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Modelling of consumption and assimilation in *Abra alba* (Mollusca, Bivalvia)

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ABSTRACT: The deposit-feeding bivalve *Abra alba* was fed over 3 different periods of time (4, 10, 48 h) on 3 species of different-sized, ^{14}C-labelled diatoms: *Navicula incerta*, *Nitzschia acicularis* and *Nitzschia* sp. Because of the complexity of the exchanges of matter between the different compartments (i.e. bivalves, CO_2, dissolved organic matter, algae) of our system, the experimental study alone was insufficient to quantify the amounts of organic matter ingested, excreted or assimilated. Therefore, we developed an analog model which allowed the calculation of such information. *A. alba* ingested *Nitzschia* sp. rather than *N. acicularis* and *N. incerta*. Comparison of results in the presence and absence of *A. alba* suggests that bivalve activity affected the metabolism of sedimented diatoms: *N. incerta* seemed stimulated whereas *N. acicularis* and *Nitzschia* sp. were inhibited. The adaptative dark metabolism of these species is probably different for the same conditions of darkness and bioturbation.

INTRODUCTION

Organic matter available for deposit-feeders is composed of heterogeneous particles including detritus and microorganisms (Newell 1965, Fenchel 1970, Lopez et al. 1977, Nielsen & Kofoed 1982, Reise 1983, Harvey & Luoma 1984, Kemp 1987). Deposit-feeders selectively collect and ingest such particles (Odum 1968, Fenchel 1972, Hylleberg & Galucci 1975, Nielsen & Kofoed 1982, Whitlach & Weinberg 1982, Briggs 1985, Petch 1986). It is difficult to determine whether detrital, algal, or bacterial components are ingested preferentially. Furthermore, because dissolved organic matter (DOM) and faeces may also be consumed, it is difficult to quantify the amount of ingested material derived from the sediment.

Through bioturbation and predation, deposit-feeding organisms modify the balance of the different communities of microorganisms living on the sediment. The growth of these microorganisms is often stimulated by the presence of deposit-feeders (Hargrave 1970b, Murphy 1985, Branch & Pringle 1987). Many deposi-feeders also stimulate bacterial production via cultivation on aggregates ('gardening') (Hylleberg 1975, Reichardt 1988). Deposit-feeding organisms have developed several elaborate food-collecting systems (e.g. combs, sticky palps, external siphons). Such diversity, coupled with the effects of deposit-feeders on their food sources, complicates the design of experimental studies assessing the quantitative aspects of nutrition in deposit-feeding organisms. For example, the change of algal radioactivity over time (i.e. loss of DOM and CO_2) has been studied experimentally by numerous authors (e.g. Fogg 1966, Mague et al. 1980, Smith & Horner 1981, Jensen 1983, Amouroux 1986b). Because deposit-feeders are able to absorb DOM, such losses complicate quantitative studies of nutrition in deposit-feeding organisms. Dring & Jewson (1982) recommended the use of compartmental analysis (Grégoire 1972), coupled with an analog modelisation for such studies.

In this study we used this method to compare the consumption of 3 different live diatoms by the bivalve *Abra alba*. An analog model was then built to simulate the exchanges of radioactivity between the different compartments (CO_2, DOM, particulate matter, bivalves). Calculation was thus possible of the amount of organic matter actually ingested, assimilated, and excreted (in dissolved and particulate form) by the bivalves. The model also allowed distinction between faeces and non-ingested diatoms.

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MATERIALS AND METHODS

Clams. *Abra alba* (Wood), a deposit-feeding bivalve of up to ca 12 mm length, is common in all lagoons along the Languedoc-Roussillon coast of France. It burrows 3 to 5 cm deep; from below the sediment surface, *A. alba* sucks up the thin top sediment layer by movement and numerous distortions of its 4 to 5 cm long siphons. The exhalant siphon draws a regular current of water into the burrow where the faeces are stored (J. M. A. pers. obs.). In other deposit-feeders, such faecal pellets may be triturated to collect the organic matter corresponding to bacterial production ('gardening'; Hylleberg 1975). The clams were collected at a shallow station (< 1 m) of the Canet lagoon. In the laboratory they were then kept for several months in tanks provided with running natural seawater and natural muddy sediment.

Diatoms. Food sources were 3 diatoms: *Navicula incerta* (Grunow), *Nitzschia acicularis* (Wm Smith) and *Nitzschia* sp. (provided by Dr C. Riaux fromthe Roscoff Laboratory, France). *N. incerta* is 16 mm long and contains 5.9×10^{-10} g organic matter (500 °C for 5 h) per cell; *N. acicularis* is 60 mm long and contains 1.5×10^{-10} g organic matter per cell; *Nitzschia* sp. is 11 mm long and contains 1.1×10^{-10} g organic matter per cell. Diatoms were grown at 18 °C for 15 d under constant illumination (1700 lux) in F/2 medium (Guilliard & Ryther 1962). Cultures were labelled with $NaH^{14}CO_3$ (CEA) 12 h before each experiment.

Dissolved substances; filtrates. Live diatoms exude much dissolved organic matter (DOM) (e.g. Fogg 1966, Jensen 1983, Admiraal et al. 1986). After centrifugation, ^{14}C-labelled diatom cultures were deep-frozen (−40 °C), autoclaved (to break the cell walls), and filtered on a 0.2 µm filter. Filtrates containing the labelled soluble material were collected, their radioactivities measured and compared with those of filters corresponding to particulate organic matter in order to quantify the concentration of organic matter of the filtrates (Amouroux 1984). Biochemical composition of filtrates probably differs from the biochemical composition of natural exudates.

Procedure. Cultures were centrifuged, resuspended in filtered seawater and their concentration adjusted so as to correspond to a total organic dry weight of 20 mg per flask (they were not re-adjusted during experiments). Before use, bivalves were placed in filtered seawater at 15 °C in darkness for at least 24 h to empty their digestive tracts; 30 bivalves of known size, corresponding to a total of 185 mg flesh dry weight, were introduced into each flask immediately after food addition. The experimental set up consisted of a 350 ml flask containing 300 ml of filtered seawater. The liquid medium was mixed by gentle air bubbling sufficient for oxygenation without disturbing sedimentation of diatoms. At the outlet, air was passed through NaOH-traps to capture the labelled respiratory CO_2. For each run 3 replicates and a control without bivalves were carried out in darkness at 15 °C. Under these conditions, the bivalves fed and apparently were not stressed (J. M. A. pers. obs.)

Nine (3 series of 3 replicates) 4 h experiments were carried out to assess the consumption of DOM (filtrates) by *Abra alba*. Experiment duration was limited to restrict bacterial activity. Three series of experiments (4, 10, 24 h) were carried out to measure consumption of *Navicula incerta, Nitzschia acicularis* and *Nitzschia* sp. by *Abra alba*. All experiments were conducted at 15 °C in darkness. Bacterial acitvity was very low due to bivalve filtration.

At the end of experiments, radioactivity corresponding to the 4 compartments (the bivalves in toto, particulate organic matter [POM], DOM and CO_2) was measured in a Beckman liquid scintillator (see Amouroux 1984 and 1986a for details). In each control, cells were resuspended after strongly shaking the flask and then counted on a microgrid. For feeding experiments (the presence of bivalves) non-ingested diatoms were not counted at the end of the experiments since they were mixed with faeces and biodeposits of *Abra alba*.

Modelling. Analog computation (Goldstein & Elwood 1971) was used to establish continuity among experimental data and to quantify the exchanges between the different compartments. Such a model allowed the calculation of the amount of organic matter moved through the different compartments, and of the changes over time of the radioactivity corresponding to compartments that could not be measured experimentally (e.g. faeces). Fitting the model to our experimental set-up required several trials involving different assumptions. We present here only the best fitted model (i.e. the one which seems to correspond to the most valid hypotheses). The model was used as a tool to test different hypotheses relative to the tranfer of matter among the different compartments of the system studied. When the model provided a good description of our experimental data we concluded that our priorhypotheses (taken into account in the model) were confirmed.

System and differential equations: The system (Fig. 1) was considered to be closed. Its compartments were diatoms, bivalves, CO_2, DOM and faeces. Each of these should have been analysed separately during the experimental study. However, experimental measurements of radioactivity were carried out in only 4 (bivalves, DOM, CO_2, POM) compartments. It was not possible to measure radioactivity corresponding to diatoms and faeces separately. Mass transfer dynamics of the system Bivalves-Diatoms-Seawater were rep-

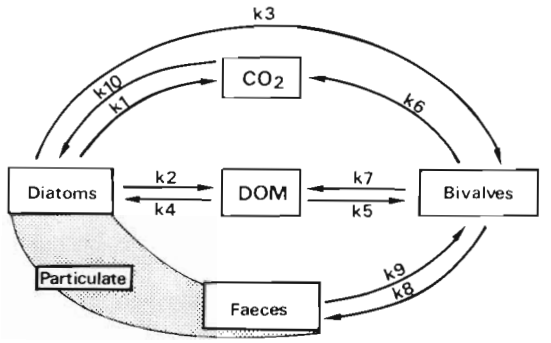

Fig. 1. Five-compartment model of 'Diatom-Bivalve' system showing exchanges studied and numbered kinetic constants of mass transfer

resented by an interaction of 'kinetic' equations reflecting the rates of exchanges between the compartments:

$$\frac{d(Diat)}{dt} = +k4\,(Diss) + k10\,(CO_2) - k1\,(Diat) - k2\,(Diat) - k3\,(Diat)$$

$$\frac{d(Biv)}{dt} = +k3\,(Diat) + k5\,(Diss) + k9\,(Faec) - k6\,(Biv) - k7\,(Biv) - k8\,(Biv)$$

$$\frac{d(Diss)}{dt} = +k2\,(Diat) + k7\,(Biv) - k4\,(Diss) - k5\,(Diss)$$

$$\frac{d(Faeces)}{dt} = +k8\,(Biv) - k9\,(Faec)$$

$$\frac{d(CO_2)}{dt} = +k1\,(Diat) + k6\,(Biv) - k10\,(CO_2)$$

$$\frac{d(Part)}{dt} = + \frac{d(Diat)}{dt} + \frac{d(Faec)}{dt}$$

where k1, k2, ..., k10 = kinetic constants of mass transfer; ( ) = radioactive content of each compartment expressed as a percentage of total radioactivity initially introduced into the system; t = time. The computer circuit simulating these equations, together with kinetic constants, is illustrated in Fig. 2

Determination of the kinetic constants: The system Bivalve-Diatom was subdivided into 2 sub-systems (i.e. Diatom-DOM-CO_2, and Bivalve-DOM-CO_2-Faeces) to permit evaluation of the kinetic constants. The first sub-system (Fig. 3) corresponds to changes over time in the specific radioacitvity of diatoms alone (control experiments); the second subsystem corresponds to the consumption of diatoms exudates by the bivalves. Experiments with filtrates allowed for the computation of k5 and k7 which correspond to the exchanges between bivalves and DOM (Fig. 1). The study of variation over time of diatoms alone (controls) allowed for the computation of k2 and k4 which correspond to the exchanges between diatoms and DOM, and of k1

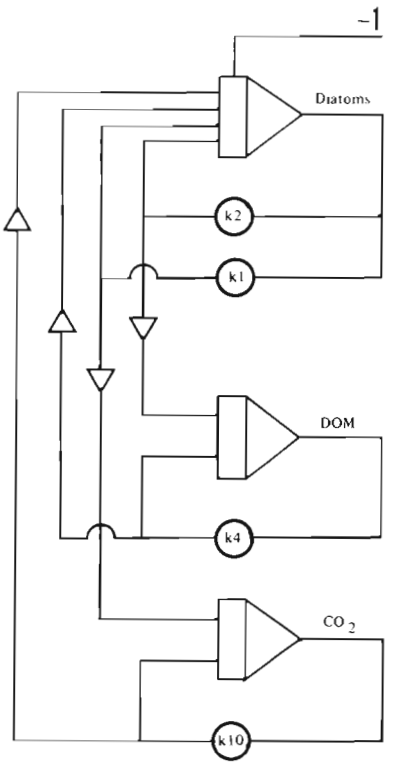

Fig. 2. Circuit diagram of computer and display constants after fitting of model 'Diatom-Bivalve' system

and k10 which correspond to exchanges between CO_2 and diatoms. These constants were introduced in the model Diatom-Bivalve-Seawater.

Calculation of the amount ingested and assimilated: The experiments alone did not allow distinction between live diatoms and those rejected in bivalves faeces. The computation of the amount of radioactivity consumed, ingested (in particulate form) and assimilated by the bivalves required computation of the cumulated amounts of radioactivity within the different compartments. This could only be achieved through modelling of the system. The amount consumed was set as the total amount of radioactivity corresponding to bivalves soft parts plus excretory products (faeces, DOM, CO_2). The amount ingested was set as the difference between total consumption (see above) and DOM consumed by the bivalves. The amount assimilated was set as the difference between total consumption and faeces produced.

RESULTS

Experimental study

Control: changes in live diatoms alone over time

The concentrations of viable sedimented diatoms were constant throughout all experiments (Table 1). In

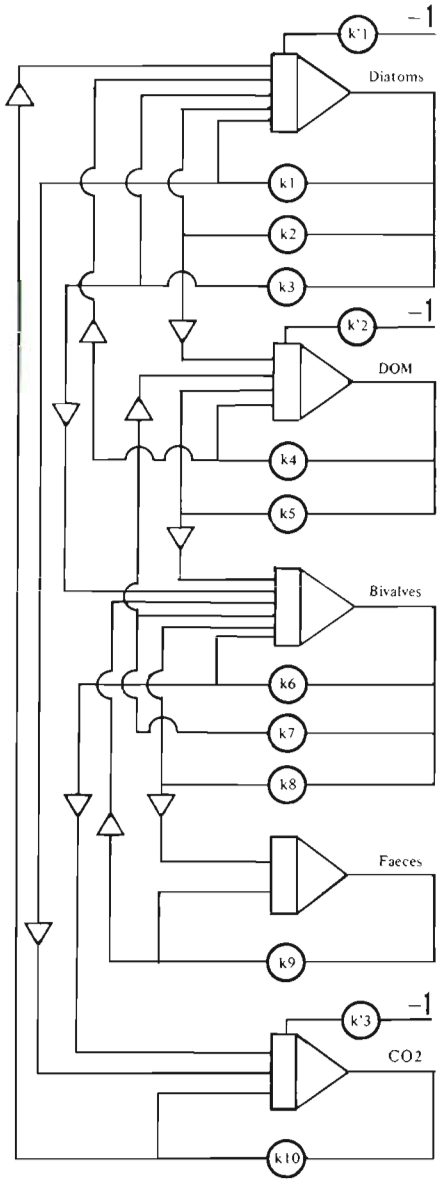

Fig. 3. Circuit diagram of computer and display constants after fitting of model 'Diatom-Seawater' system

all cases the specific radioactivity of the cells declined over time. The radioactivity corresponding to CO_2 and DOM increased rapidly during the first 10 h. Then DOM decreased slightly as CO_2 increased slowly (Table 2).

Consumption of DOM (filtrates) by the bivalves

After 4 h, the percentages of radioactivity within the bivalves were: 1.1, 2.9 and 2.3 % (means of 3 measurements) for *Navicula incerta*, *Nitzschia acicularis* and *Nitzschia* sp., respectively.

Table 1. Controls. Measurements of the concentration of the live diatoms in the flask over time. The low variations were induced by the ability of the diatoms to stick onto the walls of the flask. Values are expressed as 10^7 cells ml^{-1}

Diatom	0 h	4 h	10 h	48 h
Navicula incerta	13.1	2.8	13.3	12.5
Nitzschia acicularis	45.0	45.2	44.8	44.7
Nitzschia sp. Roscoff	61.0	61.2	60.8	60.7

Consumption of live diatoms by the bivalves

The bivalves consumed the same quantities (about 50 % after 48 h) of *Navicula incerta* and *Nitzschia acicularis* (Table 3A and B). However *N. acicularis* was consumed faster than *N. incerta* during the first 4 h. Radioactivity corresponding to DOM increased quickly during the first 4 h and then declined slightly. The bivalves quickly consumed *Nitzschia* sp. during the first 10 h. Thereafter radioactivity in the bivalves remained constant (about 60 %). Radioactivity corresponding to particulate organic matter (diatoms + biodeposits) was low and constant (less than 10 %). Radioactivity corresponding to CO_2 increased gradually to 25 % (after 48 h). Radioactivity corresponding to DOM reached 9.5 % after 10 h and then declined to 4 % after 48 h.

Modelling

Changes in viable diatoms alone over time

During the first 3 h of the experiments, *Navicula incerta* was not consumed by *Abra alba*. The time-origin of the model was shifted by 3 h. At this time, radioactivity was distributed as follows: 87 % in diatoms, 10 % in DOM and 3 % in CO_2. The radioactivity declined regularly in the particulate (diatoms + faeces) from 87 % (3 h) to 50 % (10 h) and 8 % (after 48 h). CO_2 rose from 5 % after 4 h to 35 % after 48 h. DOM remained nearly constant (ca 10 to 11 %) throughout the experiment. The amount of faeces present on the bottom was low: 5 % after 48 h. Radioactivity of diatoms decreased regularly to 3 % after 48 h. Radioactivity of diatoms decreased regularly to 3 % after 48 h. The production of faeces accumulated during 48 h was low: 19 % (Figs. 7 and 8). For fitting the model, it was necessary to modify the values of the constant of integration (relative to those used for the model of the diatoms alone; Table 4). This implies that diatom metabolism (CO_2 and DOM exchanges) differed in the presence and absence of clams. Changes in the metabolism of *N. incerta* were revealed by changes in the values of these constants. The con-

Table 2. Time-dependent variation in ^{14}C radioactivity of the 3-compartment control system. (A) *Navicula incerta*; (B) *Nitzschia acicularis*; (C) *Nitzschia* sp. Values are mean percentages of initial radioacitvity

Compartment	4 h			10 h			48 h		
			Mean			Mean			Mean
(A) *Navicula incerta*									
Particulate	91.9	–	–	80.3	79.6	79.9	35.6	57.0	46.3
DOM	7.0	–	–	7.2	9.4	8.2	29.6	16.0	22.8
CO_2	1.1	–	–	12.5	11.3	11.9	34.8	27.0	30.9
(B) *Nitzschia acicularis*									
Particulate	71.7	75.9	73.8	67.8	79.8	73.8	60.9	68.1	64.5
DOM	17.5	10.5	14.0	16.2	8.8	12.5	10.1	11.0	10.6
CO_2	10.8	13.6	12.2	16.0	11.4	13.7	29.0	20.9	24.9
(C) *Nitzschia* sp.									
Particulate	81.5	82.8	82.1	78.0	77.3	77.6	67.6	66.6	67.1
DOM	4.0	3.1	3.5	6.5	10.2	8.4	10.9	7.5	9.2
CO_2	14.5	14.1	14.3	15.5	12.5	14.4	21.5	25.9	23.7

Table 3. Time-dependent variation in ^{14}C radioactivity of the 4-compartment system Diatom-*Abra alba*: (A) *Navicula incerta*; (B) *Nitzschia acicularis*; (C) *Nitzschia* sp. Values are mean percentages of initial radioacitvity

Compartment	4 h					10 h					48 h				
	1	2	3	Mean	SD	4	5	6	Mean	SD	7	8	9	Mean	SD
(A) *Navicula incerta*															
Bivalves	4.7	4.5	6.8	5.3	1.27	31.7	21.1	28.1	27.0	5.39	45.8	45.0	49.9	46.9	2.63
Particulate	84.5	84.3	83.9	83.9	0.93	48.5	58.6	56.1	54.5	5.34	8.4	7.8	5.6	7.3	1.47
DOM	10.8	11.2	10.3	10.8	0.45	10.6	9.0	7.7	9.1	1.45	11.8	12.9	8.5	11.1	2.29
CO_2	–	–	–	–	–	7.1	6.0	7.1	6.7	0.64	34.0	34.3	36.1	34.8	1.14
(B) *Nitzschia acicularis*															
Bivalves	10.7	13.9	12.7	12.4	1.62	21.7	16.7	22.5	20.3	3.14	48.9	51.2	43.6	47.9	3.90
Particulate	65.6	62.1	63.5	63.7	1.76	59.2	62.1	52.0	38.0	5.20	20.0	16.1	26.3	20.8	5.15
DOM	10.9	12.7	11.3	11.6	0.95	9.4	10.6	11.5	10.5	1.05	7.1	3.7	2.6	4.5	2.35
CO_2	12.6	11.3	12.5	12.1	0.72	10.8	11.0	11.8	11.2	0.53	24.0	29.0	27.4	26.8	2.55
(C) *Nitzschia* sp.															
Bivalves	6.7	11.1	12.6	10.1	3.07	59.2	62.9	59.0	60.4	2.20	59.8	66.4	61.2	62.5	3.48
Particulate	75.2	71.3	71.6	72.7	2.17	14.7	16.7	15.2	15.5	1.04	8.3	7.4	10.3	8.7	1.48
DOM	3.8	3.9	2.5	3.4	0.78	10.9	8.9	8.6	9.5	1.25	5.1	3.0	4.0	4.0	1.05
CO_2	14.2	13.7	13.3	13.7	0.45	15.7	11.4	17.3	14.8	3.05	26.8	23.2	24.4	24.8	1.83

Table 4. Integration constants of the model Diatom-Seawater (controls). (A) *Navicula incerta;* (B) *Nitzschia acicularis*; (C) *Nitzschia* sp. k4 is the consumption of DOM by diatoms, k2 the production of DOM, k10 the consumption of CO_2 by the diatoms and k1 the production of CO_2

Constant	*Navicula incerta*	*Nitzschia acicularis*	*Nitzschia* sp.
k4	0.0145	0.8001	0.2006
k2	0.0135	0.1501	0.0328
k10	0.0121	0.5309	0.3331
k1	0.0436	0.1861	0.1001

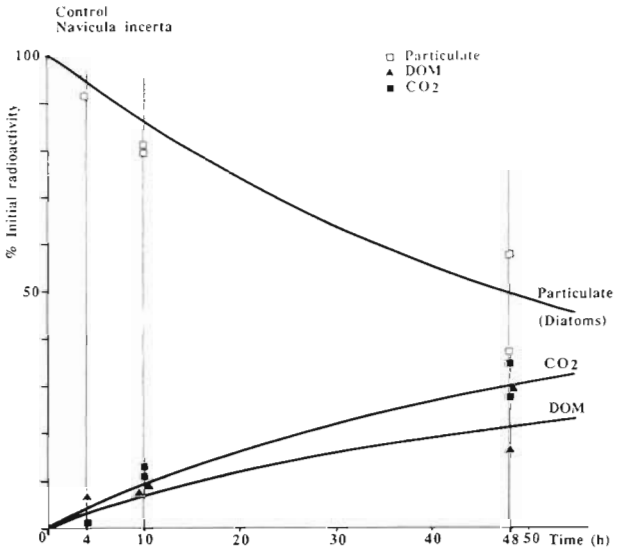

Fig. 4. Time-dependent variation in radioactivity of the different compartments of the control system Diatom-Seawater *(Navicula incerta)*. Results are expressed as percentage of radioactivity introduced at start versus time elapsed (h). Experimental data for the different experiments and compartments are pointed on the graph

stant k2 (DOM produced) changed from 0.0135 to 0.0201 (1.5 times more); k4 (DOM consumed) from 0.0145 to 0.0257 (2 times more); k1 (CO_2 produced) from 0.0436 to 0.0810 (2 times more); and k10 (CO_2 consumed) from 0.0120 to 0.0495 (4 times more) (Tables 5A and 6).

Consumption of *Nitzschia acicularis*

Nitzschia acicularis was initially consumed faster than *Navicula incerta*. Fitting the model revealed that actions of the bivalves altered the metabolism of the diatoms. Constants of integration were very different from those of the control (diatoms without bivalves). DOM production changed from 0.1500 to 0.0111 (13 times less); consumption of DOM from 0.8000 to 0.1200

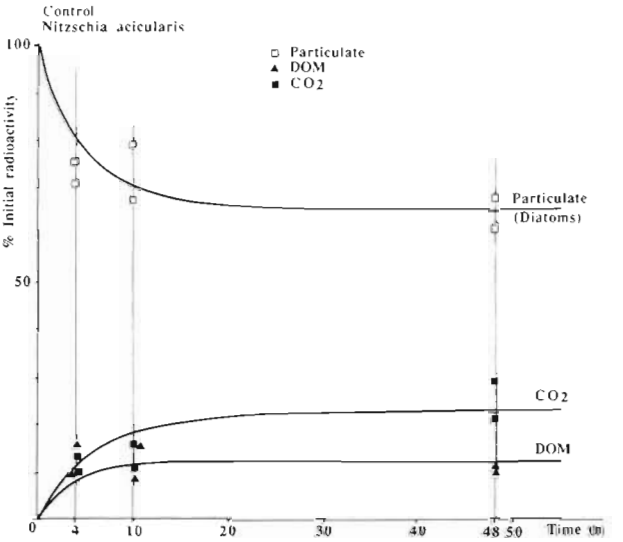

Fig. 5. Time-dependent variation in radioactivity of the different compartments of the control system Diatom-Seawater *(Nitzschia acicularis)*

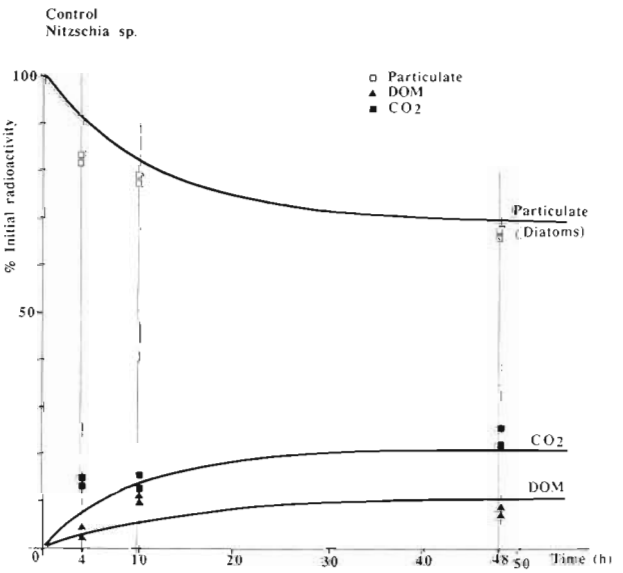

Fig. 6. Time-dependent variation in radioactivity of the different compartments of the system Diatom-Seawater (*Nitzschia* sp.)

(7 times less); production of CO_2 from 0.1860 to 0.0108 (17 times less); consumption of CO_2 from 0.5310 to 0.1306 (4 times less) (Tables 5B and 6). Radioactivity in the soft body of the bivalves increased gradually to 46 % after 48 h. During this time the radioactivity of the particulate declined gradually to 21 % after 48 h. Total CO_2 rose from 13 % after 10 h to 23 % after 48 h. DOM increased to 13 % after 4 h and then declined to 11 ‰ after 10 h, and to 4 % after 48 h; this indicates that DOM was reabsorbed first by diatoms and then by bivalves. Radioactivity of diatoms (as calculated by the

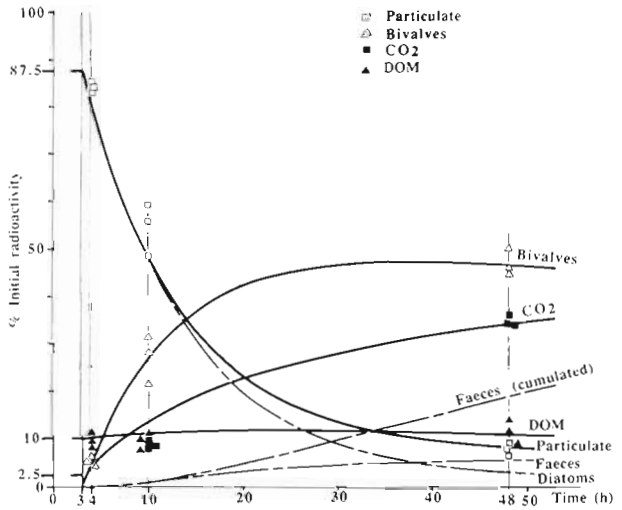

Fig. 7. Time-dependent variation in radioactivity of the different compartments of the system Diatom-Bivalve *(Navicula incerta-Albra alba)*

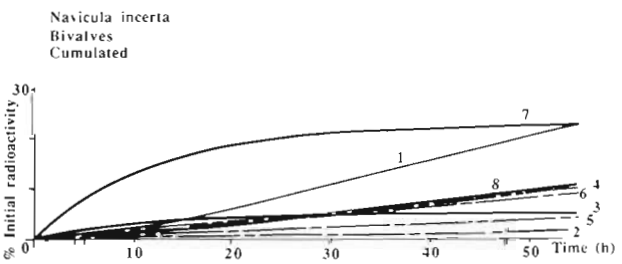

Fig. 8. Calculation of cumulated amounts of organic matter (radioactivity) transited through different compartments as a function of time during different exchanges. System Diatom-Bivalve *(Navicula incerta-Abra alba)*. (1) Faeces; (2) CO_2 consumed by diatoms; (3) DOM produced by diatoms; (4) DOM consumed by bivalves; (5) DOM consumed by diatoms; (6) DOM produced by bivalves; (7) CO_2 produced by diatoms; (8) CO_2 produced by bivalves

Table 5. Integration constants of the model Diatom-*Abra alba*. (A) *Navicula incerta*, (B) *Nitzschia acicularis*, (C) *Nitzschia* sp. Time origin for fitting the model and initial conditions on the left; comparison with the integration constants of the control on the right. Values expressed as h^{-1}

Initial condition	*Abra alba*	Control
A. *Navicula incerta*		
	k1 = 0.0811	k1 = 0.0436
	k2 = 0.0201	k2 = 0.0135
$T'_0 = T_0 + 3$ h	k3 = 0.0355	
	k4 = 0.0257	k4 = 0.0145
k'1 = 0.875	k5 = 0.0236	
k'2 = 0.100	k6 = 0.0011	
k'3 = 0.025	k7 = 0.1106	
	k8 = 0.2848	
	k9 = 0.4092	
	k10 = 0.0495	k10 = 0.0121
B. *Nitzschia acicularis*		
	k1 = 0.0108	k1 = 0.1861
	k2 = 0.0111	k2 = 0.1501
$T'_0 = T_0$	k3 = 0.1509	
	k4 = 0.1201	k4 = 0.8001
k'1 = 0.999	k5 = 0.0108	
k'2 = 0.000	k6 = 0.0051	
k'3 = 0.000	k7 = 0.0946	
	k8 = 0.2007	
	k9 = 0.3114	
	k10 = 0.1306	k10 = 0.5311
C. *Nitzschia* sp.		
	k1 = 0.0941	k1 = 0 1001
	k2 = 0.0052	k2 = 0.0328
$T'_0 = T_0 + 3$ h	k3 = 0.1023	
	k4 = 0.1431	k4 = 0.2006
k'1 = 0.900	k5 = 0.0124	
k'2 = 0.000	k6 = 0.0011	
k'3 = 0.100	k7 = 0.0751	
	k8 = 0.8992	
	k9 = 0.3064	
	k10 = 0.0361	k10 = 0.3331

model) declined steadily to 4 % after 48 h. Radioactivity of faeces increased slowly to 17 % after 48 h. The amounts of radioactivity cumulated in the different compartments were low, except for the faeces: 50 % after 48 h (Figs. 9 and 10; Tables 5B and 6).

Consumption of *Nitzschia* sp.

The consumption of *Nitzschia* sp. by *Abra alba* began 3 h after food introduction. At this time most of the radioactivity (90 %) corresponded to particulate matter (live diatoms), the remainder (10 %) was in CO_2 (DOM: about zero). After 10 h (13 h of experimentation), only 10 % of the diatoms were in particulate form. Radioactivity retained in the soft body of the bivalves was 60 % after 13 h, 65 % after 20 h and 62 % after 48 h. This implies that faeces were not abundant and were quickly reconsumed by the bivalves. CO_2 increased steadily from 10 % after 3 h to 23 % after 48 h. DOM increased to 8 % after 13 h and declined slightly to 4 % after 48 h. Calculations using the model show that faeces on the bottom were low (less than 7 %) and live diatoms less than 1 % (Fig. 11). Calculation of the cumulated amount flowing through the different compartments shows that faeces produced during the whole experiment were less than 20 % over 48 h (Figs. 11 and 12; Table 6). Diatom metabolism was modified by the activity of bivalves. Integration constants differed from those of diatoms in the absence of bivalves. k2 (production of DOM) changed from 0.0328 to 0.0052 (6 times less); k4 (consumption of DOM), from 0.2006 to 0.1431 (1.4 times less); k1 (production of CO_2) remained fairly stable from 0.10000 to 0.0941; k10 (CO_2 consumed) changed from 0.3330 to 0.0361 (9 times less) (Tables 5C and 6).

Table 6. Comparison of results after fitting the model. For each diatom species the amount of cumulated radioactivity is listed for each compartment after 50 h. (1) Faeces; (2) CO_2 consumed by diatoms; (3) DOM produced by diatoms; (4) DOM consumed by bivalves; (5) DOM consumed by diatoms; (6) DOM produced by bivalves; (7) CO_2 produced by diatoms; (8) CO_2 produced by bivalves. Values expressed as percentages of initial radioactivity

	Navicula incerta	*Nitzschia acicularis*	*Nitzschia* sp.
(1) Faeces	42.5	42.0	24.0
(2) CO_2 cons. Diat.	1.5	1.5	0.5
(3) DOM prod. Diat.	5.0	34.0	12.0
(4) DOM cons. Biv.	9.5	1.5	6.0
(5) DOM cons. Diat.	4.0	23.0	6.5
(6) DOM prod. Biv.	8.5	4.0	3.5
(7) CO_2 prod. Diat.	23.5	27.0	6.5
(8) CO_2 prod. Biv.	10.0	4.0	8.5
50 h present			
Faeces	5.5	17.5	7.0
Diatoms	2.0	4.0	1.0
DOM	10.5	4.0	0.4
Particulate	8.0	21.0	7.5
Bivalves	46.0	46.0	62.5
CO_2	36.0	28.0	23.3
Amount consumed	107.0	96.0	98.5
Amount ingested	97.5	94.5	92.5
Faeces produced	42.5	42.0	24.0
Faeces recycled	37.0	24.5	17.0
DOM consumed	9.5	1.5	6.0
Amount assimilated	54.5	54.0	74.5

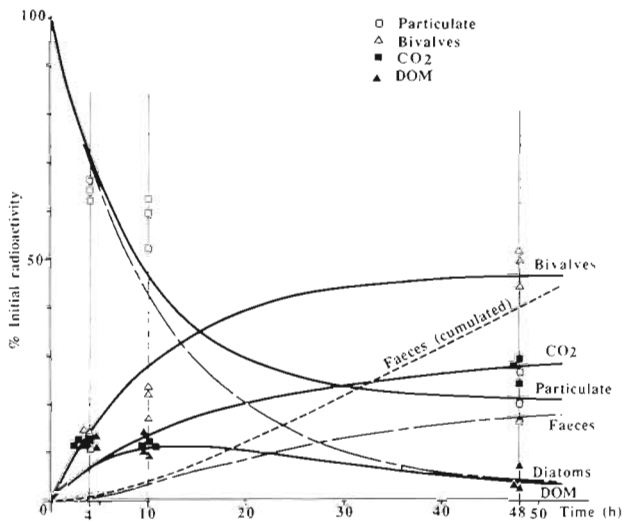

Fig. 9. Time-dependent variation in radioactivity of different compartments of the system Diatom-Bivalve *(Nitzschia acicularis-Abra alba)*

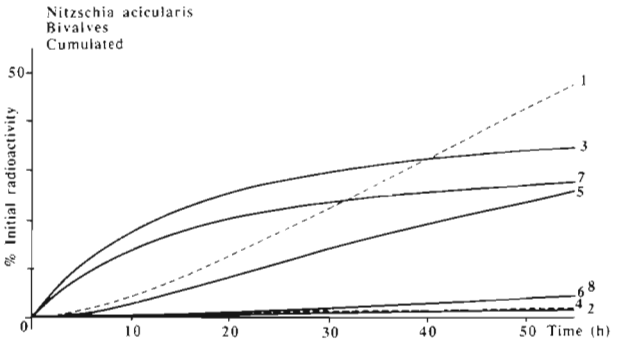

Fig. 10. Calculation of cumulated amounts of organic matter (radioactivity) transited through different compartments as a function of time during different exchanges. System Diatom-Bivalve *(Nitzschia acicularis-Abra alba)*. (1) Faeces; (2) CO_2 consumed by diatoms; (3) DOM produced by diatoms; (4) DOM consumed by bivalves; (5) DOM consumed by diatoms; (6) DOM produced by bivalves; (7) CO_2 produced by diatoms; (8) CO_2 produced by bivalves

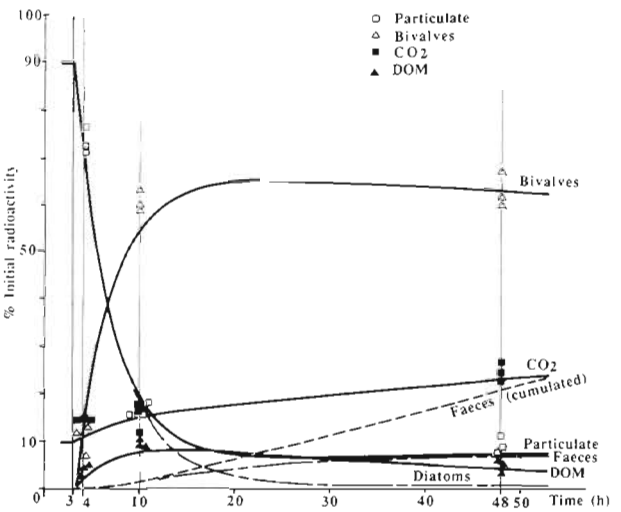

Fig. 11. Time-dependent variation in radioactivity of different compartments of system Diatom-Seawater (*Nitzschia* sp.)

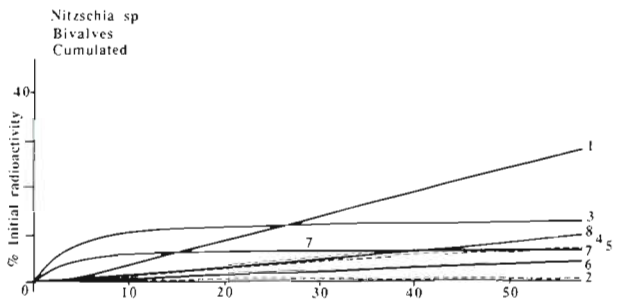

Fig. 12. Calculation of cumulated amounts of organic matter (radioactivity) transited through different compartments as a function of time during different exchanges. System Diatom-Bivalve *(Nitzschia* sp.-*Abra alba)*. (1) Faeces; (2) CO_2 consumed by diatoms; (3) DOM produced by diatoms; (4) DOM consumed by bivalves; (5) DOM consumed by diatoms; (6) DOM produced by bivalves; (7) CO_2 produced by diatoms; (8) CO_2 produced by bivalves

Consumption, ingestion and assimilation

Nitzschia sp. was most easily assimilated with 74.5 % of initial radioactivity and 98.5 % of food consumed and 92.5 % ingested by the bivalves. *Navicula incerta* was more easily consumed, with 107 % (values include recycled faeces) and 97.5 % ingested and 54.5 % assimilated, than *N. acicularis*, which was least assimilated with 54.0 %, and 96.0 % consumed and 94.5 % ingested (Table 6).

DISCUSSION

The purpose of the present study was to compare ingestion and assimilation of 3 different species of diatoms by the deposit-feeding bivalve *Abra alba*. Variation over time of controls reveals the loss in radioactivity of the 3 diatoms: *Navicula incerta* lost 200 % more DOM (22.8 % after 48 h) and 125 % more of CO_2 (30.9 % after 48 h) than did *Nitzschia acicularis* and *Nitzschia* sp. Our study shows that it is possible to describe the exchanges of matter within the system using a compartmental (in contrast to an interface) model (Amouroux & Amouroux 1988). This is probably due to the bioturbation by the bivalves which increases the homogeneity of the seawater near the bottom.

Abra alba ingests *Nitzschia* sp. rather than *Navicula incerta* or *Nitzschia acicularis*. The model permits the mathematical determination of the amounts of exudates and excretory products through POM and DOM and the amount produced or consumed by each compartment, even if these amounts are not experimentally measurable. Faeces (cumulated) produced by *Abra alba* were 42.5, 42.0 and 24.0 % of the organic carbon introduced at the beginning of experiment for *N. incerta, N. acicularis* and *Nitzschia* sp., respectively. The amounts of assimilated matter were 54.5, 54.0 and 74.5 %, respectively.

These results can be compared with those of previous studies dealing with other deposit-feeders. Hargrave (1970a) reported 60 % assimilated for the amphipod *Hyatella azteca* fed on diatoms, and 83 % for *H. azteca* fed on bacteria (experimental duration: 5 or 6 h); Kofoed (1975) found 60 to 75 % assimilated for *Hydrobia ventrosa* fed on *Nitzschia angularis* and other species of diatoms (the snails were in contact with their food for only 20 min). However the balance of the total radioactivity introduced at the beginning of their experiments (Hargrave 1970a, Kofoed 1975) was not established and the excreted DOM seems to have been as low as 4 to 8 %: a value that is equivalent to the data calculated by Nielsen & Kofoed (1982) for the crustacean *Corophium volutator* (experimental duration: 20 min). Hargrave (1970a) reported 36 % for *H. azteca*. These animals feed differently: amphipods and gastropods browse over sediment particles and select them, while bivalves suck up the water containing fine particles and flocculates. The other workers' calculations did not consider the possibility of recycling of faeces by the animals. Further, experimental conditions were not the same: Hargrave used natural autoclaved sediment, Nielsen & Kofoed used reconstituted sediment, and Kofoed used no sediment. It is not easy to use sediment as calculations are difficult and counting errors numerous. Diatom activity easily disturbs the balance by recycling of dissolved organic matter and CO_2. However, in spite of such differences in experimental procedures, the calculated percentages of assimilated food are very similar.

To achieve a good fit of the model, some modifications in the integration constants corresponding to the metabolic exchanges of algae were required. This suggests that, while feeding, the bivalves affect the metabolic rates of diatoms. The metabolic rate of *Navicula incerta* was stimulated (its 4 constants of integration increased) whereas the metabolic rates of *Nitzschia acicularis* and *Nitzschia* sp. were inhibited (their 4 constants of integration declined). The constants decreased from 0.3330 to 0.0361 for *N. incerta* and from 0.8000 to 0.1200 for *N. acicularis*. This effect is similar to the inhibition of photosynthetic processes described by Sumner & McIntyre (1982) on a system involving grazer-periphyton. The difference between *Navicula incerta* and the 2 other diatoms is presumably due to the adaptative differences in metabolic rate for the different species of diatoms (Gallagher et al. 1984, Mortain-Bertrand et al. 1988). Our experiments were carried out in darkness in order to limit the photosynthetic recycling of CO_2 while permitting good activity by the bivalves. Unfortunately the dark metabolism of the different species of diatoms is not yet well known. Our results, too, cannot constitute additional physiological information. Hence the problem of valid reference data remains unsolved for experiments employing live foods. Bioturbation of diatoms induced by *Abra alba* caused a physiological response of diatoms similar to that reported for bacteria consumed by a predator (Sumner & McIntyre 1982, Alongi 1985, Moriarty et al. 1985).

Deposit-feeders may consume organic matter from very different origins. Through bioturbation (Rhoads 1974, Aller & Yingst 1985, Murphy 1985) they disaggregate the biodeposits, mix the interface water-sediment, and recycle their own faeces (Newell 1965, Guidi & Tito de Morais 1983). Such action stimulates bacterial growth (Branch & Pringle 1987, Reichardt 1988) and dissolved excretion by microbes (Jensen 1983, Harvey & Luoma 1984, Baird & Thistle 1986). Deposit-feeders can also feed directly on diatoms or

their dissolved exudates or colloids (Moriarty 1982, Connor 1986) or on bacteria (Hylleberg 1975, Dobbs & Whitlach 1982, Reise 1983). Because of such complexity, a modelling approach is the only one that faciliates interpretation of experimental data on quantitative aspects of nutrition (ingestion, assimilation) in deposit-feeders. More studies are necessary to determine the exact effects of deposit-feeding organisms on their food sources, and to quantify actual ingestion rates. The model that we have used in this study is probably imperfect; however, it provided an adequate description of our experimental data. Furthermore, it allowed (1) determination of the influence of the bivalves on the metabolic rate of the diatoms, and (2) quantification of the amounts of organic matter which passed through the bivalves (short-term energetic budget).

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