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Modelling of consumption and assimilation in the deposit-feeding polychaete *Eupolymnia nebulosa*

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ABSTRACT: The deposit-feeding terebellid polychaete *Eupolymnia nebulosa* was fed over 3 different time periods (4, 10, and 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 (annelids, CO_2, DOM, algae) of the 'Diatom-Annelid' system, the experimental study alone was insufficient to quantify the amounts of organic matter that were ingested, consumed or assimilated by the worms. An analog model allowed quantification of such exchanges. *E. nebulosa* ingested *Nitzschia* sp. rather than *N. acicularis* and *N. incerta*. Comparison of results in the presence and absence of annelids suggested that the activity of the worms affected the metabolism of the sedimented diatoms (*N. incerta* was stimulated whereas *N. acicularis* was inhibited). This action is similar to the effect of the deposit-feeding bivalve *Abra alba* on these 2 algae.

INTRODUCTION

Food resources available to deposit-feeding organisms are diverse. They include both live cells such as benthic diatoms (Smith et al. 1985) and bacteria (Lopez & Cheng 1983), and detritus such as sedimenting phytoplankton (Graf et al. 1982, 1984, Christensen & Kanneworff 1985) and seaweed detritus (Adams & Angelovic 1970, Stuart et al. 1981, Tenore 1981). Many deposit-feeders are also able to reingest their own faeces (Hylleberg 1975), and/or incorporate dissolved organic matter (DOM) (Stephens 1968). In addition, through bioturbation and predation, deposit-feeders affect the balance of the benthic microorganism community. In the field, the production of microalgae and bacteria is often stimulated in the presence of deposit-feeders (Hargrave 1970, Branch & Pringle 1987). Such complex interactions between deposit-feeders and their food sources, coupled with the heterogeneity of these food sources, complicate the characterization and quantification of organic matter obtained from sediment by benthic deposit-feeders.

Radiotracer methods have been widely used for qualitative and quantitative studies of the portion of organic matter associated with the sediment that is actually ingested and absorbed by deposit-feeders (Adams & Angelovic 1970, Tenore 1981, Guidi & Tito de Morais 1983, Guidi 1986). However, the interpretation of such studies is often complicated by short-term recycling phenomena occurring inside closed experimental chambers (Conover & Francis 1973, Smith & Horner 1981). The loss of algal specific activity, for example, has been studied by several authors (Mague et al. 1980, Amouroux & Amouroux 1986b). Because most marine invertebrates are able to incorporate DOM (Stephens 1968), this factor also complicates quantitative studies of nutrition (Smith & Horner 1981).

It is possible to use an open, instead of a closed system, in order to avoid such bias. Pulse chase experiments are designed to minimize recycling by using very short ingestion periods (Kofoed 1975, Cammen 1980, Lopez & Cheng 1983; but see Calow & Fletcher 1972), moving the animal to unlabelled food, and then measuring specific activities of animals and faeces. Such an approach has been useful in estimating ingestion and absorption rates in several benthic deposit-feeders. However, such an approach cannot be used with large soft-body tentaculate deposit-feeders (such as the terebellid polychaete *Eupolymnia nebulosa* Montagu) because of: (1) their fragility, (2) time-periods involved in feeding activities (according to the results of the present study, *E. nebulosa*, for example, may begin to feed only several hours after the introduction of the food in the experimental chamber).

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Dring & Jewson (1982) recommended the use of compartmental analysis (i.e. measurement of the temporal changes in radioactivity within several compartments of a closed system) coupled with analog modelling (which allows the a posteriori quantification of exchanges between compartments) for such studies. Our research group has already used this approach for: (1) a 'bacteria – filter-feeder' system (*Venus verrucosa* + *Lactobacillus* sp.; Amouroux & Amouroux 1986a, 1988); (2) a 'phytoplankton – filter-feeder' system (*V. verrucosa* + *Pavlova lutheri;* Amouroux & Amouroux 1986b, 1988); and (3) a 'benthic diatom – deposit-feeder' system (*Abra alba* + *Navicula incerta, Nitzschia acicularis,* and *Nitzschia* sp.; Amouroux et al. 1989). The aims of the present study were: (1) to use a similar approach to quantify the consumption, the ingestion, and the assimilation of the deposit-feeding polychaete *Eupolymnia nebulosa* fed on 3 benthic diatoms (*N. incerta, N. acicularis,* and *Nitzschia* sp.); and (2) to compare these results with those obtained with the same algae for the deposit-feeding bivalve *A. alba* (Amouroux et al. 1989).

MATERIAL AND METHODS

Experimental study. ***Worms:*** *Eupolymnia nebulosa* (Montagu) is a very common deposit-feeding polychaete found along the Mediterranean coast of France. Although it is able to colonize very different habitats, this species preferentially lives under large embedded boulders (Grémare 1986, 1988). It is often sympatric with the hesionid *Hesione pantherina,* and a great proportion of its tubes are also occupied by the commensal polynoid polychaete *Polynoe scolopendrina. E. nebulosa* feeds on the sediment surface by means of its numerous tentacles (Dales 1955, Grémare 1988). Feeding takes place almost entirely in darkness (Lang 1984, 1986, Grémare 1988). For the present study, the worms were collected by SCUBA diving at a shallow station (< 5 m) located in the bay of Port-Vendres (western Mediterranean). They were then kept in the laboratory for several weeks in tanks provided with running ambient seawater.

Diatoms: The food provided and the experimental conditions were similar to those described by Amouroux et al. (1989).

The tested food sources were 3 different strains of diatoms: *Navicula incerta* (Grunow), *Nitzschia acicularis* (Wm Smith) and *Nitzschia* sp. (provided by Dr C. Riaux from the Roscoff laboratory, France). *N. incerta* is 16 μm long and contains 5.9×10^{-10} g of organic matter (500 °C for 5 h) per cell, *N. acicularis* is 60 μm long and contains 1.5×10^{-10} g of organic matter per cell, *Nitzschia* sp. is 11 μm long and contains 1.1×10^{-10} g of 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: Absorption of DOM by *Eupolymnia nebulosa* was studied separately from ingestion of live diatoms. After centrifugation (4000 rpm, 30′), the ^{14}C labelled diatoms 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 organic matter were collected, their radioactivities measured and compared with those of filters retaining the particulate organic matter to quantify the concentration in organic matter of the filtrates (this procedure assumes uniform labelling of the diatoms; Amouroux 1984). Although we are aware that the biochemical composition of the filtrates probably differs from that of the natural exudates, we believe that such a DOM is useful for studying recycling phenomena within the experimental chamber.

Experimental procedure: Cultures were centrifuged (4000 rpm, 30′) and resuspended in filtered seawater, and their concentrations adjusted so as to correspond to a total organic dry weight of 20 mg per flask (these were not readjusted during experiments). Before use annelids were allowed to clear their guts for 24 h in filtered seawater. Five worms of known size corresponding approximately to a total ash-free dry weight of 500 mg were introduced into each flask immediately after food addition. The experimental set-up consisted of a 3000 ml flask containing 1000 ml of filtered seawater. The liquid medium was mixed by bubbling air gently sufficient for oxygenation, but not disturbing the sedimentation of diatoms (Amouroux et al. 1989). At the outlet, air was passed through NaOH-traps to capture labelled respiratory CO_2. Three experiments involving 3 different time exposures (4, 10, and 48 h) were carried out to measure the consumption of *Navicula incerta, Nitzschia acicularis* and *Nitzschia* sp. by *E. nebulosa.* For each run 3 replicates and a control without worms were carried out in darkness at 15 °C. Under these conditions, worms fed and did not seem to be stressed.

Nine (3 series of 3) 4 h experiments were carried out to assess the consumption of DOM (filtrates) by *Eupolymnia nebulosa.* Filtrate concentrations were adjusted so as to correspond to a total organic dry weight of 10 mg l^{-1}. Five worms of known size corresponding approximately to a total ash-free dry weight of 500 mg were introduced into each flask immediately after food addition.

At the end of both experiments radioactivity corresponding to 4 compartments (i.e. annelids, particulate organic matter [POM], dissolved organic matter [DOM], and CO_2) was measured in a Beckman liquid scintillator (see Amouroux 1984, Amouroux & Amouroux 1986a, b

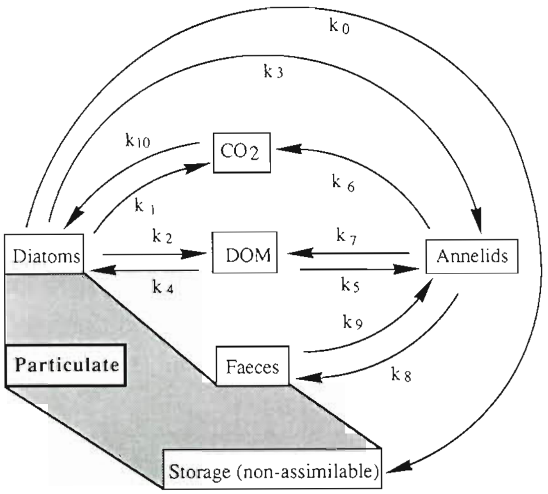

Fig. 1. Six-compartment model of 'Diatom-Annelid' system showing exchanges studied and numbered kinetic constants of mass transfer

for details). In each control, algal cells were resuspended after strongly shaking the flask and then counted on a microgrid. For feeding experiments (i.e. in the presence of annelids) non-ingested diatoms were not counted at the end of the experiments since they were mixed with faeces and biodeposits of *E. nebulosa*.

Modelling. An analog model was used to calculate the amount of organic matter which passed through the different compartments, and the changes of the radioactivity corresponding to compartments that were not measured experimentally (e.g. non-assimilable storage, faeces). Fitting the model to our experimental data required several trials involving different assumptions. We present here only the model of best fit (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 transfer of matter among the different compartments of the studied system. When the model provided a good description of our experimental data we concluded that our a priori hypotheses (taken into account in the model) were confirmed.

System and differential equations: The system was closed (Fig. 1); its different compartments were diatoms, annelids, CO_2, DOM, faeces, and NAS (non-assimilable storage compartment corresponding to the accumulation of diatoms in the worm's tube). Each of these compartments should have been analysed separately. However, experimental measurements of radioactivity were carried out in only 4 (i.e. annelids, DOM, CO_2 and POM) of these 6 compartments. It was not possible to measure radioactivity corresponding to diatoms and to faeces separately.

Mass transfer dynamics of the 'Diatom-Annelid' system were represented by an interaction of 'kinetic' equations reflecting the rates of exchanges between compartments:

$$d\,[\mathrm{Diat}]/dt = +k4\,[\mathrm{Diss}] + k10\,[CO_2] - k1\,[\mathrm{Diat}] - k2\,[\mathrm{Diat}] - k3\,[\mathrm{Diat}] - k0\,[\mathrm{Diat}]$$

$$d[\mathrm{Ann}]/dt = +k3\,[\mathrm{Diat}] + k5\,[\mathrm{Diss}] + k9\,[\mathrm{Faec}] - k6\,[\mathrm{Ann}] - k7\,[\mathrm{Ann}] - k8\,[\mathrm{Ann}]$$

$$d[\mathrm{Diss}]/dt = +k2\,[\mathrm{Diat}] + k7\,[\mathrm{Ann}] - k4\,[\mathrm{Diss}] - k5\,[\mathrm{Diss}]$$

$$d[\mathrm{Faeces}]/dt = +k8\,[\mathrm{Ann}] - k9\,[\mathrm{Faec}]$$

$$d[CO_2]/dt = +k1\,[\mathrm{Diat}] + k6\,[\mathrm{Ann}] - k10\,[CO_2]$$

$$d[\mathrm{Part}]/dt = d\,[\mathrm{Diat}]/dt + d\,[\mathrm{Faec}]/dt$$

$$d[\mathrm{NAS}]/dt = k0\,[\mathrm{Diat}]$$

where k1, k2, ..., k10 = kinetic constants of mass transfer, [X] = radioactive content of Compartment X as a percentage of the 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 kinetic constants: First we studied the sub-system 'Diatoms-DOM-CO_2'. This sub-system corresponds to the change over time of the specific radioactivity of the diatoms alone (control experiments). Controls allowed the computation of k2 and k4 which correspond to the exchanges between diatoms and DOM, and k1 and k10 which correspond to the exchanges between diatoms and CO_2. These constants were introduced in the model of the 'Diatom-Annelid' system.

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

RESULTS

Experimental study

Controls

Changes of radioactivity within the controls (microcosms containing algae without annelids) have previously been reported (Amouroux et al. 1989). The specific radioactivity of the diatoms declined rapidly,

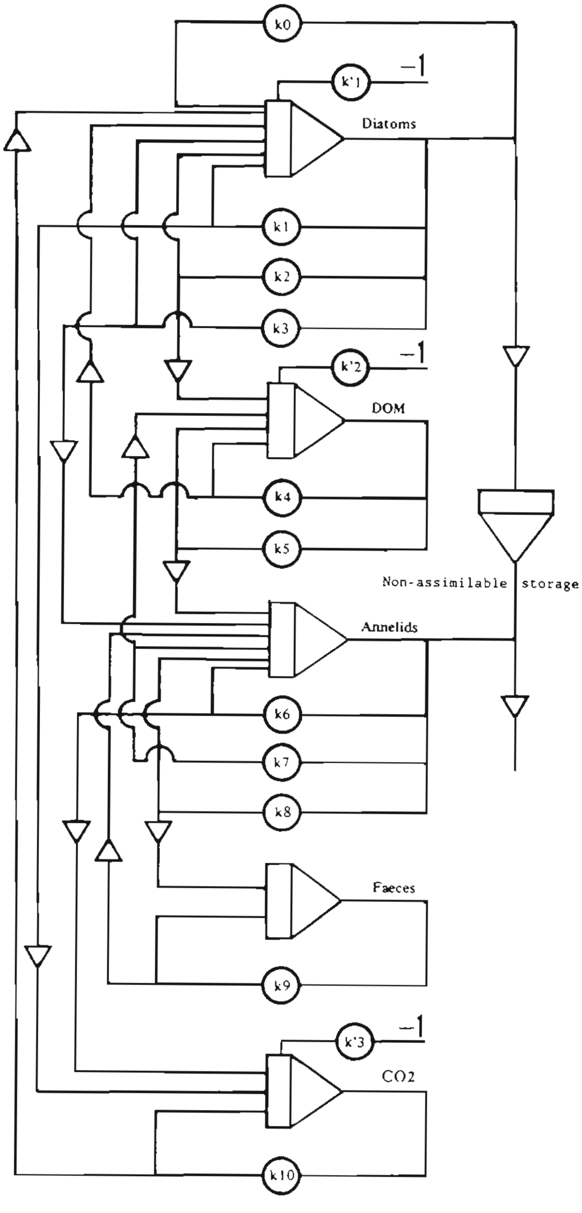

Fig. 2. Circuit diagram of the 'Diatom-Annelid' model

whereas the radioactivity corresponding to DOM and CO_2 increased over the first 10 h.

Uptake of DOM (filtrates) by annelids

After 4 h the percentages of radioactivity within the annelids were: 3.5, 10.4 and 5.4 % for filtrates of *Navicula incerta*, *Nitzschia acicularis*, and *Nitzschia* sp., respectively.

Consumption of live diatoms by annelids

Annelids incorporated the same quantities (about 20 % after 48 h) of the 3 different algae (Figs. 3, 4 and 5). However, when *Eupolymnia nebulosa* was fed on *Nitzschia acicularis*, radioactivity within the particulate matter declined more regularly and slowly than for the other 2 diatoms. For *Nitzschia* sp., CO_2 reached 45 % (48 h), which suggests a good assimilation and metabolic rate for the ingested food.

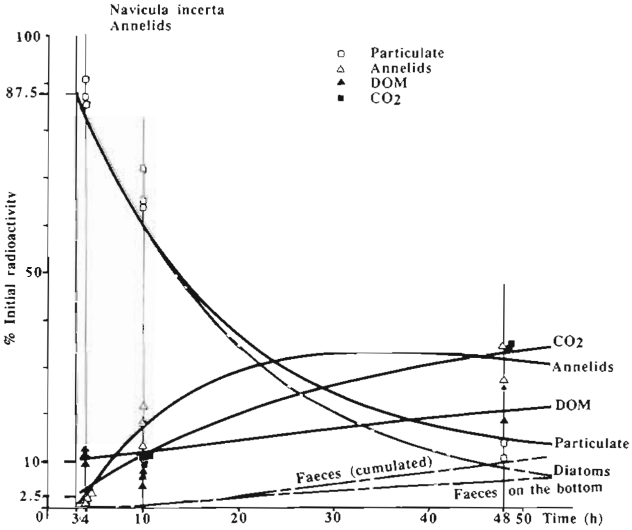

Fig. 3. Time-dependent variation in radioactivity of the different compartments of a 'Diatom-Annelid' system (*Navicula incerta–Eupolymnia nebulosa*)

Modelling

Changes in viable diatoms alone over time

The kinetic constants corresponding to the algae alone have been computed elsewhere (Amouroux et al. 1989). These values are given in Table 1.

Consumption of *Navicula incerta*

During the first 3 h of experiments, *Navicula incerta* was not ingested by *Eupolymnia nebulosa*. Therefore, the time-origin of the model was shifted by 3 h. At this time (Fig. 6), radioactivity was distributed as follows: 87.0 % in diatoms, 10 % in DOM, and 3 % in respiratory CO_2. Radioactivity declined gradually in the particulate fraction (diatoms + faeces) from 87.5 % (3 h) to 66.5 % (10 h), and 13.7 % (48 h). CO_2 rose from 5 % (4 h) to 34 % (48 h). DOM rose slowly from 10 % (4 h) to 22 % (48 h). The amount of faeces accumulated on the bottom was low: 5 % (48 h).

Fitting the model required modification of the values of the kinetic constant (relative to those found in the absence of annelids, Table 1). This suggests that exchanges of CO_2 and DOM between algae and water

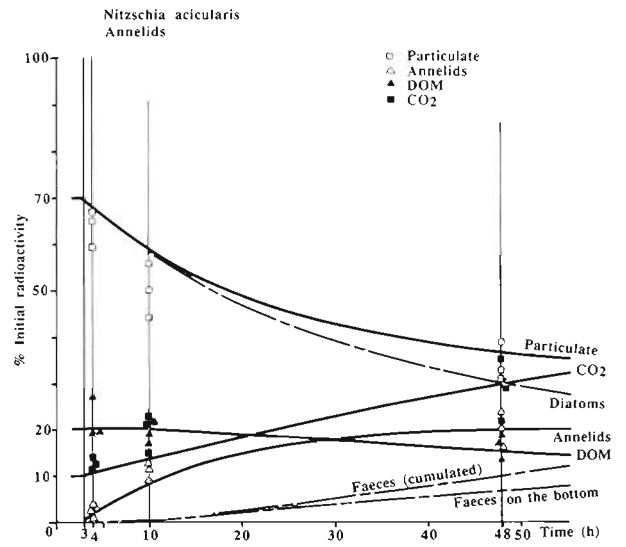

Fig. 4. Time-dependent variation in radioactivity of the different compartments of a 'Diatom-Annelid' system *(Nitzschia acicularis–Eupolymnia nebulosa)*

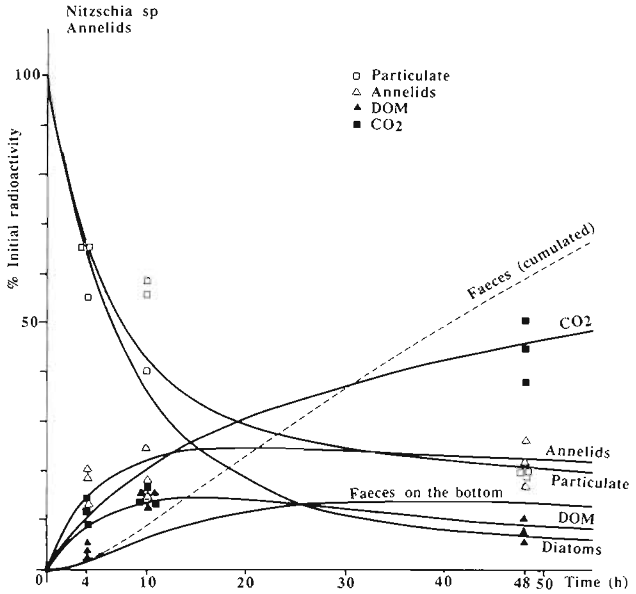

Fig. 5. Time-dependent variation in radioactivity of the different compartments of a 'Diatom-Annelid' system (*Nitzschia* sp.–*Eupolymnia nebulosa)*

are affected by the presence of annelids. For the same diatom, we reported a similar result in the presence of the deposit-feeding bivalve *Abra alba* (Amouroux et al. 1989). k2 (DOM produced by diatoms) changed from 0.0135 to 0.0422 (a 3-fold increase); DOM consumed by the diatoms, k4, remained fairly constant from 0.0145 to 0.0135; the CO_2 produced by the diatoms, k1, changed from 0.0436 to 0.0150 (i.e. 3 times less) and CO_2 consumed by the diatoms, k10, changed from 0.0120 to 0.0345 (a 3-fold increase).

Table 1. Kinetic constants of the model 'Diatom-Annelid'. (A) *Navicula incerta*, (B) *Nitzschia acicularis*, (D) *Nitzschia* sp. The time-origin and the initial conditions are noted on the left. Comparison with the kinetic constants of the controls are on the right. Values are expressed as h^{-1}

(A) *Navicula incerta*			(B) *Nitzschia acicularis*			(C) *Nitzschia* sp.		
Initial conditions	*Eupolymnia nebulosa*	Control	Initial conditions	*Eupolymnia nebulosa*	Control	Initial conditions	*Eupolymnia nebulosa*	Control
	k1 = 0.0150	k1 = 0.0436		k1 = 0.0145	k1 = 0.1860		k1 = 0.0951	k1 = 0.1000
	k2 = 0.0422	k2 = 0.0135		k2 = 0.0731	k2 = 0.1500		k2 = 0.0934	k2 = 0.0328
T'o = To + 3 h	k3 = 0.0145		T'o = To + 3 h	k3 = 0.9950		T'o = To	k3 = 0.2500	
	k4 = 0.0135	k4 = 0.0145		k4 = 0.0861	k4 = 0.8000		k4 = 0.1307	k4 = 0.2006
k'1 = 0.875	k5 = 0.0302		k'1 = 0.700	k5 = 0.0412		k'1 = 0.999	k5 = 0.0943	
k'2 = 0.100	k6 = 0.0050		k'2 = 0.200	k6 = 0.0083		k'2 = 0.000	k6 = 0.0140	
k'3 = 0.025	k7 = 0.0748		k'3 = 0.100	k7 = 0.0359		k'3 = 0.000	k7 = 0.1355	
	k8 = 0.1708			k8 = 0.0926			k8 = 0.2208	
	k9 = 0.1060			k9 = 0.1006			k9 = 0.4046	
	k10 = 0.0345	k10 = 0.0121		k10 = 0.0682	k10 = 0.5310		k10 = 0.3153	k10 = 0.3330
	k0 = 0.0000			k0 = 0.0000			k0 = 0.0242	

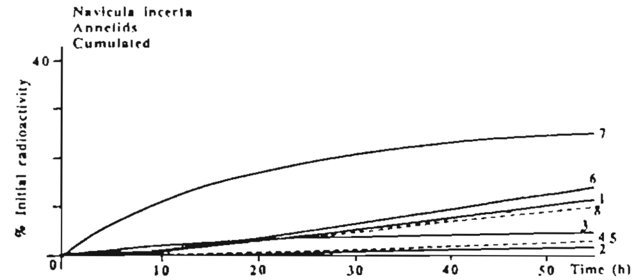

Fig. 6. Calculation of cumulated amounts of organic matter (radioactivity) passing through different compartments as a function of time during different exchanges within the *Navicula incerta–Eupolymnia nebulosa* system. (1) Faeces, (2) CO_2 consumed by diatoms, (3) DOM produced by diatoms, (4) DOM consumed by annelids, (5) DOM consumed by diatoms, (6) DOM produced by annelids, (7) CO_2 produced by diatoms, (8) CO_2 produced by annelids

Consumption of *Nitzschia acicularis*

The time-origin of the model was shifted by 3 h. At this time (Fig. 7), radioactivity was distributed as follows: 70.0 % in diatoms, 20.0 % in DOM, and 10.0 % in CO_2. *Eupolymnia nebulosa* consumed *Nitzschia acicularis* more slowly than *Navicula incerta.* The amount of radioactivity contained in the annelids rose from 1.9 % (4 h) to 19.7 % (48 h). Radioactivity of the particulate fraction declined slowly from 63.8 % (4 h) to 33.6 % (48 h). DOM declined from 21.7 % (4 h) to 16 % (48 h). CO_2 rose from 12.6 % (4 h) to 30.6 % (48 h). The production of faeces accumulated during 48 h was low (7 %). As for *N. incerta,* the kinetic constant of the diatom was affected by the presence of worms (Table 1). The value for k2 changed from 0.1860 to 0.0731 (2 times less), k4 changed from 0.8000 to 0.0861 (9.5 times less), k1 changed from 0.1860 to 0.0145 (13 times less), k10 changed from 0.5310 to 0.0682 (8 times less).

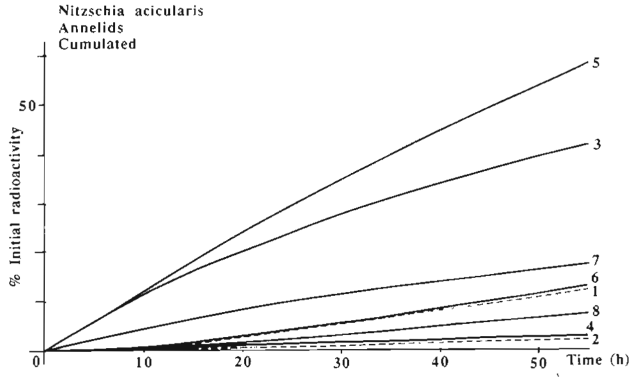

Fig. 7. Calculation of cumulated amounts or organic matter (radioactivity) passing through different compartments as a function of time during different exchanges within the *Nitzschia acicularis–Eupolymnia nebulosa* system. (1) Faeces, (2) CO_2 consumed by diatoms, (3) DOM produced by diatoms, (4) DOM consumed by annelids, (5) DOM consumed by diatoms, (6) DOM produced by annelids, (7) CO_2 produced by diatoms, (8) CO_2 produced by annelids

Consumption of *Nitzschia* sp.

The consumption of *Nitzschia* sp. by *Eupolymnia nebulosa* began immediately after the food was introduced. Therefore, the time-origin of the model was not shifted. Radioactivity (Fig. 8) in the particulate fraction (diatoms + faeces) declined gradually from 61.3 % (4 h) to 22.3 % (48 h). CO_2 rose from 12.5 % (4 h) to 45.7 % (48 h). DOM rose from 4.3 % (4 h) to 15.4 % (10 h) and then declined to 9.6 % (48 h). Radioactivity of the faeces trapped on the bottom reached 12 % (48 h). Here again, the presence of *E. nebulosa* affected the kinetic constant of the diatom (Table 1). The value for k2 changed from 0.0328 to 0.0934 (a 3-fold increase), k4 changed from 0.2006 to 0.1307 (1.5 times less), whereas k1 and k10 remained fairly constant (0.1000 vs 0.095, and 0.3330 vs 0.3153, respectively).

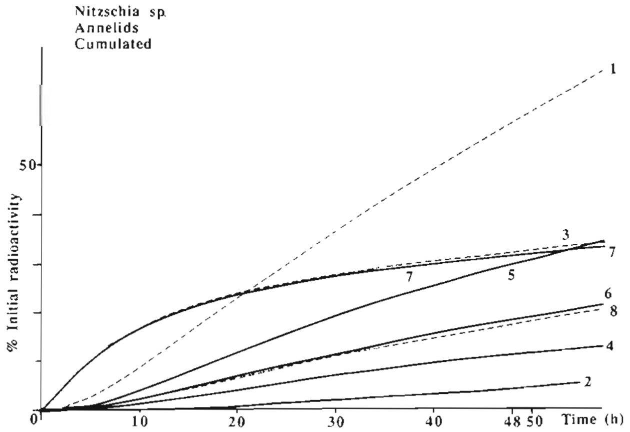

Fig. 8. Calculation of cumulated amounts of organic matter (radioactivity) passing through different compartments as a function of time during different exchanges within the *Nitzschia* sp.–*Eupolymnia nebulosa* system. (1) Faeces, (2) CO_2 consumed by diatoms, (3) DOM produced by diatoms, (4) DOM consumed by annelids, (5) DOM consumed by diatoms, (6) DOM produced by annelids, (7) CO_2 produced by diatoms, (8) CO_2 produced by annelids

Consumption, ingestion, and assimilation

The computation of the amount of radioactivity consumed, ingested (in a particulate form) and assimilated by the worms required the computation of the cumulative amounts of radioactivity within the different compartments. This could only be achieved through modelling of the system. Such cumulative amounts are presented for *Navicula incerta, Nitzschia acicularis,* and *Nitzschia* sp., in Figs. 6, 7, and 8, respectively.

Nitzschia sp. (Table 2) was the diatom most readily consumed (118.5 % vs 63 and 48 % for *Navicula incerta* and *Nitzschia acicularis,* respectively), ingested (108 % vs 60.5 and 40.5 % for *N. incerta* and *N. acicularis,* respectively) and assimilated (95 % vs 55 and 38.5 % for *N. incerta* and *N. acicularis,* respectively).

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

	Navicula incerta	*Nitzschia acicularis*	*Nitzschia* sp.
50 h cumulated			
(1) Faeces	10.0	10.0	60.0
(2) CO_2 cons Diat	1.0	1.5	4.5
(3) DOM prod Diat	5.0	40.0	32.0
(4) DOM cons Ann	2.5	2.5	10.5
(5) DOM cons Diat	2.5	55.0	30.5
(6) DOM prod Ann	12.5	11.5	18.0
(7) CO_2 prod Diat	26.0	17.0	31.5
(8) CO_2 prod Ann	9.0	7.0	17.5
50 h present			
Faeces	5.5	7.0	13.0
Diatoms	8.5	28.5	7.0
DOM	10.5	15.0	9.0
Particulate	14.5	35.5	20.5
Annelids	31.5	19.5	23.0
CO_2	33.5	30.0	47.5
Amount consumed	63.0	48.0	118.5
Amount ingested	60.5	45.5	108.0
Faeces produced	10.0	10.0	60.0
Faeces recycled	4.5	3.0	47.0
DOM consumed	2.5	2.5	10.5
Amount assimilated	55.0	38.5	95.0

DISCUSSION

The aims of this study were: (1) to compare ingestion and assimilation of 3 different species of diatoms by the deposit-feeding polychaete *Eupolymnia nebulosa,* and (2) to compare these results with similar data collected on the deposit-feeding bivalve *Abra alba* (Amouroux et al. 1989). Our procedure followed the method explained in 2 previous papers (Amouroux & Amouroux 1988, Amouroux et al. 1989). This study confirms that it is possible to describe the exchanges of matter within a 'benthic diatom – deposit-feeder' system using a compartmental in contrast to an interface model (in which the exchanges of matter between 2 compartments are proportional both to the amounts of matter within the 2 compartments, and to the surface of exchange between the 2 compartments).

Comparison with *Abra alba*

Because of several differences (volume of the microcosms, biomass of animals) in the experimental procedures used with *Abra alba* and *Eupolymnia nebulosa,* it is not possible to compare directly consumption, ingestion, and assimilation in *A. alba* and *E. nebulosa.* However, it is possible to compare the effects of these animals on the 3 diatoms.

Ingestion

The idea that deposit-feeders feed primarily on microbes associated with sediment grains, together with the assumption of the constancy of the ratio between microbial biomass and sediment grain surface (DeFlaun & Mayer 1983, Yamamoto & Lopez 1985), has led to the conclusion that smaller particles should be preferentially ingested by deposit-feeders. The theoretical basis of this hypothesis is the optimal foraging model proposed by Taghon et al. (1978). This model was derived from a previous one developed for filter-feeders by Lehman (1976). The main difference between the 2 models is the nutritional value ascribed to each particle, which is described as proportional to its volume for filter-feeders, but to its surface for deposit-feeders. Because of this difference, the model predicts the preferential ingestion of smaller particles by deposit-feeders, which has been partly confirmed by further experimental studies (Taghon 1982).

In our experiments the particles themselves constitute the food type. It is reasonable to assume that the nutritive value of one particle is proportional to its volume (see 'Materials and methods'). In this situation the filter-feeder model can be used directly. It predicts a preference for larger particles. A result of this kind has already been reported for the amphipod *Siphonocoetes dellavallei* fed on 4 different food types (Guidi 1986).

During our experiments with *Abra alba,* higher ingestion rates corresponded to the larger diatoms (*Navicula incerta* and *Nitzschia acicularis*), whereas in *Eupolymnia nebulosa,* the results were opposite (i.e. ingestion rates of *Nitzschia* sp. were higher than those obtained with *N. incerta* and *N. acicularis*).

Differences in feeding rates observed in such short-term experiments reflects the differential efficiency of feeding mechanisms (Boyd 1976, Lehman 1976). *Eupolymnia nebulosa* is a tentaculate deposit-feeder.

Upon contact with a suitable particle, its tentacles produce mucus which adheres to the particles allowing their extraction from the surrounding sediment. The particle is then transported to the mouth via the ciliary groove (Grémare 1988). As in most of the other tentaculate deposit-feeders (with the exception of the genera *Cistenides* and *Pectinaria;* Whitlatch 1974, Whitlatch & Weinberg 1982, Dobbs & Scholly 1986), *E. nebulosa* preferentially feeds on small particles (Grémare 1988). *Abra alba* sucks up the thin sediment top layer by movements and numerous distortions of its 4 to 5 cm long siphons. According to our results, this process probably results in lesser selectivity than for tentaculate deposit-feeders.

Assimilation

Both in *Abra alba* and in *Eupolymnia nebulosa, Nitzschia* sp. is better assimilated than *Navicula incerta* and *Nitzschia acicularis.* However, in *E. nebulosa* the absorption rates (%assimilated / %consumed) of the 3 diatoms are almost equivalent (87.3 % vs 80.2 and 80.2 % for *N. incerta, N. acicularis* and *Nitzschia* sp. respectively), whereas in *Abra alba* the absorption rate of *Nitzschia* sp. (75.6 %) is greater than the absorption rates of *N. acicularis* (56.2 %) and *N. incerta* (50.9 %). In *E. nebulosa,* differences in assimilation between algae reflect differences in consumption, whereas in *A. alba* differences in assimilation between algae are due to differences in absorption rates.

Effect on the algae

To obtain a good fit of the model with the experimental data requires some modification of the kinetic constants corresponding to the metabolic exchanges of the algae. This suggests that, while feeding, worms affect diatoms' metabolic rates. *Navicula incerta* seemed stimulated (increase of k2 and k10 vs a decrease of k1). *Nitzschia acicularis* was inhibited (decrease of k1, k2, k4, and k10). The results concerning *Nitzschia* sp. are more difficult to interpret. In this species and in the presence of worms, k1 and k10 remained fairly constant whereas k2 increased and k4 decreased.

It is interesting that *Abra alba* and *Eupolymnia nebulosa* have the same effect on the metabolism of *Navicula incerta* and *Nitzschia acicularis* (i.e. inhibition and stimulation, respectively). *Nitzschia* sp. seemed relatively unaffected by the presence of *E. nebulosa* whereas it was inhibited by *A. alba.* This difference is probably due to the greater rate of ingestion of *Nitzschia* sp. by *E. nebulosa* than by *A. alba.*

The inhibition of photosynthetic processes have already been described for a 'periphyton-grazer' system (Summer & McIntyre 1982, Moriarty et al. 1985). The reaction of *Navicula incerta* is more difficult to interpret. As mentioned earlier, experiments were carried out in darkness to limit photosynthesis and to permit a normal activity of worms (Grémare 1988). Dark metabolism of diatoms is not yet well-known. Therefore, the difference between *N. incerta* and the 2 other diatoms could be due to different metabolic adaptations in the 3 species (Gallagher et al. 1984, Mortain-Bertrand et al. 1988).

Finally, it is important to point out, that, at present, we do not know to what extent such interactions between diatoms and deposit-feeders depend on the small size of our experimental system. For example, metabolic products of deposit-feeders may affect growth rate of diatoms, which would cause such an interaction to diminish in a large open system.

CONCLUSION

Because of the complexity of a 'Food source – Deposit-feeder' system, a compartmental analysis coupled with analog modelling is one of the few possible ways of acquiring information on the quantitative aspects of nutrition (ingestion, assimilation, recycling) in some benthic deposit-feeders (i.e. large soft-body tentaculate deposit-feeders).

Our results show that *Eupolymnia nebulosa* exhibits higher ingestion rates with the smallest diatoms (*Nitzschia* sp.) whereas in *Abra alba* feeding rates are independent of diatom size. This is probably due to differences in feeding mechanisms. In spite of such differences, *E. nebulosa* and *A. alba* have the same effect on 2 of the 3 diatoms (stimulation of *Navicula incerta* and inhibition of *Nitzschia acicularis*). This suggests that the nature of the response of a diatom to the presence of a deposit-feeder is probably a specific characteristic.

More detailed studies are now needed: (1) to determine (and to compare) the exact effects of deposit-feeding organisms on their food sources in the laboratory and in the field, and (2) to quantify actual ingestion and absorption rates of deposit-feeders fed on different food sources.

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