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A. Grémare, J.-C. Duchêne, Rutger Rosenberg, E. David, M. Desmalades. Feeding behaviour and functional response of *Abra ovata* and *A. nitida* compared by image analysis. *Marine Ecology Progress Series*, 2004, 267, pp.195-208. 10.3354/meps267195 . hal-00125980

HAL Id: hal-00125980

<https://hal.science/hal-00125980>

Submitted on 30 Dec 2023

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Feeding behaviour and functional response of *Abra ovata* and *A. nitida* compared by image analysis

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ABSTRACT: An automated image analysis system was used to monitor sediment surface feeding activity of 2 bivalves (*Abra ovata* and *A. nitida*) inhabiting contrasting environments. A larger variety of feeding behaviours was recorded in *A. nitida*, whereas *A. ovata* mostly fed at the sediment surface. There were also clear differences in the behaviour of the 2 species during surface deposit feeding (i.e. a wider extension of the inhalant siphon in *A. ovata*, and the exhalant siphon being located below the sediment-water interface in *A. ovata* and above this interface in *A. nitida*). In *A. nitida*, increase in feeding activity resulted mostly from an increase in feeding intensity, and not from an increase in the amount of time devoted to feeding. In *A. ovata*, the most active bivalves tended to increase their activity mostly by increasing the amount of time devoted to feeding. This suggests that feeding intensity was limited in *A. ovata* but not in *A. nitida*. Food dilution and food addition experiments were carried out to assess the functional response in the 2 species. The results of the food dilution experiments were statistically insignificant due to high inter-individual variability. Food addition significantly affected feeding activity in *A. ovata* and *A. nitida*, although in different ways. In *A. ovata*, feeding activity was highest at intermediate food concentrations, and inhibited at the highest ones. In *A. nitida*, increased feeding activity was induced at higher concentrations than in *A. ovata*, and feeding activity was greatest at the highest food concentration. Such discrepancies in feeding behaviour and functional response in closely related species characterise the difficulty in delineating functional groups in benthic deposit-feeders.

KEY WORDS: Deposit feeding · Behaviour · Image analysis · Bivalves

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INTRODUCTION

The food sources of benthic deposit-feeders are diluted within an inorganic matrix of sediment grains. Benthic deposit feeders are thus adapted to feed on a poor food source, and this requires high selectivity, and/or high ingestion rates, and/or high absorption efficiencies (Lopez & Levinton 1987). In spite of such adaptations, there is evidence that benthic deposit feeders are food limited (Lopez & Levinton 1987) and likely to react rapidly to changes in the quantity and the quality of food (Tenore & Chesney 1985, Grémare et al. 1988). In coastal areas (Grémare et al. 1997), and to a lesser extent in deep environments (Neuer et al. 1997), there may be important temporal changes in the input of particulate organic

matter to the sediment-water interface. Such changes are often linked to seasonal pelagic primary productivity with coupling between pelagic and benthic systems related to water depth and productivity (Graf 1992).

Theoretical studies have attempted to relate the intensity of feeding activity in benthic deposit feeders with the availability of food. This effort has resulted in 2 distinct theories, the optimal foraging and the compensatory intake theories. Based on a model maximizing energy gain (i.e. the difference between the energy derived from the food, and feeding costs), the optimal foraging theory postulates the existence of a positive correlation between ingestion rates and food values (Taghon et al. 1978). The compensatory intake theory was derived from the observation of a log-linear rela-

tionship between the body weight and the ingestion rates of a large variety of invertebrates fed on various substrates (Cammen 1981). It postulates the existence of a negative relationship between ingestion rates and food value. These 2 theories are not necessarily exclusive and may co-exist due to the existence of a maximal possible energy gain (Phillips 1984) and/or the existence of a trade-off between gut passage time and absorption efficiency (Taghon & Greene 1990). According to this last model, optimal gut-residence time is negatively correlated with food value. Ingestion rates thus increase with food value until absorption is saturated, and then decrease to maintain absorption at its maximum. More recently, Jumars (2000) showed that the relationship between food concentration and ingestion rates is also affected by the biochemical composition of the food. Based on the chemical reactor theory, this author suggested: (1) the existence of a negative correlation between ingestion rates and food concentrations for simple food requiring a single hydrolytic step, and (2) maximal absorption rates at intermediate food concentrations for complex food requiring multiple hydrolytic steps. This would result in a positive correlation between ingestion and food concentration, only in the lower quality range of a complex diet. It has also been suggested that adaptations to different environments may result in different feeding behaviour. This point has been raised recently for the existence of a minimal threshold of particle concentration inducing suspension feeding in interface feeders (Riisgard & Kamermans 2001). The relationships between sedimentary organics and feeding activity may also differ in deposit feeders inhabiting sediments with different organic contents.

Many experimental studies aimed at relating food availability with the bioenergetics of benthic deposit feeders have been based on production measurements (Grémare et al. 1988, 1989, Marsh et al. 1989, Forbes & Lopez 1990, Tsutsumi et al. 1990, Bridges et al. 1994, Charles et al. 1995). Few studies have investigated the effect of food availability on feeding behavior in benthic deposit-feeders (Taghon & Greene 1990, Linton & Taghon 2000), partly because until recently it was only possible to quantify feeding rates through the measurement of fecal production (Taghon & Greene 1990).

The interactions between sedimentary organics and benthic deposit feeders are not restricted to nutrition, and encompass all bioturbation processes through which benthic deposit feeders affect the fate of sedimentary organics. These interactions depend both on the biochemical characteristics of sedimentary organic matter and on the diversity of benthic deposit feeders. Bioturbation was first assessed by computing mixing coefficients accounting for the functioning of the whole community (e.g. biological diffusion coefficient in classical diagenetic models; Boudreau 1986a,b). Attempts

were later carried out to categorize benthic fauna in functional groups based on their size, morphology and feeding behaviour (François et al. 1997). The latest attempt has modeled bioturbation induced by selected benthic deposit feeders based on a set of equations describing the behavior of individual animals (Boudreau et al. 2001, Choi et al. 2002). These last 2 approaches underline the need for further assessment of: (1) benthic infaunal foraging patterns, and (2) their relationship with major environmental parameters such as sediment grain size, food quality and food availability.

An automated image-analysis system developed to study larval motion proved appropriate to assess feeding activity in both suspension and deposit feeders (Duchêne et al. 2000, Duchêne & Queiroga 2001, Duchêne & Rosenberg 2001, Hollertz & Duchêne 2001). This system allowed for a quantitative assessment of: (1) activity patterns, and (2) relationships linking food availability and feeding activity in benthic deposit feeders. Based on experiments involving the bivalves *Abra ovata* and *A. nitida*, the present study tackled 2 specific questions: (1) Are there differences in the feeding behavior of 2 closely related species? (2) Are there specific differences in feeding activity as a function of food concentration?

MATERIALS AND METHODS

Bivalve collection and maintenance. *Abra ovata* is a shallow-water species with a vertical distribution from 0 to 14 m (Denis 1981). Its horizontal range goes from the north of France to the Atlantic coast of Morocco and to the Mediterranean (Denis 1981). *A. ovata* typically inhabits sandy mud and is characteristic of areas featuring strong salinity changes (e.g. semi-enclosed areas such as coastal lagoons) (Clanzig 1987). Specimens of *A. ovata* were hand-collected in a shallow (<50 cm depth) area of the Lapalme Lagoon (NW Mediterranean) during July 2002. The annual temperature range in this lagoon is between 4 and 30°C (Wilke & Boutière 2000). The bivalves were kept at the Observatoire Océanologique de Banyuls, France, in tanks with flow-through ambient seawater (38 psu; 22°C) until the end of the month. They were then packed in sealed cool-boxes with air and taken to the Kristineberg Marine Research Station, Sweden, where all activity experiments were conducted during August 2002. The bivalves were progressively adapted to 15°C temperature and then kept for >6 d in flow-through ambient seawater (34 psu; 15°C) before being used in activity experiments. The total shell length of the bivalves used was between 9 and 14 mm.

The vertical range of *Abra nitida* is from just sublittoral to 4400 m depth (Wikander 1980b). Its horizontal

distribution ranges from western Finnmark (North Cape, Norway) to the Mediterranean and the Atlantic coast of Morocco (Tebble 1966). *A. nitida* has been found in fine sand (Wikander 1980b) but along the Swedish coast it is mainly found in muddy sediments (R.R. pers. obs.). A first batch of *A. nitida* was dredged on 30 July 2002 in the Brofjord (58°20'8 N; 11°24'0 E) between 24 and 28 m depth (annual temperature range: 7 to 17°C) using a Warén dredge. Back at the Kristineberg Marine Research Station, bivalves were immediately transferred to tanks with flow-through ambient seawater (34 psu; 10°C) where they were kept >17 d before the start of activity experiments. A second batch of bivalves was collected in the same area with the same gear on 26 August (water temperature: 17°C). These bivalves were kept for >1 d in flow-through ambient seawater (34 psu; 15°C) before being used in experiments carried out at 15°C. The total shell length of the bivalves was between 8 and 13 mm.

Activity monitoring. *Abra ovata* and *A. nitida* are both primarily surface deposit-feeders (Wikander 1980a,b, Charles 1993). They feed with their inhalant siphon at the water-sediment interface. The movements of this siphon on the sediment surface can thus be used to assess feeding activity.

Feeding activity was monitored using an automated image system designed for the study of the water-sediment interface (Duchêne et al. 2000, Jordana et al. 2000). This system was composed of a Charged Coupled Device (CCD) connected to a signal microprocessor. The microprocessor was driven by real-time routines that controlled the frequency of picture acquisition and analysis, which was based on a pixel-by-pixel comparison between the grey levels of consecutive images. Differences between images were stored in the memory board together with corresponding images. At the end of each experiment, data were transferred to a microcomputer. They were then processed by post-treatment programmes to uncompress the raw data, aggregate the activity patterns into numeric objects and track the position and surface modifications of each of these objects. This automated image system has been used to assess feeding and burrowing activities in several benthic animals (Jordana et al. 2000, Duchêne & Rosenberg 2001, Hollertz & Duchêne 2001). During the present study, its validity was checked by comparing detected activities with the visual observation of recorded images. We used 3 automated image systems allowing for the simultaneous processing of 3 replicated experiments. In all experiments, the frequency of picture acquisition was 20 s. This frequency constitutes a good compromise between the duration and the temporal resolution of activity record. It was chosen after preliminary trials carried out on 10 individuals of *A. ovata*, which

showed a reduction of only 1.6% of detected activity relative to a 1 s frequency of picture acquisition (data available on request from J.C.D.). All experiments were carried out in darkness using red light.

For each experiment, 3 activity indices were computed. Percentage of time active (ACT) was calculated for a single bivalve. Mean activity per individual (MAC) was defined as the average surface area modified by a single bivalve per unit of time. It was based on the whole activity record. Mean activity per time active (MATA) was defined as the average surface area modified by a single bivalve per unit of time when this bivalve was active. MAC is thus indicative of mean feeding activity whereas MATA is indicative of feeding intensity.

Experiments with natural sediment. The sediment used in these experiments was collected in the Gullmarsfjord from a 60 m deep station using a 0.1 m² Smith-McIntyre grab. It consisted of mud (median diameter of 14 µm) with an organic carbon and nitrogen content of 2.6 and 0.4% DW, respectively. This sediment was sieved on a 1 mm mesh before all experiments to remove the macrofauna, which could have interfered with feeding activity measurements.

Experimental boxes of 17.5 × 11.5 × 7.5 cm were filled with a 5 cm thick layer of sediment. Four PVC cylinders (3.2 cm diameter × 3 cm height) were placed on the bottom of each box as shown in Fig. 1A,B to keep the bivalves separated for analyzing individual activity. For each experiment, 4 bivalves of each species were measured to the nearest mm, placed on the sediment surface (each above a PVC cylinder), and

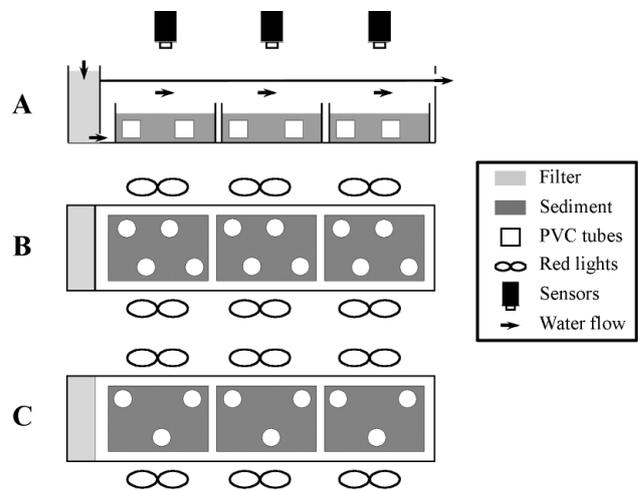


Fig. 1. (A) Lateral view of the experimental set-up showing the position of the PVC tubes, the 3 experimental boxes within the aquarium, and the 3 automated sensors. (B) Top view of the experimental set-up used during the natural sediment and sediment dilution experiments. (C) Top view of the experimental set-up used during the food addition experiment

allowed to burrow. Confinement within cylinders was not expected to interfere with feeding activity since: (1) the inhalant siphon was free to move in the upper 2 cm of the sediment, and (2) *Abra ovata* appears to search for the contact with a hard surface as it is often found within shells of dead cockles in the field (A.G. pers. obs.). After a 24 h acclimation, the 3 experimental boxes were put in a large aquarium (65 × 15 × 14 cm) with temperature-controlled flowing ambient seawater (34 psu; 15°C for *A. ovata* and 10°C for *A. nitida*). After an additional 1 h, each box was monitored by a single automated image analysis system (Fig. 1A) and individual bivalve feeding activities were recorded for 12 h as described above. Overall, 10 and 6 replicated experiments were conducted for *A. ovata* and *A. nitida*, respectively. The shapes of the relationships linking MAC and MATA in both species were assessed using appropriate regression models.

Temperature experiments. The effect of temperature on the feeding activity of *Abra nitida* was assessed by carrying out replicated experiments at 10 and 15°C. In both cases, 4 bivalves were measured to the nearest mm and used as described above, but individual activities were recorded for 8 h only. The effects of temperature on *A. nitida* individual activity indices were assessed using Mann & Whitney *U*-tests. The means of individual activity indices in *A. ovata* and in *A. nitida* were also compared using Mann & Whitney *U*-tests based on the results of the 15°C experiments (standardised for an 8 h duration in *A. ovata*).

Sediment dilution experiment. This experiment was designed to compare the activity of bivalves inhabiting natural sediment, and the same sediment mixed with various proportions of glass beads to reduce its organic content (Forbes & Lopez 1990). There were 5 treatments for *Abra ovata*: natural sediment (i.e. same sediment as the one used in the experiments with natural sediment), 15, 25, 35 and 50% glass beads (mean average diameter of 30 µm; Poudres et Grenailles Métalliques) by volume. For *A. nitida*, only the natural sediment and the 15 and 35% glass bead treatments were used. The organic carbon and nitrogen contents of the sediments were assessed using a Perkin Elmer 2400 CHN analyser. The experimental set-up and procedure were strictly identical to those described for the temperature experiments. The experiments were conducted at 15°C for *A. ovata* and at 10°C for *A. nitida*. There were 6 replicated boxes per sediment for both species. The effect of sediment types on the 3 main activity indices were assessed using Kruskal-Wallis non-parametric ANOVAs.

Food addition experiment. Three bivalves of each species were measured to the nearest mm, placed on the sediment surface of experimental boxes and allowed to bury. After 24 h acclimation, their individual activities were recorded for 3 h as described for the other experiments (Fig. 1C). A known amount of phyto-detritus (*Tetraselmis* 3600 Premium Fresh, Reed Marine Culture) was then gently and evenly added on the sediment surface of each box using a Pasteur pipette. Individual activities were then monitored for an additional 6 h. The organic carbon content of the *Tetraselmis* paste was assessed using a Perkin Elmer 2400 CHN analyser. Six concentrations corresponding to the addition of 0 (control), 0.7, 1.4, 2.8, 5.6 and 28.6 mg C m⁻² were tested with 3 replicated boxes per species and concentration. Experiments were conducted at 15°C for *Abra ovata* and 10°C for *A. nitida*. Activity indices recorded before and after food addition were compared using Wilcoxon signed-rank tests.

RESULTS

Feeding behaviour and activity patterns

The activity of 356 bivalves (190 *Abra ovata* and 166 *A. nitida*) was monitored for a total of 4000 h of individual activity recording (2200 h and 1800 h for *A. ovata* and *A. nitida*, respectively). Examples of the sediment surface area affected by *A. ovata* and *A. nitida* activity during the whole course of an experiment are presented in Fig. 2.

There were marked differences in the feeding behaviour of the 2 species. In *Abra ovata*, the inhalant siphon usually exhibited strong movements outside the sediment. During an activity event, the inhalant siphon typically explored the sediment in circles

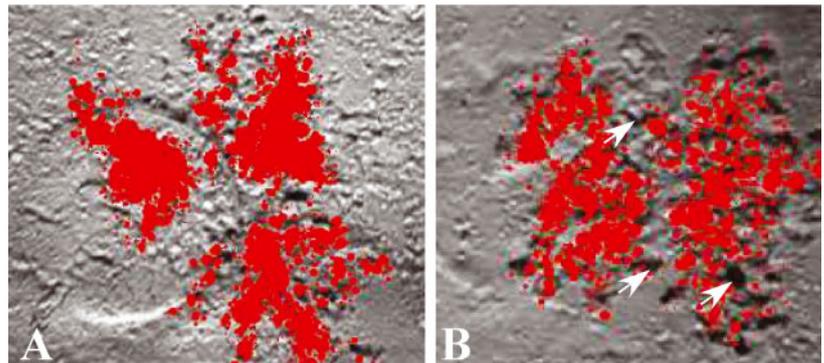


Fig. 2. *Abra ovata* and *A. nitida*. Examples of activity patterns on the sediment surface by *A. ovata* (A) and *A. nitida* (B). The shaded area shows the cumulated activity of the bivalves after 1 h recording. White arrows show the large feeding pits of *A. nitida*

around an orifice in the sediment corresponding to the end of a siphonal channel. The inhalant siphon then took patches of sediment and retracted periodically. Before leaving its present siphonal channel, the inhalant siphon usually expelled a little patch of sediment, which closed this orifice. Then the siphon started another sequence of activity from a new location. In *A. nitida*, the inhalant siphon usually did not emerge much from the sediment surface and worked in the immediate vicinity of the orifice of the siphonal channel where it first appeared. Sediment uptake by the inhalant siphon thus typically resulted in the creation of feeding pits corresponding to the end of siphonal channels. The inhalant siphon typically remained in a given channel for only a few minutes before switching to another location.

The exhalant siphon also behaved differently in the 2 species. It mainly remained beneath the sediment surface in *A. ovata*, whereas it was most often seen outside the sediment in *A. nitida*, resulting in the production of piles of fecal pellets on the sediment surface. In *A. ovata*, water was exhaled beneath the sediment surface, often leading to slight displacement of the superficial sediment above. Sometimes, however, the exhalant siphon came so close to the sediment surface that it was possible to see defecated sediment formed in a circular pattern around the siphon, but fecal pellets were never deposited in piles on the sediment surface.

Abra nitida exhibited a larger variability of feeding behaviour than *A. ovata*, especially when bivalves were very active. In some cases, the inhalant siphon remained for several minutes >0.5 cm above the sediment surface, with only small lateral oscillations and no sediment uptake. Such behaviour was probably associated with filtration (see description of the corresponding activity pattern, below). Very active *A. nitida* also exhibited shell displacement beneath the sediment surface, which was not observed for *A. ovata*.

Examples of the 4 main activity patterns recorded for *Abra ovata* are presented together with the corresponding periodograms in Fig. 3. The first pattern was characterised by a low activity level (less than 0.1 cm² modified between 2 consecutive images) and 3 periodicities as indicated by corresponding spectral analyses. The longest periodicity was usually close to 15 min and corresponded to the time between 2 consecutive extensions of the siphon out of the feeding pit. Examination of the records showed that: (1) the inhalant siphon always remained in the same pit, (2) its extension was always limited to a few millimetres, and (3) it had no impact on the water-sediment interface. These bivalves were not surface deposit-feeding and were most likely just respiring. The second pattern was characterised by higher activities (i.e. up to 0.4 cm²

modified between 2 consecutive images) and by the persistence of 3 periodicities. In this case the longest periodicity lasted for ca. 10 min. The examination of records showed bivalves featuring limited extension of their inhalant siphons yet they ingested significant amounts of sediments. This pattern was thus associated with 'moderate' surface deposit-feeding. The third pattern was characterised by even higher activities and by the merging of activity peaks. This resulted in a longest periodicity close to 7 min. The examination of the records showed actively feeding bivalves extending their siphons over distances of ca. 1 cm while ingesting significant amounts of superficial sediments. This pattern was suggested to be characteristic of 'normal' surface deposit feeding. The fourth pattern was characterised by extremely high and almost continuous activities, resulting in a single and even shorter (i.e. close to 5 min) periodicity. It was characteristic of intensive surface deposit feeding with great (up to 6 cm) extension of the inhalant siphon on the sediment surface and ingestion of superficial sediments in great amounts.

Typical examples of the 3 main activity patterns recorded for *Abra nitida* are presented in Fig. 4, together with corresponding periodograms. The first pattern was characterized by the succession of low activity (i.e. less than 0.04 cm² modified between 2 consecutive images) events with a periodicity close to 25 min. The visual examination of the records showed that these events corresponded to the positioning of the inhalant siphon into the water column with no impact on the sediment surface. This pattern was probably indicative of filtration, as it was especially frequent during food addition experiments at the period when food was added, and it lasted until all food seemed to have settled on the sediment. The second pattern was characterized by higher individual activities (i.e. more than 0.1 cm² modified between 2 consecutive images) and by the succession of activity peaks at variable frequency. This pattern was associated to active feeding at the water-sediment interface. The third pattern was characterized by very intense activity events (i.e. more than 1 cm² modified between 2 consecutive images) corresponding to shell displacement. It was associated with very active bivalves and was mostly recorded during the 15°C and the food addition experiments.

Natural sediment experiment

In *Abra ovata*, large inter-individual variability was found for all individual activity indices. ACT was between 0 and 90%, with a mean value of 40.5% of experiment duration. MAC was between 0 and

19.5 $\text{cm}^2 \text{h}^{-1}$ with an average of 4.2 $\text{cm}^2 \text{h}^{-1}$. MATA was between 0 and 24 $\text{cm}^2 \text{h}^{-1}$ with a mean value of 6.4 $\text{cm}^2 \text{h}^{-1}$. None of these indices correlated significantly with the size of the bivalve ($p = 0.740$, $p = 0.854$ and $p = 0.734$ for ACT, MAC and MATA, respectively). All 3 activity indices correlated posi-

tively pair-wise between each other. The relationship between MAC and MATA was best fitted using a 2-parameter exponential to a maximum regression model (Fig. 5). There were 2 outliers in this regression model. The activity records of these 2 bivalves showed marked changes in their feeding behaviour

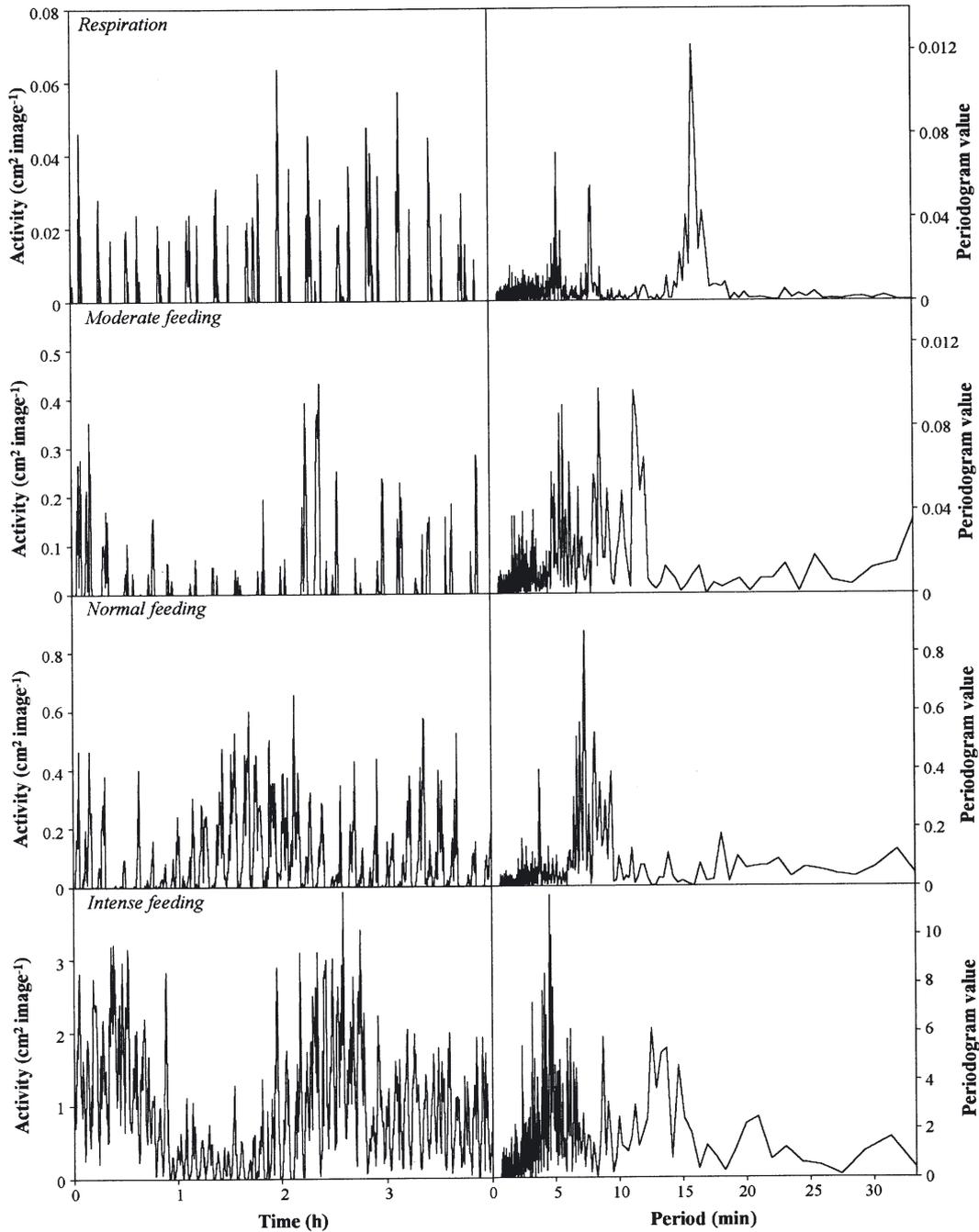


Fig. 3. *Abra ovata*. Presentation of the 4 main activity patterns recorded during the present study. The panes on the left are extracts of crude activity records; those on the right are the corresponding periodograms computed for the whole individual activity records. Note the different scales

during the course of the experiment. The fitting of this regression model can thus be considered as indicative of the constancy of the feeding behaviour both between and within bivalves.

Individual activities were highly variable in *Abra nitida* as well. All individual activity indices were significantly higher at 15 than at 10°C (Fig. 6). Mean values increased from 24.9 to 54.6%, 0.85 to 7.99 cm² h⁻¹, and 2.54 to 11.06 cm² h⁻¹, for ACT, MAC and MATA, respectively. There was no clear temperature effect on the relationship between activity indices (Fig. 7). When pooling the results of the 10 and 15°C experiments, all 3 activity indices correlated positively pair-wise to each other. As opposed to what was observed in *A. ovata*, the relationship between MAC and MATA

was best fitted using a simple linear-regression model (Fig. 7).

Temperature experiment

At 15°C, average ACT and MAC were significantly higher in *Abra nitida* than in *A. ovata* (Mann & Whitney *U*-tests, $p = 0.006$ and $p = 0.030$, respectively). This difference was not significant ($p = 0.067$) for MATA due to high variability. When discarding the portion of the records corresponding to shell displacement, differences between species were non-significant both for MAC and MATA (Mann & Whitney *U*-tests, $p = 0.053$ and $p = 0.121$, respectively).

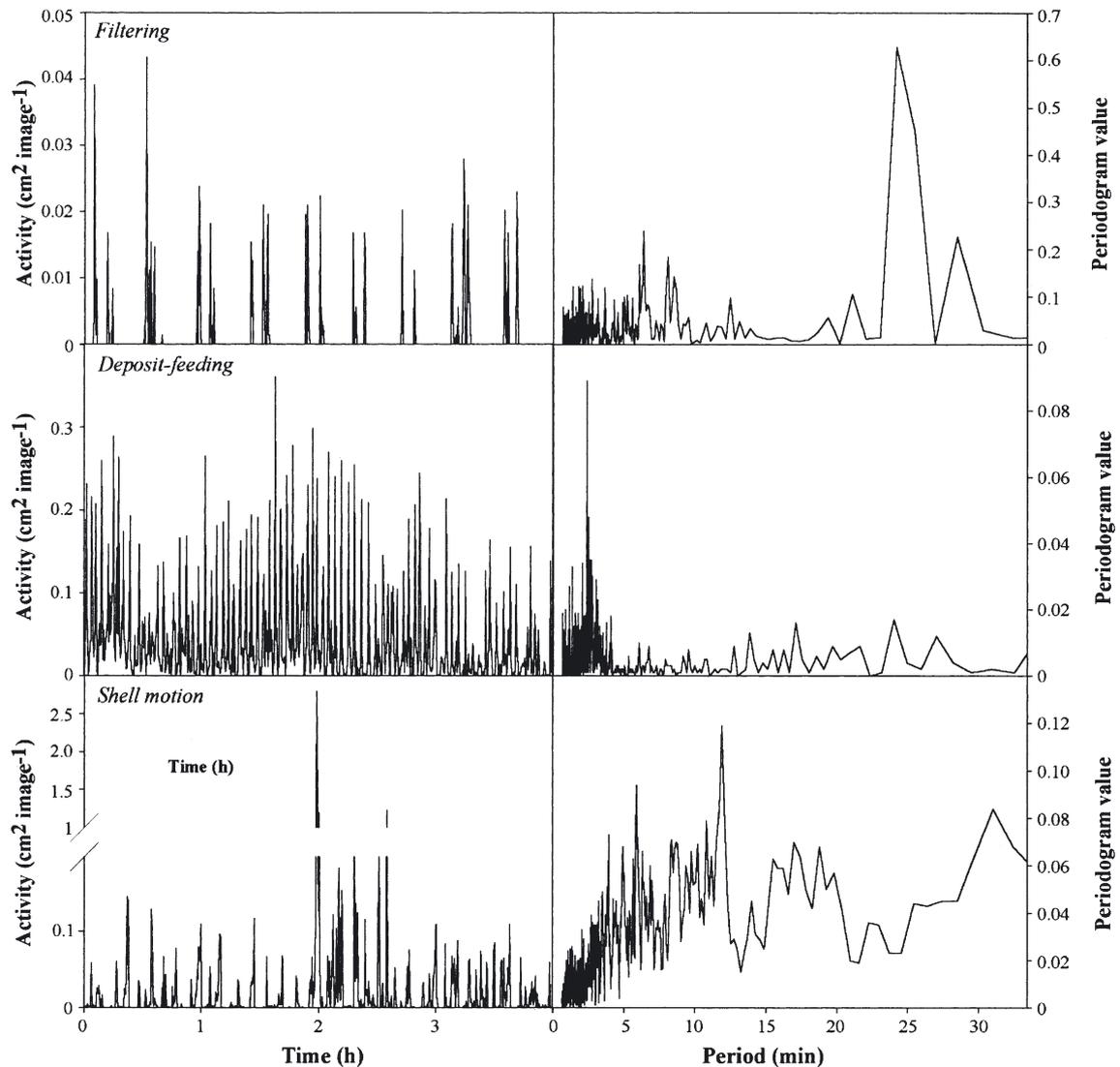


Fig. 4. *Abra nitida*. Presentation of the 3 main activity patterns recorded during the present study. The panes on the left are extracts of crude activity records; those on the right are the corresponding periodograms computed for the whole individual activity records. Note the different scales

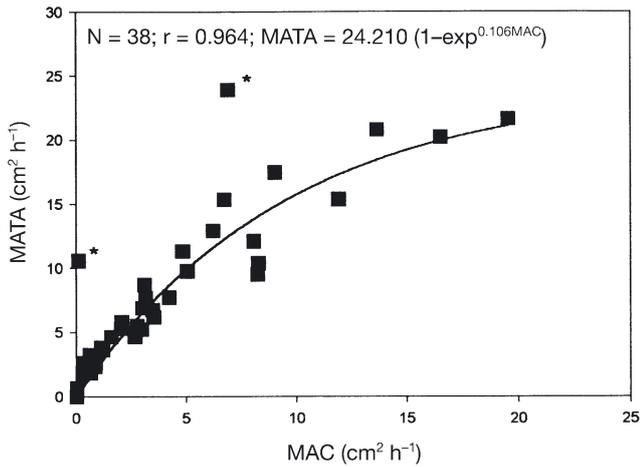


Fig. 5. *Abra ovata*. Relationships linking mean activity per individual (MAC) and mean activity per time active (MATA) during experiments (10°C) involving natural sediment. Outliers are indicated by an asterisk. See 'Activity monitoring' for further details

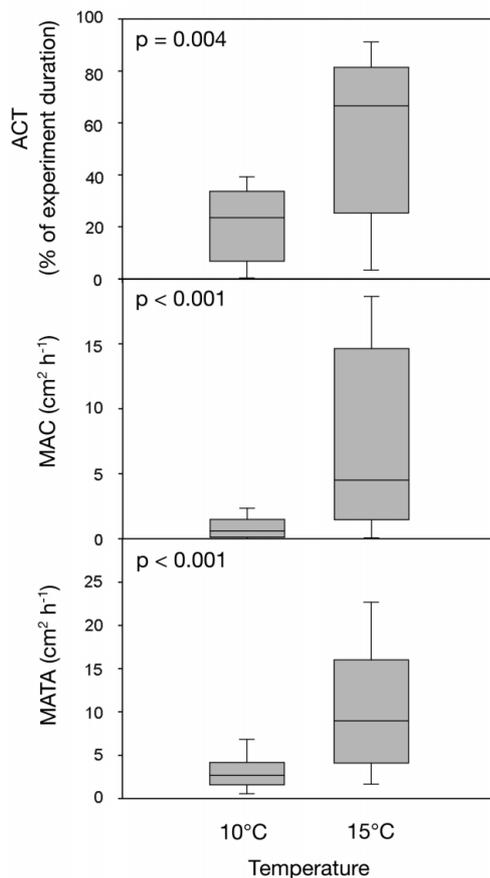


Fig. 6. *Abra nitida*. Boxplots (median, 25 and 75 percentiles) of the percentage of time active (ACT), mean activity per individual (MAC), and mean activity per time active (MATA) recorded at 10 and 15°C. See 'Activity monitoring' for further details. p corresponds to the probability of the Mann & Whitney U -tests used to compare activity indices

Food dilution experiment

The organic carbon and nitrogen contents in the different treatments were between 0.7 and 2.6, and 0.2 and 0.4% dry weight (DW), respectively (Table 1). Box-plots of ACT, MAC and MATA recorded for both species and for all the tested concentrations are presented in Figs. 8 & 9. The results suggested that *A. ovata* increased its feeding activity when glass beads were present, but bead concentration had no effect. The mean value of ACT, for example, increased from 30.7 to 44.6% of experiment duration in the presence of beads. This trend was even more pronounced for MAC and MATA, with corresponding increases from 4.8 to 12.8 $\text{cm}^2 \text{h}^{-1}$ and from 9.1 to 20.4 $\text{cm}^2 \text{h}^{-1}$, respectively. However, it should be stressed that, due to within-treatment variability, the effects of sediment type on all 3 activity indices were not significant. The distributions of both MAC and MATA were moreover slightly asymmetric because some bivalves were very active when glass beads were present in the sediment.

In *Abra nitida*, activity indices were much lower and their average values were not significantly affected by the presence of glass beads within the sediment. The distribution of the 3 activity indices tended to become asymmetric in the presence of glass beads, as reported for *A. ovata* (Fig. 9).

Food addition experiment

For all 3 activity indices (except ACT at the 2.8 mg C m^{-2} treatment), there were significant increases after

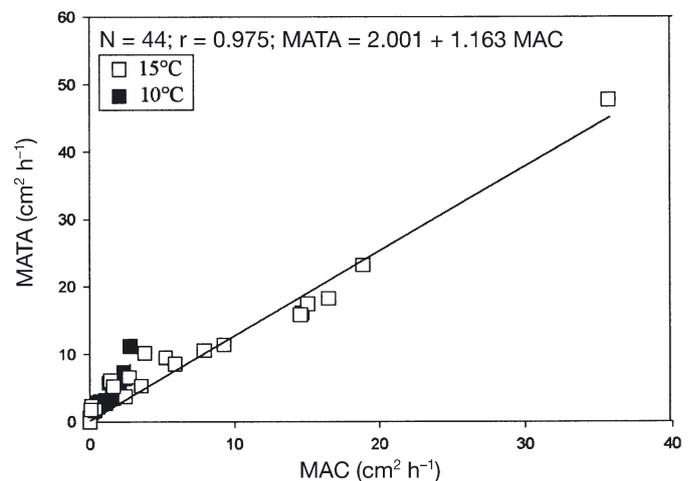


Fig. 7. *Abra nitida*. Relationships linking mean activity per individual (MAC) and mean activity per time active (MATA) during experiments (10 and 15°C) involving natural sediment. Outliers are indicated by an asterisk. See 'Activity monitoring' for further details

Table 1. Organic carbon and nitrogen contents of the various sediments used during the glass bead experiments. DW: dry weight

% beads	Organic carbon (% DW)	Nitrogen (% DW)
0	2.6	0.4
15	1.6	0.3
25	1.3	0.2
35	1.0	0.2
50	0.7	0.2

food addition for food additions between 0.7 and 2.8 mg C m⁻² in *Abra ovata* (Fig. 10). There was no significant change in *A. ovata* activity at the 5.6 mg C m⁻² treatment, but at the highest food ration (28.6 mg C m⁻²) activity was drastically reduced.

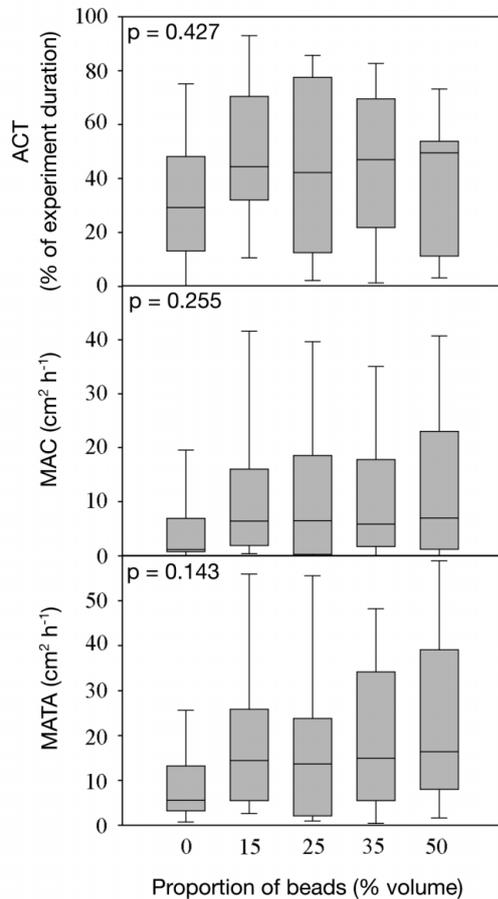


Fig. 8. *Abra ovata*. Box-plots (median, 25 and 75 percentiles) of the activity indices recorded during the sediment dilution experiments. ACT: percentage of time active; MAC: mean activity per individual; MATA: mean activity per time active. See 'Activity monitoring' for further details. p corresponds to the probability of the Kruskal-Wallis ANOVA used to compare activity indices among treatments

For all 3 indices, in *Abra nitida* there was no significant effect of food addition at the 0.7 mg C m⁻² treatment (Fig. 11). All 3 indices significantly increased after food addition for the 1.4, 2.8 and 28.6 mg C m⁻² treatments. Such an increase was not statistically significant for the 5.6 mg C m⁻² addition. Besides changes in activity indices, we also noticed 2 changes in the behaviour of *A. nitida* at the highest food addition. The first one consisted in the occurrence of long periods of activity with the inhalant siphon extended in the water column with no modification of the sediment surface. This pattern was interpreted as reflecting water filtration. The second consisted in the occurrence of short events of very intense activity corresponding to shell displacement. These 2 activity patterns were never recorded in *A. ovata*.

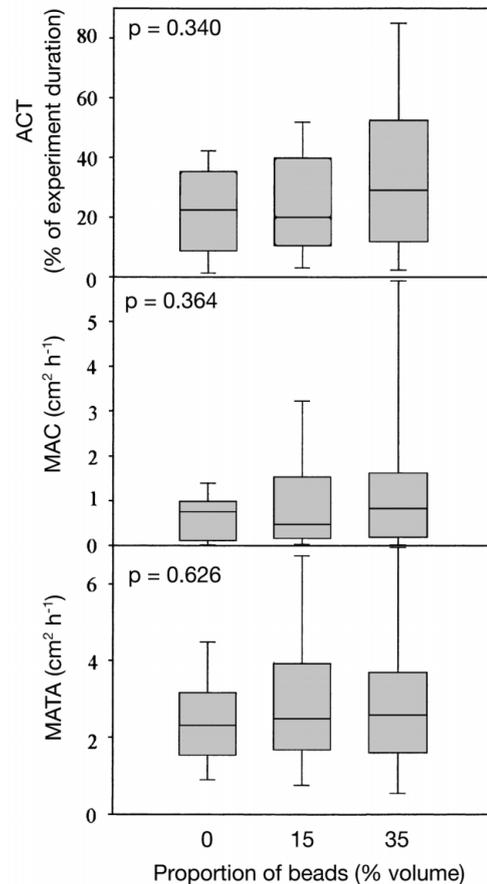
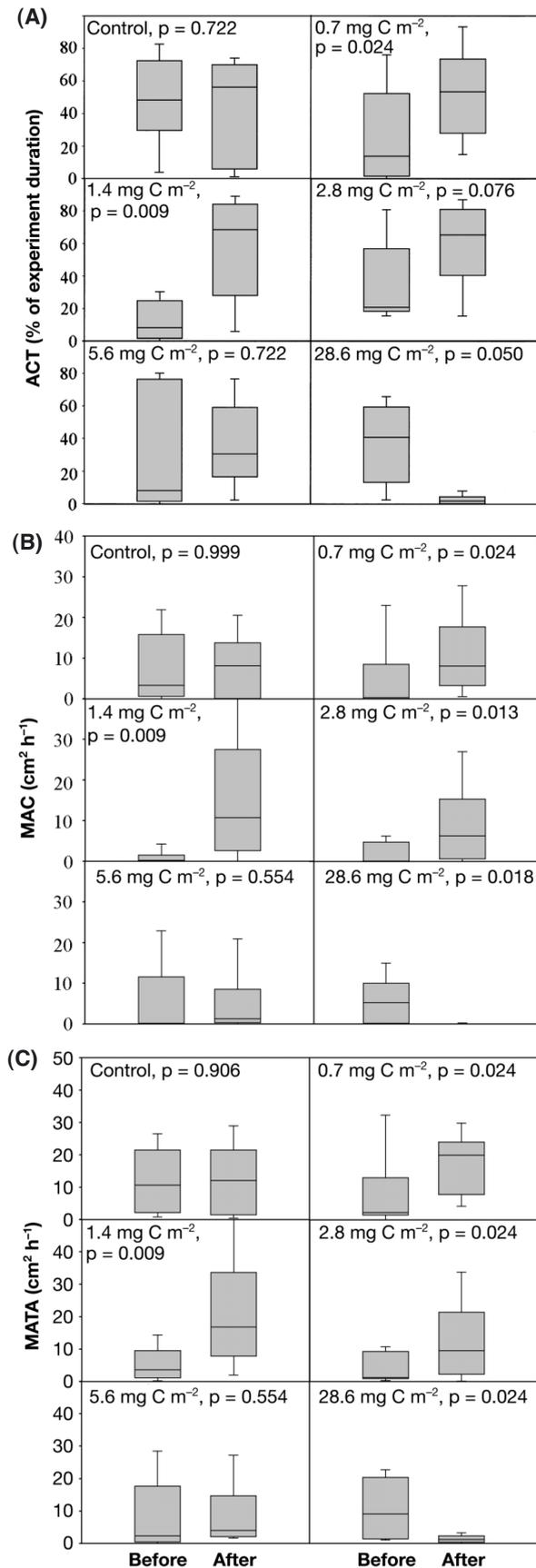


Fig. 9. *Abra nitida*. Box-plots (median, 25 and 75 percentiles) of the activity indices recorded during the sediment dilution experiments. ACT: percentage of time active; MAC: mean activity per individual; MATA: mean activity per time active. See 'Activity monitoring' for further details. p corresponds to the probability of the Kruskal-Wallis ANOVA used to compare activity indices among treatments



DISCUSSION

Differences in feeding behaviour between *Abra ovata* and *A. nitida*

During the present study, *Abra nitida* exhibited a larger variability in feeding behaviour (including suspension-feeding and shell motion) than *A. ovata*, which was almost always surface deposit-feeding. The rationale for the occurrence of suspension-feeding in *A. nitida* relies on the observation of the inhalant siphon extended above the sediment surface for long periods of times. This behaviour was related to suspension-feeding because it mostly occurred immediately following food addition, when part of the added phyto-detritus was still in suspension as indicated by the reduced transparency of the recorded images. The possibility of suspension-feeding in *Abra alba*, which also is considered a deposit feeder, was documented by Rosenberg (1993) based on clearance experiments. Observations from the present paper are based on a much larger data set. It should, however, be stressed that they are derived from visual observations and not from actual clearance measurements. Additional experiments coupling activity monitoring and clearance measurements are needed to establish the occurrence of suspension-feeding in *A. nitida*.

Clear differences were also found in the behaviour of *Abra ovata* and *A. nitida* when they were surface deposit-feeding. In *A. ovata*, the exhalant siphon almost always remained beneath the sediment surface, which was also where fecal pellets were produced. Conversely, *A. nitida* most often extended its exhalant siphon into the water and produced piles of fecal pellets on the sediment surface. We also observed that *A. ovata* extended its inhalant siphon further away from the aperture of the siphonal channel, which was not the case for *A. nitida* when surface deposit-feeding. *A. nitida* is thus deposit-feeding within the sediment, which may be an adaptation to avoid siphon nipping by sediment surface feeding predators. On the other hand, when extending the siphon into the water column during periods of suspension feeding, this may be a trade-off between obtaining fresh phyto-detritus and risk of sub-lethal predation. To our knowledge, there has been no report on siphon nipping in *A. nitida*. Conversely, and based on gut content analy-

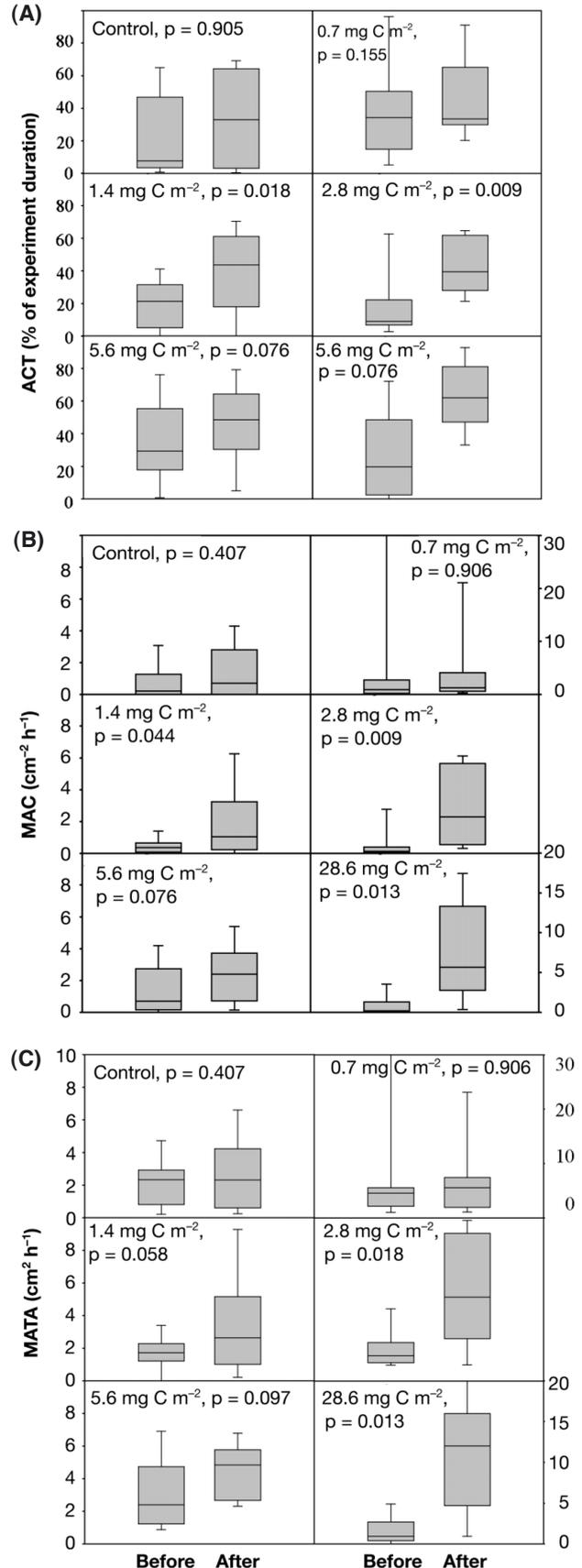
Fig. 10. *Abra ovata*. Box-plots (median, 25 and 75 percentiles) of (A) the percentage of time during which a single bivalve was active (ACT), (B) mean activity per individual (MAC), and (C) mean activity per time active (MATA), recorded before and after food addition. See 'Activity monitoring' for further details. p corresponds to the probability of the Wilcoxon signed-rank test used to compare activity indices before and after food addition

sis, J.Y. Bodiou (pers. comm.) found that the siphons of *A. ovata* may be subject to nipping by juvenile *Solea vulgaris*. Unfortunately no quantitative data are available on the proportion of bivalves affected and their regeneration rates. Our observations also show that *A. ovata* closed the aperture of the siphonal channel before changing its feeding location, whereas *A. nitida* did not.

Wikander (1980b) compared the feeding behaviour in *Abra nitida* and *A. longicallus* based on a limited set of visual observations. He reported that in *A. longicallus*, fecal pellets were deposited beneath the sediment surface in cavities left by the inhalant siphon, whereas they were deposited on the sediment surface by *A. nitida*. These results are in full agreement with ours regarding *A. nitida* (see also Persson & Rosenberg 2003), and further suggest that *A. ovata* and *A. longicallus* behave in a similar way regarding faeces production. Wikander (1980b) also reported the occurrence of large extensions of the inhalant siphon in *A. longicallus*, but he did not detect any differences in siphon extension and closure of the siphonal channel in *A. nitida* and *A. longicallus* when surface deposit-feeding. Results of the present study are based on more observations and on recorded images, which allows for a repeated and precise assessment of the feeding behaviour. The present results show that the inhalant siphon of *A. nitida* always remains restricted to the proximal vicinity of the aperture of the siphonal channel over a wide range of activity levels, as indicated by the results of the 15°C and food addition experiments.

Differences in feeding behaviour also affected the functional responses of the 2 species. MAC is the product of ACT and MATA. The slope of the relationship between MAC and MATA can be used to infer whether bivalves increase their mean feeding intensity by increasing the percentage of time devoted to feeding and/or their feeding intensity. Based on the results of the natural sediment experiments, we found that in *Abra nitida*, the relationship between MAC and MATA was linear, with a slope greater than 1. This suggests that an increase in mean feeding activity mostly results from an increase in feeding intensity. In *A. ovata*, the relationship between MAC and MATA was best described by a 2 parameter exponential to a maximum model. For low ACT, the slope of the regression model

Fig. 11. *Abra nitida*. Box-plots (median, 25 and 75 percentiles) of (A) the percentage of time during which a single bivalve was active (ACT), (B) mean activity per individual (MAC), and (C) mean activity per time active (MATA), recorded before and after food addition. See 'Activity monitoring' for further details. p corresponds to the probability of the Wilcoxon signed-rank test used to compare activity indices before and after food addition



was greater than 1, indicating that the bivalves increase their mean feeding activity mostly by increasing their feeding intensity. For high MAC, the slope of the regression model was smaller than 1, indicating that very active bivalves tend to increase their mean feeding activity by mostly increasing the percentage of time they devote to feeding. Differences in feeding behaviour may account for such a discrepancy between the 2 species. In *A. ovata*, feeding intensity may indeed be limited because the extension of the inhalant siphon is itself limited. In *A. nitida*, the restricted extension of the inhalant siphon resulted in much more frequent changes in the feeding pit as indicated by the spectral analysis of individual activity in surface deposit feeding bivalves. In this species increase in feeding activity thus mostly relies on more frequent switches between feeding pits accounting for the linear relationship between MAC and MATA.

Differences in the feeding behaviour of 2 closely related species such as *Abra ovata* and *A. nitida* underline some of the difficulties in assigning species to separate functional groups. Functional groups have been proposed as a way to deal with biocomplexity by pooling together organisms sharing the same functions (e.g. nutrition ethology and/or bioturbation). Regarding benthic fauna, functional grouping was first applied to feeding (Fauchald & Jumars 1979) and then to sediment reworking (François et al. 1997). In both cases, functional groups have been mostly defined based on size and morphology. Classification of benthic animals into functional groups is a useful ecological tool to generalise animal activity patterns in relation to food availability (Pearson & Rosenberg 1987). The concept needs, however, to be developed further. By showing that feeding behaviour may slightly differ in closely related species, our results suggest that monitoring of feeding activity should be considered as an addition for an improved definition of functional groups in benthic deposit feeders.

Effect of food availability on activity

During the present study, the organic content of natural sediment was manipulated through sediment dilution using glass beads and through food addition using phyto-detritus. In both *Abra ovata* and *A. nitida*, there was no significant effect of food dilution, but a positive effect of food addition, although on different ranges of food concentrations.

Dilution experiments are efficient in manipulating the organic content of the sediment without altering the composition of sedimentary organics (Linton & Taghon 2000), whereas food addition experiments, e.g. with phyto-detritus, are designed to mimic particulate

organic matter inputs corresponding to sedimentation events (Duchêne & Rosenberg 2001). These 2 types of experiments are also associated to different experimental designs. During dilution experiments, treatments are usually applied to different batches of animals, whereas during food addition experiments the same animals are successively submitted to different levels of food concentrations. Therefore, within-treatment variability tends to be lower during food addition than during food dilution experiments. Due to high inter-individual variability in the activity level in *A. ovata* and *A. nitida*, differences in experimental design may thus partly explain the lack of significance of the results of our food dilution experiment.

Based on the results of the food addition experiments, feeding activity was greatest at intermediate sediment organic concentration for *Abra ovata*, whereas feeding activity increased progressively with concentration above a threshold for *A. nitida*. In experiments with the polychaete *Abarenicola pacifica* (Taghon & Greene 1990) feeding rates tended to be maximal at intermediate sediment organic concentrations, whereas in the polychaete *Capitella* sp. I (Linton & Taghon 2000), feeding rates increased progressively with sediment organic concentration and then levelled off. In *A. pacifica* the shape of this relationship is in agreement with that which we found for *A. ovata*. Conversely, the relationship between sediment organic concentrations and feeding rates in *Capitella* sp. I is in agreement with that which we found for *A. nitida*. The occurrence of maximal feeding rates at intermediate sediment organic concentration was predicted by optimal foraging theory for deposit feeders, either due to a limitation of the net energy gain (Phillips 1984) or more probably to a trade-off between absorption efficiency and gut residence time (Taghon & Greene 1990). More recently, Jumars (2000) pointed out the potential effect of the nature of the food, and based on the optimization of absorption rates in several types of chemical reactors, predicted that ingestion rates and food concentrations should only correlate positively for complex foods at low concentrations. During our food addition experiments, *A. ovata* and *A. nitida* were given the same food and nevertheless showed different functional responses.

To our knowledge, the present study is the first attempt to assess the functional response of closely related deposit feeding species inhabiting contrasted environments relative to organic matter availability. Such differences are clear when comparing the organic carbon contents of sediments from the Gullmarsfjord in west Sweden (2.6% DW) and the Lapalme lagoon in the Mediterranean (1.7% DW). Temporal changes in primary productivity also differ between these 2 areas. The spring bloom is much more pro-

nounced and restricted in time in the Gullmarsfjord (Belgrano et al. 1999) than in Mediterranean lagoons (Jarry et al. 1990). Differences in the adaptation of *Abra ovata* and *A. nitida* to their environments may thus account for differences in the functional response of these 2 species. Adaptation to higher sediment organic concentrations may also contribute to explain that the functional response of *A. ovata* is apparently similar to that of another equilibrium species such as *Abarenicola pacifica*, whereas the functional response of *A. nitida* is closer to that of *Capitella* sp. I, an opportunistic species well fitted to respond to organic enrichment (Grémare et al. 1988, 1989). Due to the magnitude and the limited duration of the spring bloom in its habitat in the Gullmarsfjord (Belgrano et al. 1999), one could even argue that *A. nitida* behaves to a certain extent as a species adapted to rely on an abundant food source available for a short period of time only. More generally, differences in the functional responses of *A. ovata* and *A. nitida* underline the difficulty in generalizing ecophysiological results obtained on animals adapted to a particular environment.

Besides changes in the mean values of feeding activity, the results of the present study suggest that change in food availability may also induce qualitative changes in the feeding behaviour. In *A. nitida*, food addition induced important switches in feeding behaviour, such as the onset of suspension-feeding and shell motion. The parametrisation of individual activity constitutes one of the key questions in individual-based models of sediment transport (Boudreau et al. 2001, Choi et al. 2002). In such models, the behaviour of individual animals is cued by the generation of random numbers at each time step. The addition of particles is considered in such models (Choi et al. 2002). So far, this has only consisted of adding particles with characteristics similar to those of the initial sediment. In the future, addition of particles could nevertheless be used to simulate the sedimentation of phytoplanktonic blooms. The present results then suggest that the equations used by Boudreau et al. (2001) to describe the behaviour of deposit feeders should be different before and after a bloom, due to the quantitative and qualitative effects of food availability on feeding.

Acknowledgements. The support of the EU programme Access to Remote Infrastructure to J.C.D. and A.G. is acknowledged together with the help of the staff of the Kristineberg Marine Research Station.

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Editorial responsibility: Kenneth Tenore (Contributing Editor), Solomons, Maryland, USA

*Submitted: February 11, 2003; Accepted: October 3, 2003
Proofs received from author(s): February 4, 2004*