the corresponding benthic metabolic activity (Osinga *et al.* 1996). The rates of carbon mineralization determined for our 3 stations are not vastly different compared to the levels of variability that often characterize measurements of benthic metabolism. May samples were among the most variable, with coefficients of variation (CV) of 62 and 119 % in replicate cores for oxygen consumption at Emerald Basin and the Slope respectively. The other oxygen data were characterized by CV = 7-35 %. Rowe *et al.* (1994) found similar rates of shelf and slope oxygen uptake to ours, and values of CV = 12-78 % for incubated cores from the mid-Altlantic shelf and deep-sea. An obvious factor related to intersite differences is water depth, which may result in an exponential decline in sediment oxygen consumption from shelf to slope (Rowe *et al.* 1988). The greatest spatial contrast in benthic oxygen demand occurs over the largest depth contrast, Emerald Basin to the Slope, but the change in oxygen uptake between these stations was not large. Rowe *et al.* (1994) found that middle slope sediments (1000 m) had oxygen demand rates similar to those on the shelf, a result closely aligned with our observations. They suggested that enhanced rates mid-shelf reflected the importance of this zone as a depocenter, a suggestion made for our Slope station in previous studies (Grant *et al.* 1987), and for onshelf basins herein. Increased benthic mineralization has also been observed in depositional areas of the North Sea (Lohse *et al.* 1995).

The biomass of microbes and fauna influence sediment metabolic fluxes, and the density of macrofauna is higher on the Slope compared to both Emerald Basin and Cabot Strait (Grehan *et al.* 1994). In addition, another significant influence on solute flux, bioturbation (Christensen *et al.* 1984, DeMaster *et al.* 1994), appears to be comparable at the 3 sites as indicated by bioturbation potential based on feeding mode and vertical distribution of macrofauna (Grehan *et al.* 1994). Macrofauna thus influence both respiratory and bioturbation processes, but there is no obvious intersite correlation between macrofaunal density and sediment respiration rates. Temperature, which also affects rates of sediment respiration, undergoes little seasonal change at any of the sites, but is always warmer in Emerald Basin (Table I). Given a Q_{10} of 3 for eastern Canadian shelves (Grant *et al.* 1991), the increased temperature of Emerald Basin could also account for enhanced metabolism.

Organic input remains as one of the most important regulators of sediment carbon consumption. Primary production in the overlying water column provides an indication of the potential for deposition of phytodetritus. Scotian Slope waters are characterized by nitrate enrichment, yielding substantially higher primary production than Emerald Basin (Fournier *et al.* 1977, Mousseau 1996). This local production complements the lateral input of shelf production to slope sediments (Grant *et al.* 1987). In contrast, the waters of Cabot Strait may be nutrient-poor with decreased primary production (Fournier *et al.* 1977). The significant seasonal difference in oxygen consumption at Emerald Basin (December peak) is not unreasonable since there are peaks of pelagic chlorophyll in November (Fournier *et al.* 1977, Mousseau *et al.* 1996).

Sediment photopigments may also provide a record of phytoplankton deposition (Duineveld *et al.* 1997). Our available data suggest that concentrations in surface sediments of the Slope have only about 10-30 % of the chlorophyll as Emerald Basin in June although winter values may be similar (R. Thompson, unpublished data; Desrosiers *et al.* in press). Sediment POC and PN is also reduced on the Slope compared to Shelf sites (Fig. 2), but probably contribute only a small portion of the variance in sediment oxygen demand (Smith 1978), largely because there is refractory material involved that is not available for mineralization (Grant & Hargrave 1987).

Silverberg *et al.* (in press) discuss the available sediment trap measurements for the Scotian Shelf and Gulf of St. Lawrence, and there are few data that can be extrapolated to longer than a daily rate. Most other useful types of data including geochronology and carbon burial are compromised by bioturbation influence on profiles. These authors calculated that benthic metabolism in Emerald Basin and Cabot Strait consumes 6 and 9 % respectively of the organic carbon in annual primary production. A previous study estimated a value of 16 % for the Scotian Shelf (banks and basins) (Grant *et al.* 1991). Due to uncertainty in the input terms and the relatively similar rates of carbon consumption in Silverberg *et al.* (in press) compared to the present study, our results would not alter these estimates for the benthic mineralization of primary production.

Methodological comparisons

The range of approaches available for estimating benthic carbon consumption is broad, and there are several studies which address methodological comparisons. Previous studies have examined box core versus in situ estimation of solute fluxes (Miller-Way *et al.* 1994) and oxygen profiles (Reimers & Smith 1986). Our comparison of shipboard incubations using a multicorer and subcores from a boxcore, show good agreement at most stations and sampling dates (Fig. 5). The December measurements in Emerald Basin indicate the degree of variance possible between methods, but these samples were taken after an annual November peak in primary production (see above), and there is likely patchiness in benthic biomass and rate processes that contribute to this discrepancy. Therkildsen & Lomstein (1993) suggested that variation in macrofauna biomass in incubation cores resulted in high variance in their measurements of sediment oxygen consumption.

It is more difficult to compare rates of oxygen consumption based on incubation versus microelectrode profile methods, since the latter depends on choice of diffusion coefficient. Hofman *et al.* (1991) describe the use of incubations in bell jars to derive apparent oxygen diffusion coefficients for use in flux calculations based on profiles. Reimers & Smith (1986) did similar comparisons between landers and boxcore microelectrode profiles. The Scotian Shelf oxygen fluxes derived from microelectrodes utilize molecular diffusion coefficients (Silverberg *et al.* in press). Given the presence of burrowing macrofauna and bioturbation at these sites (Grehan *et al.* 1994; Muslow *et al.* 1998) and the degree of sediment pelletization, there is likely enhanced diffusion of solutes through the sediment column. Therefore, it is expected that oxygen consumption rates from microelectrodes are consistently lower at these sites.

CO_2 fluxes compared between profile and incubation methods are rather disparate for several reasons. Like oxygen profiles, diffusion is assumed to be molecular and does not include the effects of bioturbation (Mucci *et al.* in press). In addition, profiles of carbonate species are characterized by precipitation at depth and dissolution near the surface, a relationship that changes with station due to variation in sulfate reduction and its influence on alkalinity (Mucci *et al.* in press). The depth resolution of profiles is 0.5 cm, and sharp gradients over smaller depth intervals would not be detected or integrated into the flux calculations. The extent to which net incubation fluxes from cores of fixed length reflect these interactions has not been ascertained, and it is apparent that CO_2 release does not necessarily represent a straightforward measure of total system metabolism (Anderson *et al.* 1986 Therkildsen & Lomstein 1993).

Given the high levels of porewater dissolved organic carbon (DOC) in these sediments (Mucci *et al.* in press), it is likely that carbon release takes forms other than carbonate, making CO_2 release a potential underestimate of carbon efflux. DOC release has previously been shown to be important in benthic carbon budgets (Hulth *et al.* 1997). Measured fluxes of DOC in our cores (analyzed with high temperature combustion; up to ~ 150 mmol C m^{-2} d^{-1}) were extremely large compared to other CO_2 fluxes, especially if dissolution corrections are applied to the latter. DOC can be released as a colloid due to disturbance of surface sediments (Farke & Riemann 1980), such that apparent fluxes are analogous to resuspension rather than metabolism. Regardless, we expect production and release of DOC to be a significant pathway for early diagenesis, but one that is not accounted for by inorganic carbon fluxes.

Oxygen consumption appears to be the most robust measure of total benthic metabolism, assuming that storage of reduced sulfides is not problematic. Canfield (1993) suggested a similar conclusion, even where most of the oxygen demand was chemical. Since anaerobic respiration affects both oxygen consumption (through COD) and CO_2 release, a CO_2/O_2 close to 1 as in our work, reveals little about the relative importance of other electron acceptors. Either estimate of carbon consumption by sediments cannot account for all of the mineralization estimated from sulfate reduction. Rates of oxygen consumption may be most reliably extrapolated to the field, since carbon dioxide release is subject to the problems discussed above, and sulfate reduction via the aliquot technique is subject to disturbance artefacts. Several shipboard methods of measuring oxygen uptake produce acceptably similar results. The boxcore subcores provided similar rates to the multicorer, despite the potential disturbance associated with subcoring and refilling of supernatant water. These latter steps require extreme care in order to avoid excessive disturbance. Multicorer incubations should incorporate controls for the metabolic rates in the supernatant water. Microelectrode profiles are prone to error with respect to choice of diffusion coefficient, but it is interesting that the microelectrode approach did not differ more from incubation methods considering the pelletized nature of the sediments and assumption of molecular diffusion. Because no single method provides insight into all of the sediment metabolic processes, several complementary methods are necessary, and more work is required in which 2-3 methods are compared across both seasonal and spatial dimensions. In most cases, alteration of boundary layer flow remains a persistent problem when sediments are isolated in cores or chambers (Lohse *et al.* 1996).

The general implication of these results is that the middle slope of the Scotian Shelf has levels of carbon mineralization that are comparable to rates in muddy depocenters on the shelf. At all sites, sulfate reduction is an important pathway in carbon mineralization. Moreover, if we integrate sulfate reduction to the full 35 cm sampling depth, sediment column sulfate reduction increases by factors of 73 to 91 % (data not shown). In sands, diagenesis may be limited to surface sediments (Van Raaphorst *et al.* 1990). Thus, compared to sandy banks that comprise most of the shelf, the relative importance of fine shelf sediments is even further accentuated because (1) anaerobic processes dominate fine shelf sediment respiration and involve a greater length of sediment column than organic-poor sands (2) the Slope must be included as a processor of organic carbon on the continental margin, especially in the event of significant offshelf transport.

ACKNOWLEDGEMENTS. – We wish to thank the crews of CSS Parizeau, Hudson and Alfred Needler for help with field work. D. Capone, M. Marvin, and R. Chambers graciously provided advice on measurements of sulfate reduction. We are grateful to A. Mucci, N. Silverberg, and P. Hall for providing insight into the companion data, and to D. Adler, B. Hargrave, W. van Raaphorst, and an anonymous reviewer for comments on the manuscript. This study was supported by the Natural Sciences and Engineering Research Council as part of the Canadian Joint Global Ocean Flux Study.

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Reçu le 2 juillet 1998 ; received July 2, 1998
Accepté le 2 septembre 1998 ; accepted September 2, 1998

VIE MILIEU, 1998, 48 (4) : 271-284

TEMPERATURE EFFECTS ON MICROPHYTOBENTHIC PRODUCTIVITY IN TEMPERATE INTERTIDAL MUDFLAT

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DYNAMICS
MICROPHYTOBENTHOS
MUD SURFACE TEMPERATURE
PHOTOSYNTHETIC RESPONSE
TIME SCALES

ABSTRACT. – Based on field measurements and computer simulations, we describe the temporal (short- and long-term) and spatial dynamics of the mud surface temperature (MST) on temperate intertidal mudflats. We then document the photosynthetic responses of natural assemblages of epipelic microalgae to such variations by means of field observations and laboratory experiments. This synthetic work is an attempt to put into perspective our knowledge about the scales of variation of one major physical forcing (MST) and the relevant ecophysiological responses of microalgae.

DYNAMIQUE
ECHELLES DE TEMPS
MICROPHYTOBENTHOS
RÉPONSE PHOTOSYNTHÉTIQUE
TEMPÉRATURE DE SURFACE DE LA VASE

RÉSUMÉ. – Effets de la température sur la productivité du microphytobenthos des vasières intertidales tempérées. Nous décrivons les dynamiques temporelle (à court et à long terme) et spatiale de la température de surface de la vase à partir de mesures de terrain et de simulations numériques. Nous présentons ensuite quelques réponses photosynthétiques des Algues épipéliques à ces variations sur la base d'observations *in situ* et d'expérimentations en laboratoire. Ce travail synthétique vise principalement à faire coïncider les échelles de variation d'un forçage physique (en l'occurrence, la température de surface de la vase) avec les réponses écophysiologiques appropriées des microalgues.

INTRODUCTION

Estuaries are among the most productive ecosystems in the world due to the high primary productivity yield of their intertidal areas (Schelske & Odum 1962). When those flats are devoid of macrophytic vegetation, such as in the 'european type' estuary – according to McLusky's classification (1989) –, microphytobenthos may become the main primary producer (Admiraal 1984, Colijn & de Jonge 1984) and can contribute substantially to the total carbon budget of the whole estuary (de Jonge 1995, de Jonge & van Beusekom 1995, de Jonge & van Beusekom 1992). In that case, production is essentially realized by the community of motile epipelic microalgae (Pinckney & Zingmark 1991) – referred to as epipelon (Round 1971) – once they have migrated upwards in the photic zone of the mud. This vertical migration seems to be determined by an endogenous rhythm (Aleem 1950, Callame & Debyser 1954, Hopkins 1963, Palmer & Round 1965, 1967, Round & Palmer 1966, Round 1979, Paterson 1986, Serôdio *et al.* 1997) : in outline, epipelic algae migrate upwards to the surface of the sediment at the beginning of diurnal emersion periods and migrate downwards in anticipation of submersion or night periods. Such a rhythm is controlled by the time difference between the tidal and diurnal cycles ; therefore, it completely determines the window within which epipelic algae can photosynthesize at the surface of the sediment, in the form of a very thin biofilm, as a function of the available incident irradiance.

Meanwhile, the mud surface temperature (MST) in temperate mudflats exhibits large (up to 10 °C) and rapid (at a rate of 2-3 °C h^{-1}) changes during diurnal emersion periods (Harrison 1985 ; Harrison & Phizacklea 1987). Those changes are due first to the variation in the supply of sunlight energy heating the mud – which is likewise entirely controlled by the phase difference between the tidal and diurnal cycles – and second to the effect of local meteorological conditions and sedimentological properties. Although such MST variations are susceptible to force the photosynthetic capacity (photosynthetic rate at light saturation) of epipelic algae at the surface of the sediment, the issue had been poorly documented (Colijn & van Buurt 1975, Henriksen *et al.* 1983).

Recently, we have addressed different aspects of this topic in a few articles which dealt with the effect of short-term (Blanchard *et al.* 1996, Blanchard & Guarini 1996) and long-term (Blanchard *et al.* 1997) temperature changes on the potential production of epipelic algae, as well as with the dynamics of MST (Guarini *et al.* 1997). However, as each point has been analysed separately with very specific objectives, there is a comprehensive view missing. Therefore, we propose herein to synthesize into a single consistent frame all our data which come from the same site (Marennes-Oléron Bay, France), in order to assess critically the relevance of the methods and the main results. It is also our goal to emphasize the different aspects of the relationship between temperature and microphytobenthos photosynthesis which should be taken into account by ecologists if we are to understand the effect of temperature dynamics on that of microphytobenthos production.

To achieve our goal, we shall proceed into 2 steps. Firstly, we shall present recorded temporal series of mud temperature under different meteorological conditions to provide a schematic representation of mud temperature variations undergone by epipelic diatoms and other benthic organisms. We shall further show model simulations of long-term time series and large-scale spatial series in MST. Secondly, we shall formalize and analyse the response of microphytobenthos photosynthetic capacity to short-term time scale temperature changes as a startpoint to test the effect of high frequency/high amplitude MST changes. In addition, we shall point out the response of microphytobenthos photosynthetic capacity to long-term time scale temperature changes which will give us the opportunity to discuss the problem of interaction between high- and low-frequency MST changes, that is the acclimation strategy to temperature changes.

CHARACTERIZING MST DYNAMICS : FROM MEASUREMENTS TO MODELLING

Analysis of the short-term time scale dynamics

Continuous *in situ* recordings are necessary to characterize the short-term dynamics of mud surface temperature. We thus provide (Fig. 1) a few examples of such recordings describing MST variations during a tidal cycle at 3 different periods and under 3 different meteorological conditions. In all 3 cases, the short-term dynamics is charaterized by a succession of daily oscillations resulting from the combination of both the tidal and diurnal cycles. The amplitude of each oscillation, however, is variable from one day to the next when the meteorological conditions are unstable (for instance, Fig. 1 upper and middle graphs). On the contrary, the oscillation characteristics exhibit a consistent scheme under stable anticyclonic meteorological conditions without cloudiness (Fig. 1 lower graph) : the minimum and maximum temperatures together with the amplitude of temperature variation tend to increase from neap tides towards spring tides. It nevertheless turns out that these predictible temperature variations, indirectly induced by the tidal cycle, can be completely masked by the meteorological conditions (Fig. 1 upper graphs) which appear to be predominant in this respect.

Similar recordings of mud temperature at different depths in the mud (Fig. 2) show that the daily oscillations are still detectable at a depth of 5 cm but the amplitude is about twice as less as at the surface. At a depth of 15 cm, the oscillations are strongly deadened and they are no longer detectable at a depth of 30 cm. So, it is clear that the whole community of photosynthetically active microalgae, meiofauna, and macrofaunal organisms inhabiting the top 5 cm of the sediment undergo large and rapid temperature variations. Most of these organisms cannot avoid those variations by escaping deeper in the mud; they have to cope with those high frequency variations. It is further worth noting that there is a time lag of several hours between the peaks of highest temperatures at the surface and at a depth of 15 cm, due to temperature diffusion across the sediment (Fig. 2).

Assuming no meteorological interferences, such as in the situation depicted in figure 1C, we can further schematize the diel MST variations as a function of the tidal phasing. Let us take the example (Fig. 3) of a semi-diurnal tide when the tidal cycle is in opposition with the diurnal cycle during neap tides (slack high water coincides with midday) – correlatively, both cycles are in phase during spring tides.

In the former case (Fig. 3A), MST is in equilibrium with the water temperature during nocturnal high tide (phase 1), then MST decreases at the beginning of low tide until sunrise (phase 2). From sunrise onwards, MST rapidly increases (at a rate of about 2-3 $^{o}C\ h^{-1}$) until the onset of submersion some time before noon (phase 3), which then corresponds to a drop in MST due to the rapid equilibrium with water temperature (phase 4). MST remains constant during the course of submersion; the water temperature during the day is higher than during the night because the water height at the point of temperature recording is small. The difference between the

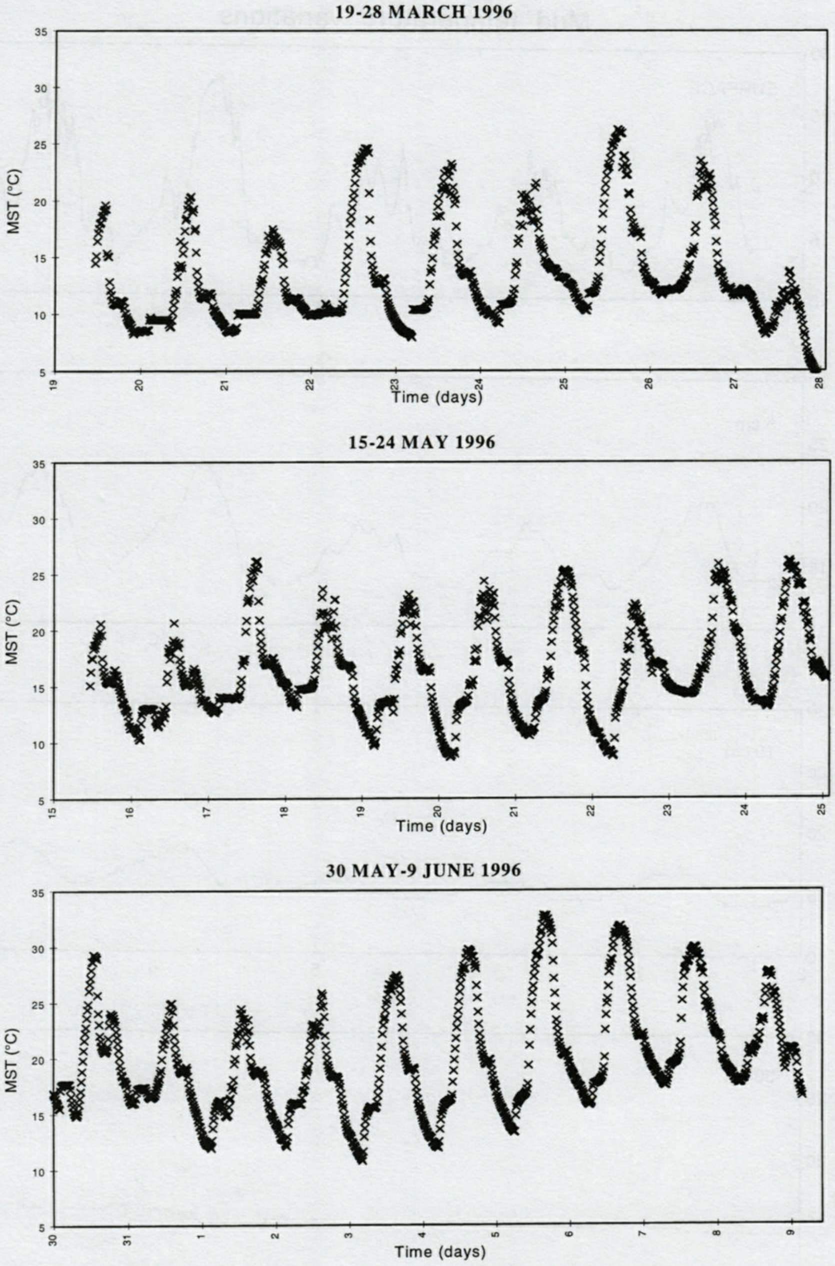


Fig. 1. – MST time series in March (upper graph), May (middle graph) and June (lower graph) from an intertidal mudflat close to La Rochelle on the French Atlantic coast (modified from Guarini *et al.* 1997).

water temperature during the day and during the night is large when the water height is small, and it is small when the water height is large. MST starts again to increase when late afternoon emersion occurs because sunlight is still strong enough (phase 5). At sunset, MST goes on decreasing (because of heat loss) until it reaches a minimum when high tide comes back (phase 6). After a rapid equilibrium with water temperature, MST is back to phase 1.

In the case where slack low tide coincides with midday (Fig. 3B), MST is in equilibrium with water temperature during the early morning high tide (phase 1) ; water temperature tends to increase after sunrise – due to the supply of sunlight energy – because the water height is small in the highest part of the mudflat. During the diurnal emersion period (phase 2), MST increases steadily and rapidly (at a rate of about 2-3 °C h^{-1}) until noon, and starts to decrease in early afternoon. At the beginning of the afternoon high tide, MST quickly reaches an equilibrium with water temperature (phase 3). Finally, compared to water temperature, MST decreases during the nocturnal emersion period (phase 4) before getting back to phase 1.

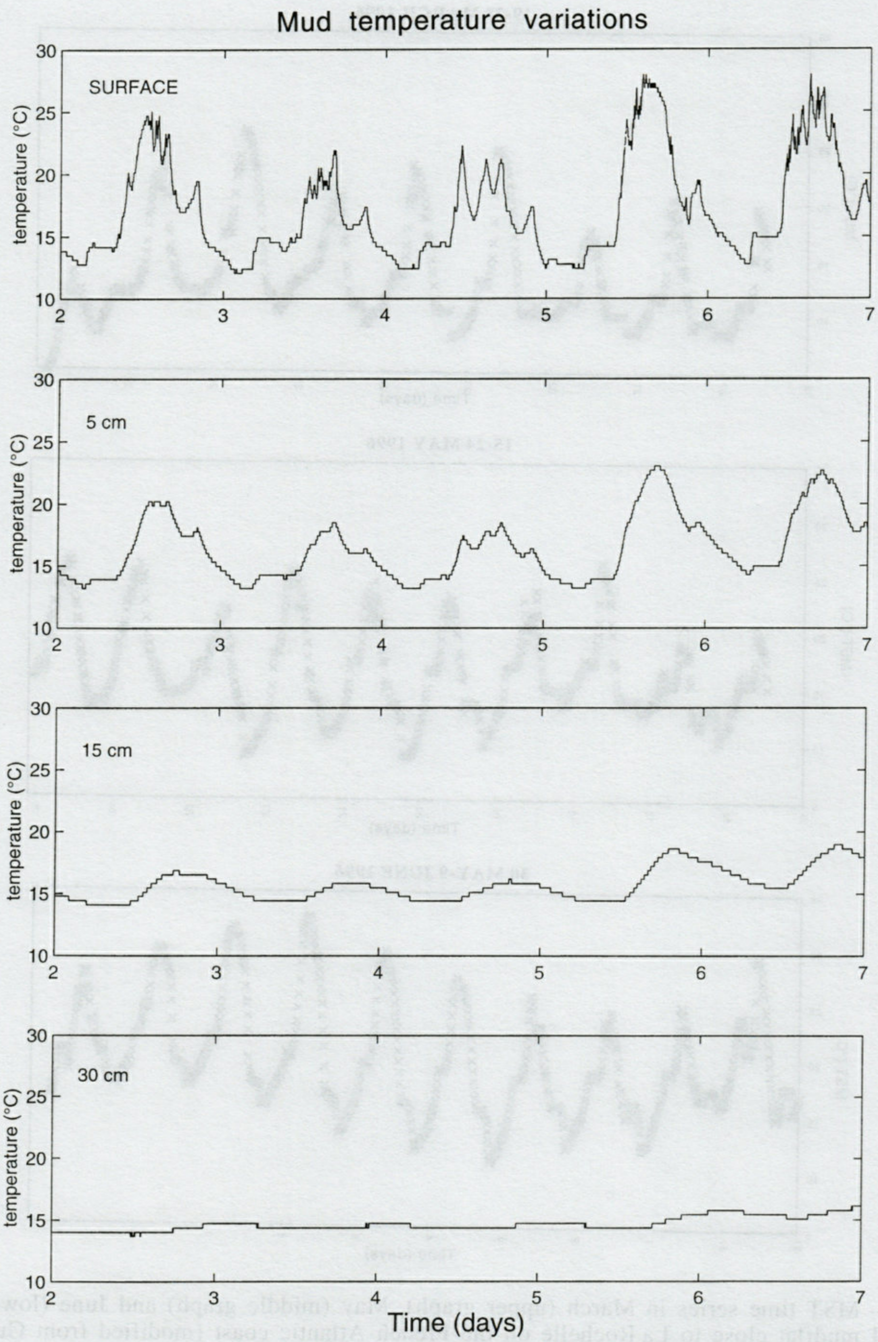


Fig. 2. – MST time series as a function of depth in July from an intertidal mudflat in the Humber estuary, U.K.

Therefore, according to the tidal phasing, these successions of phases are typical of MST dynamics, and should be taken into account when studying metabolic responses of intertidal organisms inhabiting mudflats.

Modelling MST dynamics

In consideration of the ecological implications of MST dynamics, its prediction in space and time is thus of prime importance. However, as MST measurement at any time and at any point on a mudflat is practically impossible, it is necessary to have recourse to modelling. Therefore, we have modelled MST dynamics of intertidal mudflats (Guarini *et al.* 1997).

Basically, the temporal evolution of MST, TM (z_0,t), is governed by the first law of thermodynamics with isobaric transformation :

$$\rho_M C_{P_M} \frac{\partial T_M(z_0,t)}{\partial t} = R_S + R_{Atm} - R_M - S_{Mud \rightarrow Air} - V_M$$

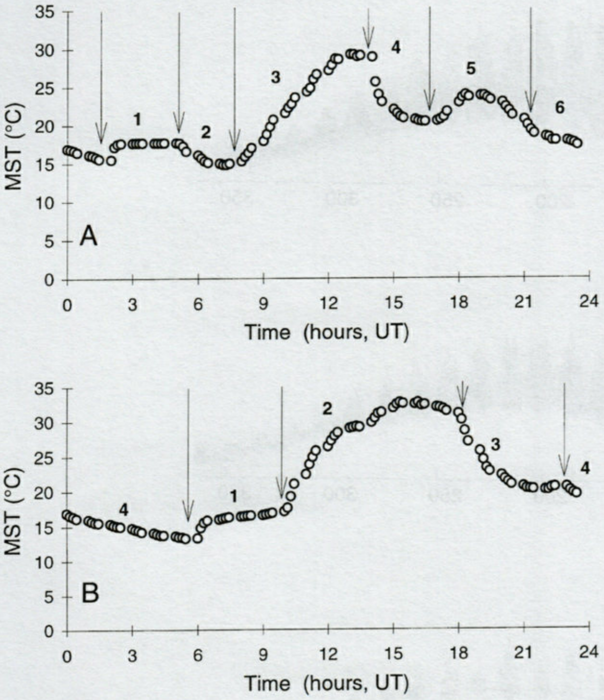


Fig. 3. – Schematic representation of MST short-term time scale dynamics. A : during neap tides, B : during spring tides. Numbers represent the different phases of MST variation cycle (see text for explanation).

where rM is the mass of mud per unit of volume (kg m^{-3}); CPM is the specific heat capacity of mud at constant pressure (J kg^{-1} K^{-1}); TM is the temperature of the mud (°K); z is depth (m); t is time (s); the right-hand term is the Heat Energy Balance with (Fig. 4): the fluxes of radiation coming from the sun (R_S), from the atmosphere (R_{Atm}, infra red radiation), from the receiving surface (R_M), the sensible heat flux by conduction due to the difference between the temperature of mud and air ($S_{Mud \rightarrow Air}$), and the flux of evaporation (V_M) depending on the mud water content. During the submersion periods, the Heat Energy Balance is simply a sensible heat flux described as the product of thermal conductivity and of a finite-difference approximation of the temperature gradient between mud and overlying water.

Spatialization of the local equation is provided by an hydrodynamic model (Le Hir *et al.* 1993) which calculates the total water height variations over the intertidal area – and hence the duration of the emersion period.

Simulating long-term time series and large-scale spatial series

Modelling allows to work at scales relevant to the functioning of the ecosystem, that is simula-

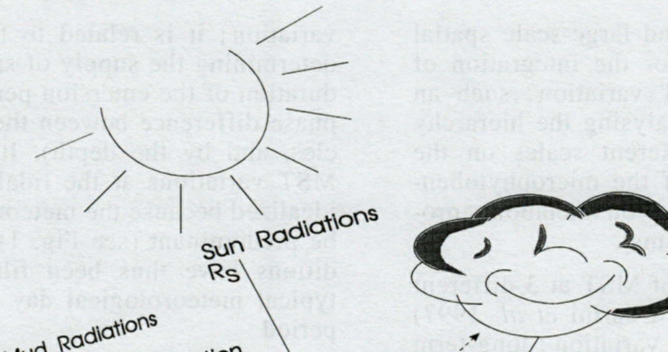


Fig. 4. – Diagrammatic representation of the thermodynamic MST model (from Guarini *et al.* 1997).

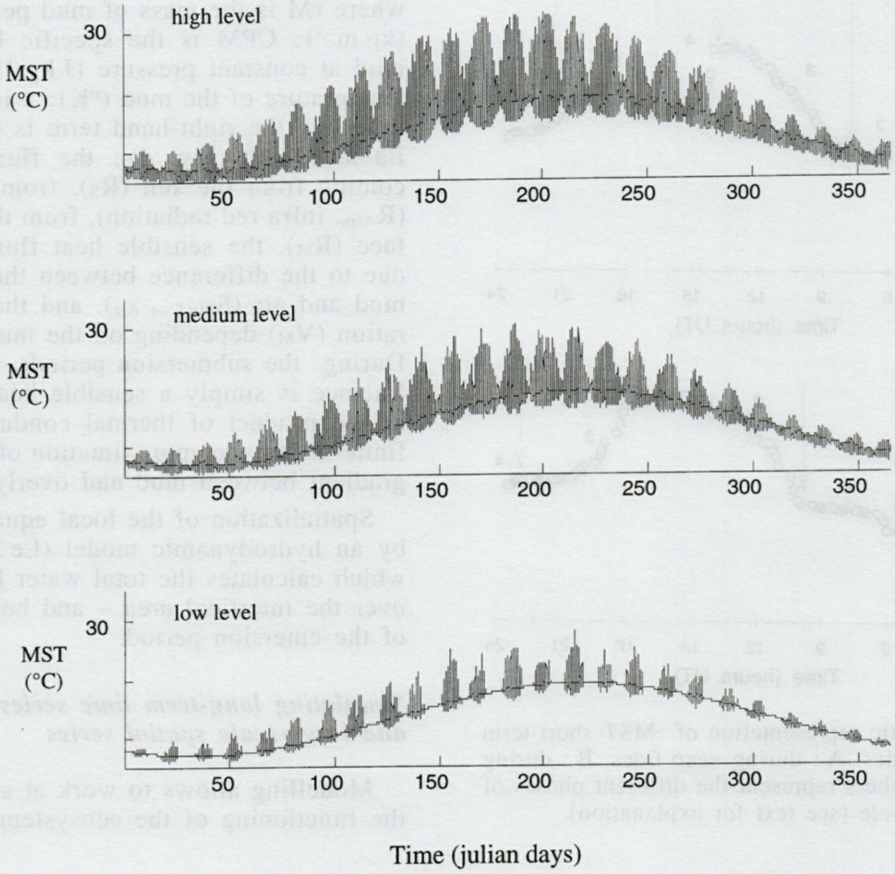


Fig. 5. – Whole-year simulation of MST at different levels (high, medium, low) on the Brouage mudflat in Marennes-Oléron Bay (along the French Atlantic coast) in 1996 (modified from Guarini *et al.* 1997).

ting long-term time series and large-scale spatial series in order to account for the integration of the different scales of MST variation; such an information is crucial for analysing the hierarchy of the effects of these different scales on the ecophysiological response of the microphytobenthic photosynthesis (and also on metabolic processes of all benthic organisms).

A whole-year simulation of MST at 3 different levels on a mudflat (Fig. 5, Guarini *et al.* 1997) clearly points out 3 scales of variation : long-term (seasonal), medium-term (within the 14-day lunar cycle) and short-term (within the day due to the succession of emersion-submersion periods). In addition, there are interactions among scales so that short-term variations are influenced by long- and medium-term changes. The influence of the topographic level (equivalently, the emersion duration) is also clear; MST variations at shorter time scales tend to be less important at low levels on the mudflat. Both the amplitude (short-term changes) and the average value of MST variations increase from winter to summer, with the larger changes occurring during diurnal emersion periods. At the scale of the tidal cycle, the major feature is the change of the amplitude of MST variation; it is related to the temporal windows determining the supply of sunlight energy and the duration of the emersion period (controlled by the phase difference beween the tidal and diurnal cycles, and by the depth). It is worth noting that MST variations at the tidal scale in figure 5 are idealized because the meteorological influence can be predominant (see Fig. 1); meteorological conditions have thus been filtered out by using a typical meteorological day for the corresponding period.

Further spatializing MST variations at the scale of the whole mudflat allows to describe the MST spatio-temporal evolution during an emersion period. Thus, in the simulation which we propose herein (Fig. 6), the MST difference in April 1996 at spring tide, between the highest and lowest levels of the emerged parts of the flat, increases during ebb tide as the emerged surface area increases and as the mud is exposed for longer periods of time (from 2 °C at low tide – 4 hr to 14 °C at low tide + 2 hr). The temperature gradient is roughly uniform during ebb tide. Then at low tide the gradient is clearly not uniform : MST tends to homogenize on high and mid-levels of the mudflat (where the highest MSTs are reached)

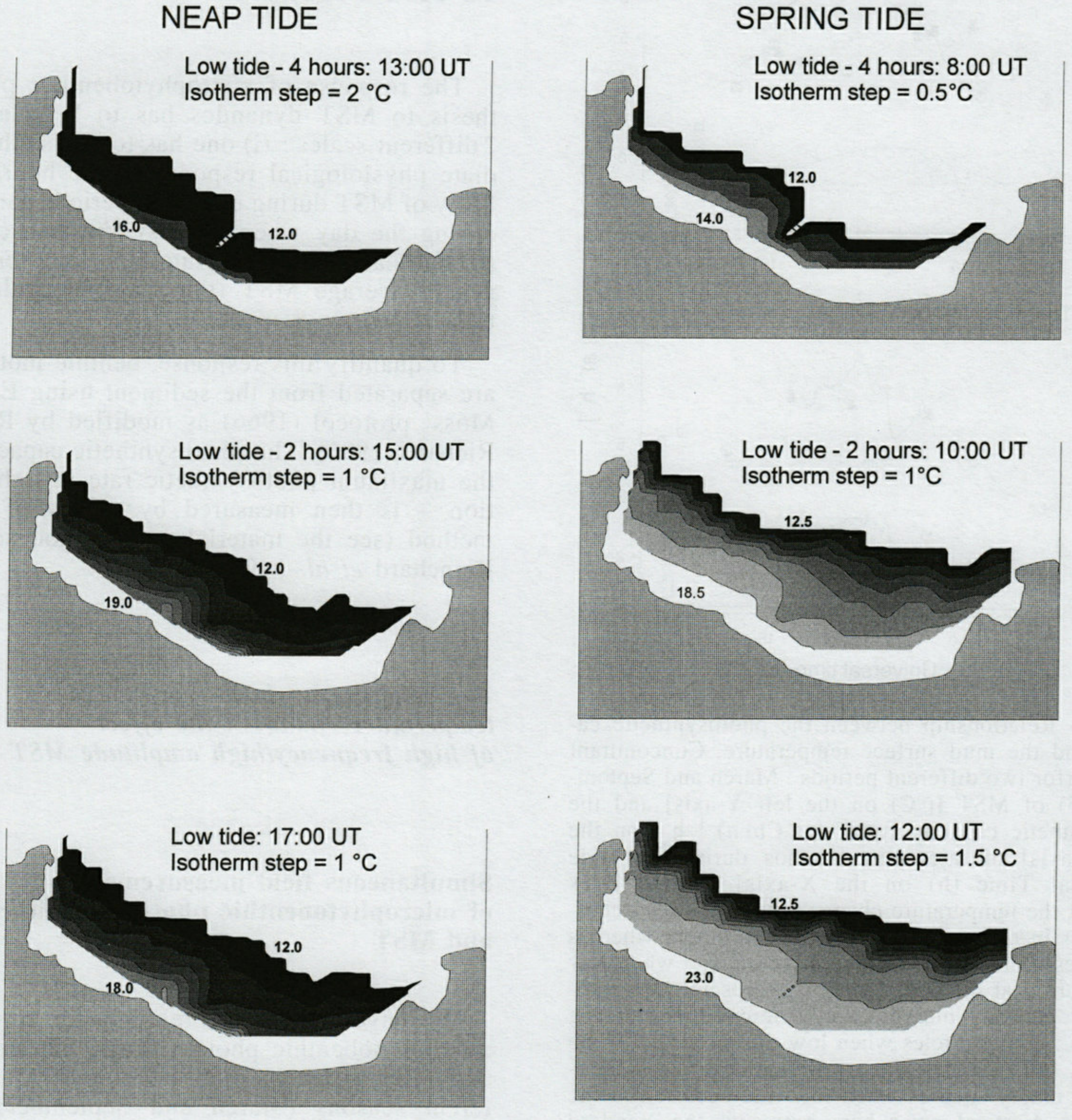


Fig. 6. – Spatial simulation of MST over an entire mudflat. Two situations are presented (spring and neap tides) at different times of low tide (at low tide – 4 h, at low tide – 2 h, at low tide and at low tide + 2 h) during a spring month in a mudflat of Marennes-Oléron Bay along the Atlantic French coast. The surface area is about 50 km^2 (modified from Guarini *et al.* 1997).

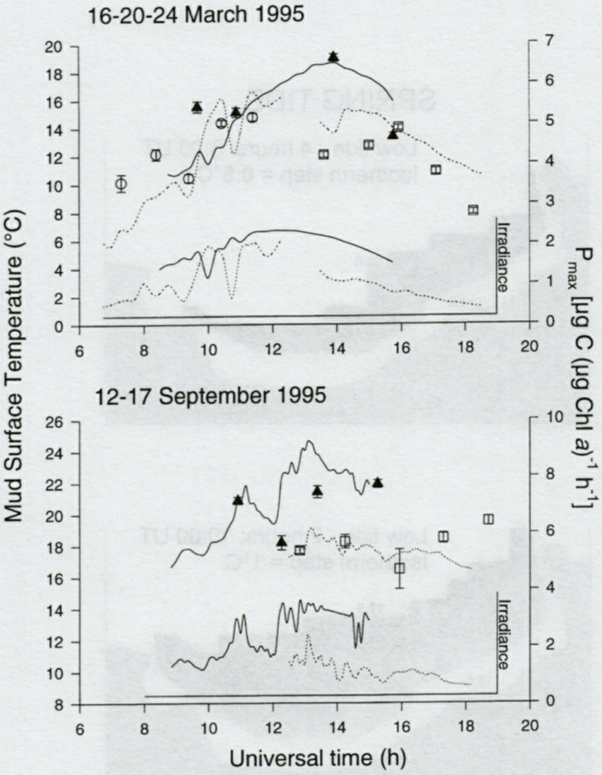


Fig. 7. – Relationship between the photosynthetic capacity and the mud surface temperature. Concomitant changes (for two different periods : March and September 1995) of MST [(°C) on the left Y-axis] and the photosynthetic capacity [µg C (µg Chl a)$^{-1}$ h^{-1} on the right Y-axis] of microphytobenthos during low tide [Universal Time (h) on the X-axis]. Dotted lines represent the temperature change when low tide occurred either in the morning or in the afternoon, whereas solid lines represent the temperature change when low tide occurred at midday. Symbols represent the photosynthetic capacity measured at different times during emersion : empty circles when low tide occurred in the morning, full triangles when low tide occurred at midday, and empty squares when low tide occurred in the afternoon. Vertical error bars represent the standard error on P_{max} determined by the curve fitting procedure (modified from Blanchard and Guarini 1996).

and the gradient becomes steeper at the water front. During flood tide, the gradient becomes again roughly uniform : MST gets colder in the mid-level part of the flat and the flooding tide cools the surface mud (with a short equilibrium period) in the lowest part of the mudflat. At neap tide, there are several differences with the spring tide pattern because the phase difference between the tidal and diurnal cycles is maximum : (i) the maximal MST reaches only 19 °C in the highest part of the emerged flat at 15 : 00 UT during ebb tide, (ii) MST starts to decrease before low tide and (iii) the MST gradient is not uniform and becomes steeper landwards instead of seawards.

RESPONSE OF MICROPHYTOBENTHOS PHOTOSYNTHETIC CAPACITY TO MST DYNAMICS

The response of microphytobenthos photosynthesis to MST dynamics has to be analysed at 2 different scales : (i) one has to assess the immediate physiological response to the hourly variability of MST during emersion periods particularly during the day when photosynthesis occurs, and (ii) one has also to evaluate how long-term changes in average MST (the seasonal cycle) affect this immediate response.

To quantify this response, benthic motile algae are separated from the sediment using Eaton and Moss' protocol (1966) as modified by Riera and Richard (1996). The photosynthetic capacity – i.e. the maximum photosynthetic rate at light saturation – is then measured by means of the ^{14}C method (see the material and method section in Blanchard *et al.* 1996).

The response to short-term time scale temperature changes : the effect of high frequency/high amplitude MST changes

Simultaneous field measurements of microphytobenthic photosynthetic capacity and MST

We have studied the relationship between the microphytobenthic photosynthetic capacity (P_{max}) and MST (Blanchard & Guarini 1996) at 2 different seasons (March and September) and in 3 different tidal conditions : (i) when low tide occurred in the morning, 3 hours before midday (9 : 00 UT), (ii) when low tide occurred at midday (12 : 00 UT), and (iii) when low tide occurred in the afternoon, 3 hours after midday (15 : 00 UT). In each case, the photosynthetic capacity was assessed at different times of the emersion period, and temperature was continuously recorded. Results (Fig. 7) clearly show a marked difference in MST recordings between the different tidal conditions, both in spring and autumn ; measurements of the photosynthetic capacity further show that there is a good agreement with MST changes. The highest values tend to occur around midday when there is the maximum supply of sunlight energy, while the lowest values occur early in the morning or late in the afternoon. It thus turns out that microphytobenthic photosynthesis at the surface of the sediment during diurnal emersions is related to MST dynamics.

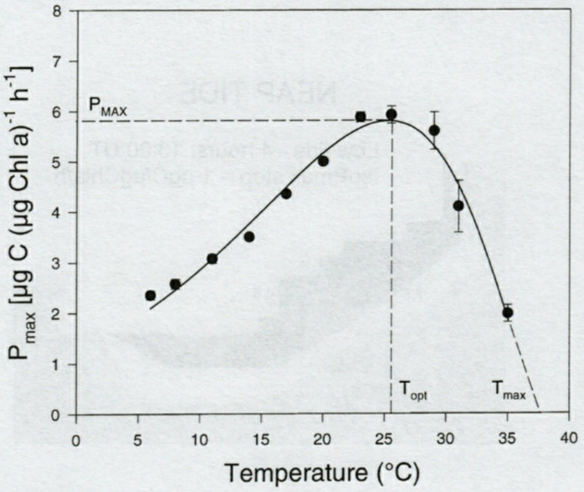
Experimental determination of the short-term temperature effect on P_{max} and mathematical formulation

Because there seems to be a relationship between MST changes in the field and the photosynthetic capacity of natural assemblages of benthic microalgae, it was necessary to assess and quantify the physiological response of microphytobenthos to a temperature change (Blanchard *et al.* 1996). As a first step, the photosynthetic capacity was measured in the laboratory at different temperatures : the effect of an increase in the range 5-35 °C at a rate of 3 °C h^{-1} – similar to what occurs in the field – was tested. Results (Fig. 8) show that the shape of the relationship is typical of a short-term temperature effect on light-saturated photosynthesis (Davison 1991) : a progressive increase up to an optimum temperature, beyond which P_{max} declines rapidly. We have proposed an original non-linear model to fit those experimental data :

$$P_{\max}(T) = P_{MAX}\left(\frac{T_{\max}-T}{T_{\max}-T_{opt}}\right)^{\beta}\ \exp\left\{-\beta\left(\frac{T_{\max}-T}{T_{\max}-T_{opt}}-1\right)\right\}$$

where T (°C) is temperature ; $P_{\max}$ is the photosynthetic capacity (µgC µgChl a^{-1} h^{-1}) ; P_{MAX} (µgC µgChl a^{-1} h^{-1}) is the maximum value of $P_{\max}$ at the optimum temperature, T_{opt} (°C) ; $T_{\max}$ (°C) is the lethal temperature at which $P_{\max}$ decreases to zero ; β is a dimensionless shapeparameter.

So far, this mathematical relationship has been parameterized for an increase in temperature in the range 5-35 °C (Blanchard *et al.* 1996), but a different set of parameters might then be necessary for describing the response of $P_{\max}$ to the decrease in temperature. This possibility has not been tested yet, although it is crucial for assessing the complete response of microphytobenthic photosynthesis to short-term time scale MST dynamics. Therefore, we think that additional research is required on the following issues : (i) in the range of suboptimal temperatures ($T < T_{opt}$), is the photosynthetic response to the decrease in temperature (from T_{opt} downwards) symmetrical to that of the increase (towards T_{opt}) ? (ii) does an exposure to supraoptimal temperatures (but still sublethal, $T_{opt} < T < T_{max}$) impair the photosynthetic response in the suboptimal range, and if so, to what extent ? (iii) in case of an impairment, what is the ability of the microphytobenthic community to resume its initial photosynthetic capacities ? Although far from being exhaustive, these issues represent the minimum basis to investigate accurately the complete response of microphytobenthic photosynthesis to short-term time scale MST dynamics.



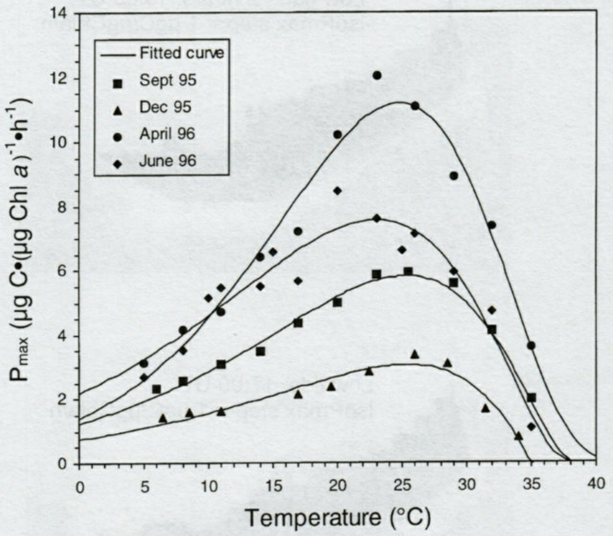


Fig. 8. – Above, response of the photosynthetic capacity P_{max} to a rapid increase in temperature. Experimental data from September 1995 (symbols) and the fitted curve (solid line) are presented. T_{opt} is the optimum temperature for photosynthesis, P_{MAX} is the maximum value of P_{max} at T_{opt}, T_{max} is the lethal temperature when P_{max} drops to 0 (modified from Blanchard *et al.* 1996). Below, seasonal influence on the relationship between the photosynthetic capacity and temperature. Squares for September 1995, triangles for December1995, circles for April 1996, diamonds for June 1996, and the solid line represents the model equation fitted to each data series (from Blanchard *et al.* 1997).

Spatializing the photosynthetic response at the scale of the ecosystem

By combining the equation describing the physiological response of microphytobenthos to short-term temperature changes with the thermodynamic model of MST (§1.2.), it becomes possible to

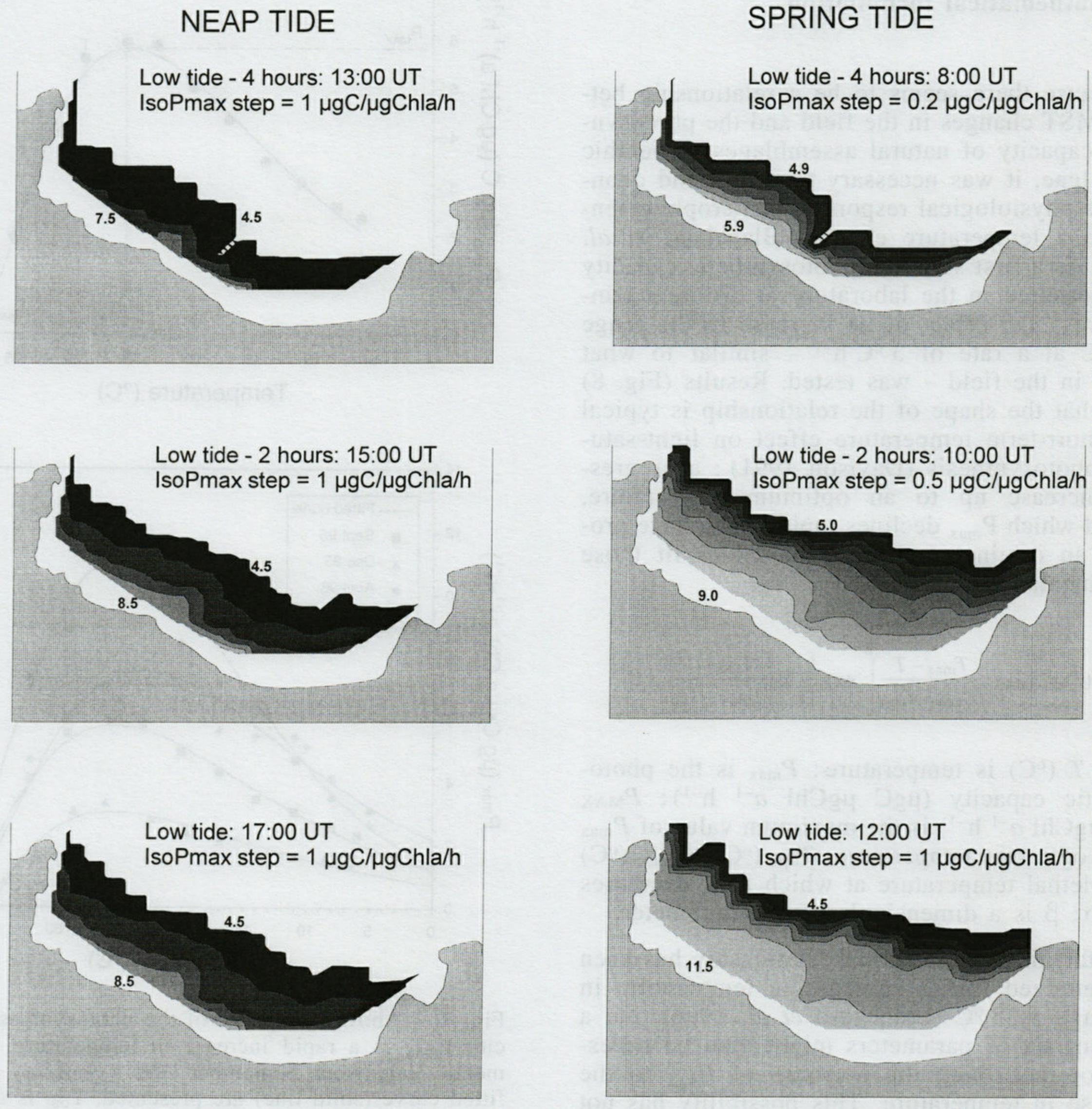


Fig. 9. – Simulation of the spatio-temporal dynamics of P_{max} in April 1996 at spring tide (left-hand side) and neap tide (right-hand side). Spatialized series are provided at 4 different times during a diurnal emersion period : at low tide – 4 h, at low tide – 2 h, at low tide and at low tide + 2 h. The iso-P_{max} steps are also provided (modified from Guarini *et al.* 1997).

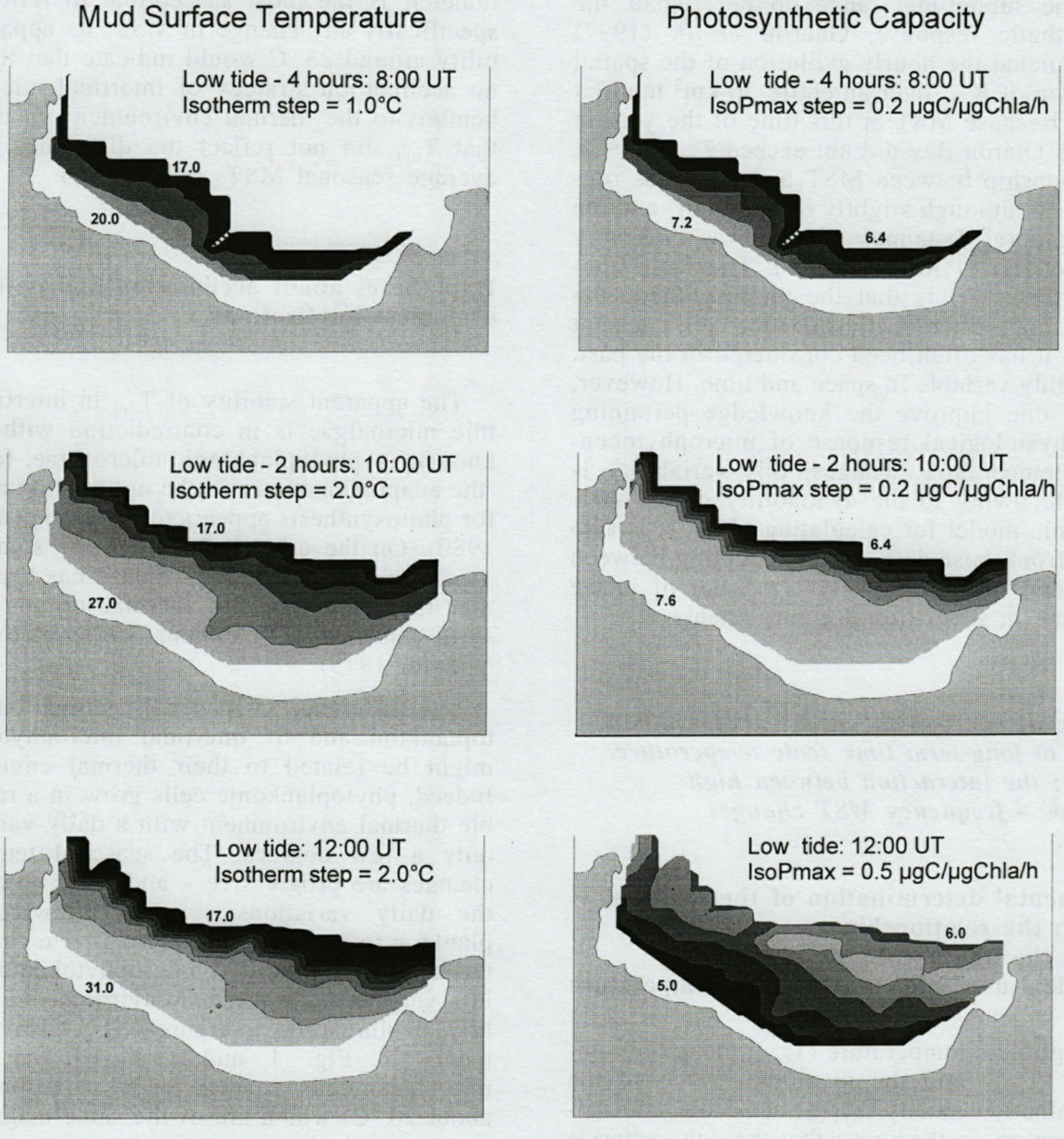


Fig. 10. – Simulation of the spatio-temporal dynamics of MST (left-hand side) and P_{max} (right-hand side) in June 1996, spring tide (from Guarini *et al.* 1997).

analyse the spatio-temporal dynamics of microphytobenthic P_{max} at the scale of a whole mudflat. For instance, assuming that any temperature changes in the suboptimal range do not impair the photosynthetic response, Guarini *et al.* (1997) have simulated the hourly evolution of the spatial distribution of P_{max} over an entire 50 km^2 mudflat (Fig. 9). Because MST at this time of the year in Marennes-Oléron Bay did not exceed T_{opt} (25 °C), the relationship between MST and P_{max} was roughly linear (although slightly exponential) and the spatio-temporal dynamics of P_{max} was thus very similar to that of MST (Fig. 6). The main conclusion, therefore, is that the photosynthetic capacity of microphytobenthos cannot be a constant value, as it has often been considered in the past, but is highly variable in space and time. However, provided one improve the knowledge pertaining to the physiological response of microphytobenthos to temperature changes, this variability is predictible owing to the availability of the thermodynamic model for calculating MST. It is also obvious from those data that the coupling between physics and biology is very tight and of prime importance in such littoral environments.

Response of microphytobenthos photosynthetic capacity to long-term time scale temperature changes : the interaction between high – and low – frequency MST changes

Experimental determination of the seasonal effect on the relationship between the photosynthetic capacity of intertidal microphytobenthos and temperature

The optimum temperature (T_{opt}), the lethal temperature (T_{max}) and the maximum value of the photosynthetic capacity (P_{MAX}) are ecophysiological parameters in the sense that they characterize the adjustment of the physiological status of microalgae to the environment; so, any change in the environmental conditions might be reflected by a change in the value of the parameters. Therefore, studying the way physiological parameters change as a function of the change of different environmental variables allows to define acclimation strategies, that is the way organisms and populations cope with variations of their environment.

Based on this principle and on the analysis of the simulation of whole-year temperature variations (Fig. 5), we have measured the response of microphytobenthic P_{max} to a rapid increase in temperature (such as in Fig. 8, above) at the 4 different seasons (Blanchard *et al.* 1997). Results (Fig. 8, below) show that the photosynthetic response changed between seasons, but the only parameter which changed significantly was the maximum value of P_{max}; T_{opt} and T_{max} did not change throughout the year. Since T_{opt}, as a parameter, is the most susceptible to reflect more specifically any change in MST, its apparent stability around 25 °C would indicate that there was no acclimation strategy of intertidal microphytobenthos to the thermal environment, in the sense that T_{opt} did not reflect the difference between average seasonal MSTs (see Fig. 5).

Hypotheses about acclimation and potential ecological implications

The apparent stability of T_{opt} in intertidal benthic microalgae is in contradiction with what is known for phytoplanktonic microalgae, for which 'the adaptative nature of the optimum temperature for photosynthesis appears to be quite general' (Li 1980). On the other hand, there are some analogies with macroalgae for which it has been shown that the photosynthetic thermal optima did not shift seasonally (Yokohama 1972, Mathieson & Norwall 1975).

The difference in seasonal acclimation of phytoplankton and of intertidal microphytobenthos might be related to their thermal environment. Indeed, phytoplankonic cells grow in a rather stable thermal environment with a daily variation of only a few degrees. The seasonal temperature changes are progressive – and large compared to the daily variations –, thus allowing phytoplankton to acclimate to the long-term change. On the opposite, intertidal microphytobenthos grow in a very unstable thermal environment; the whole-year simulation in figure 8 (but also measurements in Fig. 1 and 2) shows that benthic microalgal cells undergo daily variations (up to about 20 °C) which are of the same magnitude as the seasonal changes in mean temperature. Therefore, the weight of the high frequency/high amplitude temperature variations is such that it may prevent benthic cells from acclimating to low frequency variations (a mask effect) : the result is that the optimum temperature (T_{opt} = 25 °C) is several degrees higher than the highest mean monthly seawater temperature (around 18-19 °C, Fig. 8), like in the case of several macroalgal species (Healey 1972, Mizusawa *et al.* 1978, Bolton 1983). To explain this feature of macroalgal photosynthesis, it has been suggested by Zupan and West (1990) – based on Berry & Bjorkman' review (1980) on higher plants – that the energy expenditure required for lowering the photosynthetic temperature optimum to a relatively low growth temperature may not be compensated by the increase in photosynthetic rate at that lower temperature.

The apparent stability of T_{opt} has important ecological implications. The whole-year simulation of MST (Fig. 5) clearly points out that MST exceeds T_{opt} ($T > 25$ °C) during diurnal emersion periods in spring tide conditions in the summer time at the highest levels on a mudflat. This implies that microphytobenthic photosynthesis is potentially thermo-inhibited during these periods. To account for the spatial extend of this thermo-inhibition, we provide a simulation of MST and P_{max} over an entire mudflat in Marennes-Oléron Bay, at different times of low tide in spring tide conditions in June 1996 (Fig. 10). MST exceeds T_{opt} in the highest part of the mudflat 2 hours before low tide and reaches 35 °C two hours after low tide. As a consequence, P_{MAX} (the maximum value of P_{max} at $T_{opt} = 25$ °C) is achieved rapidly at the beginning of low tide; afterwards, the supraoptimal MSTs on the major part of the surface area induce thermo-inhibition of photosynthesis, with extreme values at high levels on the flat in the second half of the emersion period : the higher the topographic level – and hence the emersion duration – the stronger the inhibition. At the time of maximum inhibition, about 75 % of the surface area is expected to be inhibited with a photosynthetic rate being reduced down to 30 % of its optimal value. Therefore, by comparing with a Spring situation where no thermo-inhibition occurs ($MST < T_{opt}$), the spatial pattern of P_{max} distribution is characterized by an inverse gradient with the highest values in the lowest parts of the mudflat, and the lowest values in the highest parts (Fig. 10).

CONCLUSION

On the whole, it seems that the combination between modelling and the use of an ecophysiological approach to analyse the potential effect of a physical variable on a metabolic rate at different scales – in the present case, the effect of temperature on photosynthesis – is very promising. It has already been established that MST dynamics controls intertidal microphytobenthic photosynthesis at a very short-term time scale. In that respect, this finding clearly points out that the dynamics of the primary production system of intertidal microphytobenthos differs from that of phytoplankton where the control by temperature occurs at longer time scales.

However, data accumulated so far on this topic are scarse and only represent the first steps of what should be, in our opinion, a more important and systematic approach. Indeed, many uncertainties remain about the photosynthetic response of intertidal benthic microalgae to temperature dynamics, at the different time scales.

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Reçu le 29 juillet 1998 ; received July 29, 1998
Accepté le 29 septembre 1998 ; accepted September 29, 1998

VIE MILIEU, 1998, 48 (4) : 285-294

BENTHIC BOUNDARY LAYER PROCESSES AND SESTON MODIFICATION IN THE BAY OF FUNDY (CANADA)

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SESTON
MODIOLUS MODIOLUS
PLACOPECTEN MAGELLANICUS
BENTHIC BOUNDARY LAYER
SUSPENDED PARTICULATE MATTER

ABSTRACT. – The Bay of Fundy is characterized by large tidal amplitudes, strong currents and high suspended particulate loading. Particle dynamics in the water column and benthic boundary layer in the Bay of Fundy were studied with standard oceanographic sampling equipment and a new specialized sampler to elucidate conditions in areas supporting the two most productive macrofaunal species, the mussel, *Modiolus modiolus*, and the scallop, *Placopecten magellanicus.* Suspended particulate matter (SPM) concentrations in the water column ranged from 0.55 to 138.4 mg L^{-1}, while SPM values in the benthic boundary layer (5 to 50 cm from the seabed) ranged from 2.7 to over 1500 mg L^{-1}. Seston concentration and composition were found to vary greatly throughout the course of a tidal cycle, with periodic dilution of the organic content due to resuspended sand. Examination of the particle size distributions suggests that flocculation plays a major role in packaging the material ingested by these benthic suspension feeders.

SESTON
MODIOLUS MODIOLUS
PLACOPECTEN MAGELLANICUS
COUCHE LIMITE BENTHIQUE
MATIÈRE PARTICULAIRE EN SUSPENSION

RÉSUMÉ. – La grande amplitude des marées, des courants forts et l'importance des apports fluviaux de particules en suspension caractérisent la Baie de Fundy (Canada). La dynamique particulaire dans la colonne d'eau et dans la couche limite benthique de la baie a été étudiée à l'aide de l'équipement classique. Un nouvel appareil a été développé pour étudier les conditions de l'environnement où vivent les deux espèces de la macrofaune les plus productives, la Moule *Modiolus modiolus* et le Pétoncle *Placopecten magellanicus.* Les concentrations de particules en suspension dans la colonne d'eau varient entre 0,55 et 138,4 mg L^{-1}. Dans la couche limite benthique (5 à 50 cm du fond), les valeurs varient de 2,7 à plus de 1500 mg L^{-1}. La concentration et la composition du seston sont très variables pendant le cycle de marée, avec une dilution périodique des matières organiques due à la remise en suspension du sable. L'examen de la distribution de la taille des particules suggère que la floculation joue un rôle majeur dans la compaction du matériel particulaire que les suspensivores benthiques ingèrent.

INTRODUCTION

The bay of Fundy is a large (11,149 km^2) embayment lying between the provinces of Nova Scotia and New Brunswick on the east coast of Canada (Fig. 1). It is well known for large tidal amplitudes and high suspended particulate loading and there is evidence that the tidal amplitude is still increasing (Godin 1995). The unique environment of the Bay of Fundy ecosystem is formed in large part by the tidal energetics of this macrotidal estuary. The most appreciated aspect of this is the increased productivity in the outer Bay, due to turbulent mixing and upwelling (Garrett *et al.* 1978). However tidal energy input also has significant ramifications for the benthos and benthic faunal distributions. The benthic boundary layer (or bottom Ekman layer) is the region of the water column where the effects of fluid drag on the seafloor result in a layer where the flow velocity decreases to zero. This induces significant velocity gradients within a few meters of the seabed, as well as transverse flows, and produces shearing and turbulence. The balance between fluid shear and gravitational settling of suspended particles produces seston concentration gradients close to the seabed. Boundary-layer shear also can disaggregate flocculant material, thereby changing its settling rate. In this region the downward ver-

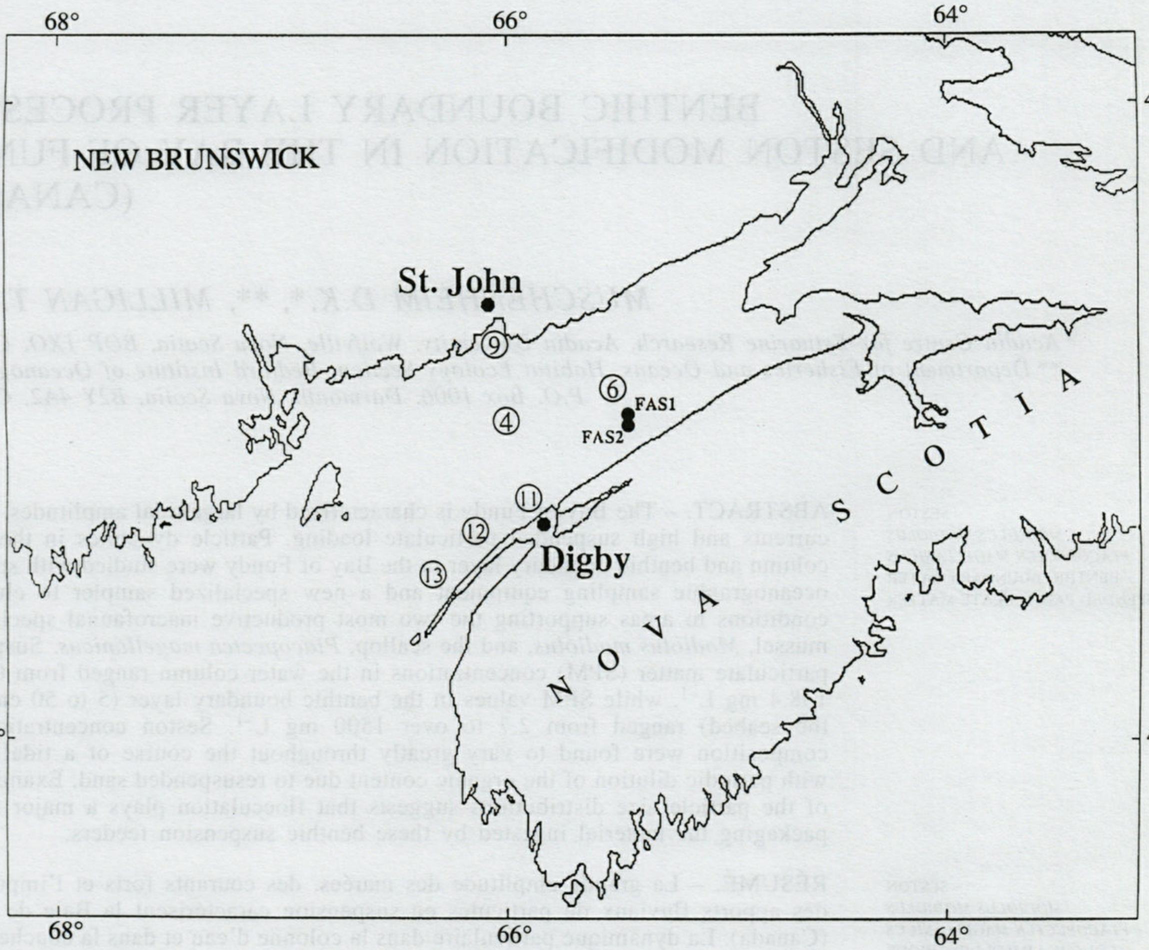

Fig. 1. – The Bay of Fundy, showing stations sampled during D38 and H20.

tical transport of euphotic zone production is modified by interaction with resuspended seabed sediments. In a macrotidal estuary this seston modification is especially significant for benthic suspension feeders.

The results of benthic macrofaunal surveys within the Bay of Fundy show that secondary production estimates, based on biomass data, are dominated by suspension-feeding organisms (Wildish & Peer 1993, Wildish *et al.* 1986). The two species producing the highest mean biomass (whole organism, wet) are the bivalves *Modiolus modiolus* (Linnaeus, 1758), with a mean annual production of 485 m^{-2}, and *Placopecten magellanicus* (Gmelin, 1791), which produces 203 gm^{-2} yr^{-1} (Wildish & Peer 1983). *M. modiolus*, the horse mussel, is notable for forming raised reefs, which are concentrated in the shallower, landward half of the Bay (Wildish *et al.* 1983). The second most productive macrofaunal species is the commercially important sea scallop, *P. magellanicus*, primarily found in the outer Bay (Peer *et al.* 1980). Wildish & Fader (1998) have shown that large-scale (tens of kilometers) benthic distributions in the Bay of Fundy may be affected by the distribution of tidal mixing. Within this picture, the finer-scale (tens to thousands of meters) distribution of suspension feeders is likely controlled by conditions within the benthic boundary layer.

Horizontal transport of seston occurs not only in the upper water column but also in the near-seabed region, the benthic boundary layer. Strong vertical gradients in flow speed and suspended particle concentration, as well as in the composition of the seston, determine the conditions under which suspension feeders must capture and ingest food particles (Jumars & Nowell 1984, Muschenheim 1987a,b, Muschenheim & Newell 1992). Quality and availability for active suspension feeders are affected not only by seston organic content but also by flow speed, through its effect on resuspension of seabed sediments and its potential for inhibiting particle intake (Wildish *et al.* 1987). Superimposed on this picture is the tidal signal, which results in varying bottom shear stresses and a consequent variability in the vertical seston profile. Previous studies over productive scallop grounds have shown that the concentration and nature of the suspended particulate matter (SPM) in the benthic boundary layer can change significantly over a single tidal cycle (Muschenheim *et al.* 1995, Muschenheim 1998).

The purpose of this paper is to present and contrast conditions in the benthic boundary layer over grounds typical of the two most productive macro-invertebrate species in the Bay of Fundy, *Modiolus modiolus* and *Placopecten magellanicus*. We examine conditions in the benthic boundary layer which determine the *in situ* quality and availability of seston.

METHODS

Data were collected during two research missions to the outer and mid Bay of Fundy. C.S.S. *Dawson* mission 87038 (D38) and C.C.G.S. *Hudson* mission 97020 (H20) were conducted in Sept., 1987 and June, 1997, respectively. Fig. 1 shows the locations of the stations sampled for this study. Water column samples for SPM were taken with a General Oceanics (D38) or SeaBird Electronics (H20) rosette sampler, using 5L Niskin bottles. Depth and salinity data were obtained with either a Guildline (D38) or SeaBird model 9 (H20) CTD. SPM values from the benthic boundary layer were obtained with the BOSS (Benthic Organic Seston Sampler) device (Muschenheim & Newell 1992, Muschenheim *et al.* 1995, Milligan *et al.* 1998), which takes simultaneous samples at several (10 during D38, 7 during H20) heights from 0.05 to 0.5 m above the seabed. Use of specialized sampling gear, such as BOSS, is a requisite for studies of benthic suspension feeders and their particulate food resources. Standard water sampling equipment, such as Niskin bottles, do not sample effectively close to boundaries. In addition, when large, fast-falling flocs form a significant proportion of the seston, they will be undersampled by water bottles, which damp fluid turbulence in the enclosed volume. Since water bottles typically sit at their sampling depth for one to several minutes before they are triggered any fast-falling material, such as large mineral grains or flocculated detritus, will settle through the enclosed volume and exit the bottle before it closes. Laying the bottle horizontally poses another problem. Entrapped particles would settle to the lower side, but any flow through the bottle before closing would introduce additional particulate material which, due to lowered fluid turbulence, would also settle. The net effect in this case is an oversampling bias.

During D38 six stations in the mid and lower Bay were sampled (Fig. 1). At one station (12) in the lower Bay sampling occurred at 3-hr intervals over 13 hours to cover a complete tidal cycle. Tidal currents in the water column were measured with a hull-mounted Ametek Straza acoustic doppler current profiler (ADCP). As configured, the ADCP was capable of resolving 3-dimensional flow velocities at 1-m depth intervals in the upper 80 % of the water column. The geometry of the acoustic beam precluded obtaining reliable data in the benthic boundary layer, but the data were useful for determining relative current velocities and directions at various stage of the tidal cycle. During H20 two stations in the mid Bay were sampled at 2-hour intervals over a complete tidal cycle. One station (FAS1) was located over a large *Modiolus* reef while the other (FAS2) was located 2 km away over "normal" seafloor. No current measurements were made concurrently to this sampling.

Bulk SPM concentrations were determined by filtering samples (Niskin or BOSS) through 25 mm diameter, 8 μm washed and tared Millipore SCWP filters. Kranck & Milligan (1979) showed that these filters have equivalent retention efficiencies to 0.4 μm Nucleopore filters. Blank corrections were performed to control for variations in weighing conditions. The filters were dried to constant humidity and weighed. Percent organic content was determined by weight loss after removal of the organic fraction through ashing at 60°C in a low temperature plasma ashing apparatus (Hollahan 1966, Milligan & Kranck 1991). The samples were then re-hydrated and sonified to disaggregate the component mineral grains. The particle size spectrum of the disaggregated inorganic fraction was determined using either a Coulter model TAII or a Coulter Multisizer IIe electroresistive particle counter using the methods described in Kranck & Milligan (1979) and Milligan & Kranck (1991).

RESULTS

Sampling in the mid and outer Bay of Fundy revealed significantly higher SPM concentrations in the benthic boundary layer than in the overlying water column. Values within 50 cm of the seabed showed high variances, related to the champing bed shear stresses throughout the course of the tidal cycle. These changes affected not just the average SPM concentration but also the shape of the concentration gradient near the seabed as well as the particulate composition of the seston. Table I shows the range of concentrations encountered using the BOSS sampler within 0.5 m of the seabed. Although water column SPM values seldom exceeded 20 mg L^{-1}, values in the benthic boundary layer ranged from 2.7 to over 1000 mg L^{-1}. The highest values obtained were in the nepheloid layer of the St. John River plume as it exited St. John harbour (Station 9) and exceeded 1500 mg L^{-1} (Fig. 2). The SPM concentration gradient often underwent a 2 order-of-magnitude increase within 50 cm of the seabed.

Stations 4 and 6, in the middle Bay, had somewhat lower benthic boundary layer seston values than the coastal stations, with values at Station 4 ranging from 2.83 to 35. mg L^{-1} within 50 cm of the seabed (Fig. 3) and 4.90 to 232.8 mg L^{-1} at station 6 (Fig. 4). Close to the Nova Scotia shore benthic boundary layer SPM values also were higher than in the mid-Bay. Stations 11, 12 and 13 were all in approximately 90 m depth close to

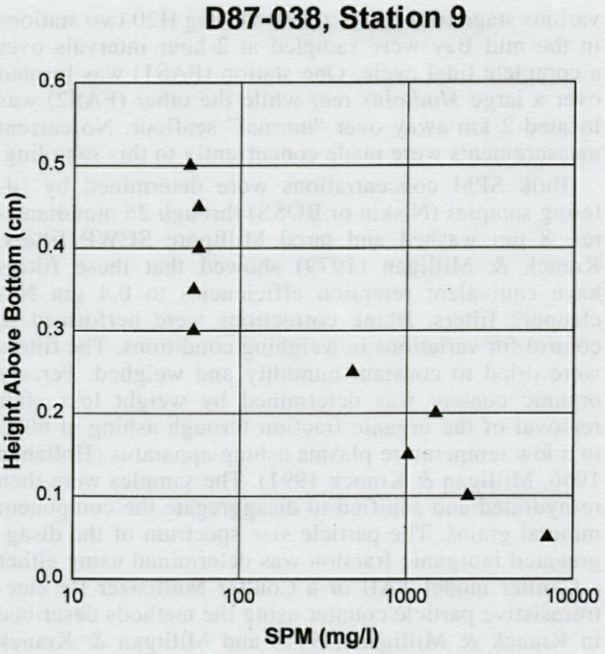

Fig. 2. – SPM concentrations within 0.5 m of the seabed at Station 9 (D38).

the Nova Scotia coast and all exhibited SPM values that changed by up to two orders of magnitude within 50 cm of the seabed.

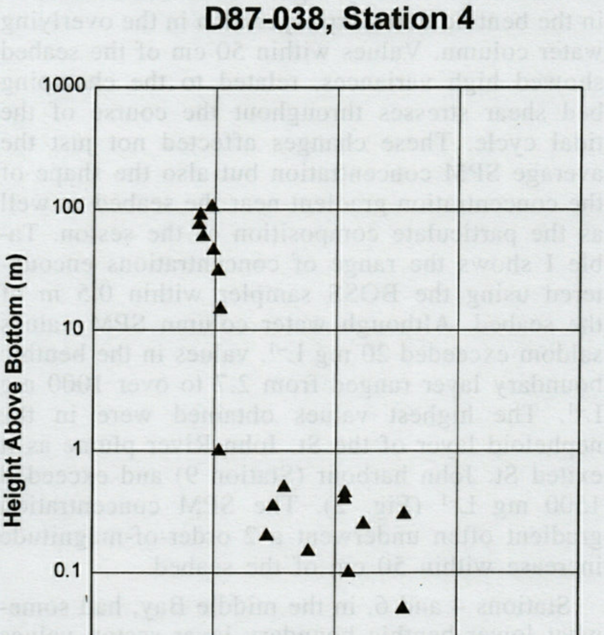

Fig. 3. – SPM concentrations from the sea surface to the seabed at Station 4 (D38).

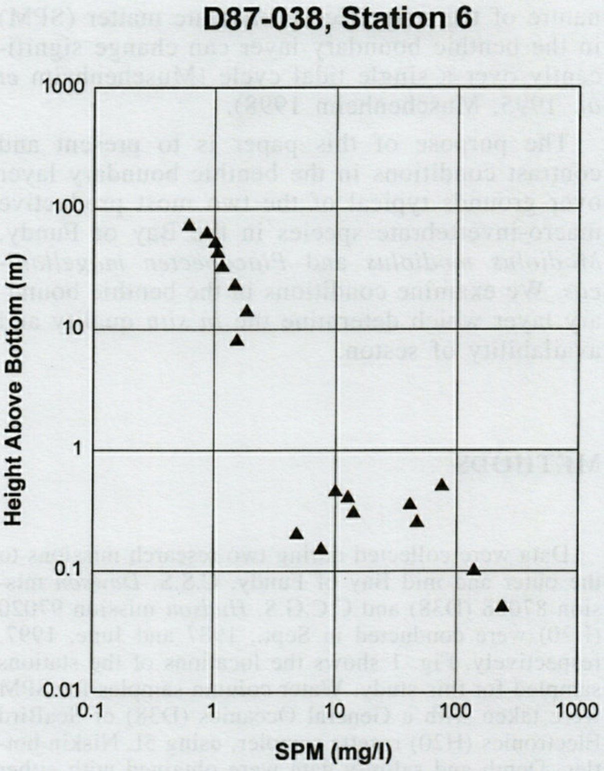

Fig. 4. – SPM concentrations from the sea surface to the seabed at Station 6 (D38).

Station 12, at a site representative of productive sea scallop (*Placopecten magellanicus*) ground, was occupied for a period of 13 hrs to study temporal changes occurring over the course of a tidal cycle. Fig. 5 shows tidal current rate at 20 m above bottom during the sampling period. Fig. 6A-C shows SPM concentration profiles within 50 cm of the seabed over three successive samplings, each taken three hours apart. The particle size spectrum of the inorganic fraction is shown in Fig. 7a-c. Fig. 6A shows a nearly uniform concentration profile around 45 mg L^{-1}. Fig. 6B, sampled three hours later, shows the effect of sand-size particles from bed resuspension under strong current flow (Fig. 7b), with SPM values increasing from approximately 10 mg L^{-1} at 50 cm from the seabed to over 1,000 mg L^{-1} at just 5 cm above the seabed. Two hours later (Fig. 6C) the SPM concentration profile has again become fairly uniform, with a slightly lower mean value, possibly due to the influx of less sediment-laden water from the Gulf of Maine on the flood tide. The particle size spectrum of the inorgnic components (Fig. 7a-c) shows the change from a flat particle size spectrum to one dominated by resuspension of sand-sized particles in the 200 µm size range and back to the nearly flat distribution within a period of six hours. Changes in the organic content of the seston during this period are shown in Table II. At lower current velocities the

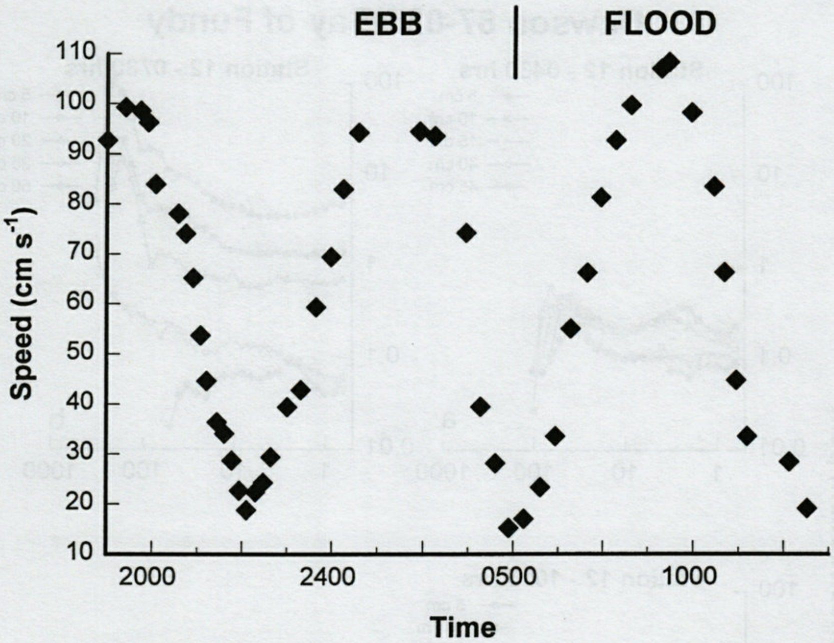

Fig. 5. – Tidal current velocity at 20 m above the seabed at Station 12 (D38). Water depth was 90 m.

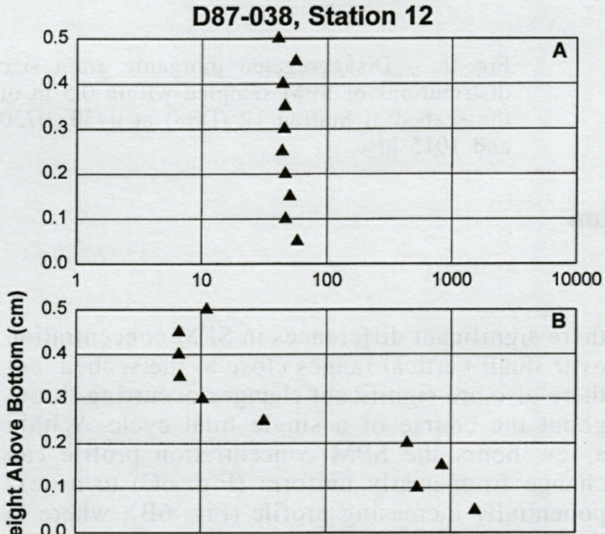

Fig. 6. – SPM concentrations within 0.5 m of the seabed at Station 12 (D38), sampled at 0430 (A), 0730 (B) and 1015 (C) hrs.

percent organic matter values within 50 cm of the seabed were extremely high, at around 50 %, but this value dropped to around 10 % as flow rate increased. Again this illustrates the greater proportion of inorganic particles in suspension.

Two 13-hr stations, FAS1 and FAS2, were occupied in the mid-Bay region during H20. At FAS1, located over a *Modiolus* reef, the bulk SPM concentration in the benthic boundary layer ranged from 1.54 to 198.53 mg L^{-1} with a mean of 40.58 mg L^{-1}, while that in the water column ranged from 0.55 to 12.54 mg L^{-1} with a mean value of 2.31 mg L^{-1}. These ranges are similar to those observed during D38 at stations 4 and 6 (Fig. 3, 4), which are in the same region of the Bay as FAS1 and FAS2 (Table I). At FAS2, approximately 2 km from FAS1 and outside of the *Modiolus* reef, the mean benthic boundary layer SPM concentration was similar, at 40.76 mg L^{-1}, while the range was 11.31 to 273.40 mg L^{-1} and the mean water column value was 2.61 mg L^{-1}. At both stations the mean SPM concentration within 25 cm of the seabed was roughly twice that observed between 25 and 50 cm. The average organic content of the seston at both FAS1 and FAS2 was 12-13 %. At FAS1 %OM values within 25 cm of the seabed were typically 1.5 times as high as those at 25-50 cm. At FAS2 there was little difference in %OM with height above the seabed. Figure 8 shows representative particle size spectra for the disaggregated inorganic component of the seston at FAS1 and FAS2. Both were taken at equivalent stages (slack water, ebb) of the tidal

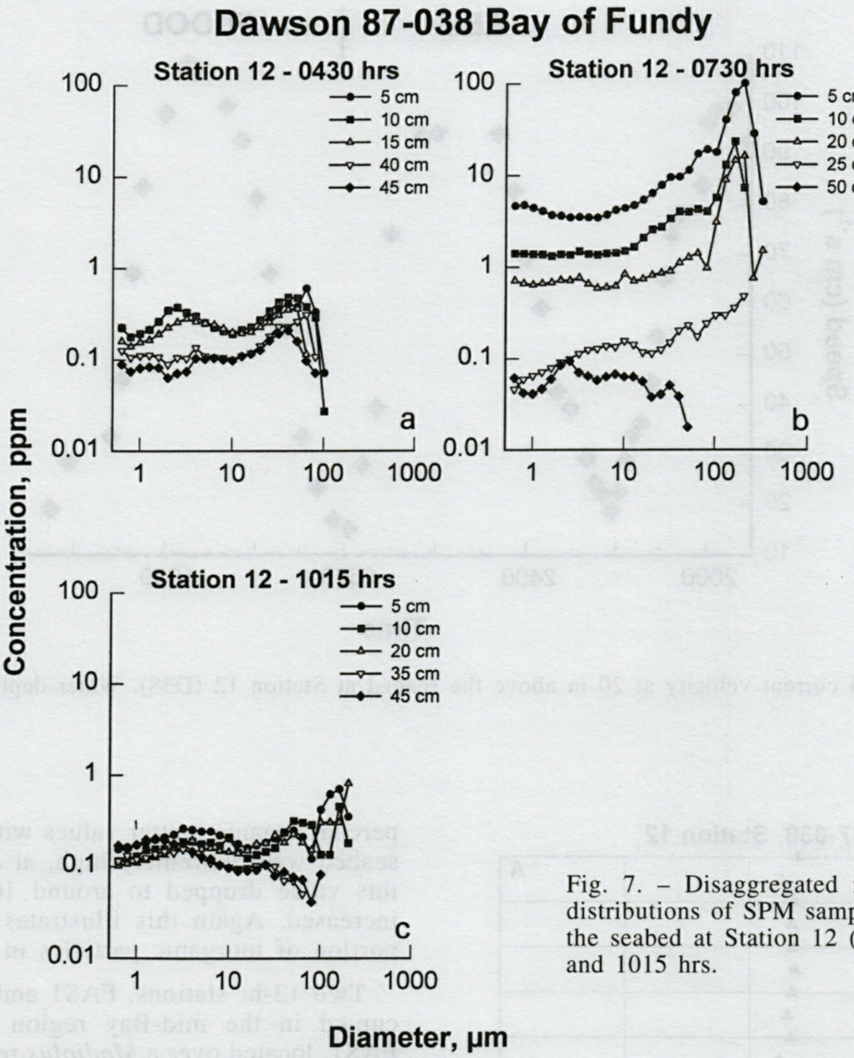

Fig. 7. – Disaggregated inorganic grain size distributions of SPM sampled within 0.5 m of the seabed at Station 12 (D38) at 0430, 0730 and 1015 hrs.

cycle. They are plotted with a vertical offset of one decade to facilitate comparison of samples from different heights within the benthic boundary layer. Particle size analysis of the inorganic fraction showed a consistent peak at around 20 µm with a secondary peak at 5 µm appearing occasionally. The 5 µm peak was much more pronounced at the second 13-hr station (Fig. 8). No evidence of sand resuspension was seen at either of these stations.

DISCUSSION

Although measurements from the two research cruises were taken ten years apart, the methods used, and the results obtained, were similar. Results from D38 and H20 show that the benthic boundary layer is a dynamic environment. SPM concentration and composition changes significantly with proximity to the seabed. Not only are there significant differences in SPM concentration over small vertical ranges close to the seabed, but there also are significant changes occurring throughout the course of a single tidal cycle. Within a few hours the SPM concentration profile can change from nearly uniform (Fig. 6C) to an exponentially increasing profile (Fig. 6B), where in the values within 5-10 cm of the seabed are one to two orders of magnitude higher than those at 50 cm and above.

Vertical mixing of high quality seston down to the benthic boundary layer is one aspect of the picture, but hydrodynamic conditions within the benthic boundary layer determine what particulate materials are available for ingestion within the near-bed region. The results from the 13-hr station in 90 m depth near Digby, on the Nova Scotia coast (Stn 12.) show that the quality of the seston undergoes great temporal variation. The change in the bulk organic content of the seston (Table II) from 51.5 % to 9.5 % in three hours represents a drastic dilution effect due to the presence of

Table I. – SPM (mg L^{-1}) in the water column (W) and benthic boundary layer (B).

STN#	min	max	mean	s.d.	n
04(W)	0.73	1.10	0.92	0.15	8
(B)	2.70	36.70	14.20	12.60	10
06(W)	0.61	1.84	1.19	0.39	8
(B)	4.80	241.30	59.60	76.60	10
09(W)	10.10	138.40	28.80	29.60	36
(B)	25.30	1520.00	385.70	494.70	10
11(W)	0.83	3.15	1.72	0.79	6
(B)	16.20	924.00	232.30	342.40	10
***12(W)**	0.70	4.39	2.69	1.88	4
(B)	6.70	1559.80	132.80	294.20	50
13(W)	0.95	2.85	1.78	0.86	4
(B)	13.40	104.00	27.90	27.10	10
***FAS1 (W)**	0.55	12.54	3.16	1.85	34
(B)	3.34	198.53	40.58	42.28	48
***FAS2 (W)**	0.94	9.14	3.12	1.85	35
(B)	11.31	273.40	40.76	42.28	49

* 13-hr stations with multiple samplings

suspended sands, as evidenced by Fig. 7b. In fact, these values are averages over the full 50 cm above the seabed sampled by BOSS. The average % organic matter content within the bottom 25 cm, where most benthic suspension feeders obtain their ration, was reduced to around 3 % by sand resuspension. Sand resuspension of this order also has been observed over productive offshore scallop grounds on Georges Bank (Muschenheim *et al.* 1995). Abrasion of gill surfaces would be a possible deterrent to feeding during this period.

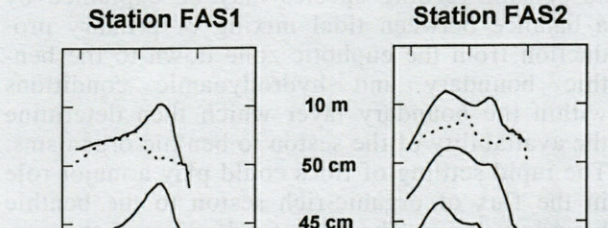

Fig. 8. – Disaggregated inorganic grain size distributions of SPM at Stations FAS1 and FAS2 (H20). The curves depict relative particle sizes at 10 (dashed line), 0.50, 0.45, 0.35, 0.25, 0.15, 0.10 and 0.05 m (solid lines) above the seabed. Note that the size distributions are offset to illustrate the height above bottom (see text).

Table II. – SPM and Percent Organic Content of 3 sequential samples from Station 12.

SAMPLE TIME (GMT)	CURRENT SPEED 20 m OFF BOTTOM (cm s^{-1})	SPM (mg L^{-1}) [± 1 s.d.]	% ORGANIC MATTER [± 1 s.d.]
0430	23.1	47.6 [5.5]	51.6 [16.1]
0730	99.3	346 [520.7]	9.5 [8.7]
1015	38.7	22.3 [11.9]	30.4 [12.7]

Examination of Figure 6 and Table II shows the role that the tidal stage plays at this site. In addition to the dilution effect of resuspended sands, a difference in seston content is seen between the ebb and flood stages of the cycle. Tidally related differences in the seston also have been seen by Cranford *et al.* (1998). This site (station 12) is typical of productive sea scallop bottom, so the scallops must have mechanisms to deal with these resuspension events. We propose that scallops would cease feeding during this portion of the tidal cycle, either due to hydrodynamic inhibition from the strong current speed (Wildish *et al.* 1987), or due to the dilution of the food quality of the seston by resuspended sands.

It is likely that *Placopecten* survives the periods of sand resuspension by virtue of the high quality ration it can obtain in the interim quiescent periods and that is possibly the only reason that they can thrive in that area. In the southeastern Bay of Fundy, seston organic content is extremely high during periods of slack or moderate current. This is likely related to centrifugal upwelling of nutrient rich Gulf of Maine water, resulting in high primary productivity near the Nova Scotia coast (Garrett & Loucks 1976). Benthic suspension feeders, such as *Placopecten* or *Modiolus*, would feed preferentially during this portion of the tidal cycle. The reduced levels of turbulent kinetic energy during these periods are likely to promote formation of flocs composed of suspended detrital particles rich in organic matter. Flocculation promotes rapid vertical transport in estuarine and oceanic areas (Postma 1967, Kranck 1984, Muschenheim & Milligan 1996) and brings large amounts of organic-rich material to the benthic boundary layer in relatively short periods of time (Cranford *et al.* 1998). Rapid aggregation of fine particles during periods of reduced turbulent stresses (slack water) produces flocs with settling velocities on the order of millimeters per second (Kranck & Milligan 1992, Milligan 1995, Sternberg *et al.* in press). This process augments the benthic-pelagic link due to turbulent mixing. Wildish & Fader (1998) concluded that the *Modiolus* reefs are associated only with transitional and well-mixed water masses, stating that *Modiolus* and other benthic suspension feeders are exposed to the highest quality seston in the bottom waters of transitional and well-mixed water masses. They also point out that, throughout the Bay there is poorer seston quality in bottom waters than is available in surface waters. It is probably true that, on average, the quality of seston in the near-bottom waters is lower than that in the euphotic zone but during slack current periods rapid settling of flocs would provide periodic transport of high quality seston to the benthos (Cranford *et al.* 1998).

The high organic content over the productive scallop ground near the Nova Scotia coast is in contrast to conditions over the *Modiolus* reef in the central Bay, where the %OM was relatively constant at 12-13 %, but no sand resuspension was observed. Comparison of the disaggregated inorganic grain size distributions of the suspended sediment in the benthic boundary layer at stations FAS1 and FAS2 shows a marked depletion of particles in the 5 µm range at FAS1 at both high and low water slack tide (Fig. 8). The overall concentration of fine inorganic particles in this range over the *Modiolus* reef is almost an order of magnitude less than that of the low biomass region. Particles in this range correspond to the modal diameter in the overlying water, which is dominated by non-oxidizable planktonic material remaining after the removal of organics. The apparent lack of material in this size range would result from preferential removal of these sizes over the *Modiolus* reef. Ingestion of particles in this size range would be augmented by breakup of the large macro-flocs responsible for the rapid settling of the fine grained material into microflocs as suggested by Eisma (1983). Seston depletion over beds of filter feeding molluscs has been shown previously (Frechette & Bourget 1985, Newell C.R. 1990, Muschenheim & Newell 1992). The small inorganic grains probably reached the benthic boundary layer bound up in flocs, which gave them sufficient settling velocity to reach the near-seabed region. The results from D38 and H20 show that large changes in SPM concentration occur in the mid-Bay region as well as in the coastal areas. The positioning of *Modiolus* reefs likely depends on a balance between availability of high-quality seston mixed down from the euphotic zone and benthic boundary layer conditions that permit sufficient time to ingest the high quality seston without excessive periods of sand resuspension and consequent dilution of the organic content. Therefore transitional or well-mixed regions provide sufficient food supply but regions of more moderate current flow (i.e. deeper, offshore areas in the mid-Bay) are not as subject to long periods of suspended inorganic particle transport.

The reason why these high density assemblages of *Modiolus* form raised reefs is not clear. One potential explanation is that raising them higher in the benthic boundary layer places them above the region of major inorganic material transport and into a more constant organic-rich seston source (Muschenheim 1987b). Avoidance of abrasion by bedload and suspended load sand transport may also play a role but, in contrast to what was observed at station 12, little or no sand resuspension was observed at the mussel reef sampled during H20. If the BOSS sampler sat directly on the reef, it would have been at least a meter or more above the ambient seabed and sand resuspension would likely not have been seen. However there also was no resuspended sand at the site outside the *Modiolus* reef. The seabed in this particular portion of the Bay is composed of longitudinal ridges, running parallel to the major flow axis, with flat sand in between (Wildish & Fader 1998, Wildish *et al.* 1998). If the BOSS deployments at FAS2 were on top of one of these ridges then they also would have been sampling at least a meter above the normal seabed level and would likely have missed the zone of suspended sand transport. It is thus not possible to determine whether *Modiolus* is excluded from this area due to sand transport or for other reasons.

CONCLUSIONS

Results from these observations in the Bay of Fundy indicate that distributions of some benthic suspension-feeding species may be explained by a balance between tidal mixing of primary production from the euphotic zone down to the benthic boundary and hydrodynamic conditions within the boundary layer which then determine the availability of the seston to benthic organisms. The rapid settling of flocs could play a major role in the flux of organic-rich seston to the benthic boundary layer. The high food value of the vertically transported seston may be diluted by resuspension of inorganic particles for varying portions of the tidal cycle.

Application of specialized sampling gear, in addition to more standard measurements, is necessary to reveal patterns of seston availability and is most useful when coupled with in situ current measurements. Conditions just above the seabed, where benthic suspension feeders obtain their food resources are not well predicted by conditions just a few meters higher in the water column. Sequential sampling through the course of a tidal cycle is much more revealing than spot sampling and generally more can be learned about near-seabed conditions by time-series sampling at one location than by an equivalent number of samples taken over a broader area.

Future work on this topic should focus on coordinated studies of the vertical distribution and transport of seston throughout the water column and near-bed region, including floc formation and breakup as a function of turbulent energy level. Modelling studies focussing on the relative contributions of tidal mixing and floc settling in the vertical transport of organic-rich particulate food resources are an important next step.

ACKNOWLEDGEMENTS. – The authors wish to thank the officers and crews of the Canadian research vessels Dawson and Hudson for invaluable assistance and logistical support at sea. Technical field and lab assistance was provided by K. Azetsu-Scott, K. Kranck, E. Petticrew, K. Saunders, T. Schell, M. Scotney and D. Wildish. K. Saunders prepared the figures. We thank D. Wildish and G. Fader for useful discussions and insights and two anonymous reviewers for constructive criticism. This research was supported by an N.S.E.R.C. Visiting Fellowship to DKM and by the Department of Fisheries and Oceans, Canada.

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Reçu le 27 octobre 1998 ; received October 27, 1998
Accepté le 30 novembre 1998 ; accepted November 30, 1998

VIE MILIEU, 1998, 48 (4) : 295-307

EXPERIMENTAL STUDY OF THE EFFECT OF KAOLINITE ON THE INGESTION AND THE ABSORPTION OF MONOSPECIFIC SUSPENSIONS OF *PAVLOVA LUTHERI* BY THE FILTER-FEEDING BIVALVE *VENUS VERRUCOSA*

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INGESTION
ABSORPTION
PHYTOPLANKTON
FILTER-FEEDERS
BIVALVES
KAOLINITE

ABSTRACT. – We investigated the ingestion and the absorption of the filter-feeding bivalve *Venus verrucosa* Linné fed on *Pavlova lutheri* Droop in the presence of different concentrations of kaolinite (i.e., between 0 and 50 mg.1^{-1}). We used ^{14}C-sodium bicarbonate to label the algae. In the presence of bivalves, the exchanges of radioactivity between compartments were always dominated by the transfer between POM and bivalves. However, there were significant differences in radioactivity partitioning among compartments depending on the concentration of kaolinite. The observed transfers resulted from the interactions between ingestion, absorption, biodeposition, and recycling of biodeposits. The coexistence of these processes did not allow to determine directly ingestion rates and absorption efficiencies, which required the use of mathematical modelling. The model used during the present study is identical to the one previously designed to describe the utilisation of a suspension of *Escherischia coli* by *Venus verrucosa.* It simulates the exchanges of radioactivity between compartments and allows the quantification of ingestion and absorption. It is complicated by the occurrence of pseudofaeces production at the highest kaolinite concentration. Our results show no significant differences in both ingestion rates (10 mgDW.h^{-1} at 0 and 5 mg.1^{-1} of kaolinite) and absorption efficiencies (about 57 % at 0 and 5 mg.1^{-1} of kaolinite) below the threshold of pseudofaeces production. Filtration and thus ingestion rates were significantly reduced for a kaolinite concentrations of 50 mg.1^{-1}. Apparent absorption efficiency was also much lower (about 34 %) during the 50 mg.1^{-1} experiment. In addition, the highest concentration of kaolinite induced higher biodeposition and recycling rates of labelled material. These results are discussed in view of the existing literature.

INGESTION
ABSORPTION
PHYTOPLANCTON
FILTREURS
BIVALVES
KAOLINITE

RÉSUMÉ. – Nous avons étudié l'effet de différentes concentrations de kaolinite (entre 0 et 50 mg.1^{-1}) sur l'ingestion et l'absorption du Bivalve filtreur *Venus verrucosa* Linné nourri avec *Pavlova lutheri* Droop. Les algues ont été marquées avec du ^{14}C bicarbonate de sodium. Dans les enceintes expérimentales contenant des Bivalves, les échanges de radioactivité les plus importants interviennent toujours entre les compartiments MOP et Bivalves. La répartition de la radioactivité entre compartiments est cependant significativement affectée par la concentration de kaolinite. Les transferts de radioactivité observés résultent de l'interaction entre les processus d'ingestion, d'absorption, de biodéposition, et de recyclage des biodépôts. La coexistence de ces processus ne permet pas la détermination directe des taux d'ingestion et des efficacités d'absorption qui requiert l'élaboration d'un modèle mathématique. Le modèle utilisé est semblable à celui ayant été développé pour décrire l'utilisation d'une suspension d'*Escherischia coli* par *Venus verrucosa.* Il simule les échanges de radioactivité entre compartiments et permet le calcul de l'ingestion et de l'absorption. Ce modèle est compliqué par la production de pseudofaeces à la concentration de kaolinite la plus élevée. En dessous du seuil de production des pseudofaeces, nos résultats ne montrent pas de différences significatives tant pour ce qui concerne les taux d'ingestion (10 mgPS.h^{-1} à 0 et 5 mg.1^{-1} de kaolinite) et les efficacités d'absorption (environ 57 % à 0 et 5 mg.1^{-1}

de kaolinite). Les taux de filtration et donc d'ingestion sont par contre significativement réduits à une concentration de kaolinite de 50 mg.l^{-1}. L'efficacité d'absorption apparente est également beaucoup plus faible (environ 34 %) à cette concentration. De plus, la concentration de kaolinite la plus élevée induit une augmentation de la biodéposition et du recyclage du matériel radioactif. Ces résultats sont discutés au vu de la littérature existante.

INTRODUCTION

The quality of the particulate organic matter (POM) available to coastal benthic invertebrates shows important temporal changes (Berg and Newell 1986, Fegley *et al.* 1992). Part of this variability is seasonal and mostly reflects changes in the relative importance of the different components of the POM pool (Tenore 1988). However, modifications in POM quality may also result from impulsional events and especially meteorological processes controlling sediment resuspension. In a recent study (Charles *et al.* 1995), we investigated temporal changes in the quality of sediment-trap collected materials by using a bioassay approach based on the measurement of ingestion rates and absorption efficiencies by the bivalve *Abra ovata.* Our results strongly suggest the existence of a negative effect of bottom sediment resuspension on absorption efficiency. They are further supported by similar data concerning growth rates (Baudart 1994, Grémare *et al.* 1997). The existence of a negative relationship between sediment resuspension and absorption efficiency of sediment trap material may result from 2 different mechanisms : (1) a simple dilution of a relatively rich food source (i.e., originating from the water column) by a more refractory material originating from the sediment, or (2) a direct effect of the particulate inorganic matter (PIM) load on absorption.

This second hypothesis is apparently supported by the results of several studies assessing the effect of resuspended bottom sediment on growth in suspension-feeding bivalves (Winter 1976, Kiorboe *et al.* 1980, 1981, Langdon and Siegfried 1984, Urban and Langdon 1984). These authors indeed reported an enhancement of suspension-feeding bivalves' growth rates in the presence of low concentrations of PIM. One of the invoked explanation being an increase in absorption rates either due to a "grinding effect" (Murken 1976 cited by Urban and Langdon 1984) or to a modification in gut residence time (Bayne *et al.* 1987). However, most of the experimental studies carried out since then have failed to detect any significant increase in ingestion rates and absorption efficiencies associated to the augmentation of the PIM load (Bricelj and Malouf 1984, Robinson *et al.* 1984, Hawkins *et al.* 1986, Bayne *et al.* 1987, Iglesias *et al.* 1992).

Such a discrepancy may be due to the fact that most of these scientists (Kiorboe *et al.* 1981, Mohlenberg and Kiorboe 1981, Iglesias *et al.* 1992, Navarro *et al.* 1992) have used natural sediment which act both as an "inert turbidity producing agent and a food supplement" (Bricelj and Malouf 1984). Along the same lines, Bayne *et al.* (1987) stated that changes in absorption efficiencies of the blue mussel *Mytilus edulis* may result from an interaction between average particle size and organic content resulting from the introduction of PIM. In order to unravel such interactions, it seems thus more appropriate to use : (1) radiolabelled food sources (Bricelj and Malouf 1984), and (2) artificial substrates such as kaolinite for manipulating the concentration of PIM (Robinson *et al.* 1984, Bayne *et al.* 1987, Cranford & Gordon Jr 1992, Urban & Kirchnan 1992).

The aim of the present study was to assess changes in ingestion rates and absorption efficiencies of the filter-feeding bivalve *Venus verrucosa* fed on a monospecific suspension of *Pavlova lutheri* and submitted to increasing concentrations of kaolinite.

MATERIALS AND METHODS

Biological material : Monospecific cultures of *Pavlova lutheri* (INSERM, Villefranche-sur-Mer) were grown on a F/2 medium (Guillard and Ryther 1963) at 18 °C under constant illumination (1700 lux). After 8 days, the algae were labelled for 48 hours with ^{14}C sodium bicarbonate (ISOTOPCHIM, specific activity ; 2109MBq.mmol^{-1}). The excess of label was then subsequently removed by 2 centrifugations (3000 rpm for 10 min).

The clam *Venus verrucosa* is abundant all along the coasts of France and more specifically on the Atlantic and the Channel where it is submitted to an intensive exploitation. Although it is not heavily harvested on the French Mediterranean coast, *V. verrucosa* is also present in most of the infralittoral biota of the Mediterranea (Amouroux 1982). The clams used during the present study have been collected from shallow water (about 1.5 m depth) in Port-Vendres harbour, France, during April 1994. To prevent any significant contamination with other biota, they were carefully scrubbed and were allowed to clear their guts for 24 h before use. Clams were adapted to the experimental temperature 48 hours prior to each experiment.

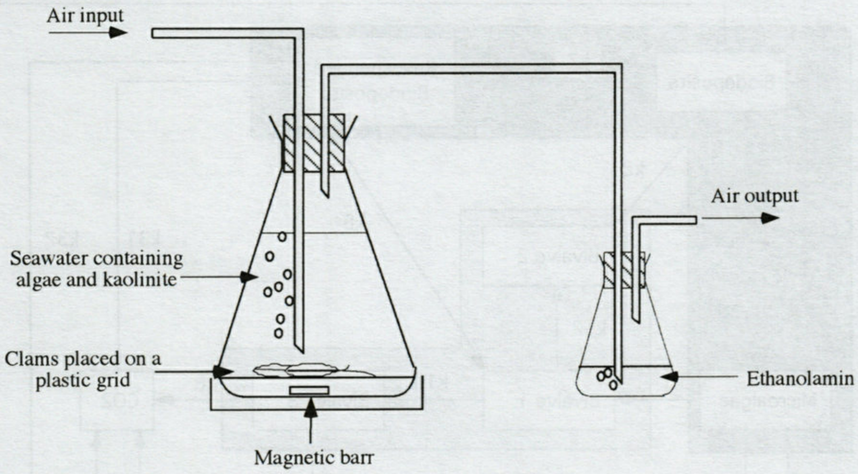

Fig. 1. – Experimental set-up used during the feeding experiments

Generality on the experimental approach : The experimental approach used during the present study combines compartmental analysis and analog modelling (Grémare *et al.* 1991). Compartmental analysis consisted in measuring temporal changes of the partitioning of radioactivity between the different compartments (i.e., Particulate Organic Matter, Bivalves, Dissolved Organic Matter, and CO_2) of a closed system. Modelling then allows the transfers of radioactivity between compartments to be computed.

Compartmental analysis : Five bivalves corresponding to a total flesh dry weight of 5 g were introduced into each experimental chamber, which was filled with 1 litre of filtered (1.2 µm) seawater and 10 mg dry weight of labelled *Pavlova lutheri*. The dry weights of the clams were calculated from the length-weight relationships proposed by Amouroux (1982). The seawater was mixed by bubbling air. At the outlet, air was passed through ethanolamin traps to capture the labelled gaseous CO_2 (Fig. 1, Amouroux 1982).

Experiments were carried out at 15 °C in total darkness. Three chambers were used for incubation in the presence of bivalves and three further chambers as controls (i.e., incubation of *P. lutheri* alone in seawater containing either 0 or 50 $mg.l^{-1}$ of kaolinite). Five incubation periods (1, 4, 10, 20 and 50 h) and 4 concentrations of kaolinite (0, 5, 10 and 50 $mg.l^{-1}$) were tested. These concentrations have been retained after preliminary trials showing that *V. verrucosa* was producing pseudofaeces for kaolinite concentrations superior to 10 $mg.l^{-1}$ (Chaabeni 1994).

The changes in the partitioning of the radioactivity within experimental chambers containing microalgae, seawater, plus eventually bivalves and kaolinite were monitored according to Charles *et al.* (1992a).

At the end of each experiment, the bivalves were recovered, rinsed with tap water, dissected and individually hydrolysed in 10 ml 1*N* NaOH at 60 °C for 24 h. Their radioactivity was assessed by liquid scintillation counting of two 1 ml subsamples each. The total radioactivity of the "bivalves" compartment was taken to be the sum of the radioactivity of all 5 bivalves.

The seawater was filtered through a 0.2 µm Nuclepore membrane to separate dissolved from particulate organic matter (POM). Membranes were hydrolysed in 20 ml 1*N* NaOH at 60 °C for 24 h. Two 1 ml subsamples were counted by liquid scintillation to evaluate the radioactivity of the POM compartment.

Two 1 ml subsamples of the ethanolamin traps were counted by liquid scintillation to determine the radioactivity of gaseous CO_2. 200 ml of the filtered seawater was then placed in a stoppered bottle and acidified (2 ml of 95 % H_2SO_4). The resulting CO_2 (which corresponds to dissolved CO_2) was captured on an ethanolamin trap. The radioactivity of the CO_2 compartment was considered to be the sum of the radioactivity of gaseous and dissolved CO_2.

Two 5 ml subsamples of filtered seawater were taken after acidification and counted by liquid scintillation to determine radioactivity of dissolved organic matter (DOM).

All radioactivity measurements were carried out on a Beckman LS5000 CE liquid scintillator. Dynagel (Baker) was always used as scintillation cocktail except for CO_2 where 5 % of PPO and 0.5 % of bis MSB (Packard) was used. All counts were checked for chemiluminescence, corrected for quenching, and then expressed as % of the total radioactivity within each experimental chamber. Counting efficiencies were always > 90 %.

Modelling : Our model is similar to the one used by Charles *et al.* (1992b). Its structure is presented in Fig. 2. The system was closed, and initially considered to be composed of six compartments : microalgae, bivalves, DOM, CO_2, biodeposits, and resuspended biodeposits. We introduced, three second-order time-delays to account for the time lags between ingestion and (1) production of faeces, (2) production of DOM, and (3) production of CO_2 by bivalves. In the model this resulted in the subdivision of the bivalve compartment into three subcompartments : Bivalves 1 (radioactivity in the anterior part of the digestive tract), Bivalves 2 (radioactivity which has not been absorbed by the bivalves), and Bivalves 3 (radioactivity which has been absorbed by the bivalves).This procedure introduced an intermediary step in the transfers from the bivalve compartment to biodeposits, DOM and CO_2 compartments.

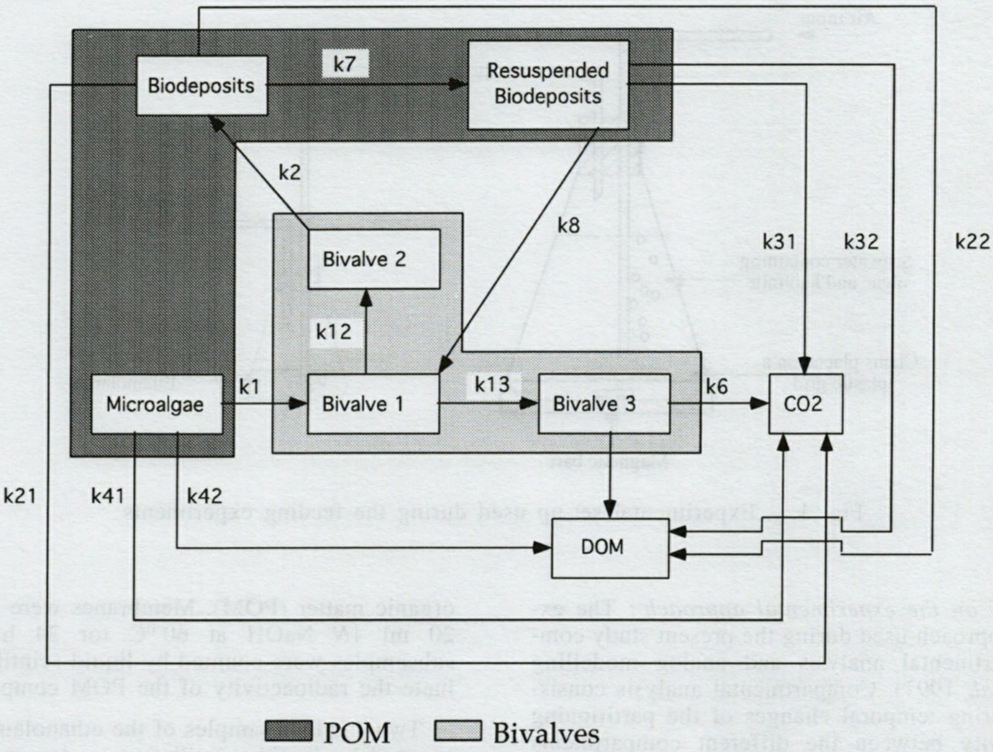

Fig. 2. – Modelling. Diagram of the "Microalgae-Bivalve" system showing exchanges studied and numbered kinetic coefficients of mass transfer.

Therefore, in its final form, the model was composed of eight compartments :

Mass transfer dynamics of the system "bivalves-microalgae-seawater" were represented by an interaction of "kinetic" equations reflecting the rate of exchanges between the compartments :

$d\,[\mathrm{Micr}]/dt = -\,(k_1+k_{41}+k_{42})\,[\mathrm{Micr}]$
$d\,[\mathrm{Biv\ 1}]/dt = k_1\,[\mathrm{Micr}] + k_8\,[\mathrm{Resbio}] - (k_{12}+k_{13})\,[\mathrm{Biv\ 1}]$
$d\,[\mathrm{Biv\ 2}]/dt = k_{12}\,[\mathrm{Biv\ 1}] - k_2\,[\mathrm{Biv\ 2}]$
$d\,[\mathrm{Biv\ 3}]/dt = k_{13}\,[\mathrm{Biv\ 1}] - (k_6+k_5)\,[\mathrm{Biv\ 3}]$
$d\,[\mathrm{DOM}]/dt = k_5\,[\mathrm{Biv\ 3}] + k_{42}\,[\mathrm{Micr}] + k_{32}\,[\mathrm{Res\ bio}] + k_{22}\,[\mathrm{Biodep}]$
$d\,[\mathrm{Biodep}]/dt = k_2\,[\mathrm{Biv\ 2}] - (k_7+k_{22}+k_{21})\,[\mathrm{Biodep}]$
$d\,[\mathrm{CO_2}]/dt = k_6\,[\mathrm{Biv\ 3}] + k_{41}\,[\mathrm{Micr}] + k_{21}\,[\mathrm{Biodep}] + k_{31}\,[\mathrm{Res\ bio}]$
$d\,[\mathrm{Res\ bio}]/dt = k_7\,[\mathrm{Biodep}] - (k_8+k_{31}+k_{32})\,[\mathrm{Res\ bio}]$
$d\,[\mathrm{POM}]/dt = d\,[\mathrm{Micr}]/dt + d[\mathrm{biodep}]/dt + d[\mathrm{Res\ bio}]/dt$
$d\,[\mathrm{Biv}]/dt = d\,[\mathrm{Biv\ 1}]/dt + d\,[\mathrm{Biv\ 2}]/dt + d\,[\mathrm{Biv\ 3}]/dt$

where ki = kinetic coefficients of mass transfer (h^{-1}), k_1 = filtration of microalgae by bivalves, k_2 = biodeposition by bivalves, k_5 = production of DOM by bivalves, k_6 = production of CO_2 by bivalves, k_7 = resuspension from biodeposits, k_8 = filtration of resuspended biodeposits by bivalves, k_{12} = transit along the digestive tract of bivalves, k_{13} = absorption by bivalves, k_{21} = production of CO_2 by biodeposits, k_{22} = production of DOM by biodeposits, k_{31} = production of CO_2 by resuspended biodeposits, k_{32} = production of DOM by the resuspended biodeposits, k_{41} = production of CO_2 by microalgae, k_{42} = production of DOM by microalgae and [X] corresponds to radioactive content of compartment X (expressed as percentage of total radioactivity initially introduced into system).

Modelling was carried out on a Macintosh microcomputer using the software Stella®. POM (i.e., the sum of microalgae, biodeposits, and resuspended biodeposits) was used together with DOM, CO_2, and bivalves (i.e., the sum of bivalves 1, bivalves 2, and bivalves 3) when fitting the model to the experimental data. The values of k_{41} and k_{42} (0.0035, and 0.0032, respectively) were deduced from the fitting of a submodel to the changes in partitioning of the radioactivity in the control chambers. It was assumed that biodeposits and resuspended biodeposits were producing DOM and CO_2 at the same rate as the microalgae compartment (i.e., $k_{21} = k_{22} = k_{31} = k_{32} = 0.0006$). Due to the low amounts of radioactive DOM and CO_2 recorded during the study, this assumption was not essential when fitting the model to the experimental data (see also Charles *et al.* 1992b).

Calculation of ingestion rates and absorption efficiencies : Ingestion rates and absorption efficiencies were computed from the values of the kinetic coefficients of the fitted models as proposed by Charles *et al.* (1992b). Initial ingestion rates were computed using the following formula :

$$I = k_1.\ [\mathrm{Micr}]$$

were I is the ingestion rate ($\mathrm{mgDW.h^{-1}}$), k^1 is the kinetic coefficient corresponding to the filtration of microalgae (h^{-1}), and [Micr] is the quantity of microalgae initially introduced in the system (mgDW). Absorption efficiency was defined as the ratio between the quantity of absorbed and ingested organic matter. The

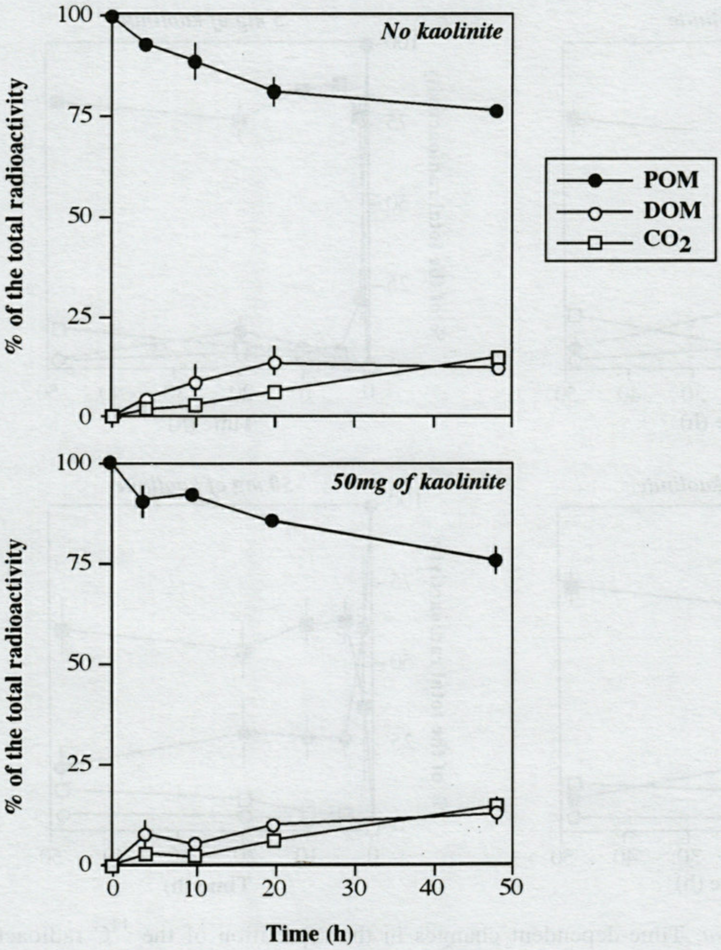

Fig. 3. – Controls. Time-dependent changes in the repartition of the ^{14}C radioactivity.

amount of ingested organic matter was taken as the cumulative amount of radioactivity resulting from the transfer from microalgae to bivalves. The amount of absorbed organic matter was computed by two different methods : either as the difference between the quantity of ingested organic matter and the amount of radioactivity transiting between the compartments bivalves 1 and bivalves 2, or as the cumulative amount of radioactivity transiting between the compartments bivalves 1 and bivalves 3. The first of these two procedures leads to an overestimation of absorption, where as the second one leads to an underestimation of absorption (Grémare *et al.* 1991 ; Charles *et al.* 1992b ; Charles 1993).

RESULTS

Compartmental analysis

Controls

Figure 3 shows the changes in the partitioning of radioactivity within the control chambers for two concentrations of kaolinite (i.e., 0 and 50 $mg.l^{-1}$). The effect of kaolinite concentration and time (i.e., experiment duration) on the amounts of radioactivity corresponding to POM, DOM and CO_2 were assessed by using two-way ANOVAs. For all these compartments, there was a significant effect of experiment duration ($p = 0.0001$, $p = 0.011$ and $p = 0.0001$, respectively). On the contrary, kaolinite concentration did not have any significant effect ($p = 0.30$, $p = 0.42$, $p = 0.30$, respectively). It was thus possible to use the average radioactivity (i.e., between the 0 and the 50 $mg.l^{-1}$ experiments) to describe changes in the repartition of radioactivity within the controls. Radioactivity of POM declined over time to represent 74.9 % of the total radioactivity after 48 hours. Meanwhile, radioactivity corresponding to DOM increased from 0 to 11.7 % of the total radioactivity. Radioactivity of CO_2 also increased significantly with incubation duration. This compartment accounted for 13.4 % of the total radioactivity after 48 hours of incubation.

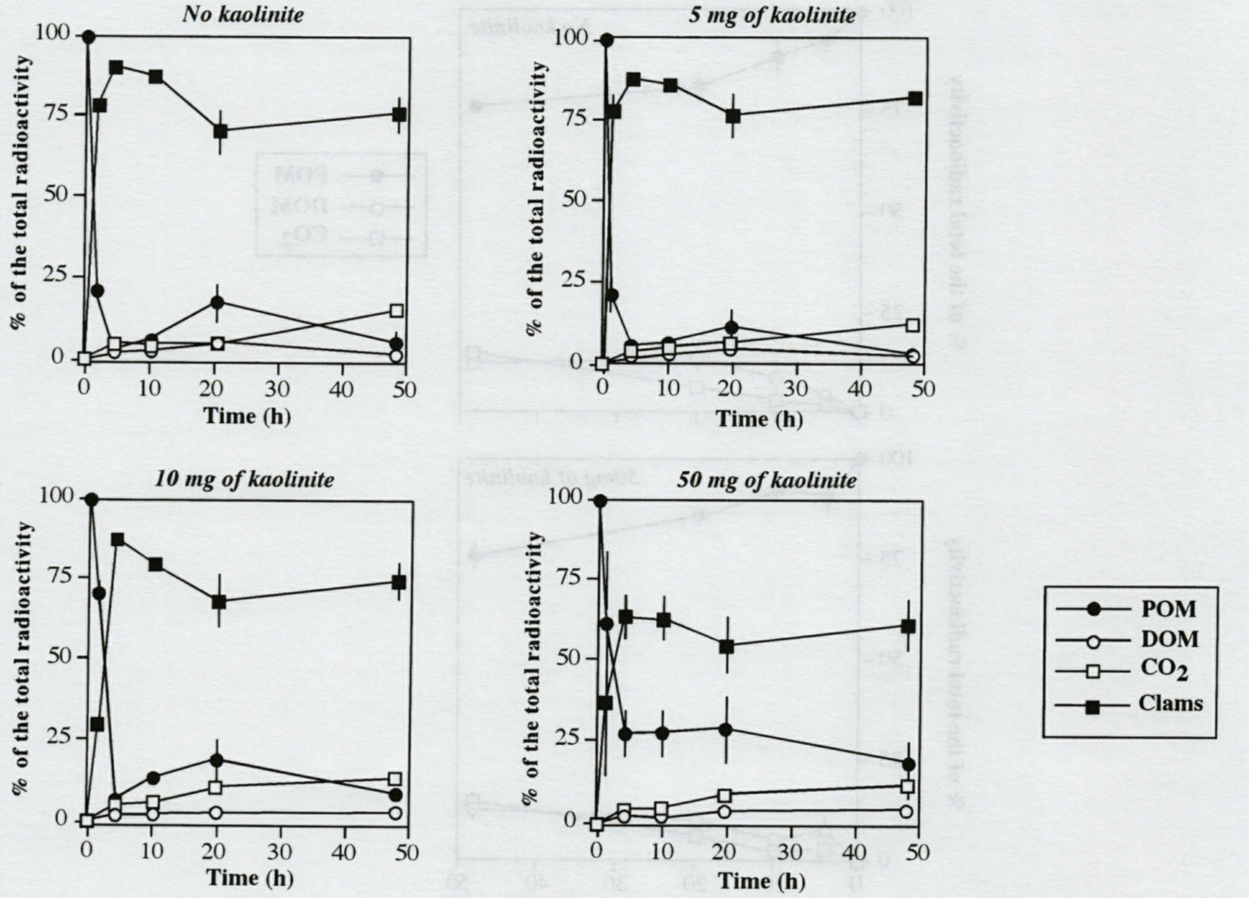

Fig. 4. – *Venus verrucosa.* Time-dependent changes in the repartition of the ^{14}C radioactivity within experimental chambers containing bivalves.

Clams

Figure 4 shows changes in the partitioning of radioactivity within the experimental chambers containing *Venus verrucosa.* For all the tested compartments (i.e., POM, bivalves, DOM and CO_2), there was a significant effect of incubation duration two-way ANOVAs, $p = 0.0001$ in all cases). For POM, bivalves and DOM, there was also a significant effect of kaolinite concentration (two-way ANOVAs, $p = 0.0001$ in all cases). There was no significant effect of kaolinite concentration on the amount of radioactivity corresponding to CO_2 (two-way ANOVA, $p = 0.23$).

The radioactivity within the clams themselves drastically increased during the first hour of the experiments. After 1 hour, radioactivity corresponding to the bivalves represented 78.7 and 78.6 % of the total radioactivity in the experimental chambers containing 0 and 5 mg.1^{-1} of kaolinite, respectively. This proportion was much lower for the chambers containing higher concentrations of kaolinite (29.6 and 37.6 % of the total radioactivity for the 10 mg.1^{-1} and 50 mg.1^{-1} experiments, respectively). For all tested concentrations, the radioactivity corresponding to the clams was maximal after 4 hours of experiment. These maxima were close to 90 % except for the chambers containing 50 mg.1^{-1} of kaolinite where bivalves accounted for only 64.5 % of the total radioactivity after 4 hours. The period between 4 and 20 hours was then characterised by a slight decrease of the radioactivity corresponding to the bivalves preceding a stabilisation at 48 hours.

Temporal changes of the radioactivity corresponding to POM were inverted relative to those concerning bivalves thereby suggesting that the major exchanges of radioactivity occurred between these two compartments. The first 4 hours of the experiments corresponded to an important decline due to the filtration of the labelled microalgae by the clams. The period between 4 and 20 hours usually corresponded to a slight increase in the radioactivity corresponding to POM thus probably reflecting biodeposition by the clams. The final proportion of the total radioactivity corresponding to POM was much higher for the chambers containing 50 mg.1^{-1} of kaolinite than for the other 3 tested concentrations (19.8 versus only about 5.5 % of the total radioactivity).

Table I. – Kinetic coefficients of mass transfers corresponding to the fitted models.

	Concentration of kaolinite ($mg.l^{-1}$)			
k_i	0	5	10	50
k_1	1.0000	1.0000	0.9000	0.2600
k_2	0.0750	0.0750	0.0900	0.2000
k_5	0.0000	0.0000	0.0000	0.0002
k_6	0.0058	0.0045	0.0046	0.0046
k_7	0.0700	0.1100	0.1000	0.1000
k_8	1.000	1.0000	0.2600	0.2600
k_{12}	0.0750	0.0750	0.0900	0.2000
k_{13}	0.1000	0.1000	0.1000	0.1000
k_{21}	0.0035	0.0035	0.0035	0.0035
k_{22}	0.0032	0.0032	0.0032	0.0032
k_{31}	0.0035	0.0035	0.0035	0.0035
k_{32}	0.0032	0.0032	0.0032	0.0032
k_{41}	0.0035	0.0035	0.0035	0.0035
k_{42}	0.0032	0.0032	0.0032	0.0032

Radioactivity of DOM always remained very low (i.e., less than 5.3 % of the total radioactivity).

CO_2 radioactivity was not significantly affected by the concentration of kaolinite. It increased slowly but significantly during the incubation period to represent about 14.5 % of the total radioactivity after 48 hours.

Modelling

Table I shows the kinetic coefficients of the fitted models. The fittings of the models to the experimental data concerning the 4 tested concentrations of kaolinite are presented in Figure 5. The cumulative quantities of ingested microalgae and recycled biodeposits in the presence of the 4 tested concentrations of kaolinite are shown in Figure 6. The corresponding quantities of radioactive biodeposits and CO_2 produced by the bivalves are presented in Figure 7. The computation of these quantities provides more specific information on the different processes occurring between microalgae and bivalves.

During the first 4 h of incubation, the predominant process was the filtration of the algal sus-

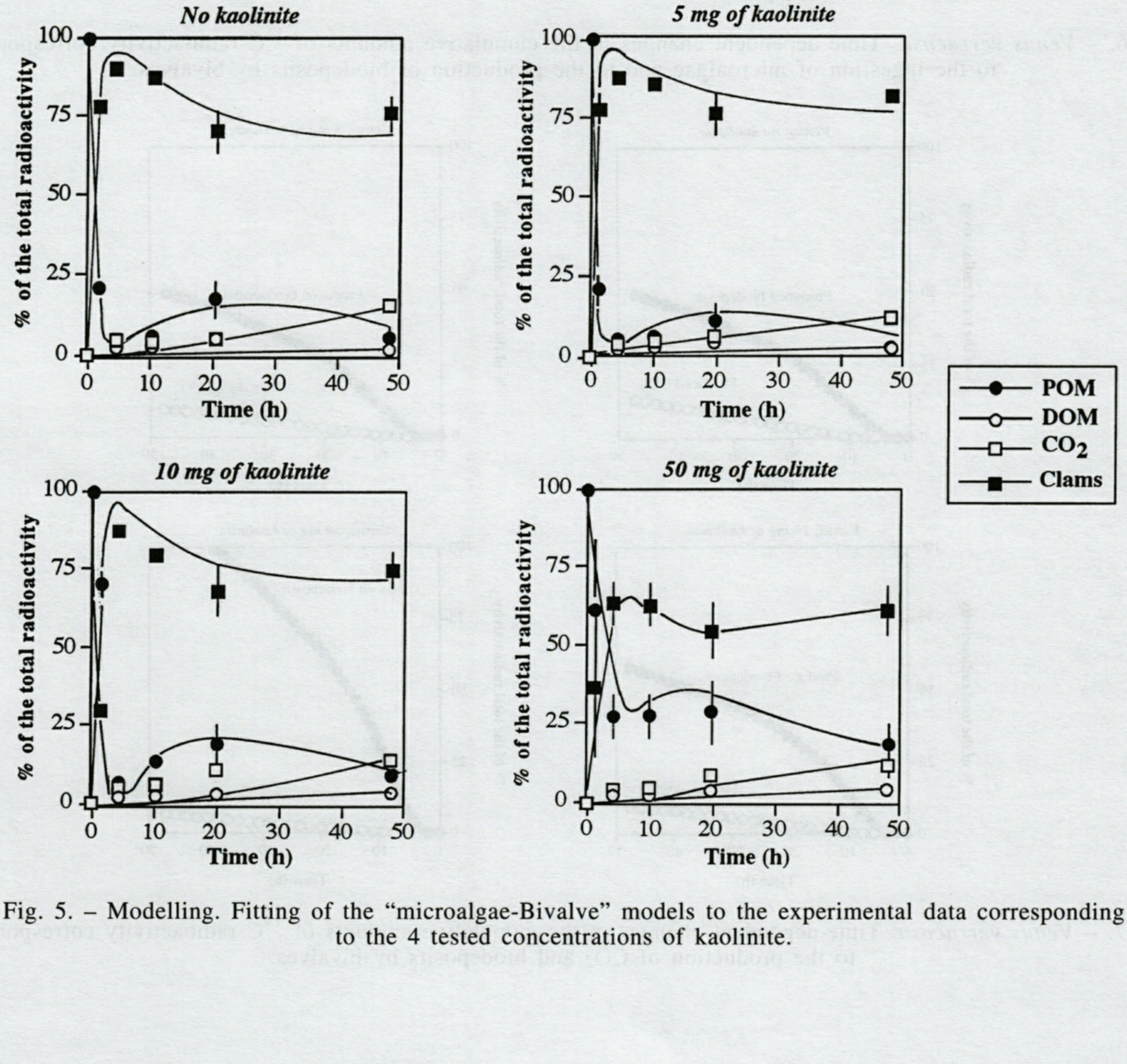

Fig. 5. – Modelling. Fitting of the "microalgae-Bivalve" models to the experimental data corresponding to the 4 tested concentrations of kaolinite.

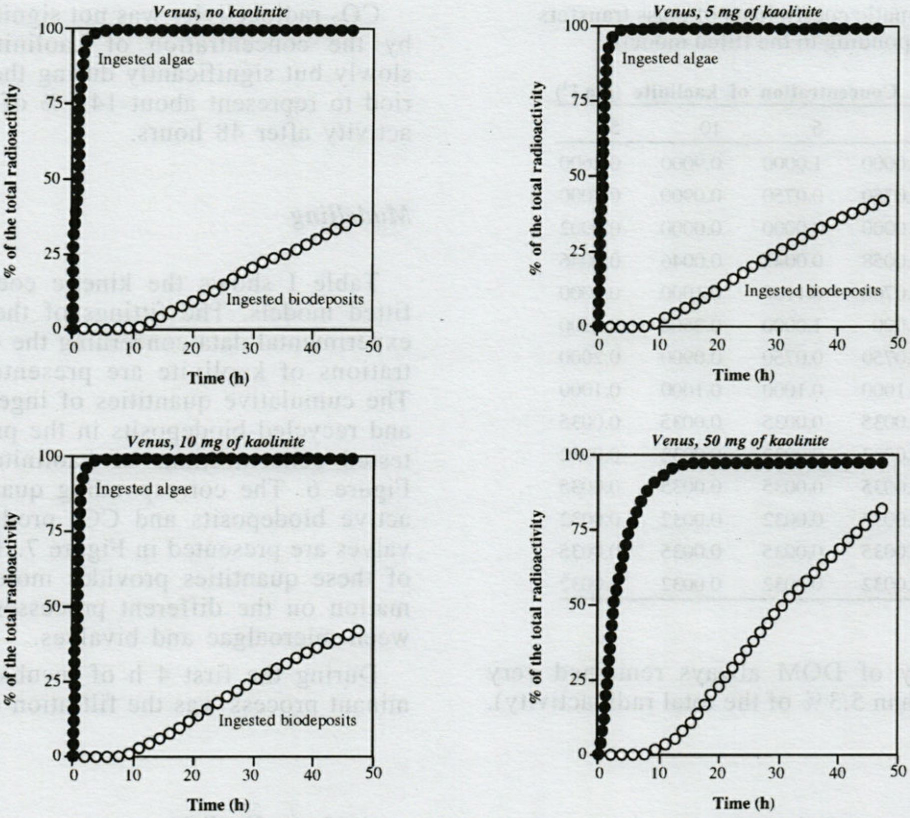

Fig. 6. – *Venus verrucosa.* Time-dependent changes in the cumulative amounts of ^{14}C radioactivity corresponding to the ingestion of microalgae and to the production of biodeposits by bivalves.

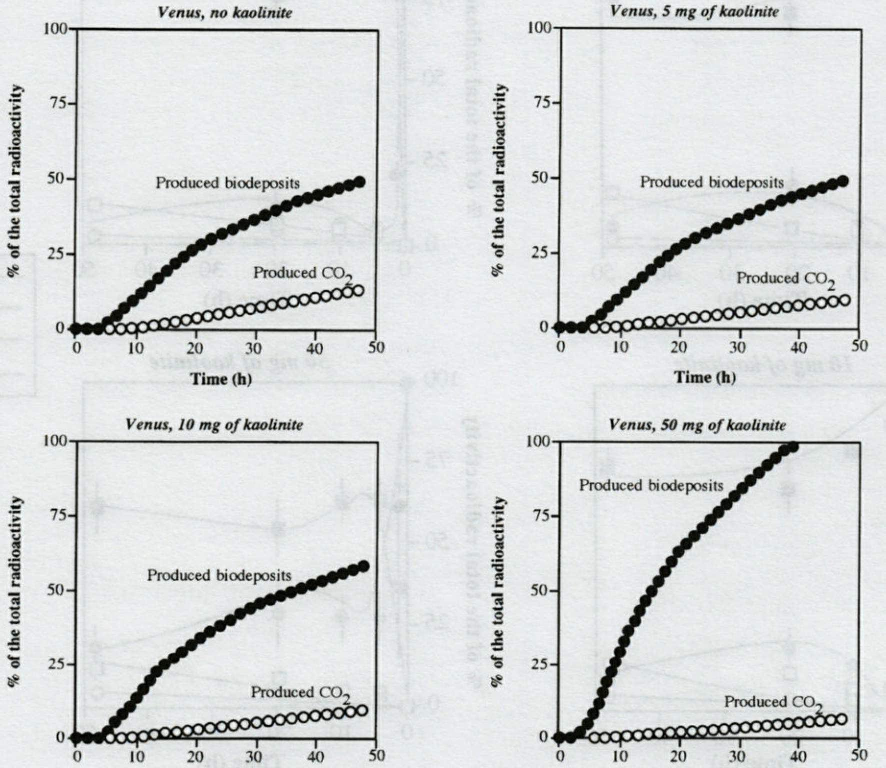

Fig. 7. – *Venus verrucosa.* Time-dependent changes in the cumulative amounts of ^{14}C radioactivity corresponding to the production of CO$_2$ and biodeposits by bivalves.

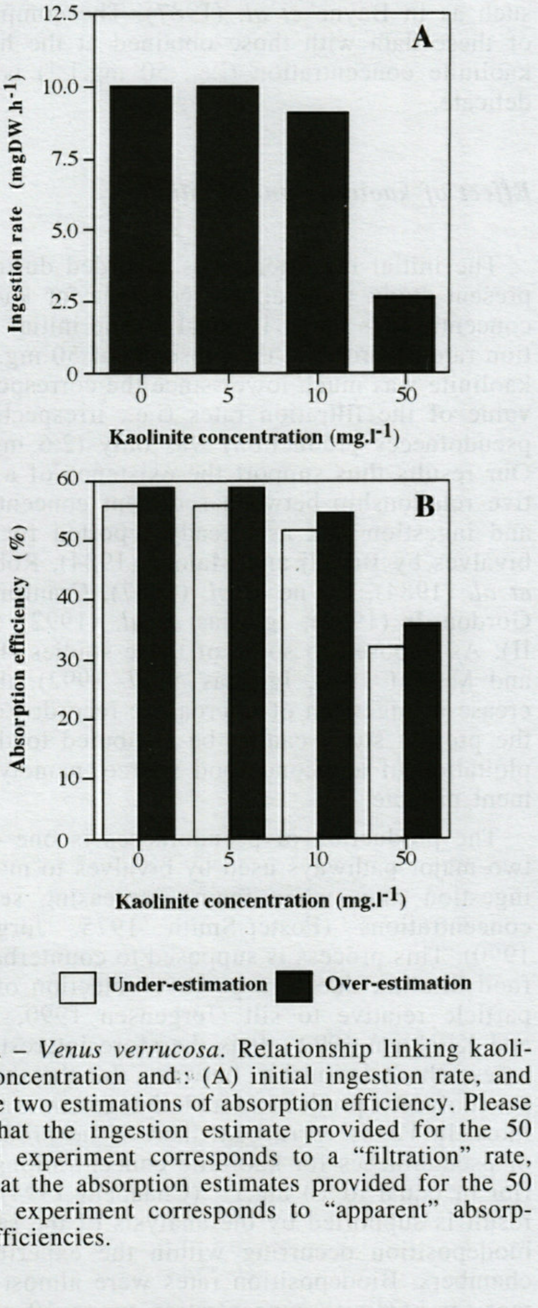

Fig. 8. – *Venus verrucosa*. Relationship linking kaolinite concentration and : (A) initial ingestion rate, and (B) the two estimations of absorption efficiency. Please note that the ingestion estimate provided for the 50 mg.l^{-1} experiment corresponds to a "filtration" rate, and that the absorption estimates provided for the 50 mg.l^{-1} experiment corresponds to "apparent" absorption efficiencies.

pension by the bivalves, which resulted in a decrease in POM radioactivity and in an increase in bivalve's radioactivity. After that, production of biodeposits predominated until 20 h of incubation, resulting in increased POM radioactivity and in decreased bivalve's radioactivity. The recycling of these biodeposits then allowed to reach an equilibrium between POM and Bivalves.

In the presence of low concentrations of kaolinite (i.e., 0, 5 and 10 mg.l^{-1}), radioactivity ingested as microalgae reached almost 99 % of the initial radioactivity after only 4 h incubation. This proportion was only 66.5 % in the experimental chambers containing 50 mg.l^{-1} of kaolinite. For all tested concentrations, consumption of resuspended biodeposits began to be significant after 8 hours of incubation. The recycling of biodeposits was positively correlated with kaolinite concentration. At the end of the experiments, it represented between 35.2 (no kaolinite) and 81.6 % of the total radioactivity (50 mg.l^{-1}).

The cumulative amount of radioactivity corresponding to the production of biodeposits by the bivalves began to be significant after 4 hours of incubation. It increased with kaolinite concentration. After 48 hours of incubation, it represented between 49.0 (no kaolinite) and 109.8 % of the total radioactivity (50 mg.l^{-1}).

The cumulative amount of radioactivity corresponding to the production of CO_2 by the bivalves correlated negatively with kaolinite concentration. At the end of the experiments, it represented between 7.6 (50 mg.l^{-1}) and 13.7 % of the total radioactivity (no kaolinite).

Ingestion and absorption

The ingestion rates determined for the 4 concentrations of kaolinite ranged between 2.6 and 10 mgDW.h^{-1} corresponding to specific ingestion rates ranging between 0.52 and 2 mgDW.gDW^{-1}.h^{-1} (cf. Fig. 8A). Ingestion rates seemed to correlate negatively with kaolinite concentrations. Ingestion rates (10 mgDW.h^{-1}, specific ingestion rate of 2 mgDW.gDW^{-1}.h^{-1}) were strictly identical in the absence or in the presence of low concentration (i.e., 5 mg.l^{-1}) of kaolinite. They were only slightly lower (9 mgDW.h^{-1}, specific ingestion rate of 1.8 mgDW.gDW^{-1}.h^{-1}) for the intermediate concentration (10 mg.l^{-1}). At last, ingestion rates were much lower (2.6 mgDW.h^{-1}) for the high kaolinite concentration (50 mg.l^{-1}, specific ingestion rate of 0.52 mgDW.gDW^{-1}.h^{-1}).

The absorption efficiencies for the 4 tested concentrations of kaolinite are presented in Fig. 8B. Absorption efficiencies were also affected by the concentration of kaolinite. The two estimations of absorption (between 55.3 and 58.6 %) were identical in the absence and in the presence of low concentration (i.e., 5mg.l^{-1}) of kaolinite. Absorption was only slightly lower (between 50.9 and 54.2 %) for the intermediate concentration (10 mg.l^{-1} of kaolinite). As observed for ingestion, absorption was much lower (between 32.3 and 35.3 %) for the high kaolinite concentration (50 mg.l^{-1}).

DISCUSSION AND CONCLUSION

Structure of the model

The model is designed to simulate the exchanges of radioactivity within the experimental chambers containing bivalves. Since the radioactivity is exclusively associated to the microalgae, the kinetic coefficients and thus the ecophysiological parameters derived from the fitting of the model to experimental data thus refers to the consumption of microalgae. The major problem in the modelling process was the simulation of pseudofaeces production. In fact, the application of analog modelling to the analysis of the transfer in aquatic food chains assumes that we are dealing with continuous phenomena (Amouroux and Amouroux 1988, Amouroux *et al.* 1989, Grémare *et al.* 1989, 1991). In closed experimental systems, this is probably not the case for pseudofaeces production since this process is cued by total sestonic concentration which rapidly declines during the time-course of the experiment (see the results of the compartmental analysis). During the present study we have chosen to simulate the pseudofaeces production by a transit through the compartments bivalves 1 and bivalves 2 (i.e., the same pathway as for faeces production) due to the impossibility to experimentally separate faeces from pseudofaeces. Moreover, the creation of a direct link between microalgae and biodeposits (i.e., corresponding to the production of pseudofaeces) would have presented the drawbacks of : (1) using two different types of models depending on kaolinite concentrations, and (2) introducing another kinetic coefficient allowing to adjust the balance between POM and bivalve radioactivity at high silt concentrations.

Nevertheless, this choice has important consequences. Indeed, below the threshold of pseudofaeces production, the constant k_1 strictly corresponds to ingestion whereas below this concentration it corresponds to filtration (i.e., total retention of the material, which will either be rejected as pseudofaeces or as faeces).

The same precaution should be observed when comparing absorption efficiencies recorded for kaolinite concentrations below and above the threshold of pseudofaeces production. Below this threshold the kinetic coefficient of mass transfer k_2 corresponds to defecation whereas above this threshold it accounts both to the production of faeces and pseudofaeces. Thus the absorption efficiencies computed below the threshold of pseudofaeces production are real (i.e., true absorption efficiencies) whereas those computed above the threshold are only "apparent" (for a similar problem see Iglesias *et al.* 1992).

During our experiments pseudofaeces production only occurs during the experiments carried out with a kaolinite concentration of 50 mg.1^{-1} (see discussion below). Results of the modelling approach thus allow for a direct comparison of both ingestion rates and absorption efficiencies recorded at low sediment concentration (i.e., below the threshold of pseudofaeces production) such as in Bayne *et al.* (1987). The comparison of these data with those obtained at the highest kaolinite concentration (i.e., 50 mg.1^{-1}) is more delicate.

Effect of kaolinite on ingestion

The initial ingestion rates recorded during the present study were almost constant for kaolinite concentrations up to 10 mg.1^{-1}. The initial ingestion rate recorded in the presence of 50 mg.1^{-1} of kaolinite was much lower since the corresponding value of the filtration rates (i.e., irrespective of pseudofaeces production) was only (2.6 mg.1^{-1}). Our results thus support the existence of a negative relationship between sediment concentration and ingestion rate as already reported for other bivalves by Bricelj and Malouf (1984), Robinson *et al.* (1984), Bayne *et al.* (1987), Cranford and Gordon Jr (1992), Iglesias *et al.* (1992) (Table II). As opposed to some of these studies (Bricelj and Malouf 1984, Iglesias *et al.* 1992), the decrease in ingestion of microalgae recorded during the present study cannot be attributed to the exploitation of a second food source, namely sediment particle.

The production of pseudofaeces is one of the two major pathways used by bivalves to maintain ingestion rates when facing increasing sestonic concentrations (Foster-Smith 1975, Jørgensen 1990). This process is supposed to counterbalance food dilution due to a positive selection of food particle relative to silt (Jørgensen 1990, Urban and Kirchnan 1992). It is therefore interesting to assess the relationship between the threshold of pseudofaeces production and changes in ingestion rates. In *Venus verrucosa*, there is no production of pseudofaeces for kaolinite concentrations inferior or equal to 10 mg.1^{-1} (Chaabeni 1994). This result is supported by the analysis of the rates of biodeposition occurring within the experimental chambers. Biodeposition rates were almost constant for kaolinite concentration up to 10 mg.1^{-1}. They were then much higher for the 50 mg.1^{-1} experiment. Since in our model there is no differentiation between biodeposits produced as faeces and pseudofaeces (see above), we believe that this increase reflects the onset of production of radioactive pseudofaeces (i.e., containing microalgae). Thus, during the present study, there was only a slight decrease (i.e., 10 %) in ingestion rates in the absence of pseudofaeces production. This result is different from what has been reported (i.e., an average decrease of 53 %) for *Mytilus edulis* fed on *Phaeodactylum tricornutum* in the presence of low silt concentration (Bayne *et al.* 1987).

The effect of sediment concentration on ingestion selectivity in bivalves has already been stu-

Table II. – Review of the litterature data regarding the effect of sediment concentration on the nutrition of filter-feeding bivalves. SFG : Scope for growth, a : apparent absorption efficiency, 1 : at low concentration, h : at high concentration.

Species	Food	Sediment type	Selectivity	Ingestion	Absorption	SFG	Growth	References
C.edule	*T.suecica*	Natural	Positive^{l}	Negative	Negative	-	-	Iglesias *et al.* 1992
C. virginica	*I. galbana*	Kaolinite + starch	Negative	Not significant	-	-	-	Urban & Kirchnan 1992
C. virginica	Artificial diets	Kaolinite	-	-	-	-	Positive^{l}	Langdon & Siegfried 1984
C. virginica	*I. galbana* *T. pseudonana*	Kaolinite	-	-	-	-	Positive	Urban & Langdon 1984
M. mercenaria	*P. paradoxa*	Natural	Negative	Negative	Negative	-	-	Bricelj & Malouf 1984
M. edulis	*D. marina*	Natural (H_2O_2)	Not significant	Positive	-	-	Positive	Winter 1977
M. edulis	*P. tricornutum*	Natural	Not significant	Maximal^{l}	Negative^{h}	-	-	Kiorboe *et al.* 1980
M. edulis	*P. tricornutum*	Natural	-	-	-	-	Positive^{l}	Kiorboe *et al.* 1981
M.edulis	*P. tricornutum*	Natural (ashed)	-	-	Negative	-	-	Hawkins *et al.* 1986
M. edulis	*P tricornutum*	Natural (ashed in most cases)	-	Negative	Negative	Negative (Not significant)	-	Bayne *et al.* 1987
P. magellanicus	*T.suecica*	Bentonite	-	Negative	-	-	Negative	Cranford & Gordon 1992
S. soldissima	*I. galbana*	Attapulgite	-	Negative	Negative	-	-	Robinson *et al.* 1984
S. subtruncata	*P. tricornutum*	Natural	-	-	-	-	Positive^{l}	Mohlenberg & Kiorboe 1981
V. verrucosa	*P. lutheri*	Kaolinite	-	Negative^{h} Not significant^{l}	Negative^{a,h} Not significant^{a,l}	-	-	Present study

died in several species (Kiorboe *et al.* 1980, Iglesias *et al.* 1992; Bricelj and Malouf 1984, Urban and Kirchnan 1992) (Table II). The results are somehow contradictory. Employing a dual tracer technique, Urban and Kirchnan (1992) reported that an increase in kaolinite concentration significantly reduces the ability of the American oyster *Crassostrea virginica* to preferentially ingest rice starch rather than the microalgae *Isochrysis galbana.* The existence of a negative correlation between silt concentration and selection efficiency has also been reported for *Mercenaria mercenaria* fed on a mixture of *Pseudoisochrysis paradoxa* and natural sediment (Bricelj and Malouf 1984). Based on the comparison of chlorophyll *a* contents in the suspension and in the pseudofaeces, Kiorboe *et al.* (1980) concluded that selection efficiency of *M. edulis* was independent of silt concentration. To our knowledge, the only published result suggesting the existence of a positive effect of silt concentration on selection efficiency has been obtained for the cockle *Cerastoderma edule* in the presence of low concentrations of silt (Iglesias *et al.* 1992). It is however important to point out that during these two last studies elevated silt concentration also induced a reduction in ingestion rates. In other word, in most cases selection efficiency does not totally compensate food dilution. This observation is supported by the diminution of retention efficiency of several bivalves submitted to high sestonic concentrations (Palmer and Williams 1980, Wilson 1983, Barillé *et al.* 1993). Besides this, there are some indirect lines of evidence suggesting that the sorting of particles is probably not very efficient in *Venus verrucosa.* Indeed, the ratio of the ingestion rates between the 5 and the 50 mg.1^{-1} experiment was greater than 3.8, which is very comparable to the corresponding dilution of microalgae (ratio from 1 to 4). Thus, the production of pseudofaeces by *V. verrucosa* apparently does not induce a significant increase in the concentration of microalgae within the ingested material as observed by Kiorboe *et al.* (1980) for the selective filter-feeding bivalve *M. edulis.* The major cause of the decrease in ingestion rates of *V. verrucosa* when submitted to increasing concentrations of kaolinite is thus probably the rejection of (labelled) microalgae in the pseudofaeces, which is also consistent with the increased bio-deposition rates recorded during the 50 mg.1^{-1} experiment (see above).

Effect of kaolinite on absorption

The existing data strongly suggest a negative effect of silt concentrations on ingestion rates of filter-feeding bivalves (Table II). However, the literature data regarding the effect of silt concentration on the nutrition of filter-feeding bivalves are less clear for absorption efficiencies than for ingestion rates. This is partly due to the range of variation in measured absorption efficiencies and to methodological problems. During the present study, we found that absorption efficiencies of *Pavlova lutheri* by *V. verrucosa* were almost constant below the threshold of pseudofaeces production. This result can be compared with those of Bayne *et al.* (1987) regarding the blue mussel *M. edulis* submitted to a mixture of algae and silt at low concentrations. These authors reported a significant decrease in net absorption efficiencies (as measured by the ash ratio method). However these authors also observed negative absorption efficiencies for the low quality diets suggesting that there might have been some problems with the experimental procedure. Thus, gross absorption efficiencies (measured based on the use of ^{14}C labelled food) and digestion efficiencies (based on chlorophyll *a* measurements) were assessed during a second set of experiment. In this last case, there was no clear relationship between diet quality and either digestion or gross absorption efficiency, which is in good agreement with the data recorded during the present study.

As stated in the first section of the discussion, absorption efficiency recorded for the 50 mg.1^{-1} experiment is only "apparent" which complicates the comparison with data recorded below the threshold of pseudofaeces production. Iglesias *et al.* (1992) recorded both true and apparent absorption efficiencies of the cockle *Cerastoderma edule* fed on a mixture comprising different proportions of *Tetraselmis suecica* and silt. They reported that the difference between true and apparent absorption efficiencies was positively correlated with the total sestonic concentration and the proportion of silt in the diet. The difference between true and relative absorption efficiencies reached 13.1 % for a mixture of silt and algae and as much as 23.1 % for silt. These values are of the same order of magnitude than the difference between the absorption efficiency of *V. verrucosa* during the 10 mg.1^{-1} (50.9-54.2 %) and the 50 mg.1^{-1} experiment (32.3-35.3 %). It is thus not possible to reach a definitive conclusion on the effect of silt on true absorption of *V. verrucosa* based on the sole results of this set of experiments.

Impact of resuspension on the utilisation of POM by benthic invertebrates

The results of the present study show that the impact of the presence of kaolinite in suspension mainly occurs above the threshold concentration of pseudofaeces production. This suggests that below this threshold, the presence of mineral particles originating from the bottom sediment would have only little effect on the utilisation of phytoplankton by *Venus verrucosa.* Above this threshold, the situation is slightly different since there is an important decrease of ingestion rates. It is difficult to reach a definitive conclusion relative to absorption efficiencies since the values computed below and above the threshold of pseudofaeces production are not directly comparable (see the first and the third section of the discussion).

These results are in relatively good agreement with the existing literature assessing the effect of silt concentration on filtration by suspending bivalves which supports the existence of a decline in both ingestion rates and absorption efficiencies at high silt concentrations. However, the analysis of this literature also suggests that the response to silt concentration is species (Palmer and Williams 1980) or even population specific (Bayne *et al.* 1987). The exact assessment of the effect of sediment resuspension on the bioenergetics of suspension-feeding bivalves will thus necessitate an increase in the number of the biological models tested.

Moreover, suspension-feeders are not the only organisms present at the water-sediment interface. The nutrition of surface and sub-surface deposit-feeders is also likely to be affected by resuspension events (Charles *et al.* 1995). Deposit-feeders are adapted to exploit a very poor food source (Lopez and Levinton 1987), they are thus often able to sort particles with a very high efficiency depending on an array of parameters including size, density, and organic coating (Jumars *et al.* 1982). However, in these organisms, the sorting process is not depending on any critical concentration of silt. Therefore, it would be very interesting to assess the effect of kaolinite concentration on the rates at which benthic deposit-feeders exploit a given food source in order to better understand the exact effect of sediment resuspension on the functioning of benthic trophic network.

ACKNOWLEDGEMENTS. – This work was partly funded through the "Programme National d'Océanographie Côtière".

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Reçu le 28 mai 1998 ; received May 28, 1998
Accepté le 10 août 1998 ; accepted August 10, 1998

VIE MILIEU, 1998, 48 (4) : 309-319

BRYOZOAN FILTER FEEDING IN LAMINAR WALL LAYERS : FLUME EXPERIMENTS AND COMPUTER SIMULATION

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AMBIENT FLOW VELOCITY
BOUNDARY LAYER
SUSPENSION-FEEDING
LOPHOPHORS

ABSTRACT. – Particle paths and velocities have been determined from video recordings above single-line colonies of bryozoans (*Celleporella hyalina, Electra pilosa, Alcyonidium hirsutum, Membranipora membranacea, Flustrellidra hispida*) placed at the bottom of a laminar flow flume in zones of constant velocity gradient (1 to 4 s^{-1}). The laminar wall layer simulated viscous sublayers found in the field for smooth surfaces. Incurrents to lines of 3 to 10 zooids typically distort paths of particles approaching the colony at heights 1 to 2 mm above the level of lophophore inlets and they capture particles from paths 0.7 to 1.2 mm above this level. The experiment was simulated numerically by computing the full three-dimensional laminar flume flow for the case of a line of 10 zooids that were modelled as sink-source pairs. Computed paths of discrete "fluid particles" show how the fraction of captured particles per zooid decreases downstream. Similar results were obtained by computing the continuous concentration distribution in the flow resulting from specifying uniform upstream concentration and sinks at zooids. Computed particle paths show the cross sectional area of approaching flow cleared of particles by the 10 zooid line colony to be about 16 times the frontal area of a simulated lophophore. Fluid particles were captured from paths about 1.3 mm above the sink. At twice the flowrate, the area cleared of particles reduced to about 7 times the frontal area while feeding rate increased by about 19 %.

HYDRODYNAMISME LOCAL
COUCHE LIMITE
SUSPENSIVORES
LOPHOPHORES

RÉSUMÉ. – Alimentation par filtration des Bryozoaires dans des couches laminaires : essais au laboratoire et simulation informatique. Les trajectoires et les vitesses des particules ont été déterminées à l'aide d'enregistrements video effectués au-dessus de colonies de Bryozoaires formant une colonne unique (*Celleporella hyalina, Electra pilosa, Alcyonidium hirsutum, Membranipora membranacea, Flustrellidra hispida*) placée à la base d'un écoulement laminaire dans des zones de gradient linéaire de vitesse (1-4 s^{-1}). L'écoulement laminaire simule les sous-couches visqueuses existant dans la nature le long de parois lisses. La trajectoire de particules approchant une colonne de 3 à 10 zooïdes est typiquement modifiée à une hauteur de 1 à 2 mm au-dessus de l'ouverture des lophophores et ceux-ci capturent les particules dans les couches situées entre 0,7 et 1,2 mm au-dessus de ce niveau. Les essais de laboratoire ont été simulés numériquement en calculant l'écoulement laminaire tri-dimensionel dans le cas d'une colonne de 10 zooïdes considérés comme des paires d'entonnoir capteur-source. Les trajectoires calculées des « particules de fluide » montrent comment la proportion de particules capturées par zooïde décroit vers l'aval de l'écoulement. Des résultats semblables ont été obtenus en calculant les taux de concentration en aval de la colonie provenant de concentrations uniformes en amont de la colonie, et d'un nombre donné d'entonnoirs par zooïde. Les trajectoires calculées des particules montrent que la proportion de section transversale d'écoulement qui est vidée de particules est équivalente à 16 fois la zone frontale d'un des lophophores simulés. Les particules de fluide sont capturées dans les trajectoires situées à environ 1,3 mm au-dessus des entonnoirs. Pour un courant deux fois plus fort, la surface vidée de particules est réduite à environ 7 fois la zone frontale, mais le taux de capture augmente d'environ 19 %.

INTRODUCTION

Bryozoans are active filter feeders working an energy-consuming lophophore filter-pump (Bullivant 1968, Gordon 1974, Ryland 1976, Winston 1978, Gordon *et al.* 1987, Grünbaum 1995, Riisgård & Goldson 1997, Riisgård & Manríquez 1997). Water from near the surface of a bryozoan colony is pumped downward by the lateral cilia on the crown-tentacles of the individuals. The flow velocity at the entrance of the lophophores is typically 2 to 3 mm s^{-1} (Riisgård & Manríquez 1997, Nielsen & Riisgård 1998). In encrusting colonial bryozoans, which form a continous and often fairly smooth layer, the filtered water moves laterally along the substratum between the individual lophophores, and finally in e.g. *Membranipora villosa*, the water emerges from 'chimneys' as a jet of substantial speed (about 20 mm s^{-1}) (Lidgard 1981).

Due to their small size bryozoans must be able to cope with thin boundary layers and steep velocity gradients above surfaces of marine macroalgae, rocky outcrops etc. on which they live. Therefore, it may be expected that the feeding success, choice of habitat, colony form and distribution are closely related to the way in which bryozoans deal with the flowing surrounding water (Okamura 1984, 1985, Eckman & Okamura 1998).

For a long time it has been recognized that a variety of processes of biological interest are strongly influenced by water motions at the boundary with the sea floor (Jumars & Nowell 1984, Jumars 1993). It has also been realized that the processes in the bottom boundary layer may be modelled in flumes (Nowell & Jumars 1987, Fréchette *et al.* 1989, Emlet 1990, Hart *et al.* 1991, Butman *et al.* 1994, O'Riordan *et al.* 1993, 1995, Anthony 1997). Nowadays, flumes with widely different size, shape and flow characteristics are used for manifold purposes (Wildish & Kristmanson 1997). But so far the use of flumes in benthic filter-feeding biology has mainly dealt with studies of boundary layer flows in supplying phytoplankton to mussels and other macro-benthic filter feeders. Thus, most studies deal with the 'logarithmic' layer where the velocity varies as the logarithm of the distance above the bottom. The logarithmic layer is turbulent but below this layer, due to viscous damping, there exists a thin layer of essentially laminar flow near hydrodynamically smooth surfaces. This layer is designated the viscous sublayer or the 'linear sublayer' because the velocity varies linearly with the distance above the substratum (Emlet 1990, Jumars 1993, Vogel 1994, Mann & Lazier 1996, Wildish & Kristmanson 1997).

The viscous sublayer is typically in the order of millimetres thick at low flowrates but decreases in thickness with increasing flowrate. Encrusting filter-feeding bryozoan colonies may often (or perhaps as a rule) reside within this viscosity-dominated layer (Lidgard 1981, Grünbaum 1995) although Eckman & Okamura (1998) have claimed that such conditions may occur only under restrictive circumstances or if the bryozoans foul flat blades of marine macroalgae. But in a recent study, Hurd *et al.* (1997) measured the velocity profiles of seawater flow along a blade of a giant kelp exposed to unidirectional laminar flow in a flume. At low free-stream velocities (< 2 cm s^{-1}) the boundary layer was laminar in the blade mid-region but turbulent at the blade end. However, no detailed information was given about the thickness of the viscous sublayer. At higher free-stream velocities (> 2 cm s^{-1}) the velocity boundary layer was turbulent and, depending on blade morphology, there were recirculating regions.

A detailed mathematical model of laminar feeding currents in encrusting bryozoans in the absence of external flow was recently presented by Grünbaum (1995). Closely spaced zooids forming a circular colony experience hydrodynamic interference that results in a significant reduction of feeding current per zooid as the number of zooids increases. This effect is especially strong in the absence of 'chimneys' because excurrents flowing in the substratum can only escape at the rim of the colony. For an in-line colony, however, the interference is minimal because excurrents escape to the sides of zooids. Eckman & Okamura (1998) solved the two-dimensional convection-diffusion equation for the concentration boundary layer developing in both turbulent and laminar flows over encrusted actively feeding bryozoans, and accounted for excurrents through a phenomenological model of mixing. This theoretical study shows how the per-lophophore rates of particle capture were predicted to decrease downstream of the first zooid in a colony, depending on flowrate and zooid spacing. It was also concluded that, in general, feeding was greater from turbulent flow than from laminar flow, except for closely spaced zooids where excurrent chimney effects could provide added mixing.

Due to the uppermost parts of the lophophores of encrusting bryozoans being typically raised only about 0.5 to 1.5 mm above the substratum, it seems obvious that filter-feeding in the viscous (linear) sublayer may frequently take place – or perhaps be the usual condition. Therefore, the physical environment experienced by encrusting bryozoan colonies living on brown algae, such as *Laminaria* sp., or less commonly on other algal substrates, is 'one of reduced flow within a boundary layer' (Lidgard 1981).

Our knowledge about viscous sublayers in the field is very limited and more empirical measurements are needed to understand the interactions between sessile organisms and the surrounding water (Shashar *et al.* 1996). Protected embayments may be subject only to tidal changes in water level and velocities that rarely exceed 10 cm s^{-1}. In areas that experience seawater velocities < 4 to 6 cm s^{-1}, seaweed productivity may be limited by the development of a boundary layer that reduces the transport of nutrients to the blade surface (Hurd *et al.* 1996). But this layer, inhabited by encrusting bryozoans, should perhaps also be regarded as a protected niche for these animals. Given the flexibility and closeness of tentacles these protrusions can hardly be compared to usual rigid roughness elements. Also, the boundary layer flow experiences 'suction' due to incurrents which are known to stabilize the flow or it may be obstructed by regions of spines that reduce the velocity gradient. It therefore seems relevant to consider situations of bryozoan filter feeding in a viscous layer.

The present work deals with flume studies and computer simulation of bryozoan particle capture in a viscous wall layer. The starting point – and assumption – is that filter feeding by bryozoans in nature takes place in the linear gradient region adjacent to the surface. Seen in that perspective it is of considerable interest to know how the filter feeders deal with velocity gradients in which they find themselves.

MATERIALS AND METHODS

Experimental animals and flume observations: Flume studies were performed with 5 species of bryozoans collected at low tide in the Menai Strait, UK, in May 1997 : *Celleporella hyalina, Electra pilosa, Alcyonidium hirsutum, Membranipora membranacea, Flustrellidra hispida.* Using a scalpel, the continuous encrusting layer of colonial zooids on fronds of seaweed was reduced to a single row of individuals. A rectangular piece of frond (30 × 15 mm), with the lengthwise located row, was placed in a small flume (Fig. 1). Measurements were commenced after a re-establishment period of about 24 h. In one case the bryozoans in the flume were replaced by a small glass tip (opening = 0.27 mm) connected to a thin tube thus enabling siphoning at different flowrates analogous to the pumping of a bryozoan lophophore.

Particle paths and velocities were recorded at 20 °C using a video camera (Kappa CF 11/1) attached to a horizontal placed microscope (Wild M3C), and a 50 half-frames per second video recorder (Panasonic NV-FS200 HQ). The depth of focus (about 4 mm) ensured that only particles in the mid plane of the flume were registred. The position of particles (6 µm flagellate cells of *Rhinomonas reticulata*) upstream as well as above the row of zooids were recorded and the position of the particles traced. This was done by mounting a transparent plastic sheet onto the video screen so that the tentacle contours as well as the position of suspended particles were marked with a time interval of 5 video frames = 0.1 s using a pen directly on the sheet. The length, width and height (distance from substratum with bryozoans to free water surface) of the flume were 200, 15 and 70 mm, respectively. The flow was set up by means of a pump recirculating the seawater, and the volume flow was regulated by means of an adjustable outlet placed 100 mm downstream of the bryozoans. All measurements were done at the School of Biological Sciences, University of Wales, Bangor, U.K.

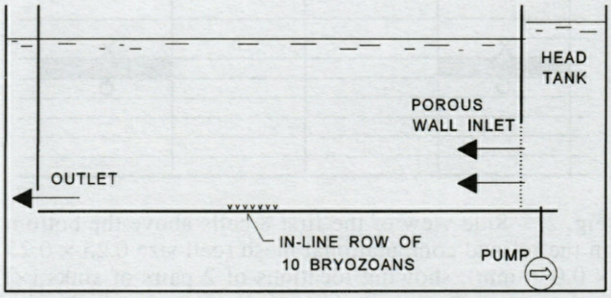

Fig. 1. – Flume (schematic) with row of 10 bryozoans positioned at bottom in mid-plane of flume chamber (200 × 70 mm by 15 mm deep), having uniform inflow through a 35 × 15 mm porous wall inlet (lower right wall) and an adjustable outlet (lower left wall).

Computational model : To ensure an accurate simulation the flow was computed in the whole flume chamber, from inlet to outlet (Fig. 1). Being interested in the trajectories of captured particles and hence the boundary layer depletion, only the net effect of cilia-driven feeding currents of each lophophore in the line of bryozoans was simulated by source-sink pairs of specified flow.

Thus, the computational domain of flume chamber (200 × 70 mm by 15 mm deep), had at the right face (lower half) a 35 × 15 mm uniform flow inlet (U = 10.9 mm s^{-1}, corresponding to a total flow of 5.7 ml s^{-1}, and at the left face (near bottom) a 5 × 15 mm outlet condition. The top was a free surface with imposed no-shear condition, and side walls were imposed the no-slip condition.

The numerical study used the finite volume method (Patankar 1980) available in a standard computer code (STAR-CD). The steady, three-dimensional Navier-Stokes equations were solved on an unstructured Cartesian mesh (about 190,000 nodes), employing a self-filtering central-difference scheme and the SIMPLE pressure-velocity coupling.

The computational mesh consisted of a coarse mesh (cell size 4 × 3.5 × 1.5 mm), refined in 6 steps to the finest mesh (cell size 0.25 × 0.25 × 0.036 mm) in which were placed a total of 10 sink-source pairs. These sink-source pairs simulated a line colony of lophophores of *Electra pilosa* (Riisgård & Maríquez 1997, Table 4 index no. #4 therein), each of strength 1.09 ml h^{-1}, located from 95.5 mm to 102.5 mm from the inlet and in cells in the midplane of the flume model. The sink of specified volume flow was located in one cell and a source of equal volume flow and of a corresponding

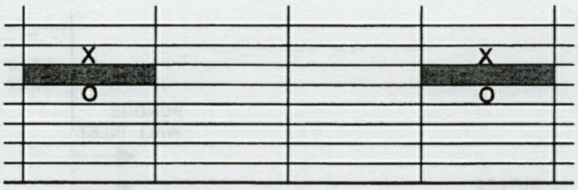

Fig. 2. – Side view of the first 8 cells above the bottom in the refined computational mesh (cell size 0.25 × 0.25 × 0.036 mm), showing locations of 2 pairs of sinks (×) and sources (○), separated by cell (cross-hatched) with impermeable horizontal faces.

downward directed momentum source was located two cells below (Fig. 2). To ensure a downward directed sink flow a horizontal cell-face between sink and source was separated by an impermeable wall.

Once a converged solution had been established, neutrally buoyant 'fluid particles' were started with the local velocity from a position 6.5 mm upstream of the first model zooid and tracked, in this way simulating the experiment. A total of 1050 particles were arranged in 21 columns of 50 particles, covering the central width of 2.5 mm and a height of 1.79 mm, which ensured that only a fraction of particles (typically about 10 %) would be captured. In this way the capture capacity in terms of upstream flow area cleared of particles could be determined. Capture was registred at a given lophophore when a particle entered its sink.

As an alternative approach to determine the theoretical feeding potential of zooids, given the steady velocity field and specifying a uniform upstream concentration of unity representing food particles, zero concentration at sources on the assumption of 100 % retention, and zero flux at all walls, the resulting concentration distribution was computed. Using a low value of diffusivity (3×10^{-9} m^2 s^{-1}) the solution of the convection-diffusion equation gave transport with negligible dispersion. Then, the value of concentration at each sink represented the feeding potential at that location since the product of volume flow and concentration at a sink equalled the feeding rate at that point.

RESULTS

Flume experiments

Figure 3 shows the upstream velocity profiles and particle trajectories above a line of 3 lophophores of *Celleporella hyalina* in two situations. In both cases (#1 and #2) it was verified that the upstream flow was laminar, and that the velocity varied linearly with height above the bottom (Fig. 3, lower fig., recorded about 50 mm upstream of the colony).

Figure 4 shows results obtained with a line of 10 *Electra pilosa*. The figure allows a comparison between individuals without long spines (Fig. 4A) and individuals with long spines (Fig. 4D). The upstream velocity profile (Fig. 4B & C) and the velocities above and within the long spines (Fig. 4E & F) clearly illustrate how the spines reduce the laminar flow velocity gradient.

The particle trajectories above a single row of zooids of 3 differently sized species of bryozoans *(Alcyonidium hirsutum, Membranipora membranacea* and *Flustrellidra hispida)* are shown in Fig. 5.

In Fig. 6 the bryozoans in the flume have been replaced by a small glass tip connected to a thin tube thus enabling siphoning at 3 different flowrates, analogous to the pumping of a bryozoan lophophore, except that flow corresponding to excurrent was not returned. It is seen that the strength of the sink highly influences the thickness of the 'feeding layer' from which particles are captured.

Computational results

Simulations were carried out with a specified volume flow of 1.09 ml h^{-1} for each sink-source pair, which corresponds to the data from the experiment shown in Fig. 4A, and for the nominal flume flow of 5.7 ml s^{-1}, as well as twice that flume flow. In both cases laminar boundary layers developed with a linear vertical velocity gradient near the bottom that decreased downstream. In the mid-plane of the flume, at positions 50 mm and 5 mm upstream of the first sink-source pair, the velocity gradient at nominal flume flow was $\partial u/\partial y = 3.1$ s^{-1} and 1.6 s^{-1}, respectively. The former value should be compared to the experimental value $\partial u/\partial y = 3.26$ s^{-1}, derived from data in Fig. 4B & C.

Figure 7 shows computed trajectories of fluid particles entering with the flow from right. For clarity only particles started in the vertical plane aligned with the sinks are shown. About 10 % of all particles released were captured. Figure 8 shows the fraction of these particles that were captured by each lophophore (+). These results obtained from trajectories are compared to those obtained from the concentration distribution (—). Also shown in the figure are corresponding results for twice the nominal flume flow, (○) and (---). In each case the sum of discrete values at the 10 zooids adds up to unity.

For the case of twice the nominal flume flow, because of the nature of the viscous boundary layer development along the bottom, velocity gradients at positions 50 mm and 5 mm upstream of the first sink-source pair increased to the values $\partial u/\partial y = 5.95$ s^{-1} and 4.8 s^{-1}, respectively. While the distribution of relative feeding rate per zooid only changes little (Fig. 8), the magnitude of feeding rate increased by about 9 % at the first zooid

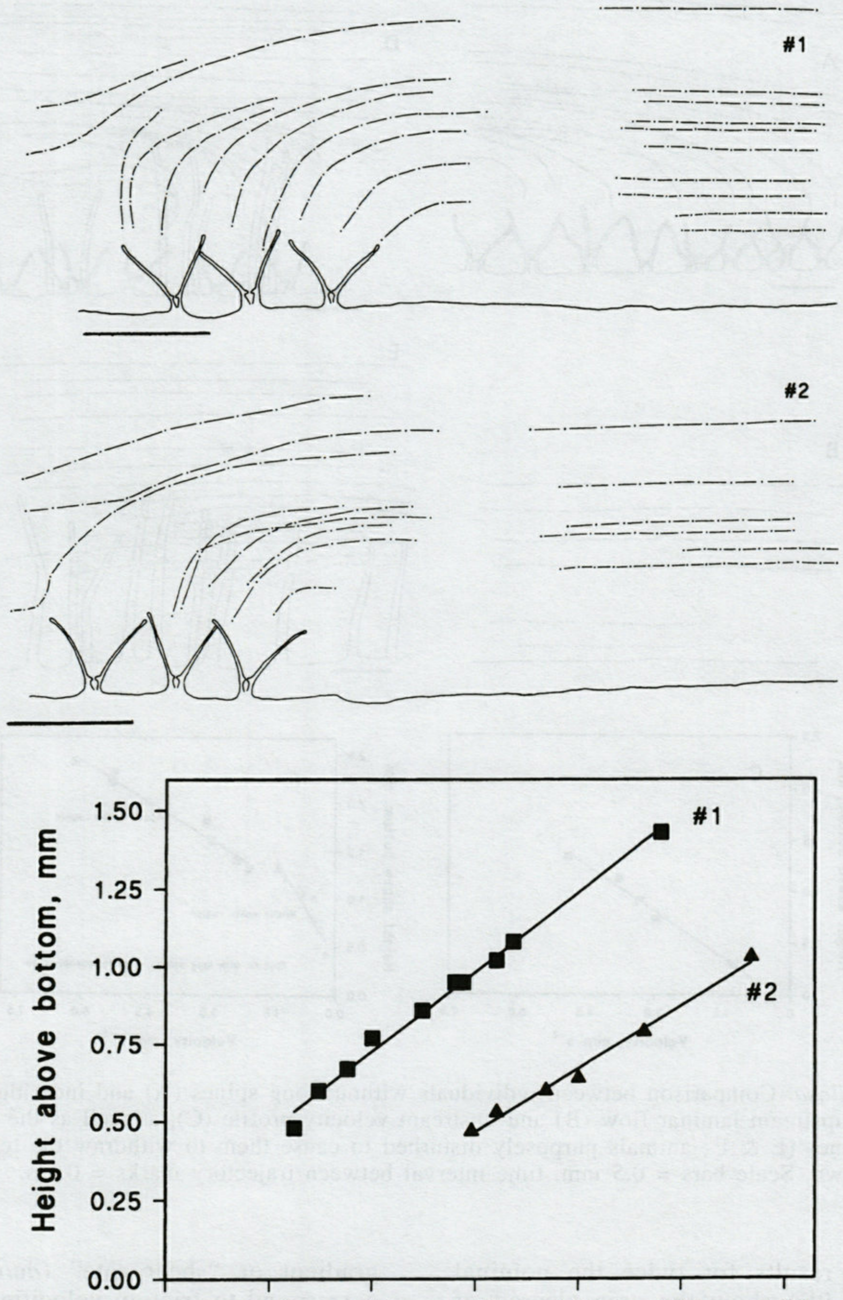

Fig. 3. – *Celleporella hyalina.* Upstream velocity profiles (#1 & #2 right side) and particle trajectories above 3 lophophores in flume. The lowest figure shows that the estimated flow velocity as a function of height above the bottom for 2 settings of the adjustable gate (Fig. 1) : 5 × 15 mm (#1) and 10 × 15 mm (#2) open outlet. Scale bar = 0.5 mm, time interval between trajectory marks = 0.1 s.

and 21 % at the 10th zooid, as compared to the case of nominal flow, hence becoming slightly more uniform at this higher flow.

Figure 9 shows a cross-section of the approaching flow, located 6.5 mm upstream of the colony where particles were started, each cross indicating that a particle started from this location was captured. Thus, the marked region gives an idea of the area of approaching flow cleared of particles. For nominal flow (Fig. 9A), the size of the area was about 16 times the frontal area of a simulated lophophore. Particles were captured from paths as high as about 1.3 mm above the sinks and as much as about 0.75 mm to the sides.

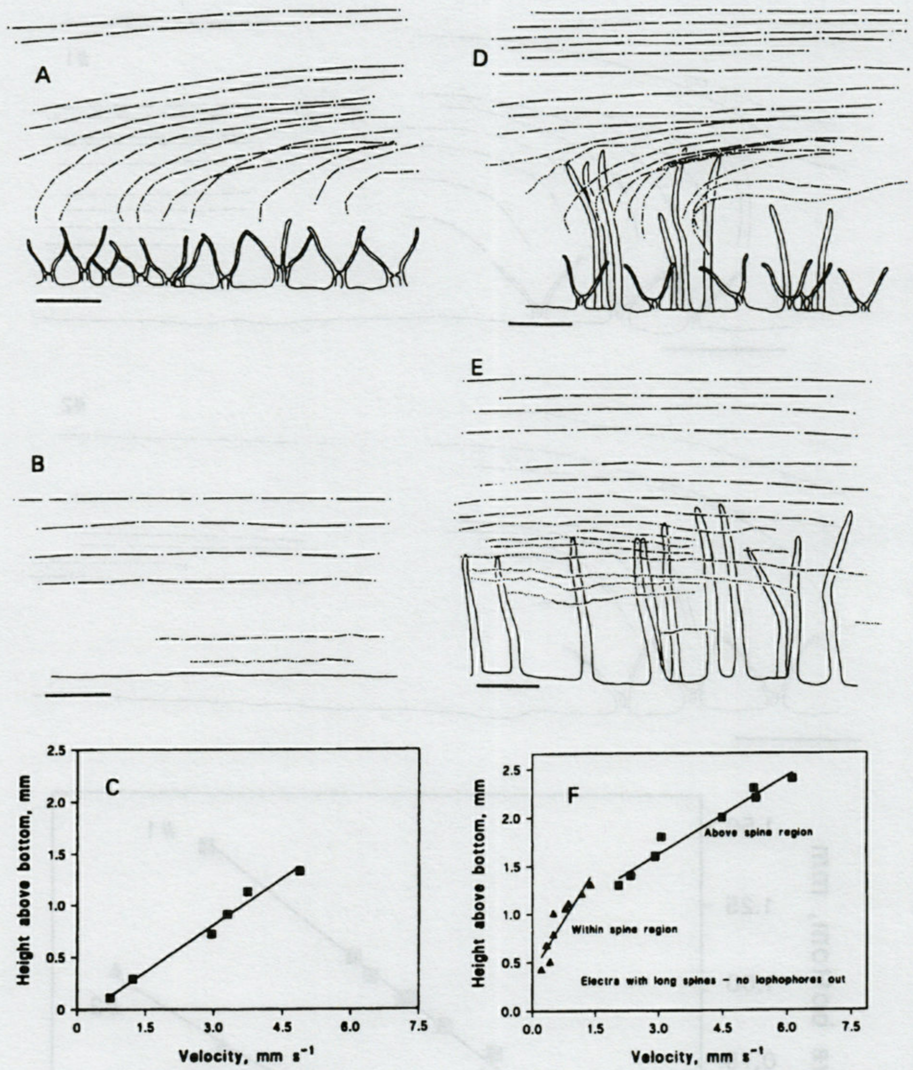

Fig. 4. – *Electra pilosa*. Comparison between individuals without long spines (A) and individuals with long spines (D) in flume. The upstream laminar flow (B) and upstream velocity profile (C), as well as the velocities above and within the long spines (E & F; animals purposely disturbed to cause them to withdraw the tentacular crowns into the casing) are shown. Scale bars = 0.5 mm, time interval between trajectory marks = 0.1 s.

Corresponding results for twice the nominal flume flow (Fig. 9B) show the area cleared of particles to be only about 8 times the frontal area of a lophophore, and particles were captured from paths about 1 mm above and 0.5 mm to the sides of the sinks. Due to the higher velocity the net flux in terms of number of particles captured per unit time increased by about 19 % on the average.

DISCUSSION

Using flume experiments and numerical simulation the present study has focussed on the feeding process in small line colonies of bryozoans in a laminar wall layer. Values of the velocity gradient or "shear rate" ($\partial u/\partial y$ = 1 to 4 s^{-1}) correspond to friction velocities or "shear velocities" ($u^* = (\upsilon\ \partial u/\partial y)^{1/2} \approx$ 3 to 6 mm s^{-1}) (Vogel 1994) that are similar to those found in the laminar sublayer of turbulent flow over smooth surfaces (e.g. Muschenheim 1987, Fréchette *et al.* 1989, Shashar *et al.* 1996).

Flow pattern

The tracking of small food particles assumed to be neutrally buoyant provided information on both particle capture and fluid motion, because slip between fluid and particle motion was negligible. Experiments have shown how feeding currents distort a laminar wall layer above single-line colonies of a number of bryozoans (*Celleporella*

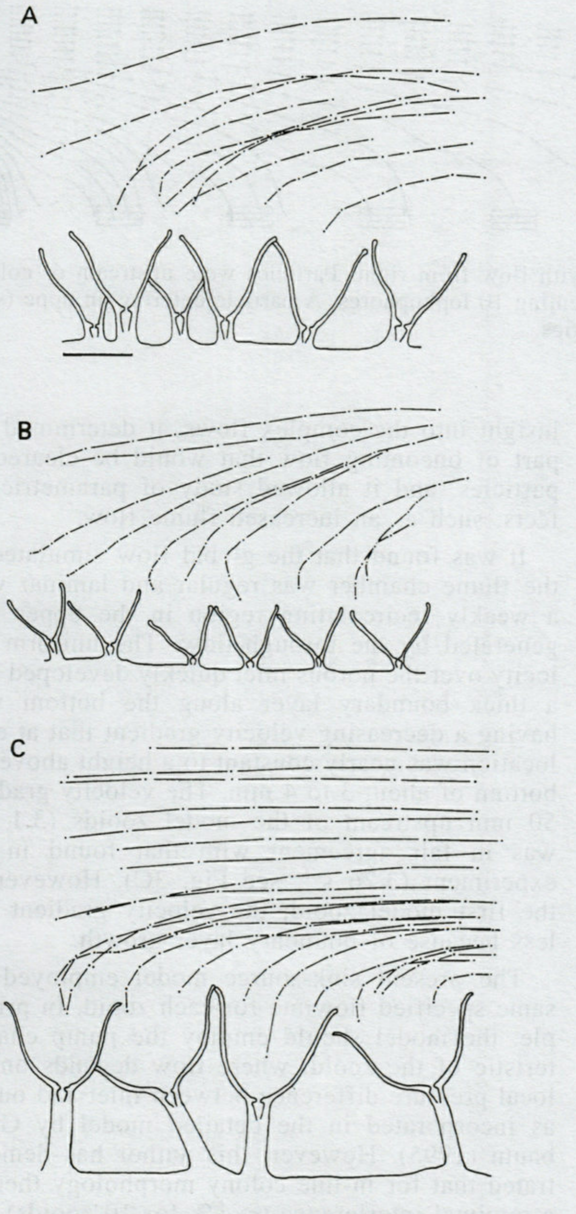

Fig. 5. – Examples of particle trajectories above the lophophores of 3 species of bryozoans in flume. (A) *Alcyonidium hirsutum*, (B) *Membranipora membranacea*, (C) *Flustrellidra hispida*. Scale bar = 0.5 mm, time interval between trajectory marks = 0.1 s.

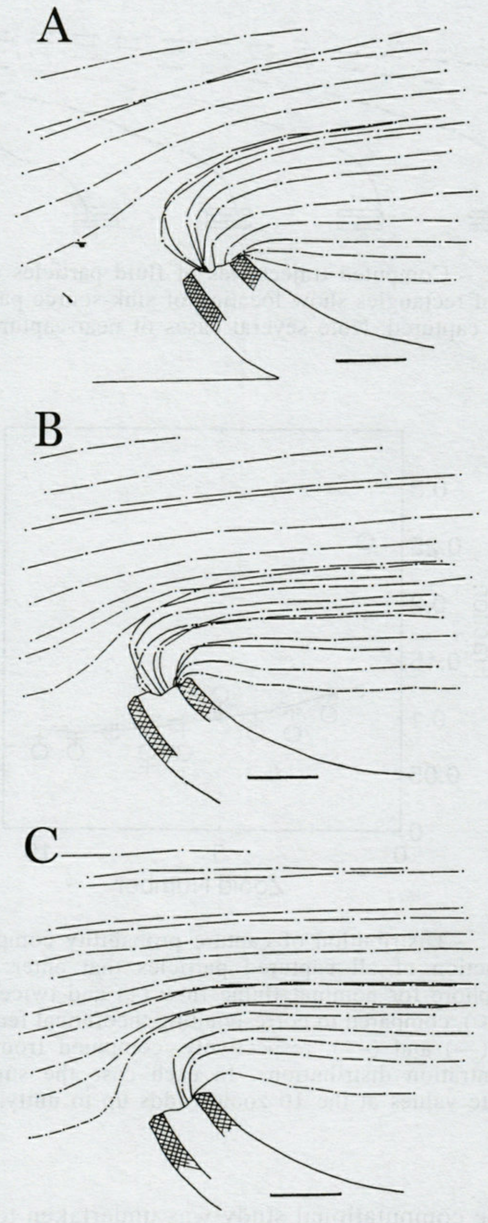

Fig. 6. – Bryozoans in flume replaced by a small glass tip (opening = 0.27 mm) and connected to a thin tube thus enabling siphoning at different flowrates (Q), analogous to the pumping of a bryozoan lophophore. (A) Q = 17 ml h^{-1}, (B) 11 ml h^{-1}, (C) 9 ml h^{-1}. Scale bar = 0.5 mm, time interval between trajectory marks = 0.1 s.

hyalina, Electra pilosa, Alcyonidium hirsutum, Membranipora membranacea, Flustrellidra hispida). Thus, incurrents to lines of 3 to 10 zooids typically distort paths of particles approaching the colony at heights 1 to 2 mm above the level of lophophore inlets and they capture all particles from paths 0.7 to 1.2 mm above the level of lophopore inlets, the higher values applying to the longer colonies of 10 zooids. Paths were observed to curve toward the zooids so that captured particles entered lophophores on nearly vertical paths. In reduced velocity gradients in the wall layer, when spines are present (Fig. 4D), particle paths even reversed direction turning upstream before entering the lophophore. This phenomenon, to be expected for flow to a strong sink, was also demonstrated by recording paths to a glass tip through which water was drawn at increasing volume flows for a fixed velocity gradient (Fig. 6). The number of particles tracked in the experiments was insufficient to deduce results on the per-zooid relative feeding rate.

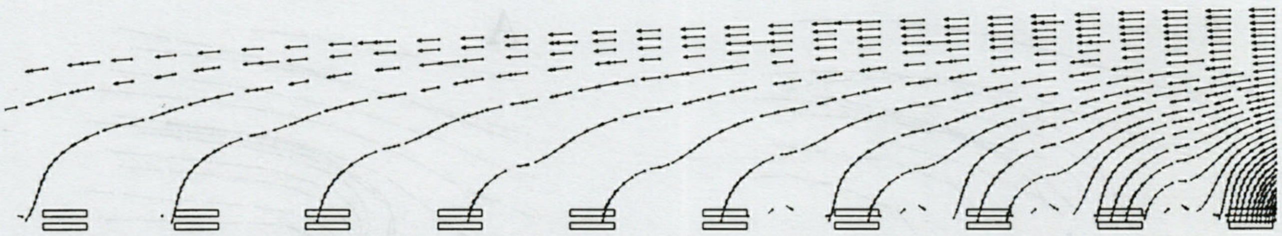

Fig. 7. – Computed trajectories of fluid particles entering with flow from right. Particles were upstream of colony. Pairs of rectangles show location of sink-source pairs representing 10 lophophores. A particle entering an uppe (sink) cell is captured. Note several cases of near-capture trajectories.

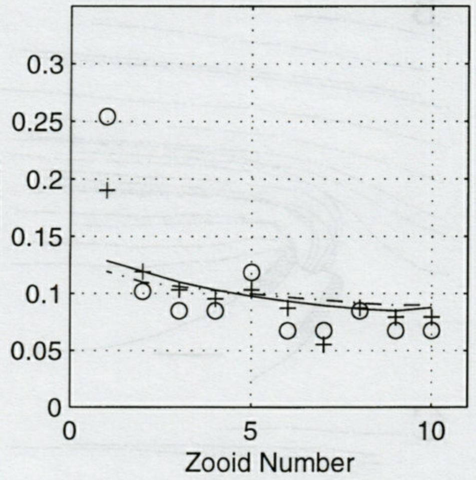

Fig. 8. – Distribution of capture probability computed as fraction of all captured particles that enter each lophophore for nominal flume flow (+) and twice that flow (○), compared to corresponding theoretical feeding rates (—) and (– –), respectively, computed from the concentration distributions. In each case the sum of discrete values at the 10 zooids adds up to unity.

The computational study was undertaken to determine the per-zooid capture rate along a 10-zooid line colony, a situation studied in one experiment (see Fig. 4A). In addition, it provided insight into the complex flows, it determined the part of oncoming flow that would be cleared of particles, and it allowed study of parametric effects, such as an increased flume flow.

It was found that the global flow simulated in the flume chamber was regular and laminar with a weakly recirculating region in the upper part generated by the through-flow. The uniform velocity over the porous inlet quickly developed into a thick boundary layer along the bottom wall having a decreasing velocity gradient that at each location was nearly constant to a height above the bottom of about 3 to 4 mm. The velocity gradient 50 mm upstream of the model zooids (3.1 s^{-1}) was in fair agreement with that found in the experiment (3.26 s^{-1}, see Fig. 3C). However, at the first model zooid, the velocity gradient was less because of boundary layer growth.

The present sink-source model employed the same specified flowrate for each zooid. In principle, the model should employ the pump characteristic of the zooid, where flow depends on the local pressure difference between inlet and outlet, as incorporated in the detailed model by Grünbaum (1995). However, this author has demonstrated that for in-line colony morphology there is a minimal interference (< 4 % for 10 zooids), i.e. each zooid will pump a volume flow essentially as an isolated zooid. This justified the use of the same volume flow for all model zooids.

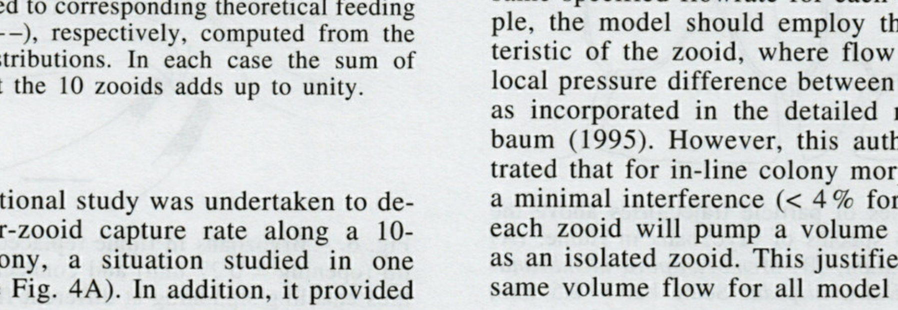

Fig. 9. – Cross section of flow 6.5 mm upstream of 10 zooid line colony, showing starting location (+) of particles captured. Nominal flow (A) and twice that flow (B). Also shown are positions of sinks (×), impermeable cell faces (- —) and sources (○) representing zooids located in sections further downstream.

Above the line colony the flow was systematically distorted due to the sinks, as seen from the particle tracks in the vertical plane through sinks (Fig. 7) being similar to those of the experiment (Fig. 4A). To the sides of each zooid, however, a complex three-dimensional flow prevailed. Downward directed source flows cleared of particles were deflected by the bottom, primarily to the sides of the line colony, creating two vortices of opposite sign aligned with the main flow and aiding the transfer of particles from the sides toward the center. Clearly, the line colony is very special and of simple geometry, but the last mentioned flow features may also be at play along edges aligned with the main flow for the normal geometry of fairly large encrusting bryozoans.

Particles that were started upstream in the vertical (symmetry) plane through sinks tended to stay in this plane (Fig. 7) dispite the induced secondary flows described above. Most of the particles from this and neighboring planes were captured (Fig. 9A), but not all because of the discrete nature of sinks leading to near-capture trajectories (Fig. 7). Particles which started further away from the center underwent complex motion and some were captured. The difference in shape of area of oncoming flow cleared of particles shown in Fig. 9A & B can be explained by the source flow induced vortices being less effective in bringing particles toward the center when flume flow was increased. Vortex centers were located about 0.7 mm above the bottom and about 0.5 mm to the sides of sink-source pairs, thus particles that started near the center of these vortices were not displaced sufficiently to be captured. Asymmetries in Fig. 9A & B are due to sink-source pairs being positioned in a plane offset 0.125 mm from the midplane of the flume chamber. Vacancies in the pattern of starting points of captured particles are due to near-capture trajectories.

Feeding rates

Feeding rates per zooid were computed in two ways; by tracking particles started upstream of the colony and recording those captured at each zooid, and by determining the concentration at each zooid given an upstream uniform distribution. The scatter in computed trajectory results for fraction of particle capture by each zooid (Fig. 8) is due to the small total number. The first zooid has about twice the capture rate of the followings zooids. For the latter, capture rate decreases moderately downstream. The computed results show that the last zooid has a slight advantage over the preceeding ones because it has no competition from downstream zooids. The present results for fraction of particle capture obtained from the concentration distribution do not show the abrupt decrease after the first zooid displayed by the trajectory results. In this regard the results are similar to those of Eckman & Okamura (1998) also obtained from concentration distributions, now for widely spaced lophophores.

The difference between the two computational schemes, although using velocity information from the same discrete mesh, lies with the *apriori* averaging of concentration over cell faces of sinks compared to the very accurate trajectories computed in small increments using interpolated velocities. The latter gives in effect a distribution of the flux of particles over the cell face of each sink. For this reason it is believed that particle tracking provides more realistic results. It dublicates the physical process and shows the sensitivity to upstream starting position of particles.

Both schemes showed that feeding rates increase with increasing flume flow, as also found by Eckman & Okamura (1998), which is to be expected with the associated thinning of the concentration boundary layer and increase in flux of particles. From particle tracking, feeding rate is proportional to the sum of products of captured particles and the velocity at their starting location (Fig. 9) which increases linearly with height above the bottom. At nominal flume flow and twice that value the number of captured particles decreased from 130 to 59, but the velocity gradient increased, leading to an increase in capture of about 19 %. From the concentration distribution, feeding rate is proportional to the product of sink flow and concentration, showing a similar increase when flume flow was doubled.

Flow control and spinosity

It has been shown that e.g. *Membranipora membranacea*, within 1 to 2 days after the colony detects a molluscan predator, can produce spines as a mean of defense (Harvell 1990, Grünbaum 1997). But spinosity in *Flustrellidra hispida* has also been found to be highly correlated with the degree of water movement (Whitehead *et al.* 1996). Thus colonies from wave-swept turbulent conditions have more spines than colonies from sheltered habitats. This suggests that spinosity may also be partially controlled by the hydrodynamic environment (Bayer *et al.* 1997). The functional significance of spinosity in *Electra pilosa* (Fig. 4) is obscure; but the spines are too small to produce local turbulence near the lophophores. On the contrary, the spines clearly dampen the flow velocity of the viscous sublayer. The hydrodynamic interference of spines with water transport in the feeding process has recently been studied by Grünbaum (1997) who found that spination in *M. membranacea* reduced the exponential growth rate in 'fast flow' (1.1 cm s^{-1}).

ACKNOWLEDGEMENTS. – H.U.R. was supported by a grant from the Danish Natural Research Council (reg. no 28-808) during his sabbatical stay at the School of Biological Sciences (SBC), University of Wales, U.K. Thanks are due to Dr. M.A. Lock for use of the flume, and to A. Goldson for collaborative work on the effect of spinosity on flow, as part of his PhD dissertation. Dr. B. Okamura is acknowledged for constructive criticism of the manuscript, Dr. N.F. Nielsen for computational advise, K. Anderson and G. Desportes for linguistic improvements, and Prof. R. Hughes for hospitality and support of H.U.R. at the SBC.

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Reçu le 18 juillet 1998; received July 18, 1998
Accepté le 11 septembre 1998; accepted September 11, 1998

VIE MILIEU, 1998, 48 (4) : 321-329

SHORT TERM VARIATIONS OF BACTERIAL COMMUNITIES ASSOCIATED WITH A MEDITERRANEAN *POSIDONIA OCEANICA* SEAGRASS BED

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DIEL CHANGES
BACTERIAL BIOMASS
BACTERIAL PRODUCTION
POSIDONIA OCEANICA

Abstract. – Diel changes in abundance and production of planktonic and benthic bacteria were examined at the water-sediment interface of a Mediterranean seagrass bed *(Posidonia oceanica* (L.) Delile) in the Bay of Calvi (Corsica). Several additional parameters (temperature, solar radiation, dissolved oxygen, DOC, Chlorophyll *a*) were also recorded in order to establish possible relations with bacterial parameters. Diel changes in abundance of total and saprophytic bacteria were relatively modest. In contrast, obvious diel cycles of bacterial production occurred, maximal values being recorded during the night. No direct coupling was observed between Chlorophyll *a* and bacterial parameters, suggesting that phytoplanktonic exudates are not critical to bacterial growth. Night time stimulation of bacterial production seems to correspond to an enlargement of cell volumes rather than to an increase in cell numbers. It could be interpreted as a consequence of nutrient release during the dark phase of seagrass metabolic activity or to predation release during the night.

VARIATIONS NYCHTÉMÉRALES
BIOMASSE BACTÉRIENNE
PRODUCTION BACTÉRIENNE
POSIDONIA OCEANICA

RÉSUMÉ. – Les variations nychtémérales des abondances et des productions bactériennes benthiques et pélagiques ont été examinées de part et d'autre de l'interface « eau-sédiment » à l'intérieur d'un herbier de Posidonies (*Posidonia oceanica* (L.) Delile) situé en baie de Calvi (Corse). Plusieurs paramètres complémentaires pouvant intervenir sur la régulation des communautés bactériennes (température, rayonnement solaire, oxygène dissous, DOC, Chlorophylle *a*) ont également été mesurés. Les changements observés au niveau des abondances totales et saprophytes sont relativement modestes. A l'opposé, de profondes modifications affectent la production bactérienne qui atteint ses valeurs maximales durant la nuit. L'absence de corrélation entre la Chlorophylle *a* et les différents paramètres bactériens semble indiquer que l'excrétion phytoplanctonique n'a qu'une influence limitée sur la croissance bactérienne. La stimulation nocturne de la production bactérienne correspond plus à une augmentation du volume moyen des cellules bactériennes qu'à un accroissement de leur nombre. Elle pourrait être reliée soit à une augmentation de l'excrétion de l'herbier pendant la nuit, soit à une baisse de la prédation durant la même période.

INTRODUCTION

It is now well established (Moriarty & Boon 1989) that there is a strong interdependence between seagrasses and their sedimentary environment. Seagrasses can offer within their foliage an ideal refuge for dense populations of benthic fauna (Bell & Harmelin-Vivien 1982, Orth & Van Montfrans 1984). They can also have a direct effect on the chemical and microbiological characteristics of sediments and water column by their production of detritus (Robertson *et al.* 1982) and their substantial nutrients demand (Brix & Lyngby 1985, Thursby & Harlin 1982). The flux of O_2 through their roots, rhizomes or leaves (Oremland & Taylor 1977, Roberts & Moriarty 1987) is greatly dependant of the time of the day (Frankignoulle & Distèche 1984). Previous studies have pointed out the existence of short-term variations of marine bacterioplankton (Wright and Coffin, 1983, Riemann *et al.* 1984, Carlucci *et al.* 1986, Delille *et al.* 1988, 1997, Delille & Cahet

1991, Zohary & Robarts 1992, Torréton *et al.* 1994). Day-night cycles of microbiological parameters can be interpreted primarily as a manifestation of the relationship between sunlight and the marine biota (Fuhrman *et al.* 1985). Seagrass environment represent an ideal zone to study such diurnal cycles.

Many reviews (Moriarty 1980, Moriarty & Pollard 1981, 1982) showed that seagrass meadows may sustain a high biomass of bacteria and that a substantial proportion of the net primary production in seagrass beds is channelled through bacterial populations. Most of the bacterial data available for seagrass sediments deal with tropical and subtropical beds of *Zoostera capricorni* (Moriarty & Pollard 1981, 1982, Moriarty *et al.* 1985 a & b) or multispecies seagrass community (Moriarty *et al.* 1990). There is a lack of information for the microbial communities associated with temperate seagrass systems, especially Mediterranean *P. oceanica* beds. Some data concern seagrass leaves and debris (Velimirov *et al.* 1981, Novak 1984) or the surrounding water column (Velimirov 1986, 1987, Velimirov and Walenta-Simon 1992, 1993). To date, except the works of Danovaro *et al.* (1994) in the Ligurian sea and of Delille *et al.* (1996) in Corsica, it seems that the only other data available for *P. oceanica* beds sediment concern heterotrophic bacterial plate counts (Bianchi 1973).

The purpose of the present study was to investigate daily variations of bacterial parameters linked to seagrass bed of the Bay of Calvi (Corsica) which is half covered by an important *P. oceanica* (L.) Delile bed.

MATERIALS AND METHODS

Study area and sampling. This study was conducted in March and May 1991 in the Bay of Calvi (Corsica) in the *Posidonia oceanica* (L.) Delile seagrass bed, that is one among the four main biocenoses observed in this Bay (Bay 1978). Samples were collected at a fixed coastal station in the *Posidonia* bed during two 24 hours cycles (on March 27-28 and on May 29-30, 1991). The sampling interval was three hours during the first experiment, and four hours during the second experiment.

Samples were collected by diving at 14 m depth. Samples taken for bacterial parameter determination were aseptically collected using sterile glass bottles for seawater (10 cm and 1 m over the bottom) and 4 cm diameter PVC coring tube for sediment (surface layer and 3 cm depth). In vegetated area the lower layer of seawater (10 cm) is located inside the seagrass bed while the upper one (1 m) is located above the canopy. Water samples assigned to dissolved oxygen were collected in standard BOD bottles. Complementary samples (DOC and Chlorophyll *a*) were collected using Niskin bottle, one meter below the surface.

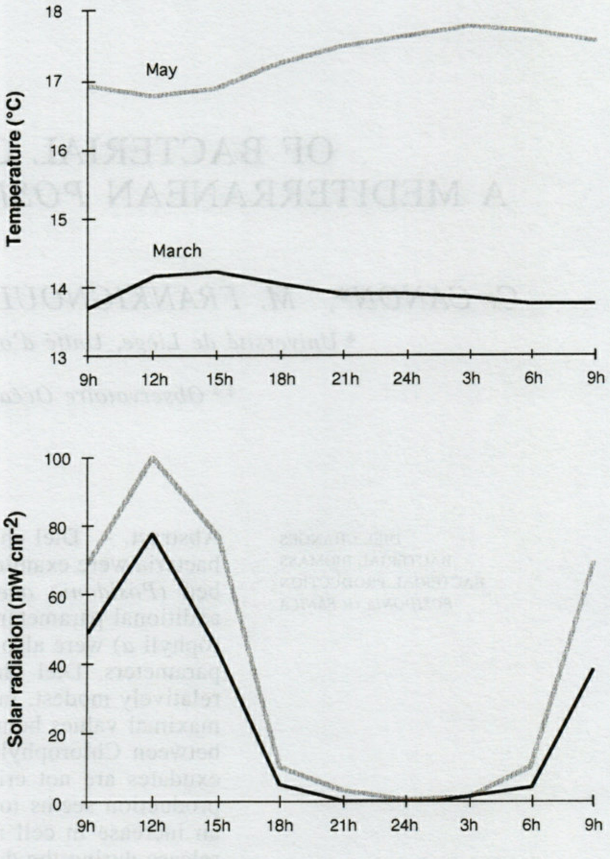

Fig. 1. – Diel changes of temperature and solar radiation during two 24 h survey.

Determination of bacterial parameter. All bacterial samples were fixed and/or analysed in the laboratory within 10 minutes of collection. Sediment cores were diluted with sterilised seawater and then homogenised for 4 minutes in a warring blender.

Total bacteria were determined by acridine orange direct count with an Olympus epifluorescence microscope according to the method of Hobbie *et al.* (1977). Biovolumes were estimated using an ocular micrometer. Frequency of dividing cells (FDC) was assessed using the method of Hagström *et al.* (1979). A minimum of 20 dividing cell per filter was counted. The calculation of *in situ* growth rate from these FDC values is not simple. According to Newell & Christian (1981), the linear regression equation depends on numerous parameters (Delille *et al.* 1988). FDC data presented here only describe relative rates of bacterial production.

Viable counts of aerobic heterotrophic culturable bacteria were made using the spread plate technique on DIFCO 2216 Marine Agar medium (Oppenheimer & ZoBell 1952). Inoculated plates were incubated for 20 days at 18 °C.

Bacterial production was measured by the rate of [H^3-methyl] thymidine incorporation into macromolecules, with modified TCA precipitation procedures of Fuhrman & Azam (1982) which has been proposed by Wicks & Robarts (1987). [H^3-methyl] thymidine (specific activity : 60 Ci mmol^{-1} ; final concentration

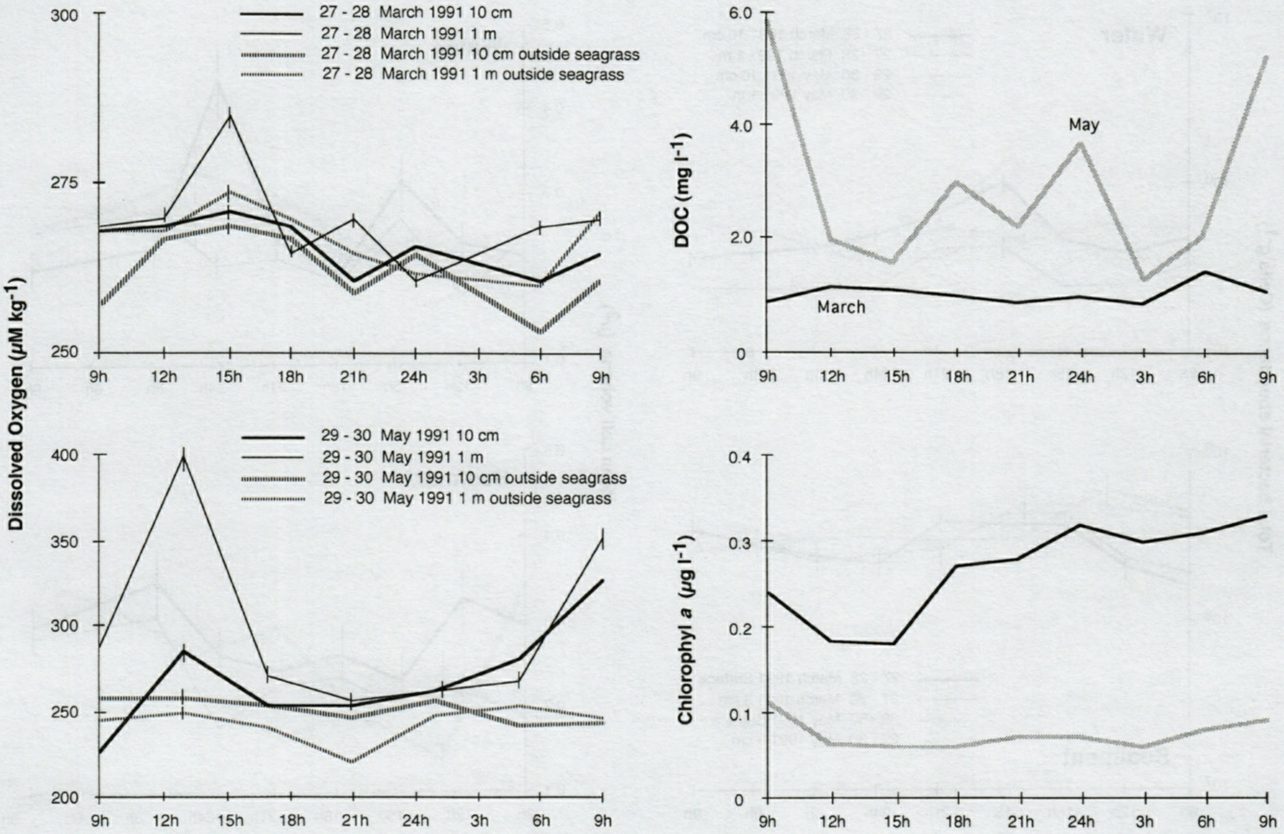

Fig. 2. – On the left, diel changes of dissolved oxygen concentrations recorded during two 24 h survey. Error bars indicate standard deviation. For avoid confusion only one complete data set are presented. Only one error bar is shown for the other sampling level. On the right, diel changes of dissolved organic carbon (DOC) and Chlorophyl *a* concentrations recorded during two 24 h survey.

20 nmol^{-1}) was added to triplicate aliquot volumes of seawater. Unfortunately, production data are not available in May.

Determination of associated parameter. The dissolved oxygen was measured in the water column using the usual Winkler method. DOC was determined by UV oxydation followed by non-dispersive IR detection. Chlorophyll *a* concentrations was estimated using the method described by Lorenzen & Jeffrey (1978). Solar radiation was monitored using a meteo station from Aanderaa instruments.

Statistical analysis. Such diel survey were to much time consuming to allow replicate analysis. One quintuplicate sampling set had been realized the day after each 24 hours cycles. Standard deviation obtained has been extrapolated to the corresponding diel study.

RESULTS

Seawater temperature presented only slight variations : from 13.7 C to 14.2 °C in March, and from 16.6 C to 18.4 °C in May (Fig. 1). In contrast, the dissolved oxygen measured in the water column above *Posidonia* bed displayed a clear diel variation (Fig. 2). The general pattern were in agreement with photosynthesis and respiration processes of seagrasses : diurnal augmentation followed by a diminution during the night. These daily variations were particularly obvious above the canopy of seagrasses (1 m seawater layer) with a maximum in the early afternoon corresponding to the maximum of solar irradiance (Fig. 1). Changes in dissolved oxygen were slighter near the bottom sediment. With a few exceptions (end of the second experiment) the values recorded at the 10 cm layer were relatively similar to those find at both layer on unvegetated area.

In March, the concentration of dissolved organic carbon (DOC, Fig. 2) was weak and did not vary significantly while the concentration in chlorophyll *a* showed a small daily variation with minimal values occurring during the afternoon. In contrast, in May, the concentrations of dissolved organic carbon were relatively high with a maximum occurring at 9 A.M. while chlorophyll *a* values were always very low.

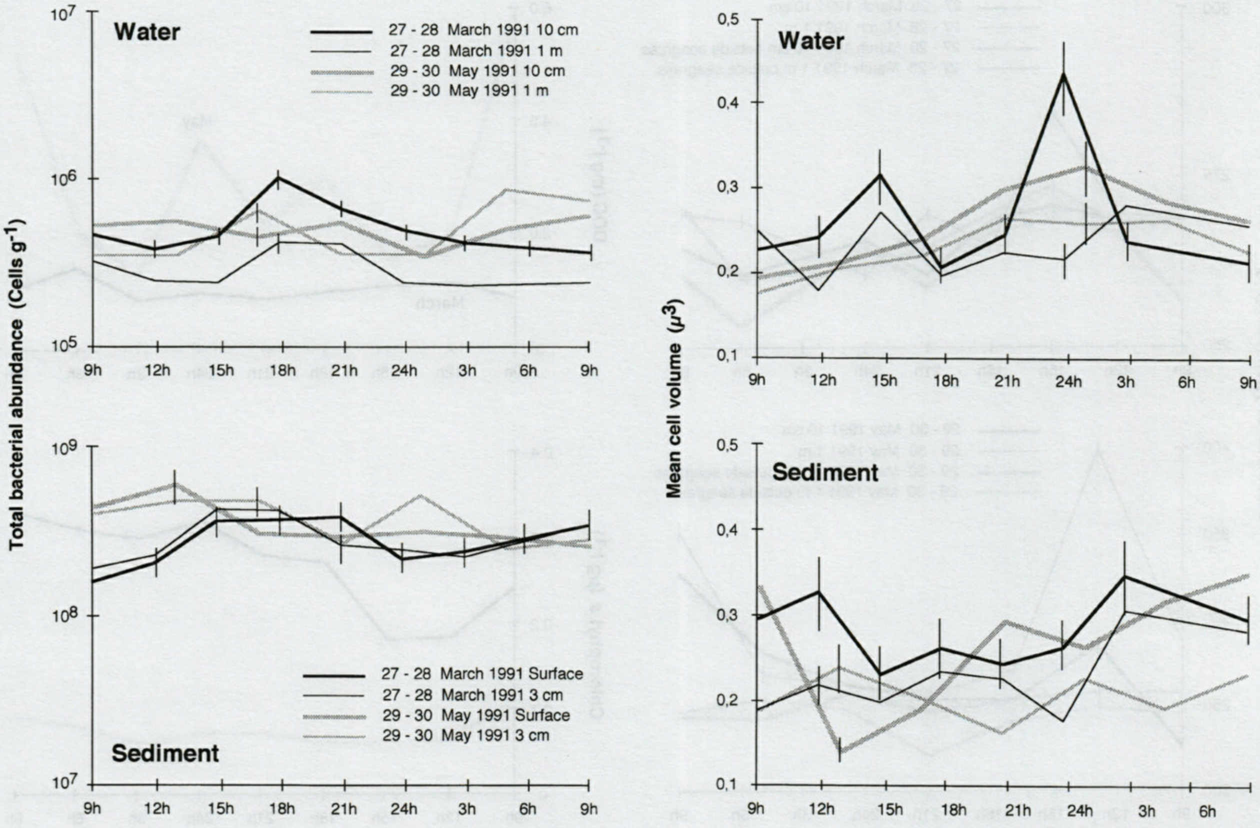

Fig. 3. – Diel changes of total bacterial abundance and mean cell volume recorded during two 24 h survey. Error bars indicate standard deviation extrapolated from a quintuplicate study. For avoid confusion only one complete data set are presented. Only one error bar is shown for the other sampling level.

Bacterial parameters

Relatively similar patterns in the distribution of total bacterial abundance were observed in both water and sediment (Fig. 3). There were only small diel changes.

In contrast, diel variations of the mean bacterial cell volume (Fig. 3) were observed during the two seasons. In March, in both water and sediment, two peaks were recorded : one in the middle of the day, the second in the middle of the night. There was only one peak recorded in May : in the night in water and in the morning in sediment. Estimations of the frequency of dividing cells (FDC) reflected a relatively similar dynamic with, in addition, an increase of the frequency of dividing cell in May when compared to March (Fig. 4). A diel variation of the percentage of free living bacteria occurred in seawater (Fig. 5), with a minimum value at the beginning of the night. A diminution of this parameter was recorded in May, corresponding to a differentiation of the two studied layers (10 cm and 1 m).

Variations in the distribution of saprophitic viable bacteria (Fig. 6) confirmed those of direct counts ; viable bacterial abundance was larger in the sediment (particularly in the surface layer) than in the water column. A slight increase of viable bacterial density appeared in May compared to March, but no clear temporal fluctuations in viable counts were detected over the two experiments.

In March, bacterial production (Fig. 7) in the water situated 10 cm above sediment had an average value of 1.9 µg C l^{-1} h^{-1} with a maximum of 8.0 µg C l^{-1} h^{-1} reached in the night. In contrast with this strong diel change inside the bed, the bacterial production was always low above the canopy (1 m seawater layer).

DISCUSSION

During the two experiments, there was no phytoplankton bloom which could interfer significantly with seagrass photosynthesis and no modification of wind pattern sufficiently efficient to induce an upwelling of nutrient rich water (Brohée *et al.* 1989) or an important current flow which could be responsible of hourly changes in coastal bacterioplankton (Bouvy & Delille 1988).

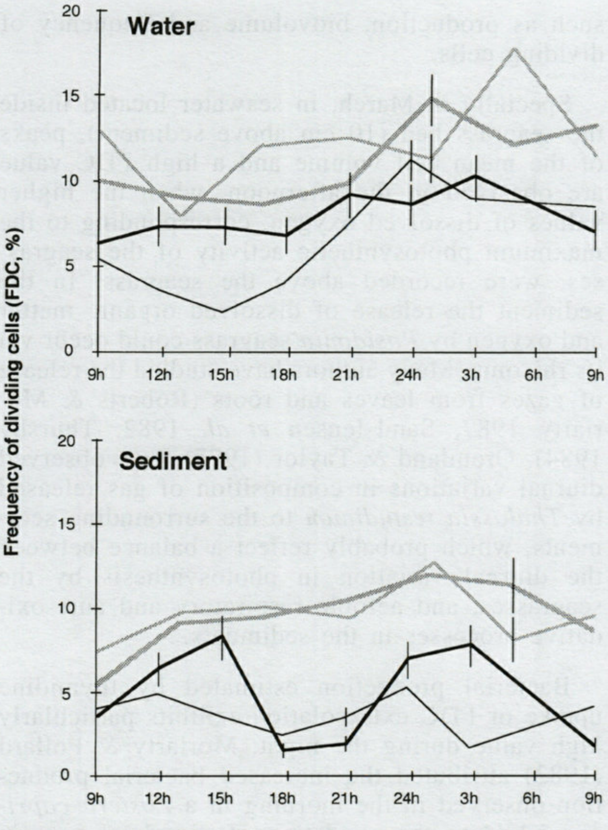

Fig. 4. – Diel changes of frequency of dividing cells (FDC) recorded during two 24 h survey (Symbols as in Fig. 3).

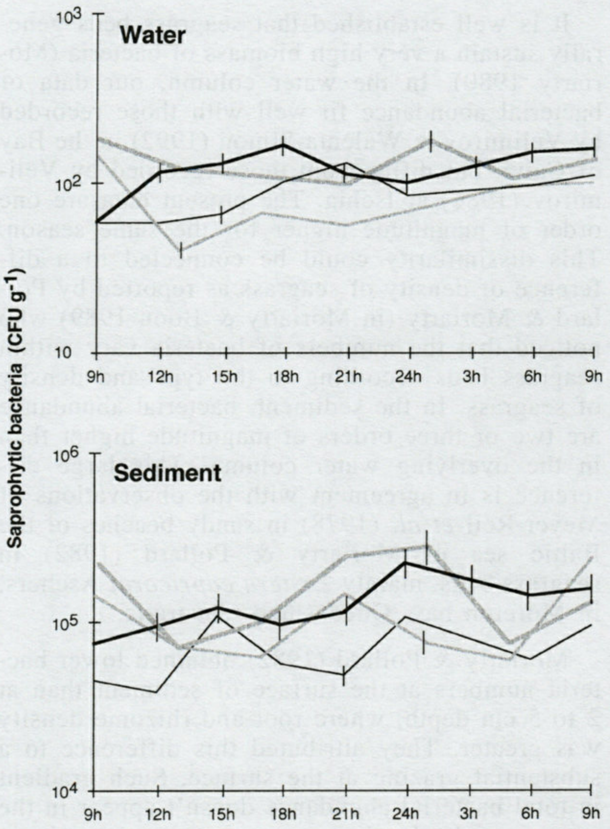

Fig. 6. – Diel changes of percentage of saprophytic bacterial abondance recorded during two 24 h survey (Symbols as in Fig. 3).

Dissolved oxygen and other parameters such as seawater temperature, total alkalinity or inorganic carbon (unpublished data) presented normal values for both seasons studied. The data are in agreement with those recorded by Frankignoulle & Bouquegneau (1990) on the same site. Very low concentrations in chlorophyll *a* were recorded during our study but they were of the same order of magnitude than those found by Brohée *et al.* (1989) in the Bay of Calvi outwards the main periods of phytoplankton bloom. This relative weakness of the phytoplanktonic biomass seems to indicate a predominance of *Posidonia* production in the autotrophic communities.

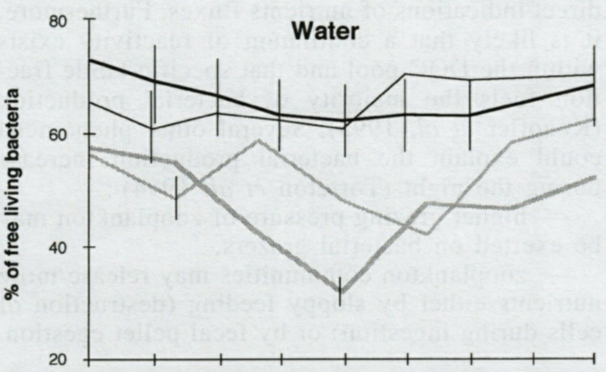

Fig. 5. – Diel changes of percentage of free living bacteria recorded during two 24 h survey (Symbols as in Fig. 3).

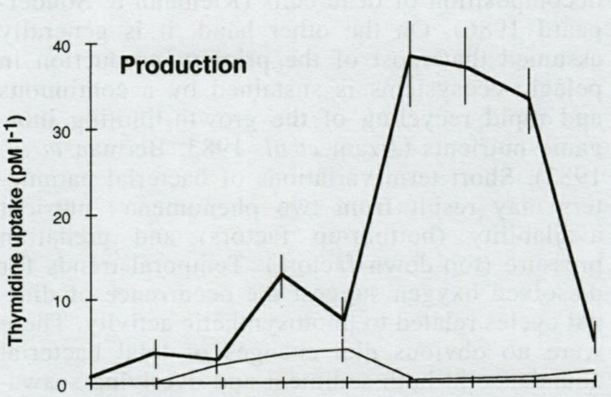

Fig. 7. – Diel changes of bacterial production recorded during March survey (Symbols as in Fig. 3).

It is well established that seagrass beds generally sustain a very high biomass of bacteria (Moriarty 1980). In the water column, our data of bacterial abundance fit well with those recorded by Velimirov & Walenta-Simon (1992) in the Bay of Calvi, but differ from those recorded by Velimirov (1986) at Ischia. The present data are one order of magnitude higher for the same season. This dissimilarity could be connected to a difference of density of seagrass as reported by Pollard & Moriarty (in Moriarty & Boon 1989) who noticed that the numbers of bacteria vary within seagrass beds according to the type and density of seagrass. In the sediment, bacterial abundance are two or three orders of magnitude higher than in the overlying water column. This large difference is in agreement with the observations of Meyer-Reil *et al.* (1978) in sandy beaches of the Baltic sea or Moriarty & Pollard (1982) in seagrass beds, mainly *Zostera capricorni* Aschers, in Moreton bay, Queensland, Australia.

Moriarty & Pollard (1982) obtained lower bacteria numbers at the surface of sediment than at 2 to 5 cm depth, where root and rhizome density was greater. They attributed this difference to a substantial grazing at the surface. Such gradient in total bacterial abundance doesn't appear in the present study. Furthermore, a greater saprophytic bacterial abundance and an enhanced FDC in March were observed at the surface than at 3 cm depth. This may be attributed to a reduced grazing pressure related to the generally low values of zooplankton biomass (10-20 mg. dry weight $m^{-3)}$ observed in the Bay of Calvi (Brohée *et al.* 1989).

The pathways mediating the transfer of nutrients between the primary producers and bacteria in seawater are extremely complex and include numerous feedback mechanisms. Heterotrophic bacteria are largely reliant on primary producers for their energy supply, either directly through excretion of dissolved organic matter (Kuosa & Kivi 1989, Suttle *et al.* 1991) or indirectly after decomposition of dead cells (Riemann & Sondergaard 1986). On the other hand, it is generally assumed that most of the primary production in pelagic ecosystems is sustained by a continuous and rapid recycling of the growth-limiting inorganic nutrients (Azam *et al.* 1983, Berman *et al.* 1987). Short term variations of bacterial parameters may result from two phenomena : nutrient availability (bottom-up factors) and predation pressure (top-down factors). Temporal trends for dissolved oxygen suggest the occurrence of diurnal cycles related to photosynthetic activity. There were no obvious diel changes of total bacterial abundance in both sediment and overlying seawater which could be connected to these photosynthetic process of seagrass beds. However, there are some metabolic modifications of the bacterial communities attested by more sensible parameters such as production, biovolume and frequency of dividing cells.

Specially in March, in seawater located inside the seagrass bed (10 cm above sediment), peaks of the mean cell volume and a high FDC value are observed in the afternoon, when the higher values of dissolved oxygen, corresponding to the maximum photosynthetic activity of the seagrasses, were recorded above the seagrass. In the sediment the release of dissolved organic matter and oxygen by *Posidonia* seagrass could occur via its rhizome. Many authors have studied the release of gazes from leaves and roots (Roberts & Moriarty 1987, Sand-Jensen *et al.* 1982, Thursby 1984). Oremland & Taylor (1977) have observed diurnal variations in composition of gas released by *Thalassia testudinum* to the surrounding sediments, which probably reflect a balance between the diurnal variation in photosynthesis by the seagrasses, and aerobic respiratory and auto-oxidative processes in the sediments.

Bacterial production estimated by thymidine uptake or FDC extrapolation exhibits particularly high value during the night. Moriarty & Pollard (1982) attributed the increased bacterial production observed in the morning in a *Zostera capricorni* bed to the exudation of dissolved organic matter during photosynthesis, whereas the nocturnal production which was, in their study, low and constant overnight, would be controlled by dissolved organic matter from a variety of sources, including decomposition of particulate matter. Despite that Jorgenson *et al.* (1981) have shown that dissolved free amino acids are released by the seagrass *Posidonia oceanica* during daylight hours and are rapidly consumed during the dark hours, exudation of nutrients during the dark phase of seagrass metabolic acivity cannot be excluded. An increase of DOC at midnight was observed in May. However, DOC concentrations are always the result of two opposite processes, production and uptake, and thus cannot give clear direct indications of nutrients fluxes. Furthermore, it is likely that a continuum of reactivity exists within the DOC pool and that specific labile fraction fuels the majority of bacterial production (Koepfler *et al.* 1993). Several other phenomena could explain the bacterial production increase during the night (Torreton *et al.* 1994) :

— higher grazing pressure of zooplankton may be exerted on bacterial grazers,

— zooplankton communities may release more nutrients either by sloppy feeding (destruction of cells during ingestion) or by fecal pellet egestion.

The period of high bacterial production corresponded to an increase of mean volumes without clear enhancement of the cell abundance. This cell volume increase may corresponded with the observations of Kjelleberg *et al.* (1982) and Amy *et* *al.* (1983) who recorded increases of cell volume during recovery of starvation.

The observed decreases of mean cell volume corresponded to increases in bacterial abundance. Furthermore, the maximal bacterial abundances recorded during the two survey corresponded to the lower values recorded for mean cell volume. Velimirov & Walenta-Simon (1992) suggested that such opposition between cell volume and abundance could be an appropriate growth strategy under unfavorable environmental conditions.

Bacterial data were of the same order of magnitude in March and May, except when regarding the percentage of free living bacteria, which was higher in March, and the frequency of dividing cells, which was more important in May. Physicochemical parameters were relatively similar in March and May. Calm weather, with wind speeds limited to 2 or 3 m/s were noticed during the two experiments. Thus, the observed differences can hardly be explained by meteorological conditions. They could result from a modification of the composition of the seagrass bed : in March it was mainly made up of young leaves, whereas, in May, we have to take into account the presence of epiphytes, and then a modification of the attachment of bacteria. Another hypothesis could be the modification of the phytoplanktonic structure : in March there was a direct trophic system with a mixture of diatoms and flagellates, while in May there were essentially flagellates and then a substantial grazing of bacteria which corresponds to a microbial loop system (Dauby 1985). This situation is usually observed in oligotrophic ocean waters and coastal waters after the spring phytoplankton bloom (Sherr & Sherr 1988).

ACKNOWLEDGEMENTS. – We want to thank M.A. Esteves from the Universidade de Aveiro (Portugal) and J. Robertson from the Plymouth Marine Laboratory (England) for the DOC and the chlorophyll *a* determinations respectively, E. Delille for technical assistance and R. Biondo, A. Norro, A. Simon and J.M. Theate for their diving assistance. This research was supported by the biogeochemical program MAST n° 0019-C and the FNRS (Belgium) in which M Frankignoulle is a Research Associate.

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Reçu le 27 février 1998 ; received February 27, 1998
Accepté le 26 mars 1998 ; accepted March 26, 1998

VIE MILIEU, 1998, 48 (4) : 331-340

TIDAL VARIATIONS IN FEEDING, ABSORPTION AND SCOPE FOR GROWTH OF COCKLES (*CERASTODERMA EDULE*) IN THE BAY OF MARENNES-OLÉRON (FRANCE)

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FEEDING PHYSIOLOGY
TIDAL REGIME
BIVALVE MOLLUSC
COCKLES
CERASTODERMA EDULE

ABSTRACT. – Physiological components of the scope for growth were measured in cockles fed natural seston in the Marennes-Oléron bay (S.W. France). Measurements were performed at different times of the tidal cycle during neap and spring tides. Thus, ambient food variability was provided by tidal fluctuations in particle availability, that ranged between approximately 10 and 170 mg total particulate matter (TPM) per litre. Tidal fluctuations in particle concentration explained a fraction (73 %) of recorded variability in organic content of seston, as derived from the resuspension of bottom materials of low organic content. The remaining variability could not be accounted by short-term changes in phytoplankton abundance since this variability appeared poorly correlated with chlorophyll and/or phaeopigment seston concentrations. Equations fitted to physiological measurements were subsequently used with data derived from the continuous recording of turbidity performed at the same time, in order to simulate temporal variations in physiological parameters and scope for growth over the tidal cycles. Results of this simulation have shown that predicted values of the physiological parameters fluctuate within narrower ranges than measured values, most variability in actual measurements being accounted for by the unexplained (i.e., not TPM dependent) variability in seston organic content. Consequently, independent estimations of seston concentration and organic content are recommended for the purpose of modelling physiology and growth in bivalves under natural conditions of food availability.

PHYSIOLOGIE ALIMENTAIRE
RÉGIME TIDAL
BIVALVE
COQUES
CERASTODERMA EDULE

RÉSUMÉ. – Les composantes physiologiques du bilan énergétique ont été déterminées sur des Coques alimentées avec du seston naturel du Bassin de Marennes-Oléron (S.O. France). Ces déterminations ont été réalisées à différents moments du cycle des marées de vives eaux et de mortes eaux. La variabilité nutritionelle provenant des fluctuations de l'abondance des particules en suspension est liée au flux de la marée et s'échelonne de 10 à 170 mg de matière particulaire totale (MTP) par litre. Les variations de la fraction organique du seston peuvent être expliquées pour 73 % par les fluctuations de la concentration en particules associées au cycle de la marée, qui comporte la remise en suspension du substrat, pauvre en contenu organique. La variabilité restante n'a pu être expliquée par les fluctuations d'abondance du phytoplancton, car elle apparaît faiblement corrélée avec les concentrations des chlorophylles et/ou des phaeopigments du seston. Les équations dérivées des mesures physiologiques sont appliquées aux mesures obtenues par enregistrement en continu de la turbidité réalisé simultanément, pour simuler la dynamique temporelle des variables physiologiques et du bilan énergétique. Les résultats de cette simulation montrent que les valeurs attendues pour ces variables varient moins que les valeurs expérimentales, la variabilité de ces dernières étant due aux changements de la fraction organique du seston non exprimés par les fluctuations en TPM. Il est donc recommandé d'effectuer des estimations indépendantes de la concentration et du contenu organique du seston en vue de modéliser la physiologie et la croissance des Bivalves à partir de conditions naturelles d´abondance nutritionnelle.

INTRODUCTION

Studies on the carrying capacity of shellfish cultivation areas tend to make extensive use of empirical physiological models of growth in filter-feeding bivalves. Their structure generally consists of a series of equations representing the various physiological processes integrated in the energy budget of the individual, and are designed to simulate scope for growth responses to key environmental factors such as temperature and variables of the food environment (Bacher *et al.* 1991, Grant *et al.* 1993, Navarro *et al.* 1997, Grant & Bacher 1998, Scholten & Smaal 1998). The predictive value of these models is determined to a great extent by the realism of experimental conditions under which physiological measurements are undertaken. On the other hand, to be practical, empirical physiological models used to predict bivalve carrying capacity need to be based on environmental variables that could be monitored continuously and autonomously.

Concerning the first aspect, since the first physiological determinations "*in situ*" using natural seston in mussels and cockles (Bayne & Widdows 1978, Newell & Bayne 1980), there has been increasing interest in the use of natural diets while performing physiological energetics measurements (Prins & Smaal 1989, Navarro *et al.* 1991, 1992, Mac Donald & Ward 1994). Additionally, the time-course of changes in seston composition and associated physiological responses are of the greatest importance in growth computations. While seasonal variation has often been addressed, there are few instances in which physiological response has been analysed within the context of short-term fluctuations such as those brought about by tides (Stenton-Dozey & Brown 1992, 1994, Cranford & Hargrave 1994, Hawkins *et al.* 1996, Soletchnik *et al.* 1996, Urrutia *et al.* 1996).

As to the second point, consideration of seston dynamics in systems strongly affected by tides, like many shallow estuaries, makes plain "the need for short term and small-scale measurements of seston concentration and composition in order to examine the food availability to suspension feeder beds" (Smaal & Haas 1997). However, the sampling effort necessary to accomplish this programme with the required frequency would be excessive if the study is intended to be conducted over a long period (e.g., seasonally). Besides, sample processing for variables of the seston relevant in the computation of the scope for growth in bivalves is considerably time consuming. On account of these difficulties alternative procedures have been developed based on a combination of fluorimetric and nephelometric measurements performed continuously (Soletchnik *et al.* 1996). Advantages of these method are evident since the required information is automatically delivered, easily stored and can be transformed into values of environmental variables compatible with the formulation of physiological models by means of the appropriated conversion factors or equations. Nevertheless, insufficient precision in these factors might compromise the possibilities of application of such measurements.

In the course of a research programme on the carrying capacity of the Marennes-Oléron Bay we recorded physiological data from cockles (*Cerastoderma edule*) exposed to tidal fluctuations in food variables (Urrutia *et al.* 1996). One aim of the present paper is to apply equations fitted to these data to values of seston parameters continuously recorded with the above referred methods during several tidal cycles. Equations were subsequently arranged in a model of the energy budget in order to explore growth responses of cockles over tidal time scales. Possibilities and limits of the model for simulating actual trends of feeding components are discussed in relation with the characteristics of the available input variables.

MATERIAL AND METHODS

Experiments were performed at Le Chapus (Marennes-Oléron Bay) during May-June 1992. During these experiments, cockles (*Cerastoderma edule*) were maintained in an open system within individual containers with flowing sea water directly pumped from 1m above the bottom of the bay, at a site covered by the tide 9 hours on average in each tidal period. Ambient food variability to cockles was provided by tidal fluctuations in particle availability, which ranged between approximately 10 and 170 mg/l total particulate matter (TPM).

Seston variables were characterized for samples taken at 1 to 2 hours intervals at the inflows of the experimental system. The following variables were determined : TPM (mg/l), particulate organic matter (POM : mg/l) and chlorophyll (CHL : µg/l) and phaeopigment (PHP : µg/l) concentrations. The organic content of the suspension was expressed by weight (f = POM/TPM). Methods of seston analysis have been reported elsewere (Urrutia *et al.* 1996).

Food processing rates were determined according to the biodeposition method (Iglesias *et al.* 1998), from collections of faeces and pseudofaeces produced by individual cockles, sampled separately and replicated over time. This method assumes conservation of the inorganic fraction of food passing the gut. Accordingly, clearance rate (CR : l/h) was calculated as the rate of inorganic biodeposition (mg/h) divided by the concentration of particulate inorganic matter (PIM : mg/l) and filtration rate (FR : mg/h) as the product of CR and total particulate matter concentration (TPM : mg/l). Ingestion rate was estimated as the difference between filtration rate and the rate of rejection of pseudofaeces (RR : mg/h). Selection (SE) and absorption efficiencies

(AE) were estimated according to procedures described elsewhere (Iglesias *et al.* 1998). All physiological measurements were standardized to a 0.5 g dry tissue cockle by using the appropriate allometric functions (Urrutia *et al.* 1996).

Physiological determinations were combined to compute rates of absorption (A : mg/h), that were subsequently converted to their energy equivalents (J/h) by applying a standard conversion factor of 20.8 J /mg organic matter (Crisp 1971). Although no measurements of oxygen consumption were undertaken in the course of these experiments, we estimated metabolic energy expenditure under the present conditions using the following equation that was fitted to an extensive set of respiration data pooled from experiments with cockles from Marennes-Oléron and Urdaibai (Spain), under different dietary conditions and seasonal temperatures (own unpublished data) :

$$R = e^{(0.047 + 0.034\ A + 0.06\ T)} \qquad (r^2 = 0.68\ ;\ P < 0.001)$$

where R stands for metabolism (J/h), A is the rate of absorption (J/h) and T is the temperature (20.5 °C in the present experiments). These estimations of metabolism allowed computation of the Scope for Growth (SFG : J/h) as the difference A-R. Since no account of energy losses in the form of ammonia excretion have been taken, this computation of SFG represents an overestimation (approximately by a 10 %).

Individual rates and efficiencies were related to the appropriated descriptors and relationships statistically fitted. Non linear regression methods were preferred over more conventional procedures based on linearization to preclude any risk of distortion into the extremes of the distribution, that tend to limit the predictive capacity of statistically based model, particularly for extrapolation purposes. All statistical analyses were undertaken by using SYSTAT for the Macintosh.

Coincidentally with these determinations, Soletchnik *et al.* (1996) deployed continuous flow nephelometric (AF mod. DRT100B) and fluorimetric (TURNER mod. 112) sensors to continuously monitor relative turbidity and fluorescence over 9 hours during three tidal cycles, two neap (27 and 28 May 1992) and one spring (1 June 1992). These recordings were converted to TPM (mg/l) and concentration of chlorophyll plus phaeopigments (CHL + PHP : µg/l), and used in the present computations in the form of discrete values taken every 15 min. Converting equations for the outputs of the nephelometer (N) and fluorimeter (F) were as follows (Soletchnik *et al.* 1991) :

$$TPM = 19.73\ N + 9.98 \qquad (r^2 = 0.91\ ;\ n = 168)$$

$$CHL + PHP = 0.46\ F - 3.97 \qquad (r^2 = 0.76\ ;\ n = 83)$$

RESULTS

1. Physiological equations

Table I summarizes the set of equations fitted to actual data of feeding parameters as a function of the reference variables from the seston. Clearance rate was expressed as an exponential function of both total particle concentration (TPM) and organic content of the suspension (**f**). The negative coefficient associated with the term for organic content stands for the fact that cockles enhance clearance rates with increasing proportion of inorganics. Rejection rate of pseudofaeces was described as a lineal function of FR, and a negative term of **f** accounting for the fact that also production of pseudofaeces decreases with increasing organic content of food. Negative effects of **f** on both filtration and rejection rates tend to compensate each other, making ingestion rate virtually independent on the organic content of seston (see Hawkins *et al.* 1998).

Table I. – Equations fitted to the physiological functions.

FUNCTION	EQUATION	PARAMETERS ± S.E.	r^2	n
Clearance rate	$CR = e^{bo+b1\ TPM+b2\ \mathbf{f}}$	b0 = 0.536± 0.265 b1 = 0.003± 0.002 b2 = -2.938± 1.824	0.837	127
Rejection rate	$RR = b0+b1\ FR+b2\ \mathbf{f}$	b0 = -6.220± 1.431 b1 = 0.948± 0.006 b2 = -23.702± 10.571	0.998	127
Selection efficiency	$SE = b0+b1\ \mathbf{f}+b2\ \mathbf{f}^2 +b3\ TPM\ \mathbf{f}$	b0 = -0.280± 0.062 b1 = 7.242± 1.120 b2 = -13.473± 4.694 b3 = 0.010± 0.003	0.980	127
Absorption efficiency	$AE = b0\ (1-e^{b1\ (\mathbf{i}\ -\ b2)})$	b1 = 0.931± 0.030 b1 = -7.433± 0.972 b3 = 0.016± 0.010	0.995	127

Efficiencies of preingestive and digestive processes are represented by net selection efficiency for organics (SE) and net absorption efficiency of ingested organics (AE). On an empirical basis, both efficiencies appear primarily determined by the organic content of filtered (**f**) and ingested (**i**) matter, respectively.

Best predictive equation for SE was a quadratic function of the organic content (Table I), which is in agreement with trends reported for SE of cockles submitted to a broad range of food qualities (Iglesias *et al.* 1992). The influence of TPM on SE has been introduced in the form of an interaction term representing the positive effect of TPM on the rate at which SE varies with **f**. Present model accounts for 98 % of tidal variability of SE and predicts negative SE at values of the organic content of the suspension below 3.5 %.

A single variable, the organic content of the ingesta (**i**), explains 99 % variability in absorption efficiency (AE), through an exponential function that predicts maximum AE of 0.93 and critical (for AE = 0) values of **i** of 1.6 %.

2. Tidal variation of growth components

Since physiological measurements were determined under natural conditions of food availabi-

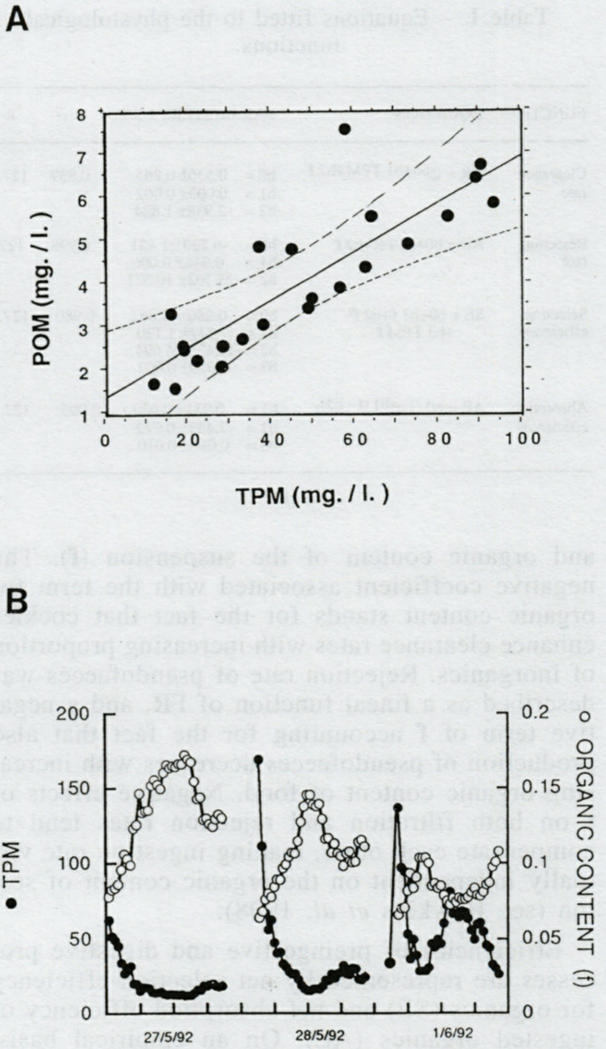

Fig. 1. – A, Regression line of particulate organic matter (POM : mg/l.) over total particulate matter (TPM : mg/l). Actual data recorded at Le Chapus (Marennes-Oléron Bay) during the experiments (circles) were fitted by linear regression using least squares. Bands for 99.9 % confidence limits are plotted (dashed lines). Regression equation : POM = 1.356 + 0.056 TPM (r^2 = 0.727 ; P = 10^{-4}). B, Time courses of total particulate matter (TPM) and organic content of seston (**f**) during two neap tides (27 and 28th May 1992) and one spring tide (1st June 1992), recorded at Le Chapus. Organic contents were derived from TPM values by applying the above regression equation.

lity, given the appropriate input, the above set of equations could be combined to simulate tidal profiles for the various components of the energy balance and the scope for growth. Particularly, the present physiological model allowed us to predict absorption rates based solely on TPM and organic content (**f**) values recorded in natural seston. TPM was directly obtained from the nephelometric recording, and the corresponding **f** values were obtained by applying to these TPM a regression equation of POM vs TPM fitted to data from Le Chapus recorded in the course of experiments (Fig. 1A). Figure 1B gives profiles for TPM over three tidal cycles, two neaps and one spring and the corresponding **f** values derived from applying the equation from Fig. 1A. Inverse relationship between these two variables can be observed as an effect of the resuspension of bottom materials of low organic content.

Using these TPM and **f** values as predictors for equations given in Table I, we have derived the panel in Fig. 2. FR was obtained by simply substituting TPM and **f** values in the equation for CR (Eq. 1). Rejection rate of pseudofaeces (RR) was obtained from FR and **f**, through Eq. 2. Ingestion rate (IR) was then computed as the difference FR-RR. Selection efficiency (SE) measuring the degree of organic enrichment following pre-ingestive selection was computed from TPM and **f** through Equation 3.

The above variables were then combined to calculate rates of organic ingestion, according to the formula :

$$\text{OIR} = \mathbf{f}\,[\text{FR} - \text{RR}\ (1\text{-SE})]$$

The organic content of ingested food (i = OIR/IR) served to estimate absorption efficiency (AE) by substitution in Equation 4 (Table I). Absorption rates were subsequently calculated as the product of OIR and AE, and rates of metabolism (R) and SFG as indicated in the Materials and Methods section.

Figure 2 shows rates of feeding, absorption and scope for growth as a function of tidal fluctuations in seston variables. Tidal profiles for most physiological parameters appear closely related to those for suspended matter indicating that TPM is the main factor determinant of components of energy budget under natural conditions of food availability. We are interested in ascertaining how much of this environmental variability in food concentration becomes buffered through the different processes of feeding and digestion taking place inside the organism. To accomplish this, we compare in Table II the coefficients of variation (CV) of the various measurements, calculated on pooled estimations for the three tidal cycles. Comparison of CVs for TPM and FR is illustrative : in spite of an almost linear relationship between both measurements, there is an increment from 73 to 99 %, indicating that the process of particle filtration tend to enhance ambient fluctuations in food supply. This arises as consequence of the negative effect of organic content on filtration rate, which results in increasing clearance rates with increasing TPM (i.e., decreasing organic content). Reduced CV for OFR, compared with FR, is a simple consequence of the inverse relationship

Table II. – Range, mean, standard deviation (S.D.) and coefficient of variation (C.V.) of values for environmental variables and physiological variables estimated over three tidal cycles. TPM and POM : total particulate matter and particulate organic matter (mg/l) ; FR, RR, IR : filtration, rejection and ingestion rates of particulate matter (mg/h) ; OFR, OIR : filtration and ingestion rate of particulate organic matter (mg/h) ; A, R and SFG : absorption rate, metabolic rate and scope for growth (Joules/h).

	MINIMUM	MAXIMUM	MEAN	S.D.	C.V.
TPM	11.69	169.20	36.31	26.62	0.73
POM	2.01	10.86	3.41	1.50	0.44
FR	12.47	397.70	57.12	56.75	0.99
RR	3.38	375.82	45.58	54.75	1.20
IR	9.08	21.88	11.53	2.04	0.17
OFR	2.14	25.53	5.10	3.48	0.68
OIR	1.90	7.13	2.39	0.68	0.28
A	27.09	119.54	33.80	11.70	0.34
R	9.00	48.85	13.49	5.02	0.37
SFG	12.81	32.13	20.30	5.47	0.27

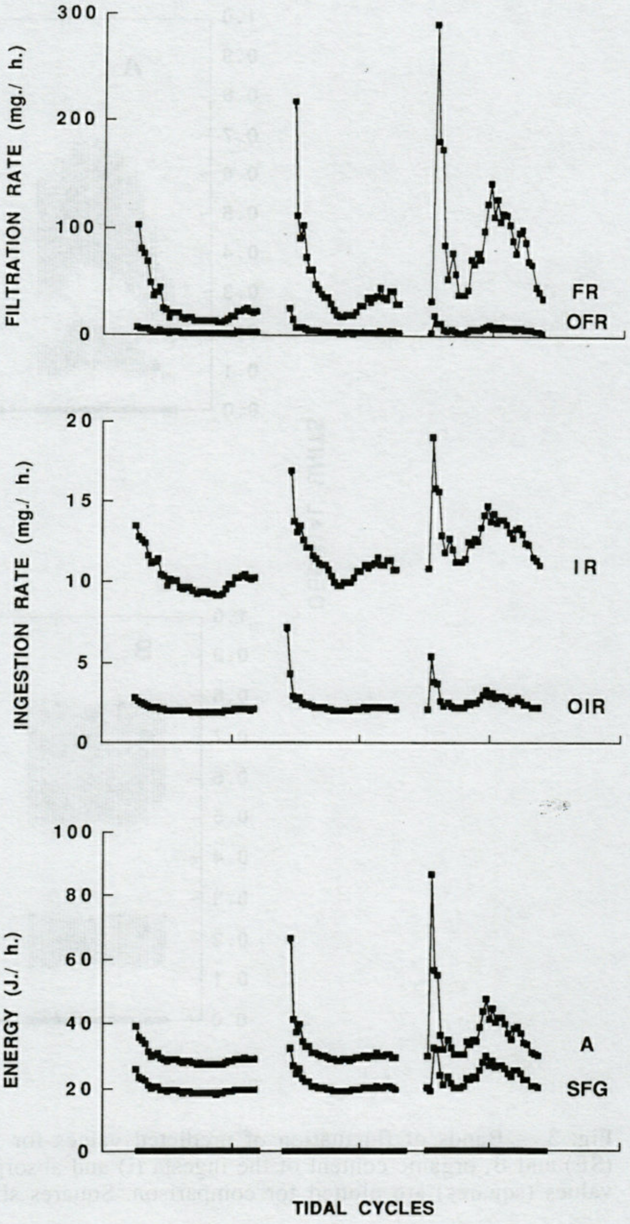

Fig. 2. – Simulated time-courses of filtration rates (FR = total filtration ; OFR = filtration of organics), ingestion rates (IR = total ingestion ; OIR ingestion of organics), absorption rate (A) and scope for growth (SFG) of cockles, during two neaps and one spring tides at Le Chapus (Marennes-Oléron Bay).

between TPM and f, also reflected in the differences in CV for TPM and POM.

Variability is greatly attenuated in the process of ingestion regulation, mainly through pseudofaeces production (CV = 17 % for IR, compared with 99 % for FR) ; however, organic ingestion becomes more variable (dependent on TPM), due to the fact that the degree of organic enrichment of filtered matter upon ingestion is a positive function of filtration rate. CV for the absorption rate increases with respect to OIR as a consequence of the positive effect of **i** (partly dependent on the organic enrichment achieved) on the net absorption efficiency of organics.

Given that water temperature was constant in these experiments, metabolic rate was a sole function of absorption, and the variability associated with both A and R and their difference (the SFG) was similar. Altogether physiological processes are shown to achieve an important attenuation of peaks of food availability that would result in less fluctuating rates of growth along tidal cycles. However, there is an important increment of growth potential during pulses of resuspension, reaching to double the mean values of scope for growth.

3. Interpreting unexplained variability in seston organic content

Variation exhibited by the different physiological measurements needs further consideration. When actual measurements of these parameters made throughout the tidal cycle were tested against the data output of fitted models, it becomes clear that actual variability is greater. This was also reflected in low correlation levels between values recorded and predicted in the same moment of the tidal cycles for most physiological rates (as an example, correlation coefficients, for n = 10, were 0.8 in the case of OFR, but droped to 0.3 for OIR and A, and to 0.2 for SFG).

These results have been the consequence of the calculation sequence, where no other variability

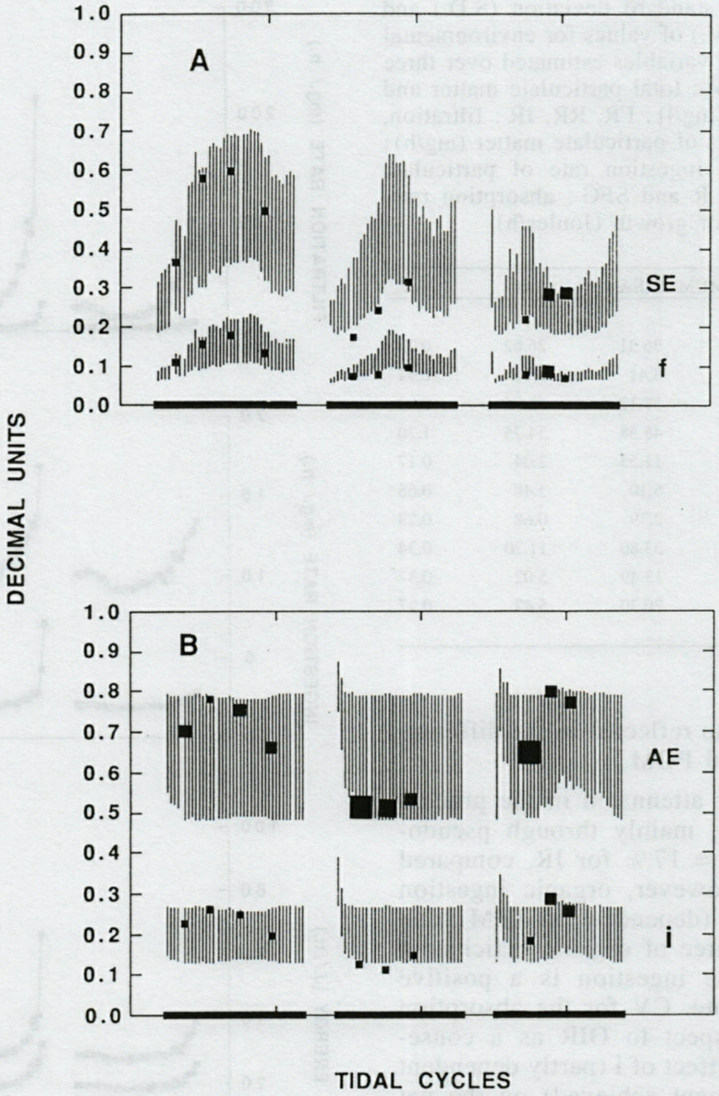

Fig. 3. – Bands of fluctuation of predicted values for A, organic content of the seston (f) and selection efficiency (SE) and B, organic content of the ingesta (i) and absorption efficiency of organics (AE). Means of actually recorded values (squares) are plotted for comparison. Squares size represents approximately 2S.E.

in the organic content of seston than that accounted by changes in TPM has been considered. However, as shown in Figure 1, at any given TPM value in the range of 10 to 100 mg/l, there is significant variation in POM, 99.9 % of which is enclosed within plotted bands in this figure.

We have considered the possibility that this unexplained variation could be accounted for by fluctuations in phytoplankton abundance, which might result, for example, from daily pulses of primary production. However, POM residuals in the above regression were not correlated with either chlorophyll ($r^2 = 0.041$; $P = 0.42$), phaeopigment concentration ($r^2 = 0.011$; $P = 0.67$) or the sum of both (CHL+PHP ; $r^2 = 0.004$; $P = 0.8$). On the other hand, a multiple regression model relating POM simultaneously to TPM and CHL + PHP explained less variability in POM (66 %) than TPM alone (73 %). These negative results precluded thus the possibility of incorporating the continuous fluorimetric measurements in the prediction of organic content of seston.

Given the importance of organic content as environmental variable affecting most processes of feeding and digestion, the unexplained character of a part of its tidal variability results in growth rates simulated through the present physiological model that can only be estimated within broad limits. To illustrate this point, recorded variation around the regression line from Fig. 1 (by convention, enclosed within 99.9 % confidence limits) was incorporated for the calculation of tidal bands of fluctuation in organic content (f) (Fig. 3A). Contour values of these bands (upper

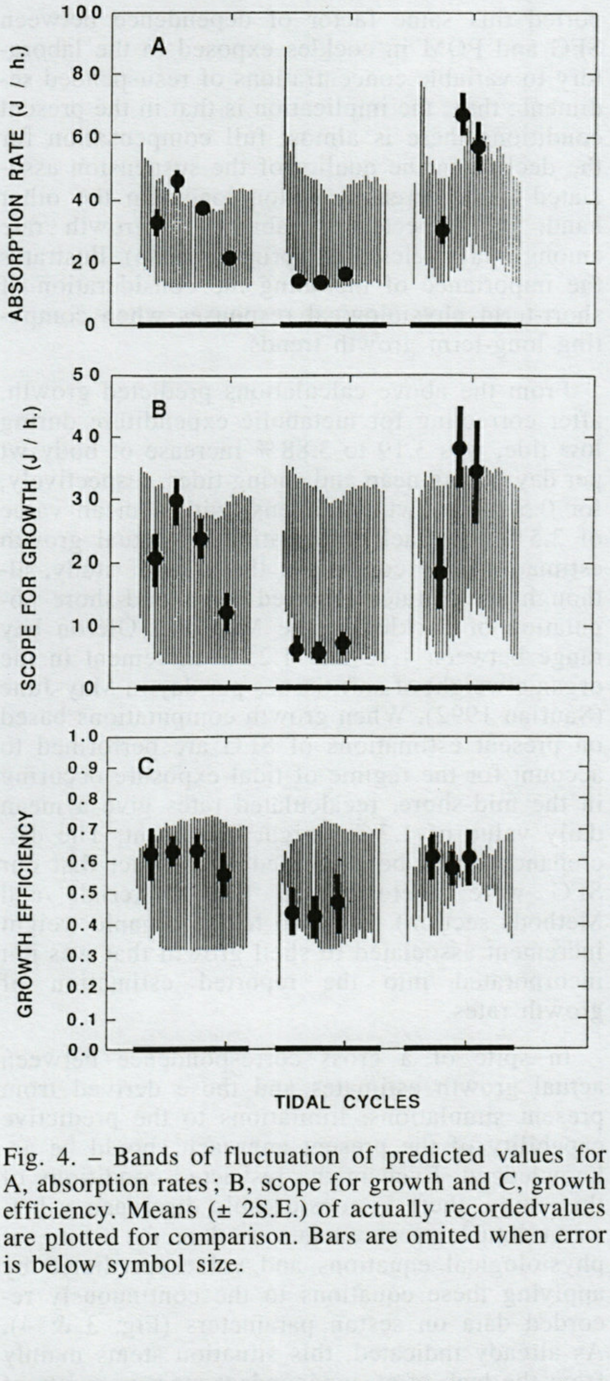

Fig. 4. – Bands of fluctuation of predicted values for A, absorption rates ; B, scope for growth and C, growth efficiency. Means (± 2S.E.) of actually recordedvalues are plotted for comparison. Bars are omited when error is below symbol size.

and lower) were subsequently applied to equations of Table I to simulate the corresponding bands for physiological variables. Results of this treatment are shown in Fig. 3 and 4, where mean values of **f** and physiological measurements actually recorded in the course of experiments are plotted for comparison.

The most important consequences of fluctuations in organic content on energy gain are mediated through its effect on selection efficiency (SE), a parameter that is predicted to closely reproduce the trends exhibited by **f** (Fig. 3A). Fluctuations in the amount of filtered organics are greatly attenuated in the process of ingestion, as a consequence of two associated factors : the ingestion rate regulation based on the mechanism of pseudofaeces, and the increase of SE with increasing organic content (i.e., decreasing TPM).

Organic content of the ingesta (**i**) is a parameter representative of the degree of organic enrichment achieved through preingestive selection, which is in turn a function of the amount of material subjected to selection (the filtration rate) and the efficiency of selection. Maximum values of **i** (Fig. 3B) were achieved coincidentally with the peak of TPM, when maximum rates of filtration occurred ; however, the range of variation in **i** became greatly increased through the effects of selection, which also resulted in a clear attenuation of tidal fluctuations at the upper levels of organic contents.

Since absorption efficiency is a saturating function of the quality of ingested food, bands for AE reproduce the behaviour of **i** in an attenuated scale. Although these bands fluctuate between 0.5 and 0.8, AE is predicted to be virtually constant over the tidal cycles, particularly in the simulated condition of higher organic content (Fig. 3B).

Changes in ingestion rate and AE that have been considered to add to produce further differentiation of curves for absorption (Fig. 4A). Computed values of the scope for growth followed the same tendency exhibited by rates of absorption (Fig. 4B). Observation of these curves indicate a marked tidal profile for the SFG ; beside, improved dietary conditions in the water column, in terms of organic content, would have a strong positive influence on growth potential, as indicated by the amplitude of the fluctuation band. As a summary of the above considerations, boundary curves in Fig. 4C showed that the growth efficiency kept fairly constant when simulated at high seston organic content, but exhibited a strong tidal dependence at low organic content. Under the poorer conditions simulated, high growth efficiencies of approximately 60 %, characteristic of richer suspensions, would be only reached during the periods of high particulate loads.

DISCUSSION

Tidally driven currents impose cyclic pulses of resuspended materials from the soft bottom. This causes abrupt changes in seston composition involving two variables, particle concentration and organic content, which have proved to determine the feeding behaviour of bivalves (Bayne *et al.* 1993, Navarro *et al.* 1994, Iglesias *et al.* 1996). In the near bottom in turbid environments like the Bay of Marennes-Oléron, both variables appear strongly correlated because organic content of seston is mainly determined (negatively) by resuspension of sediments of high mineral content. Thus, the continuous recording of suspended matter together with fitted relationship between organic and total suspended matter was used as the input to a simple model suitable to simulate the physiological behaviour of standard cockles over several tidal cycles in Marennes-Oléron.

Simulated profiles of the various physiological rates and the scope for growth reproduce the tidal variation of TPM through equations from Table I. However, since recorded reciprocal changes in TPM and organic content have been considered in this simulation, such a strict dependence suggests that cockles are able to compensate for declining organic content at high seston loads. The mechanisms by which this is accomplished have been broadly addressed elsewhere (Bayne *et al.* 1993, Iglesias *et al.* 1992, 1996, Navarro & Iglesias 1993, Urrutia *et al.* 1996, 1997, Navarro & Widdows 1997) and include the selection of organics coupled to high rates of filtration of particulate material. Although positive effects of TPM on selection efficiency appear to be almost negligible in cockles (but see Hawkins *et al.* 1996, 1998, for mussels) the organic enrichment of the ingested food achieved through maintaining high rates of filtration and pseudofaeces production is remarkable.

As an indication of the magnitude of such enrichment, it is noticeable that maximum organic contents of ingested particles occur coincidentally with peaks of TPM (see also Fig. 5 in Hawkins *et al.* 1996, for a similar behaviour in mussels), in spite of the negative relationship between TPM and organic content of filtered particles. Furthermore, the strong dependence of the absorption efficiency of organics on the quality of food entering the gut helps to explain the comparative increment of the tidal range of variation for absorption rate and SFG which overcomes the attenuating effects of ingestion regulation.

The most obvious consequence of this capacity to exploit conditions of high seston loads and low organic content is the great potential shown by this species for growth in very turbid environments, which might be considered a positive factor within broad limits. Conditions explored in the present work are adequate to illustrate this point by comparing SFG computed for a full tidal cycle during spring and neap tides. Mean SFG obtained for 9 hours of tidal immersion during the neap tides of 27 and 28 May 1992 was 181.58 Joules for a 500 mg dry wt cockle. During the spring tide of 1st. June 1992, the expected growth amounted to 221.17 Joules in specimens of that size. This represents a 22 % increment associated with an approximately 40 % increment in particulate food availability between conditions at neap and spring tides. Navarro *et al.* (1992) have reported this same factor of dependence between SFG and POM in cockles exposed in the laboratory to variable concentrations of resuspended sediment; thus, the implication is that in the present conditions there is almost full compensation for the decline in the quality of the suspension associated with increased seston load. On the other hand, the expected variability in growth rate among tidal cycles (i.e., spring vs neap) illustrates the importance of including the consideration of short-term physiological responses when computing long-term growth trends.

From the above calculations predicted growth, after correcting for metabolic expenditure during low tide, was 3.19 to 3.88 % increase of body wt per day during neap and spring tides, respectively, for 0.5 g. dry wt specimens, with a mean value of 3.5 %. We lack information on actual growth estimations for cockles in the area of study, although actual rates reported for a mid-shore population of cockles in the Marennes-Oléron bay range between 1.12 and 1.25 % increment in the organic weight of soft tissues per day in May-June (Sauriau 1992). When growth computations based on present estimations of SFG are performed to account for the regime of tidal exposure occuring in the mid-shore, recalculated rates give a mean daily value of 1.7 % weight increment. The discrepancy could be attributed to the fact that our SFG were overestimated (see Materials and Methods section), and also to the organic weight increment associated to shell growth that was not incorporated into the reported estimation of growth rates.

In spite of a gross correspondence between actual growth estimates and those derived from present simulations, limitations to the predictive capability of the present approach should be acknowledged. Even in the restricted conditions of this study, there is considerable discrepancy between actual measurements used in the fitting of physiological equations and values predicted by applying these equations to the continuously recorded data on seston parameters (Fig. 3 & 4). As already indicated, this situation stems mainly from the lack of an independent measurements of organic content in such recording, which is consequently estimated from TPM values using the equation shown in Fig. 1A. This equation explains 73 % of POM variability as dependent on TPM, but since we failed to associate the remaining 27 % to differences in phytoplankton abundance in the water column, there is a considerable degree of uncertainty regarding the estimated values of organic content over the tidal cycles. Furthermore, these effects are amplified through the various physiological processes that are strongly affected by the quality of food, to enlarge the margin of variability unexplained in terms of the recorded seston parameters.

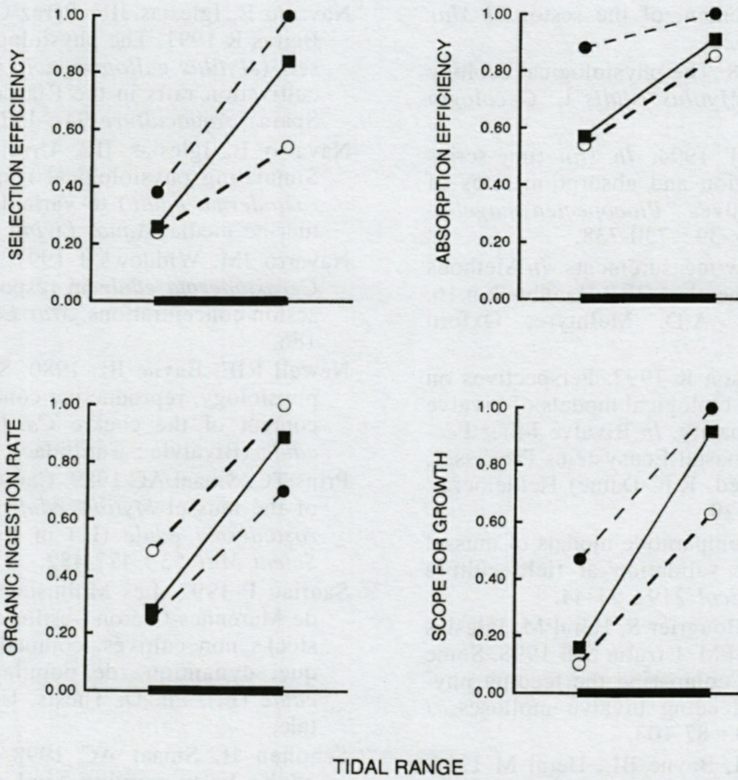

Fig. 5. – Range of variation (on a relative scale) of values of several variables obtained by simulation under conditions of maximum (full circles) and minimum (hollow circles) organic content of seston, compared with the range of variation of actually recorded values (squares).

The procedure described in the Result section, based on incorporation the bands of variation in organic content into the computation of physiological variables, allowed us to establish the magnitude of this source of variability. To illustrate graphically this point, ranges of variation of several parameters have been plotted on a relative scale in Fig. 5. Dotted lines correspond to estimations based on the extreme (maximum and minimum) organic contents of suspended food as derived from functions for upper and lower limits, and continuous lines correspond to the range of variation of actually recorded values (measurements performed at different moments in the tidal cycles). Accordingly, slopes of dotted lines for each parameter represent the amount of variability accounted for by tidal fluctuations while the variability which is associated with fluctuations around the mean organic content for each TPM value is given by the separation between dotted lines. Observation of Fig. 5 leads to the following conclusions : 1) The range of variation recorded in actual measurements of the various parameters is considerably wider, approximately covering the sum of both sources of variability. In other words, when most variability associated with organic content determinations becomes included in the physiological simulation, there is a good agreement between predicted and observed values. 2) The amount of this variability unexplained by TPM is great enough to account for most discrepancies between observed values and values predicted through the first approach presented in this paper.

For modelling purposes therefore, it is essential to have precise and independent estimations of TPM and organic content of the seston. However, in terms of continuous recording requirements, this could be a problem because of the poor correlation found, in turbid estuaries, between fluorescence and organic content.

ACKNOWLEDGMENTS. — We thank the IFREMER-URЕA team for laboratory facilities and for providing continuous recording data of seston. This work is a part of the TROPHEE project and was funded by the CEC through the contract AIR 3 CT94 2219.

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Reçu le 3 juillet 1998 ; received July 3, 1998
Accepté le 9 septembre 1998 ; accepted September 9, 1998

VIE MILIEU, 1998, 48 (4) : 341-352

NET SEDIMENTATION AND SEDIMENT-WATER NUTRIENT FLUXES IN THE EASTERN GULF OF FINLAND (BALTIC SEA)

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SEDIMENT
NITROGEN
PHOSPHORUS
GULF OF FINLAND
ESTUARIES
FLUXES

ABSTRACT. – Variation in the nutrient concentrations of sediment between the different accumulation areas, magnitude of net sedimentation and flux of nutrients from sediment to water, and main factors controlling the binding and release of nutrients was studied in the eastern Gulf of Finland. According to cluster analysis (dry weight, loss on ignition, TP and TN as variables) there are three different accumulation areas : inner Neva Estuary, open Gulf including outer estuary, and coastal areas. In these areas the net sediment accumulation of nutrients ranged from 1.5 to 2.4 g P m^{-2} and from 4.0 to 12.1 g N m^{-2}. The highest outfluxes of nutrients were calculated from the coastal areas and the lowest from the Neva Estuary. The sediment of the Neva Estuary retains P well due to good oxygen conditions, active ventilation by amphipods and possible low sulphide formation. In the coastal areas the sediment is more reduced than in the estuary due to heavy accumulation of organic matter and possible efficient sulphide formation. Iron evidently plays an important role in sediment P binding.

SÉDIMENT
AZOTE
PHOSPHORE
GOLFE DE FINLANDE
ESTUAIRES
FLUX

RÉSUMÉ. – La variation des concentrations en nutriments dans le sédiment entre les diverses zones d'accumulation, l'amplitude de la sédimentation nette et des flux de nutriments du sédiment vers la colonne d'eau, ainsi que les principaux facteurs contrôlant la liaison et le relargage des nutriments ont été étudiés dans l'est du Golfe de Finlande. Les groupements basés sur le poids sec, la perte au feu, les variables phosphore total et azote total montrent qu'il existe trois aires d'accumulation : la zone interne de l'estuaire de la Neva, le golfe, incluant la zone externe de l'estuaire, et les zones côtières. Dans ces zones, l'accumulation nette de nutriments dans le sédiment s'échelonne entre 1,5 et 2,4 g. P.m^{-2} et entre 4,0 et 12,1 g N.m^{-2}. Les flux de nutriments les plus élevés sortant du sédiment ont été mesurés dans des zones côtières, et les plus faibles dans l'estuaire de la Neva. Les sédiments de l'estuaire retiennent bien le phosphore en raison de bonnes conditions d'oxygénation, de la ventilation active due aux Amphipodes et probablement de la faible production de FeS/FeS_2. Dans les zones côtières, les sédiments sont plus réduits que dans l'estuaire par suite d'une forte accumulation de matière organique et d'une possible production de sulfures actifs. Le fer joue évidemment un rôle important dans la liaison du phosphore avec le sédiment.

INTRODUCTION

The general trophic status (chlorophyll-*a* concentration and biomasses of auto- and heterotrophic organisms) in the eastern Gulf of Finland is far higher than in the western Gulf or in the other parts of the northern Baltic (Pitkänen *et al.* 1993, Kauppila *et al.* 1994). This is principally due to the heavy nutrient load from the St. Petersburg area and the River Neva, and to the hydrodynamics of the area. According to mass balance calculations the eastern Gulf of Finland retains 69 % of the land-derived and atmospheric N load and 100 % of the P inputs (Pitkänen 1994). The suspended particulate matter is sedimented primarily in the Neva Estuary. It is also suggested, that denitrification is effective in the eastern Gulf of Finland (Pitkänen & Tamminen 1995).

The benthic flux of dissolved reactive phosphorus (DRP) and ammonium (NH) can support a significant portion of primary production in the estuaries (Nixon *et al.* 1976, Callender & Hammond 1982). Based on the measured total nitrogen (TN) and total phosphorus (TP) concentrations of the surface sediment profiles, the outflux of nutrients from sediment to water seems to be considerable in the Neva estuary and the open Gulf of Finland (Lehtoranta *et al.* 1997). Extensive deep water oxygen deficit and a high phosphorus release from sediments was observed in late summer 1996 (Pitkänen & Välipakka 1997). This internal P loading was estimated to be ca. 4 500 tons in the eastern Gulf, which corresponds about one year anthropogenic load of P to the Gulf. The importance and proportion of internal loading of nutrients is poorly studied in the eastern Gulf. Only Conley *et al.* (1997) have directly measured sediment fluxes of nutrients from one sampling site. Other outflux estimates have based on diffusion calculations (Lehtoranta *et al.* submit.).

Specific questions in this study were :

— are there variations in the nutrient concentrations of sediment and in porewater between the different accumulation areas of the eastern Gulf of Finland,

— what are the main factors controlling the regeneration and storage of nutrients in the sediment,

— what are the magnitudes of net sedimentation and sediment-water nutrient fluxes in the accumulation areas of the Gulf.

STUDY SITE

The eastern Gulf of Finland (13 000 km^2) is defined as the area east of Gogland Island (Fig. 1). The mean depth of the area is ca. 30 m and the average residence time of water ca. one year. The River Neva, discharging to the easternmost corner of the Gulf, is the largest river flowing into the Baltic Sea (mean flow ca. 2 600 m^3 s^{-1}). It corresponds to 75 % of the total inflow into the Gulf of Finland and to 20 % of the total riverine inflow into the whole Baltic Sea (Ehlin 1981). The surface salinity of the study area increases from 0 psu in the Neva Bay to 4 to 5 psu in the open eastern Gulf, whereas in near bottom waters salinities vary from 4 to 8 psu (Pitkänen *et al.* 1993).

The areas of erosion, transportation and accumulation alternate spatially due to variations in morphometry and hydrodynamical conditions. In the Finnish archipelago and in the open area east of archipelago, accumulation bottoms locate mainly in small, steeply sloped bottoms surrounded by large, shallow transportation and erosion areas (Lehtoranta *et al.* 1997). Sediment organic matter and TN contents in the accumulation areas increase while TP contents decrease from mouth of the River Neva to the open waters of the Gulf of Finland. Sediment accumulation in the eastern Gulf of Finland is characterized by greatly variable distribution of bottom types due to irregular topography with numerous depressions filled with deposits of pelitic mud (Emelyanov 1988).

MATERIAL AND METHODS

Sediment sampling and chemical analyses : The data reported here is collected from six different research cruises from years 1992-97. Samples for nutrient concentrations of the sediment were taken with gravity corers (slightly modified from Axelsson & Håkansson 1978) and a Limnos-corer (Kansanen *et al.* 1991) at 30 stations in July-August 1992 to 94 (Fig. 1). The cores were sliced into 1 cm slices from the surface to 10 cm depth. Each slice was frozen in plastic bag. Dry weight (DW, freeze drying) and loss on ignition (LOI) were analyzed according to the Finnish standard SFS 3008 (1981). Total nitrogen (TN) and total phosphorus (TP) were analysed by co-digestion using the method of Zink-Nielsen (1975). Organic matter was decomposed by strong sulphuric acid. Nitrate and nitrite were reduced to ammonia with Devarda solution. The formed ammonium sulphate was distilled and ammonium was titrated (Starck and Haapala, 1984). Inorganic phosphate complexes and organic P were converted to orthophosphate by sulphuric acid and analysed after SFS 3025 (1986).

In the years 1995-1997 the cores were sliced into 1 cm slices from the surface to the depth of 5 cm and deeper in the sediment from 5 to 7 cm, 7 to 10 cm and 10 to 15 cm. Samples were stored in plastic bags. The benthic fauna was sampled with an Ekman-sampler and the samples (three replicates) were passed through a 0.5 mm sieve.

Sediment redox potential (platinum electrode) and pH were measured (PHM62 Standard pH-meter) immediately on fresh samples. Porewater was filtered on Nuclepore polycarbonate membranes (pore size 0.4 µm) immediately after sampling under N^2-gas atmosphere with a suction pump in the temperature adjusted laboratory (+ 6 to + 9 °C). The sediment samples for total nutrient analysis were frozen (– 18 °C) and analysed as presented earlier. The concentration of oxygen was measured with Winkler method (Grasshoff *et al.* 1983). Inorganic nutrients (DRP, NH_4^+ and NO_3^- + NO_2^-) of near bottom water (siphoned from 5 cm above sediment surface) and porewater were analyzed according to Koroleff (1976). Sediment P- fractionations were based on the method of Hartikainen (1979), which is slightly modified from the method of Chang & Jackson (1957). Method is based on the ability of certain reagents to dissolve phosphate minerals : NH_4Cl is considered to extract labile loosely adsorbed phosphates, NH_4F Al phosphates, NaOH Fe phosphates and H_2SO_4 Ca phosphates. P-pools were fractioned from three sites (Fig. 1).

Calculations of diffusive fluxes of phosphorus and ammonium : The diffusive fluxes were calculated according to Fick's first law. Diffusion coefficients of phosphate and ammonium ions presented by Krom & Berner 1980 were temperature corrected by equations of Li & Gregory (1974). The sediment diffusion coefficient is influenced by sediment porosity, which was calculated by the equation presented by Yamada & Kayama (1987). The value of 2.5 g cm^{-3} was used as the density of solid matter. Sediment porosity was taken into account in using the equation presented by Ullman & Aller (1982).

Statistical analyses : The data were clustered with an average distance method (Sokal and Michener, 1958)

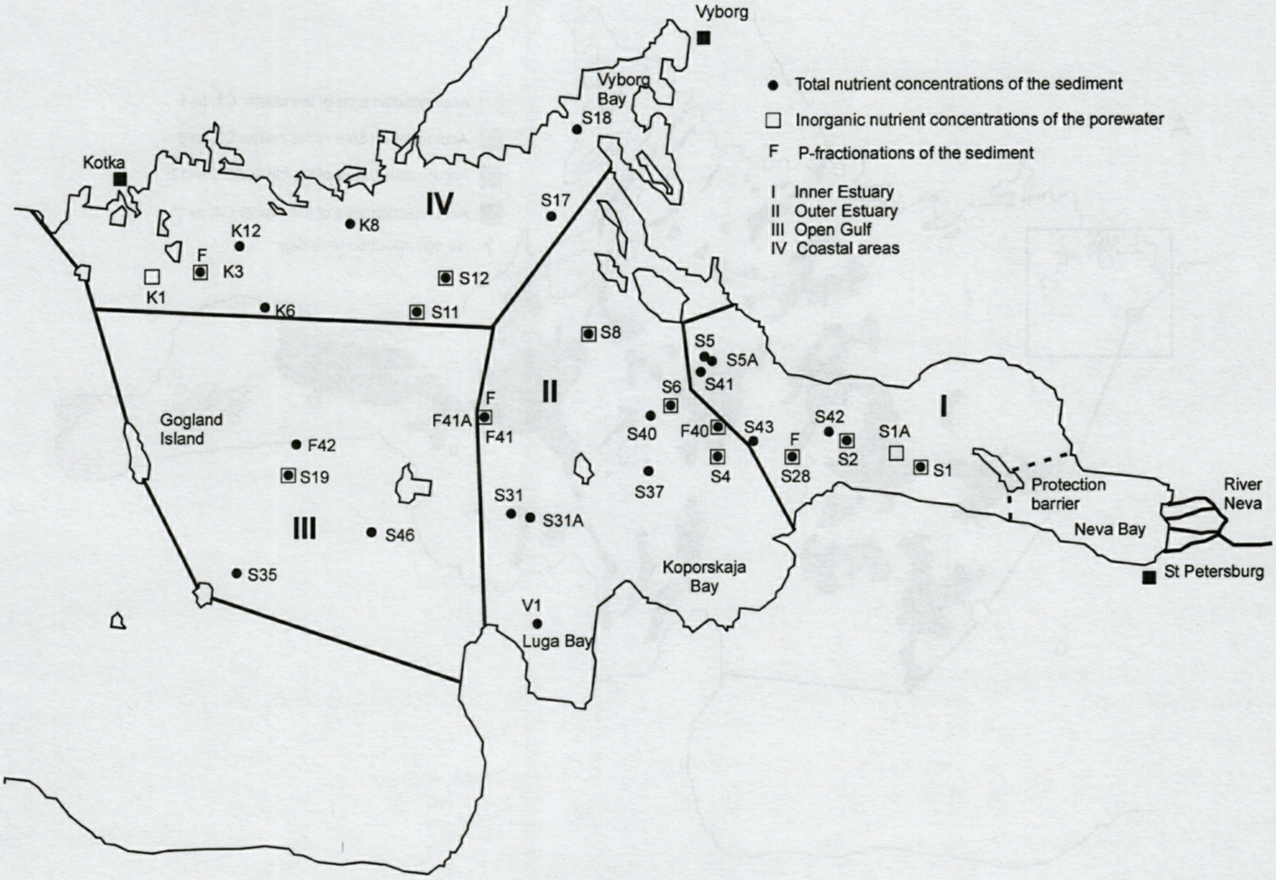

Fig. 1. – The eastern Gulf of Finland and the sampling sites.

and it tends to join clusters with small variances and is slightly biased towards producing clusters with the same variance. In this study the cluster analysis was done by sampling sites (individual directed analysis). In the cluster analysis, DW and concentration of LOI, TN and TP for each of the 1 cm sub-layers (from 1 to 10 cm) were used as discrete variables (all together 40 variables). The present data was normalised to the average of 0 and a variance of 1.

RESULTS

General character of the sediment samples

In most of the cores (mostly clayey gyttja) a light brown layer (0.2 to 4 cm thick) was found in the upper sediment. Underneath the sediment was reduced and coloured by black sulfides and a sharp smell of H_2S was present. In the black layer white filamentous bacteria, probably H_2S-oxidizing *Beggiatoa*, were found in most of the cores. At some of the organic rich sites *Beggiatoa* was also found from the very surface of the sediment. This indicated that H_2S reaches the surface.

Grouping of the sampling sites

On the basis of the cluster analysis the sites were divided into four clusters (Fig. 2A and B). In the inner estuary the sediment contained sand and the area was classified as a transport bottom (cluster C1). Cluster C2 corresponded well to the basin of the inner Neva Estuary, while the sampling sites of the cluster C3 situated in the outer estuary and in the open Gulf. Cluster C4 corresponds to the coastal areas (the Finnish archipelago, the open area east from the archipelago and the Luga Bay, where the accumulation bottoms are located mainly in small, steeply sloped bottoms surrounded by large, shallow transport and erosion areas.

In the transport area of the inner Neva Estuary (cluster C1) the surface (0-1 cm) TP concentration was low (1.1 mg g^{-1} DW, Fig. 3). In the accumulation area of the inner estuary (C2) TP decreased gradually from the sediment surface (3.7 mg g^{-1} DW) to the depth of 8 cm (1.5 mg g^{-1} DW). In the outer estuary and in the open Gulf (C3) TP concentration decreased also but the concentration was lower than in the inner estuary in the whole sediment profile. In the coastal areas

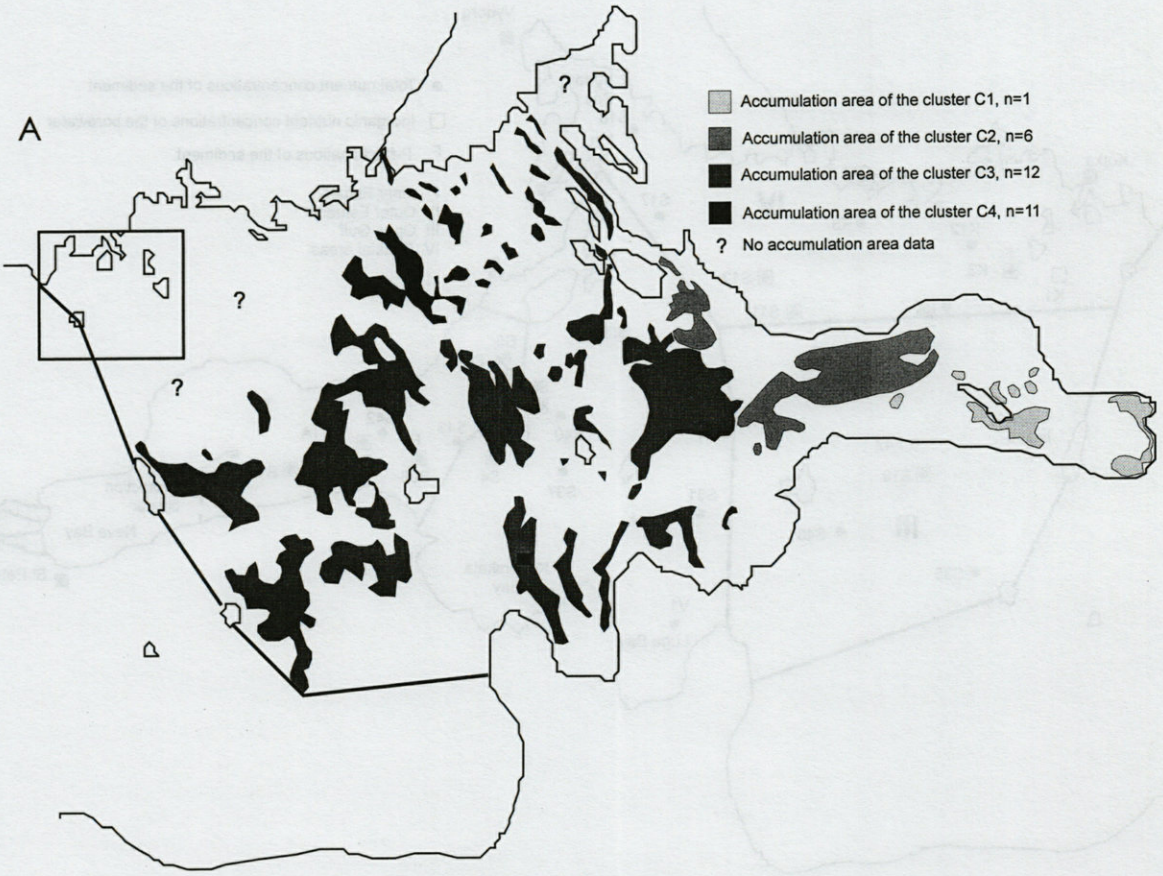

Fig. 2A. – The accumulation areas and the locations of the clusters C1-C4 in the eastern Gulf of Finland.

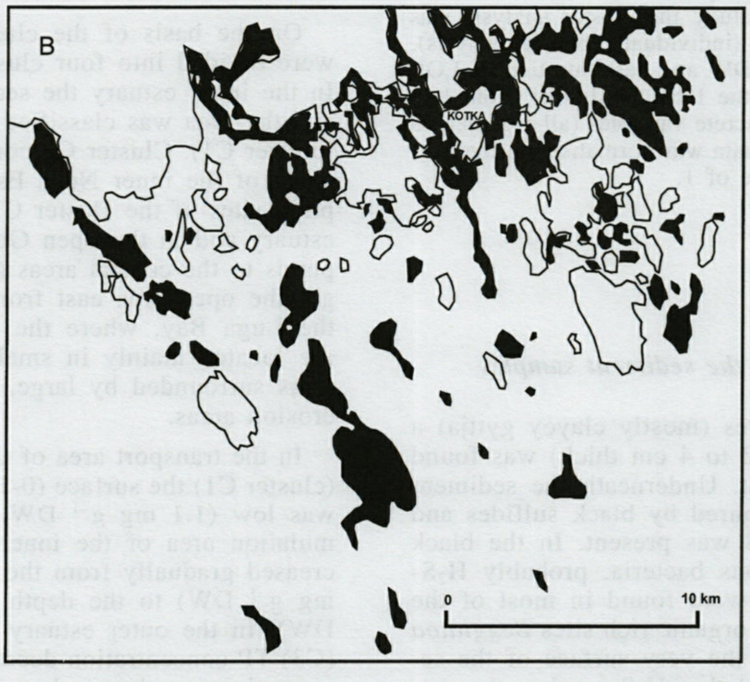

Fig. 2B. – The accumulation areas and the locations of the clusters C1-C4 in the eastern Gulf of Finland.

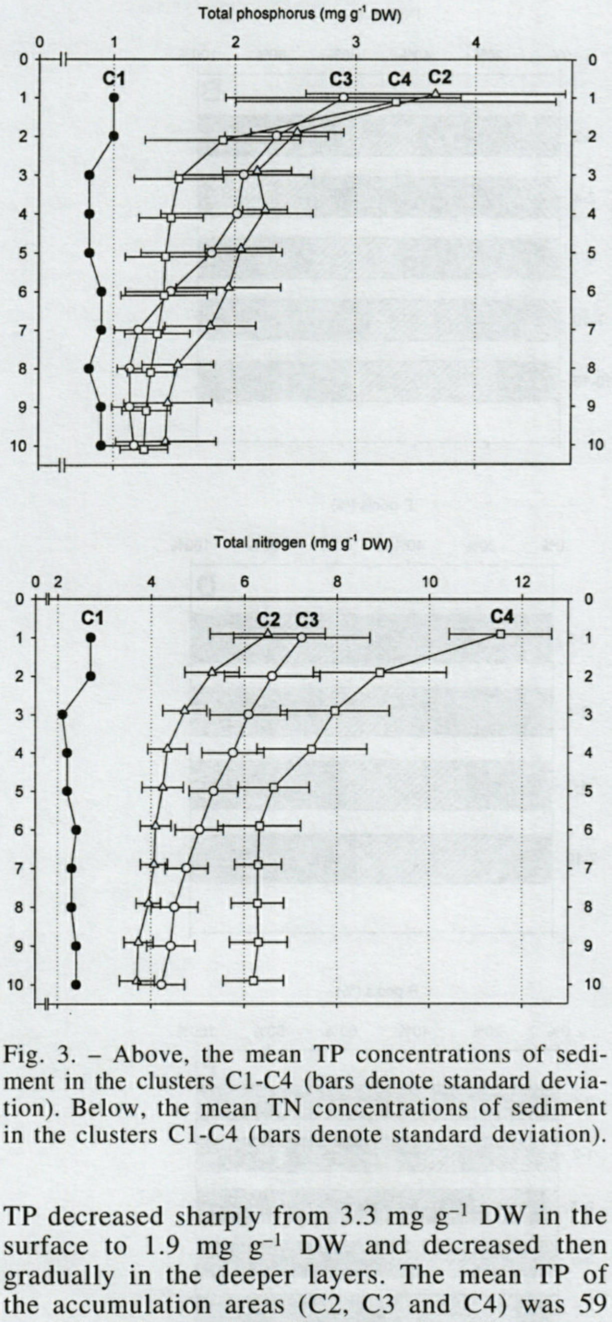

Fig. 3. – Above, the mean TP concentrations of sediment in the clusters C1-C4 (bars denote standard deviation). Below, the mean TN concentrations of sediment in the clusters C1-C4 (bars denote standard deviation).

TP decreased sharply from 3.3 mg g^{-1} DW in the surface to 1.9 mg g^{-1} DW and decreased then gradually in the deeper layers. The mean TP of the accumulation areas (C2, C3 and C4) was 59 to 62 % higher in the sediment surface (0 to 1 cm) than in the deeper sediment (9 to 10 cm).

TN concentrations of the inner estuary (cluster C1) were lower (2.7 mg g^{-1} DW, Fig. 3) than the others in the whole sediment column. The mean TN content of the studied sediment profiles of clusters C1, C2, C3 (in this order) from the River Neva mouth towards west. In the whole estuary and the open Gulf areas (clusters C2 and C3) the mean surface TN concentrations were clearly lower (6.5 to 7.2 mg g^{-1} DW) than in the coastal areas (C4, 11.5 mg g^{-1} DW). The average TN concentrations of the accumulation areas (clusters C2, C3 and C4) were 42 to 46 % higher in the sediment surface (0 to 1 cm) than in the deep layer (9 to 10 cm).

P-pools in the sediment

NH$_4$Cl-RP concentrations were low (Fig 4A, C), except in the reduced surface sediment of the coastal site K3 (Fig. 4E, F), where 11 % of P was loosely adsorbed. The high concentration of P in the oxidized surface layer (0-2 cm) could be attributed to NaOH-RP, which constituted 43 to 57 % of the TP (Fig. 4B, D). At site K3 (no brown oxidized layer) the corresponding proportion of NaOH-RP was only 9 % (Fig. 4F). NH$_4$Cl-RP and NH$_4$F-RP concentrations decreased with depth, while H$_2$SO$_4$-RP concentrations were constant. The proportion of H$_2$SO$_4$-RP increased with sediment depth. Of the buried P (sediment layer 7-15 cm), the NH$_4$Cl-RP made up 0 %, NH$_4$F-RP 0.5 – 1.7 %, NaOH-RP 12 – 16 %, H$_2$SO$_4$-RP 37 – 41 % and Res-RP 42 – 49 % of the TP.

Nutrient concentrations of the nearbottom water and porewater

There was no significant correlation between nutrient concentrations in the near-bottom water and in porewaters of the sediment surface layer. Both DRP and ammonium concentrations increased with the sediment depth. Porewater DRP concentration increased from the River Neva mouth towards west (from cluster C2 and C3 to C4, Fig. 5A). In the coastal areas (C4) NH$_4$ concentration was at the highest and there was only little variation between the inner and outer Neva Estuary and the open Gulf (clusters C2 and C3, Fig. 5B).

Redox potential was at the highest in the inner estuary (C2) and especially in the outer estuary and in the open Gulf (C3), where amphipods *Monoporeia affinis* (site S6, 4500 ind m^{-2}) or both (*M. affinis* and *Pontoporeia femorata*, site S19, 3500 ind m^{-2}) were abundant (Lehtoranta *et al.* submit.). At these sites DRP and ammonium concentrations of porewater were low while NO$_2^-$ + NO$_3^-$ concentrations were high. At bioturbated sites the brown oxidized (not oxic) layer reached the sediment depth of 5 cm. The lowest redox potentials were measured from the coastal areas (C4), where sediment burrowing animals were few in number. On the contrary to bioturbated sites, the DRP and ammonium concentrations were high and NO$_2^-$ + NO$_3^-$ concentrations very low in the porewater (3 to 10 µg l^{-1}).

Nutrient outfluxes

The calculated fluxes of nutrients from sediment to water were highest in the summer and lowest in the spring before the sinking of the spring bloom (Table I).

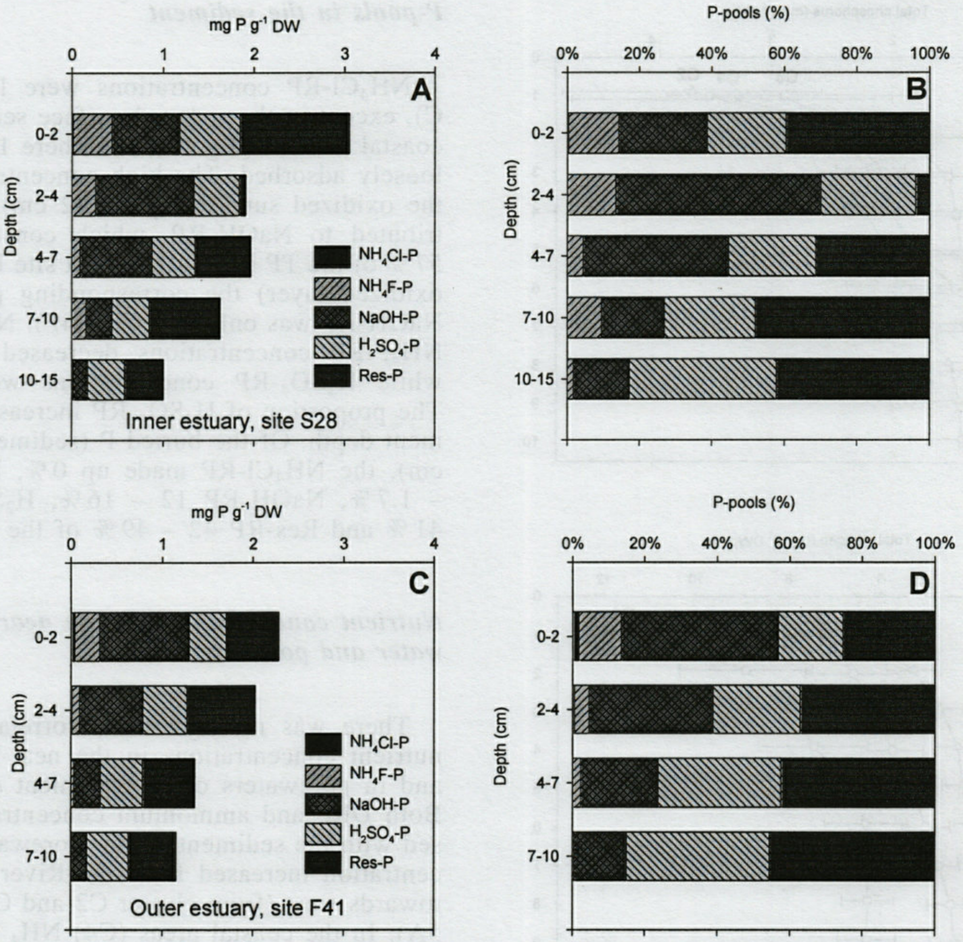

Fig. 4. – Depth distribution and proportions of particulate P fractions in the inner estuary (A and B), outer estuary (C and D) and coastal area (E and F). Data for sites S28 and F41 are from Paavilainen (1997).

DISCUSSION

Binding and burial of nutrients and nutrient regeneration in the sediment

In the very reduced surface sediment of the site K3, the NH_4Cl-RP concentration is high, which indicates the saturation of the binding sites in the sediment (Boström *et al.* 1988) and also high outflux of P from sediment. The lower proportion of NH_4F-RP compared with the high proportion of NaOH-RP suggests that Al oxides are less important in sediment P binding than Fe in the sediment surface. NH_4F is known to extract Fe-P (Petterson *et al.* 1988) and this is probably the

Table I. – Nutrient fluxes based on diffusion calculations from sediment to water. Data partly from Lehtoranta *et al.* (submitted).

Cluster	Site	DRP May (mg P m^{-2} d^{-1})	DRP August (mg P m^{-2} d^{-1})	DRP December (mg P m^{-2} d^{-1})	NH$_4^+$May (mg N m^{-2}d^{-1})	NH$_4^+$August (mg N m^{-2}d^{-1})	NH$_4^+$December (mg N m^{-2}d^{-1})
C1	S1	-	7.0	-	-	24.6	-
C2	S2	-0.1	7.2	0.2	4.3	10.2	16.9
C2	S28	-	1.2	-	-	8.6	-
C3	F40	-	1.6	-	-	5.8	-
C3	S6	-0.0	0.0	0.4	0.2	-0.8	0.4
C3	F41	-	12.0	4.7	-	18.4	29.6
C4	S12	0.6	17.4	-	5.2	29.8	-
C3	S4	-0.2	-	-	2.7	-	-
C3	S8	6.8	-	-	3.2	-	-
C4	S11b	2.3	-	-	3.7	-	-
C3	S19	-	0.2	-	-	3.0	-
C4	K1	-	-	12.9	-	-	46.5
C4	K3	-	-	3.9	-	-	32.9
C4	XV1	-	-	2.7	-	-	30.4

reason for decreasing NH$_4$F-RP concentrations with the sediment depth. In addition, the total Al concentration of the sediment was correlated poorly with TP of the sediment (Lehtoranta *et al.* submit.).

In this study NaOH-RP bound P constituted an important P reservoir in the sediment comprising about 15 % of the buried P. It is also evident that iron plays important role in the sediment P binding. In Århus Bay the dynamic pools of loosely sorbed phosphate, iron bound phosphate, and fresh organic phosphorus have constituted nearly 50 % of the total P in the uppermost 0-1 cm, but were largely depleted below the depth of 3 cm (Jensen *et al.* 1995). In their study iron and manganese bound P constituted only 3.5 % of the buried TP. The NaOH step extracts also humus compounds (Klapwijk *et al.* 1982) and this probably explains the high proportion of NaOH-RP in the deep layer of the sediment compared with the study of Jensen *et al.* (1995). Because $H_2SO_4^-$ RP concentration was almost constant with depth, no indication of P converted to apatite-P was found during early diagenesis. In Århus Bay the apatite-P concentration was uniform with depth (Jensen *et al.* 1995).

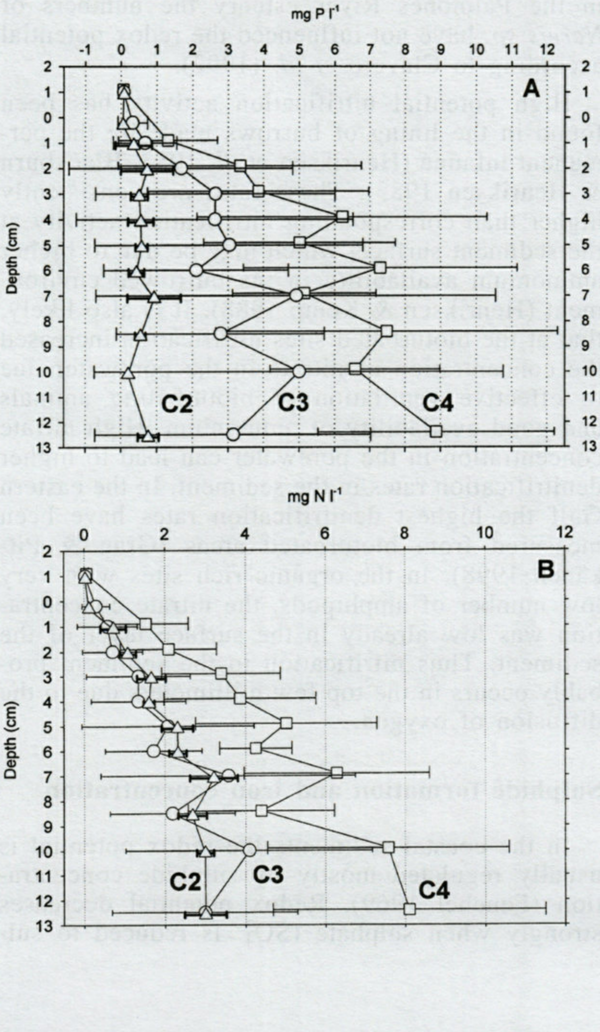

Fig. 5. – A, the average DRP– and B, NH_4^- concentrations in porewater of the inner Neva Estuary (C2), the outer Neva Estuary and the open Gulf (C3) and the coastal areas (C4). The bars denote standard deviation.

Concentration of DRP increased with sediment depth, because of the upward migration of P produced by the mineralization of organic P and the reduction of iron oxides to which P is adsorbed (Krom & Berner 1981, Balzer 1986). It has been suggested that most of the P is released in the deep sediment from iron oxides undergoing reduction (Yamada & Kayama 1987, Sundby *et al.* 1992, Jensen *et al.* 1995). DRP of porewater correlated poorly with total soluble Fe (Lehtoranta *et al.* submit.) probably due to the Fe^{2+} precipitation to ironsulphides (FeS or FeS_2, Jensen *et al.* 1995) and due to DRP released via labile organic matter mineralization (Krom & Berner 1981). The precipitation of Fe as sulphides and release of P explains also the increasing total Fe : TP ratio along sediment depth. The average TP concentration of the sediment (1.23 mg g^{-1} DW) in the deep layer (9 to 10 cm) of the sediment was close the abundance of P on the surface of the earth (0.10 to 0.12 %, Van Wazer 1961).

The concentration of TN in the sediment decreased with depth, while concentrations of porewater NH_4^+ increased with the sediment depth. Ammonium in the sediment is formed during organic nitrogen mineralization (Blackburn 1988) and through biological dissimilatory nitrate reduction (Sørensen 1978). The observed ammonium concentrations revealed that ammonium accumulated in high concentrations in the porewater. Increasing ammonium concentration along sediment depth indicated that anaerobic mineralization of organic matter continued in the deep layer. In Århus Bay nitrogen is mainly buried as organic N and only 5 % of it as adsorbed or free NH_4^+ (Jørgensen 1996). The sediment of the coastal area (C4) accumulates more organic matter than the other areas of the eastern Gulf. The burial efficiency of organic matter increases with its deposition rate (Henrichs & Reeburgh 1987). This seems to lead to increased concentrations of TN, increased burial of N and also increased accumulation of ammonium in porewater in the sediment of the coastal areas.

The controlling factors on nutrient concentrations of the sediment

Bioturbation

The accumulation of P to the layer 0 to 5 cm in the Neva estuary and the open Gulf is explained with heavy P loading from the Neva River and subsequent sedimentation of P (Pitkänen 1994, Lehtoranta *et al.* 1997) and good oxygen conditions (Pitkänen *et al.* 1993). But P is also efficiently bound in the sediment due to effective bioturbation by amphipods (Lehtoranta *et al.* submit.), low sulphide formation and higher total Fe concentration in the sediment surface compared with the other areas in the open Gulf.

Oxygen measurements with microelectrodes have revealed that the oxygen is depleted in the top few millimeters at the sediment-water interface in the Gulf of Finland (Conley *et al.* 1996). However, the sediment invertebrates ventilate oxygen rich water through their burrows down to depth of several centimeters (McCaffrey *et al.* 1980) even if oxygen is depleted within the few millimeters in the sediment surface. The vertical profiles of total nutrients and organic matter together with the brown oxidized layer in the upper sediment (redox potential ~ 350 mV) suggest that the bioturbated layer reaches the depth of 5 cm (Lehtoranta *et al.* submit.). This coincides well with depths, where the TP concentration start to decrease more rapidly in the inner and outer estuary and in the open Gulf (clusters C2 and C3). Where amphipods have been abundant, DRP and ammonium concentrations of porewater have been low, while $NO_3^- + NO_2^-$ concentrations have been high (Lehtoranta *et al.* submit.). Also Maximov (1996) have reported on the abundance of *Monoporeia affinis* in the inner and outer Neva estuary.

In the Neva estuary oligochaeta worms were abundant, but however redox potential was < 50 mV in the surface layer of the sediment. Also in the Palmones River estuary the numbers of *Nereis sp.* have not influenced the redox potential according to Clavero *et al.* (1992).

High potential nitrification activity has been found in the lining of burrows made by the permanent infauna (Henriksen *et al.* 1983, Blackburn & Henriksen 1983). These rates are consistently higher than corresponding nitrification activity at the sediment surface, which may be due to higher ammonium availability in the burrowed environment (Henriksen & Kemp 1988). It is also likely, that at the bioturbated sites nitrification increased the concentration of nitrate in the porewater due to effective ventilation of bioturbating animals and good availability of ammonium. High nitrate concentration in the porewater can lead to higher denitrification rates in the sediment. In the eastern Gulf the highest denitrification rates have been measured from bioturbated areas (Gran & Pitkänen 1998). In the organic rich sites with very low number of amphipods, the nitrate concentration was low already in the surface layer of the sediment. Thus nitrification in the sediment probably occurs in the top few millimeters due to the diffusion of oxygen.

Sulphide formation and iron concentration

In the coastal sediments the redox potential is usually regulated mostly by sulphide concentration (Fenchel 1969). Redox potential decreases strongly when sulphate (SO_4^{2-} is reduced to sul-

Table II. – The calculated nutrient outfluxes from sediment to water in the clusters C1 – C4 in the whole eastern Gulf of Finland. For EGOF/period, the outflux is assumed to be constant for the period in parenthesis (months). NB = Neva Bay, IE = inner Neva Estuary, OE = outer Neva Estuary, OG = open Gulf, CA = coastal areas, EGOF = eastern Gulf of Finland.

Cluster	area (km^2)	DRP flux late spring (t P d^{-1})	DRP flux summer (t P d^{-1})	DRP flux winter (t P d^{-1})	NH_4^+flux late spring (t N d^{-1})	NH_4^+flux summer (t N d^{-1})	NH_4^+flux winter (t N d^{-1})
NB (C1)	44	-	0.31	-	-	1.08	-
IE (C2)	266	0.03	1.16	0.05	1.14	2.50	4.49
OE,OG (C3)	1399	3.08	4.83	3.57	2.84	9.24	20.99
CA (C4)	140	0.20	2.44	0.91	0.62	4.18	5.13
EGOF	2227	2.22	14.79	5.73	6.66	32.5	42.16
EGOF/ period	-	100 (1.5)	1775 (4)	1117 (6.5)	1299 (1.5)	3900 (4)	8221 (6.5)

phides. Heavy accumulation of organic matter shifts the balance of oxidants toward anaerobic mineralization and sulphate reduction. Enhanced liberation of PO_4^{3-} occurs during anaerobic incubation in the presence of abundant sulfate and it directly correlates with sulfate reduction and iron-sulfide formation (Roden & Edmonds 1997). In the Neva Estuary the higher redox potentials in the 0 to 15 cm layers compared with potentials of the coastal areas (C4) suggest that sulphide concentration is lower in the sediment of Neva Estuary. Thus in the coastal areas phosphorus is evidently accumulated only to the very surface of the sediment due to heavy accumulation of organic matter and sulphate reduction producing low redox potential, more efficient iron oxide reduction and iron bound P release to the porewater and iron sulphide formation. In the outer estuary the total iron concentration of the sediment is about 40 % higher in the surface layer of the sediment than in the open Gulf. This may indicate higher iron oxide concentration and thus more efficient P binding in the estuary.

Outfluxes and accumulation of nutrients

Applications of the simple diffusion calculations are restricted to environments with low bioturbation and turbulence. At the bioturbated sites the bottom animals may decrease the nutrient concentration gradients between different sediment layers (Clavero *et al.* 1991), thus calculations based on diffusion may underestimate sediment-water nutrient fluxes. Calculation of ammonium diffusion is valid only for anoxic environments, where no nitrification occurs (van der Loeff *et al.* 1984). The calculated and measured fluxes have differed for more than one order of magnitude, but they are in closer agreement in reduced conditions (Enell & Löfgren 1988). For DRP the measured outflux was 1.1 to 4 times higher than calculated outflux and for ammonium 0.9 to 0.2 times lower in the easternmost Finnish archipelago (Lehtoranta, unpublished data). In the reduced sediments the measured and calculated fluxes were in closer agreement, especially for ammonium.

The annual internal load in whole study area for DRP was assumed as 2 990 t P a-1 and for ammonium 13 420 t N a^{-1} (Table II). This corresponds to about 52 % of the total land-based P load (5 800 t P a^{-1}, Pitkänen *et al.* unpublished data) and 21 % of the total land-based N load (64 000 t N a^{-1}, Pitkänen *et al.* unpublished data).

Based on ^{137}Cs datings (11 cores, data from Kankaanpää *et al.* 1997 and Mattila unpubl data) the accumulation rate varied from 0.030 to 0.253 g cm^{-1} a^{-1} (2.8 to 18.6 mm a^{-1}) in different accumulation areas. These estimates are agreement with estimates of Pitkänen (1994, from 3 to 20 mm a^{-1}). The ^{137}Cs-method is suitable for the estimate of dry matter accumulation rates in the Gulf of Finland, because the rates are high, radiocaesium activity is high and radiocaesium stratification remains well defined despite considerable mixing (Kankaanpää *et al.* 1997).

The mean sediment concentrations of 0.90 – 1.43 mg g^{-1} of P and 2.4 – 6.2 mg g^{-1} of N (the anoxic layer from 9 to 10 cm) of the present study correspond to mean accumulation rates of 1.5 to 2.4 g m^{-2} a^{-1} of P and 4.0 to 12.1 g m-^{2} a^{-1} of N (Table III). These rates are in close agreement with rates (1.4 g P m^{-2} a^{-1} and 4.9 g N m^{-2} a^{-1}) presented by Pitkänen (1994). Though average sedimentation rates are almost same in the inner estuary and coastal areas (Table III), the proportion of organic matter of the sediment is higher in the coastal areas. In the whole eastern Gulf 3 600 km^2 of the bottoms has been classified as accumulation areas (Pitkänen 1994). In this study the estimated area of accumulation is based on unpublished results of Winterhalter, Rybalko, Butylin & Spiridonov. The estimated area is smaller

Table III. – The net accumulation of nutrients of the sub-areas (clusters) and the whole eastern Gulf of Finland. Dry matter accumulation rate is an average value of the number of the sites in parenthesis. The average accumulation rate of the inner Neva Estuary was used also for the Neva Bay due to lack of accumulation rate data. The abbreviations of the areas are the same as in Table II.

Cluster	DM acc.rate ($g\ cm^{-1}\ a^{-1}$)	area (km^2)	P ($g\ m^{-2}\ a^{-1}$)	N ($g\ m^{-2}\ a^{-1}$)	P ($t\ a^{-1}$)	N ($t\ a^{-1}$)
NB (C1)	0.167(2)	44	1.5	4.0	66	175
IE (C2)	0.167(2)	266	2.4	6.2	634	1636
OE,OG (C3)	0.138(6)	1399	1.6	5.8	2259	8144
CA (C4)	0.195(3)	140	2.4	12.1	343	1696
Sum	-	-	-	-	3302	11652
EGOF	0.166 (11)	2227	2.0	6.9	3886	14050

(2 227 km^2) compared with estimate of Pitkänen (1994), partly because the lack of accumulation area data in the coastal areas of Finland. Also the large accumulation area of the Narva Bay is excluded due to lack of sediment nutrient data. Accordingly 14 100 t N a^{-1} and 3 900 t P a^{-1} have sedimented permanently in the eastern Gulf. These estimates are ca. 35 % lower than earlier estimates of Lehtoranta *et al.* (1997) and 50 % lower than estimates of Pitkänen (1994). The main reason to the difference is the smaller accumulation area used in calculations in this study.

CONCLUSIONS

Phosphorus accumulated in the top 0 to 2 cm at the organic rich coastal sediment and in the 0 to 6 cm in the sediment of the inner estuary and outer estuary and at the open Gulf. P is mostly bound to iron oxides. Thus there is a large pool of mobile P especially in the Neva estuary and the open Gulf of Finland. This part of P is not buried due to iron reduction and subsequent P release deeper in the sediment. Thus phoshate is released into porewater and diffused upwards. In the Neva Estuary the concentration of P in the sediment is high both because of heavy nutrient load and subsequent high primary production, which sinks mostly in the inner estuary and due to good oxygen conditions, bioturbation and low sulphide formation. In the organic rich coastal accumulation bottoms (the Finnish Archipelago, the open area east from the archipelago and part of the Luga Bay) the pool of mobile P is focused to the surface layer.

The sediment-water fluxes of nutrients in the sites of the inner and outer estuary of the River Neva are smaller compared with fluxes in the easternmost Finnish archipelago and in the near coastal open area to the east from the archipelago.

The abundance of amphipods has a strong effect on both the total nutrient concentration of the sediment and on porewater concentrations of inorganic nutrients via bioturbation. At the sites, where amphipods were abundant, the homogenous bioturbated layer (0 to 5 cm) containing evidently iron oxides increases the binding of P and nitrification thus providing substrate for denitrification due to active ventilation of oxygen-rich water in the burrow structures of the sediment.

ACKNOWLEDGEMENTS. – Financial support was provided by the Finnish Environment Institute and the Ministry of the Environment of Finland. I acknowledge H. Pitkänen and A.S. Heiskanen for their valuable comments on the manuscript and V. Gran, O. Sandman and N. Ignatieva for their practical assistance during the cruises and writing. I am grateful to E. Salminen and M. Sjöblom for the nutrient analysis and other laboratory work. I also like to thank the crew of R/V Muikku for the assistance in sediment sampling.

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Reçu le 5 août 1998 ; received August 5, 1998
Accepté le 20 octobre 1998 ; accepted October 20, 1998

VIE ET MILIEU : Volume 48

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Directeur gérant de la publication : A. GUILLE

Printed in France *Dépôt légal 4^e^ trimestre 1998* *Commission paritaire n^o^ 22217*

Imprimerie Louis-Jean, 05002 GAP cedex — Dépôt légal 1135 — Décembre 1998

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Eagle R.A. and P.A. Hardiman, 1977. Some observations on the relative Abundance of species in a benthic community. *In* Biology of Benthic Organisms. Edited by B.F. Keegan, P.O. Ceidigh and P.J.S. Boaden, Pergamon Press, Oxford-New York, 197-208.

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Les notes infrapaginales et les remerciements seront aussi brefs que possible.

ILLUSTRATIONS

Les figures au trait doivent être exécutées à l'encre de chine sur papier calque assez fort, bristol, carte à gratter, papier millimétré bleu. Il est exigé des lettres et chiffres «transfert» par caractères autocollants pour le lettrage et la numérotation, dont la taille tient compte de la réduction à supporter. Les figures sont regroupées au maximum en planches dont la justification pleine page est 17 × 24,35 cm une fois réduites (penser à retrancher la légende de ces dimensions); largeur d'une colonne : 8,1 cm. Méthode des «rectangles homologues» pour la réduction : tracer les diagonales d'un rectangle de 17/24,35 cm, les prolonger; tout rectangle admettant ces prolongements comme diagonales correspondra à la justification après réduction. Indiquer le numéro d'ordre des figures en chiffres arabes et le nom de l'auteur au crayon bleu au recto ou au dos. Ne pas inscrire de légende sur les illustrations.

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VIE ET MILIEU, 1998, 48 (4)

Life & Environment

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INTERFACE EAU-SÉDIMENT / SEDIMENT-WATER INTERFACE

Guest Editor : A. Grémare

Indexé dans / *indexed in* : **Current Contents**/Agriculture, Biology & Environmental Sciences, Animal Behavioural Abstracts, Aquatic Sciences and Fisheries Abstracts (ASFA), Biological Abstracts, Bowker international Serials Data base, Current Awareness in Biological Sciences, Excerpta Medica, Marine Science Content Tables, Pascal (INIST-CNRS), Science Citation Index, Zoological Record (BIOSIS).