

Marine benthic faunal activity patterns on a sediment surface assessed by video numerical tracking

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ABSTRACT: Most marine benthic macrofaunal species are buried in the sediment but feed on the sediment surface. We measured benthic faunal activity on the sediment surface in 0.25 m² box-cores from a 75 m depth in a Swedish fjord. The techniques used were video numeric tracking and electronic intelligent sensors, where the activity pattern was continuously recorded. During a 4 h recording, 24 % of the examined surface area showed infaunal activity. When phytodetritus was added to the same surfaces, the areas searched by the fauna almost doubled over the next 4 h. Thus, the main part of the sediment surface is most probably covered daily by infaunal activity, particularly when food is available. Arms of *Amphiura filiformis* and *A. chiajei* contributed to 40–80 % of the total surface area covered by faunal activity, which was >15 times that of tentaculate feeding activity of *Melinna cristata*. Time frequency recordings showed that the response of the *Amphiura* species to food supply was strong during the first 25 min, followed by a decline, which probably was related to processing and storage of food in the sediment.

KEY WORDS: *Amphiura* · *Melinna* · Video analysis · Actography · Food supply · Foraging

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INTRODUCTION

Marine sediments harbour a diverse benthic fauna, where bioturbation and feeding activities can be intense and the surficial sediment is repeatedly reworked (Rhoads 1974). Many species are buried in the sediment for protection against predators. To collect food particles at the sediment-water interface they may use tentacles (e.g. polychaetes), siphons (bivalves) or arms (brittle stars). Some of these animals are filter feeders and collect suspended food particles from the water above the bottom (Riisgård & Larsen 2000). Others are deposit feeders that are generally specialised in collecting particles from the sediment surface or within the sediment (Jumars & Wheatcroft 1989). Infaunal species may construct tubes or burrows to facilitate feeding and oxygenation of their microenvironment, or they may simply move through the sediment in a bulldozing mode like sea urchins (Fauchald

& Jumars 1979, Pearson & Rosenberg 1987). Sediment reworking rates have been summarised to be significant in many infaunal species (Diaz & Schaffner 1990). Depth of bioturbation in the sediment varies between habitats and with species composition but can extend down to depths of 20 cm or more (Dauwe et al. 1998).

Benthic species compete for the episodic input of nutritious food, and to be successful they may have to search the sediment surface more or less continuously or have sensors that can detect recently settled organic matter. Despite a high animal activity on the sediment surface, the activity pattern has never been recorded and quantified in a natural sedimentary habitat. In this study we present new information about the activity of benthic animals at the sediment-water interface and their response to food supply. The faunal activity was recorded in 0.25 m² Plexiglas boxes with natural sediment and fauna from a 75 m depth of a Swedish fjord. The techniques used were real-time video tracking and electronic intelligent sensors where the activity pattern was continuously recorded over several hours at a time.

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MATERIAL AND METHODS

Sediment with intact fauna was collected from a 75 m depth (58° 22.7' N, 11° 36.3' E) in the Gullmarsfjord on the Swedish west coast. The sampler was a USNEL spade-corer (700 kg) (Rosfelder & Marshall 1967), where transparent plexiglas boxes (47 × 47 cm, height 39 cm) were installed inside the corer before each deployment. Ten boxes were collected on 6 March 2000. Each box was closed on the bottom on board the boat and transported to Kristineberg Marine Research Station nearby. The sediment was ~30 cm high with ~15 cm of seawater above the sediment. The boxes were put in a room with a constant temperature of 8°C, and each box was continuously flushed with ~2 l filtered (1 mm meshes) seawater min⁻¹ of 34 psu, i.e., similar to natural conditions. The animals in the boxes were acclimated 3 wk until the start of the experiment on 27 March. The macrofaunal (>1 mm) composition at the sampling site was analysed by taking three 0.1 m² Smith-McIntyre grab samples in April 2000.

Samples of the top 0 to 1 cm of the sediment in 3 boxes (3 replicates in each) were freeze-dried, and nitrogen and total carbon were analysed with an NA 1500 NC analyser (Fisons, Milano). Food was added to 3 of the boxes as marine microalgae cryopaste (*Chaetoceros gracilis* and *C. muellari*, cryopreserved). A mix of 1 ml algae paste and 1 ml seawater was spread evenly on the sediment surface covered by the video system by using a pipette. As for the sediment, the algae paste was analysed for nitrogen and carbon and contained on average (±SE) 5.2 ± 0.06% nitrogen and 32.6 ± 1.8% carbon.

The activity of the benthic fauna was recorded by means of an actographic device composed of an intelligent Coupled Charged Device (CCD) camera loaded with image analysis programmes in permanent memory, connected to a desk computer (Duchêne & Nozais 1994, Nozais et al. 1997, Jordana et al. 2000). This computer was running an interface programme to store the numeric results sent by the sensor. The sensor was placed at a 60 cm distance above the sediment and recorded the activity of a 153 × 117 mm surface. A set of data was collected every 3 s. Real-time analysis resulted in a batch of numeric objects describing the movements detected on the surface, which were sent to the desktop computer and stored. Connecting a video monitor on a dedicated output of the sensor allowed us to visualise the recorded sediment surface. Alteration between original video images and computed numeric objects allowed us to visually estimate the sediment area affected by movement. Collection of image files in a Joint Photography Experts Group (JPEG) format allowed comparison of the changes of activities with location, and identification, when pos-

sible, of the species corresponding to the recorded activities. The sensor had a resolution of 744 × 568 pixels, corresponding to a resolution of 0.2 mm on the sediment surface when the 15 mm lens is used. This is supposed to be sufficient to detect most of the macrofaunal activity. The cumulative total area covered by the active animals was measured between 7 and 15 h in 10 replicate boxes. The programme scanned every image of the files and every time a new activity was detected on the surface it was graphically added to give the total sediment surface activity. When an activity on a given position was detected several times it was recorded as only 1 point of activity. This quantified newly exploited surface areas over time. This gave an asymptotic curve representative of the actual infauna activity at the water-sediment interface.

Numeric data were also analysed to separate activities of different animals. This resulted in numeric tracks over time for species easily recognisable at the sediment surface. When it was impossible to attribute an activity to a species, values were added to an 'unknown' column. Species activity was then reconstructed by adding every specific individual activity in every image. This allowed us to obtain the activity of a target species.

RESULTS

The 10 dominant benthic species collected in April 2000 in the Gullmarsfjord are listed in Table 1. The total number of species in the 3 grab samples was 53. The composition at these samples, collected of the same site, should have corresponded approximately to that in the boxes used in the activity analysis. Most of

Table 1. The 10 dominant benthic species found at 75 m in the Gullmarsfjord in April 2000. Biomass is in grams (ethanol weight). Numbers and biomass are per 0.1 m² (±SE). Feeding mode is indicated as surface deposit feeding (SD), subsurface deposit feeding (SSD) and suspension feeding (SF)

Species	Abundance	Biomass	Feeding type
<i>Abra nitida</i>	29 ± 5.4	1.3 ± 0.1	SD
<i>Amphiura filiformis</i>	24 ± 6.6	2.9 ± 1.2	SD/SF
<i>Mysella bidentata</i>	19 ± 2.7	0.1 ± 0.0	SF
<i>Heteromasus filiformis</i>	19 ± 6.2	0.1 ± 0.0	SSD
<i>Spiophanes kroeyeri</i>	18 ± 2.8	0.4 ± 0.0	SD
<i>Scalibregma inflatum</i>	16 ± 6.8	0.7 ± 0.3	SSD
<i>Thyasira equalis</i>	14 ± 5.4	0.2 ± 0.2	SSD
<i>Myriochele oculata</i>	12 ± 4.3	1.2 ± 0.1	SF
<i>Melinna cristata</i>	11 ± 3.8	2.0 ± 0.2	SD
<i>Anobothrus gracilis</i>	10 ± 3.7	0.4 ± 0.2	SD
Total community	266 ± 48	29.0 ± 4.6	

the species were either surface deposit feeders or subsurface deposit feeders. One of the dominant species, *Amphiura filiformis*, can be a suspension feeder (Loo et al. 1996) but can also feed efficiently on the sediment surface (Rosenberg et al. 1997). The mean number of *A. chiajei* per 0.1 m² was 9 ± 1.7.

On visual observations of the boxes we frequently saw arms of the brittle stars *Amphiura filiformis* and *A. chiajei* sweeping the sediment surface, the polychaete *Melinna cristata* showing its tentacles outside the tube at irregular intervals, episodic movements of the polychaete *Ophiodromus flexuosus* on the surface and at times disappearing into burrows, and the bivalve *Chlamys septemradiata* (= *Pseudamussium septemradiatum*) filtering water while attached to different objects, e.g. tubes of *Euchone papillosa*, which was filter-feeding with its crown of tentacles. The 2 *Amphiura* species were recorded in the grab samples, but their arms could not be separated into species in the images. The only larger species with a mean biomass >1 g wet weight per 0.1 m², in addition to those listed in Table 1, were the heart urchins *Brissopsis lyrifera*, *Echinocardium cordatum* and *E. flavescens*. These sea urchins were occasionally seen bulldozing within the sediment in the boxes. The contents of nitrogen and total carbon in the sediment surface were 0.3 ± 0.004 and 4.0 ± 0.15% of the dry weight, respectively.

Total benthic activity

A view of a sediment surface is shown in Fig. 1A. Most of the tubes belonged to *Melinna cristata*, but all were not active or inhabited. Some arms of *Amphiura filiformis* or *A. chiajei* were also seen in a horizontal position on the sediment surface. The area where activity was registered over 7 h is indicated in Fig. 1B. After 4 h it covered 34% of the total area. After 7 h it reached 41% of that surface. In longer recordings (4 replicates, 15 h) activity covered 54.4 ± 7.4% (SE) of the total area. Most of the movements were caused by *Amphiura* arms; we observed 8 arms in Fig. 1B. The activity of *M. cristata* covered a much smaller area close to the tube opening as indicated in the upper right corner of the image. The number of active *M. cristata* was 6. After food was added to the same patch of sediment, the area of animal activity increased significantly (Fig. 1C). Now

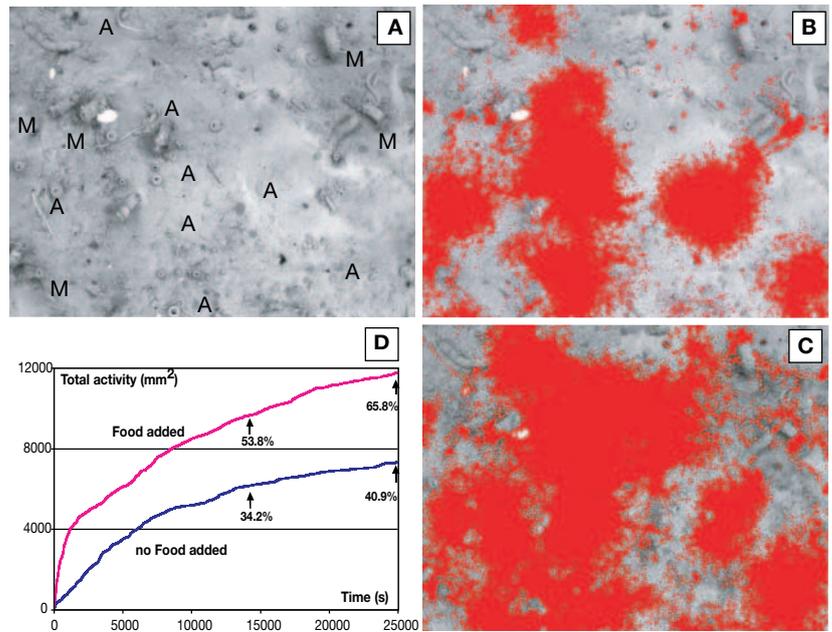


Fig. 1. Measurements of total activity at sediment-water interface. (A) Image (153 × 117 mm) of the sediment surface. A: *Amphiura* spp.; M: *Melinna cristata*. (B) Records of activity during 7 h before food addition (red surface shows areas of benthic activity). (C) Records of activity after food addition on the sediment surface. (D) Records of the total activity in mm² on the sediment without food and after food addition. Activity on sediment surface was recorded every 3 s. Arrows indicate values for 4 and 7 h

the activity covered 54% of the total area after 4 h and 66% after 7 h. No new active animals were detected. The response of the animals to food supply was immediate (Fig. 1D). The cumulative area of sediment sur-

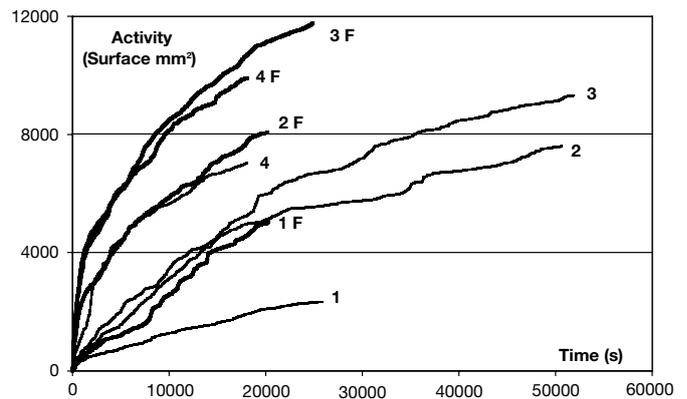


Fig. 2. Animal activity on sediment surface (in mm²) with and without food in 4 different box-cores. The same area (153 × 117 mm) of the sediment was observed before and after food was supplied (F). Number indicates replicate. Addition of food was followed immediately by a significant increase in total activity

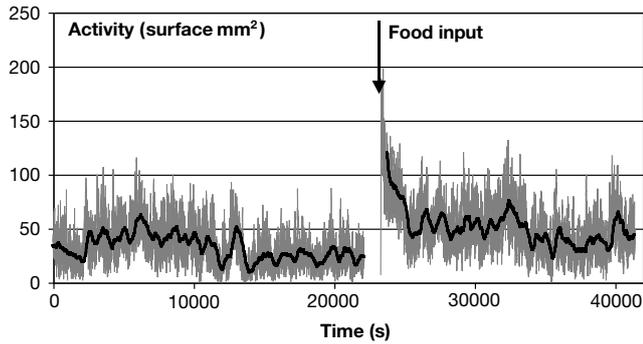


Fig. 3. Time frequency activity pattern of total fauna on the sediment surface continuously recorded for about 7 h before and 6 h after food was supplied (arrow) to the same observed area. The moving average on 144 images is shown

face covered by the animal activity was much higher with food than without and the difference increased over the 7 h of recording.

The cumulative activity pattern before and after food addition is presented in Fig. 2. The activity was different between replicates, but the response to food was rapid in all experiments. Four hours after food was added, the cumulative area searched was 1.93 ± 0.57 (SE) times greater than for the same time period without food. In total, 24.0 ± 12.4 to 41.5 ± 14.2 % of the total observed area was covered during this time by animal activity. Naturally, the magnitude of activity was dependent on numbers and species composition in the observed area.

Species living beneath the sediment surface and occasionally appearing at the sediment interface were detected as unknown patterns and added to the general background faunal activity of the sediment studied. Patterns of activity created by mobile species such as *Ophiodromus flexuosus* were detected and recorded. Replicate 1 (Fig. 2) had a low density with only 2 arms of *Amphiura* spp. Nine *M. cristata* were active. This gave, however, a rather low total activity. When food was added there was no steep increase during the first minutes. Replicate 2 was another benthic assemblage, where 7 *Amphiura* spp. arms provided a high activity (24 % of total activity without and 39 % with food addition after 4 h). A terebellid worm extended its tentacles into the site of observation during the period without food. Three *O. flexuosus* were moving across the surface. When food was added, a rapid increase was noted in *Amphiura* activity and a reduction in the extension of the terebellid tentacles. The activity of *O. flexuosus* was low with only 2 tracks visible. Replicate 3 was a mixture of active *Amphiura* spp. and *M. cristata* with a high activity (24 % of total activity without and 54 % with food addition after 4 h). Food addition induced a steep initial increase related to *Amphiura* spp. activity. Replicate 4 was characterised by a large number of *Amphiura* spp. arms (16 detected) providing a large activity both without and with food (39 % of total activity without and 50 % with food addition after 4 h, with a significant effect, $p < 0.001$). Four *M. cristata* tubes were active. A fast response to food addition resulted in a steep initial part of the curve. This was

Table 2. Relative hourly activities as a percentage of total activity of *Amphiura filiformis* and *A. chiajei* combined and of *Melinna cristata* before and after food addition. Activity during the first 25 min after food was supplied is also indicated. Mean column gives the mean value of the 1200 activity records collected every hour in mm^2

Time (h)	<i>Amphiura filiformis</i>			<i>Melinna cristata</i>			Total activity	
	Mean	SD	%	Mean	SD	%	Mean	SD
-7	9.04	10.74	70.7	0.19	0.92	1.5	12.79	11.45
-6	18.69	15.50	78.6	0.14	0.26	0.6	23.79	16.43
-5	17.92	13.18	80.8	0.21	0.64	0.9	22.17	14.59
-4	8.81	11.39	76.9	0.15	0.33	1.3	11.46	12.88
-3	2.80	4.45	40.7	0.33	0.52	4.7	6.88	5.72
-2	3.09	4.58	47.7	0.40	0.51	6.2	6.48	5.85
-1	5.65	5.30	79.6	0.27	0.34	3.8	7.09	5.56
Mean	9.43		67.9	0.24		2.7	12.95	
Food addition								
25 min	34.05	13.95	83.0	0.52	1.22	1.3	41.03	13.87
1	21.99	15.03	78.9	0.59	1.16	2.1	27.87	16.08
2	12.35	8.24	73.6	0.30	1.34	1.8	16.76	8.81
3	11.71	8.03	69.4	0.33	0.95	1.9	16.86	9.16
4	7.31	6.57	67.9	0.33	1.35	3.0	10.77	7.41
5	7.36	7.19	54.0	0.32	1.90	2.3	13.63	9.69
6	4.91	2.51	63.3	0.39	0.78	5.0	7.75	2.84
Mean	10.94		67.9	0.38		2.7	15.61	

related to *Amphiura* spp. food gathering responsible for up to 90% of the total activity in the first minutes.

Analysis of time frequency activity of all animals on the sediment surface is shown in Fig. 3. Before food was added, the activity was variable with some periodic activity, which probably mirrors periods of search for food and periods of rest. When food was supplied, the searched area initially increased by about 5 times, and a higher activity ($p < 0.001$) was maintained for at least 60 min.

Activity of *Amphiura* spp. and *Melinna cristata*

From the appearances in the images, it was possible to quantify the activities of *Amphiura filiformis* and *A. chiajei* combined, and of *Melinna cristata*. The relative activities, which are expressed as the percentage of total activity, are presented as hourly means in Table 2. The activity of the *Amphiura* species contributed 40 to 80% of total activity. The activity measured as area covered was at least 15 times greater for *Amphiura* spp. than for *M. cristata*. (Table 2).

Graphs of the cumulative activity and time frequency activity of *Amphiura* spp. and *Melinna cristata* are shown in Fig. 4. The pattern of time frequency activity of the *Amphiura* species (Fig. 4B) was similar to that of the total activity. The response to food supply was very strong during the first 25 min contributing 83% of the total (Table 2). After that a steep decrease was recorded followed by a secondary increase. The activity of *M. cristata* increased after food was supplied (Fig. 4C), but this was not as rapid as for *Amphiura* spp. The activity pattern was erratic compared with that of *Amphiura* spp. When several individual *M. cristata* were feeding simultaneously it showed up as a high peak of short duration extending for 3 to 6 s.

Besides *Amphiura* spp. and *Melinna cristata* other animals were also active on the sediment surface, but some of these were not identified in the images. Among those species excluded from measurements of individual activity were *Ophiodromus flexuosus* (a species that often came in and out of the video field), *Abra nitida* and *Spiophanes kroeyeri* (where activity was due to defecation as seen in the video recordings).

DISCUSSION

In this study we introduced a new technique to measure activity of benthic animals on a sediment surface. In the experimental set-up, we used box-cores in a laboratory system that allows most benthic animals to survive for several months (Berge et al. 1986). Their activity is assumed to be close to that in nature as they were

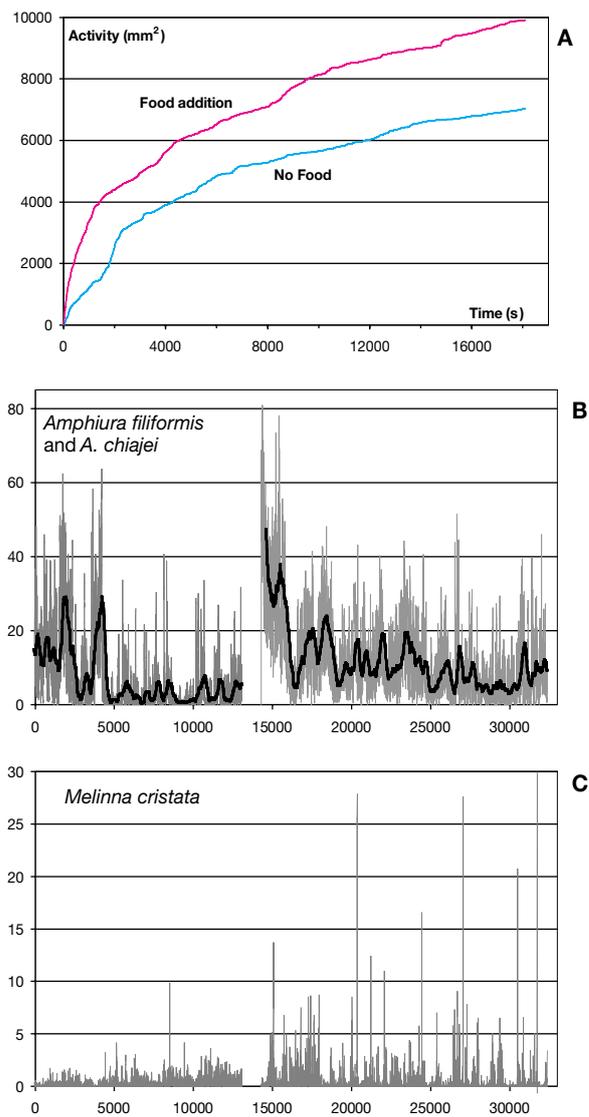


Fig. 4. (A) Total cumulative activity and (B) time frequency activity of *Amphiura filiformis* and *A. chiajei* and (C) of *Melinna cristata* on a sediment surface before and after food addition

collected together with the sediment, and salinity and water temperature were similar to that of their natural habitat. The electronic intelligent sensors detected movements of particles or of animal appendages at distances of only 0.2 mm. This means that most movements of macrofauna and possibly of meiofauna would be recorded. The records included digitised pictures of the sediment. This allowed us to detect changes in the position of a particular individual. However, the activity of subsurface deposit feeders at intervals also shows signals at the surface. Among the dominants in the studied community, only *Scalibregma inflatum* might have had a high activity in the sediment. The sea

urchins contributed negligibly to the activity as they rarely appeared in the area where recordings were made. Thus, the main activity recorded in this study must have been due to animals moving on the sediment surface. As the technique records only the sediment surface, the activity of several non-observed species inside the sediment was underestimated.

The curves of total activity presented in Fig. 2 are saturation-like curves. They reached an asymptote, and combined to a spatial expansion rate that is specific of the density and activity on the observed sediment. Over time some animals are likely to change their position in the sediment to be able to explore other parts of the sediment. Consequently, the curve would not reach an asymptote, but rather increase slowly as individual animals move inside the sediment. This movement was visible in the longer recordings: on a sediment without food addition the activity covered an average of 41% of the total surface after 7 h and 54% after 15 h. Species living in tubes, such as *Melinna cristata*, remained in their position. In contrast, motile species such as *Bryssopsis lyrifera* and *Amphiura filiformis* moved in slow motion. When the activity curve becomes rather linear, its slope is related to the number of animals exploring new sections of the sediment. A dynamic survey of the sediment must take those moving phases into consideration. The continuous numeric recording with records of an image from time to time allows control of spatial position of the animals as well as a time frequency analysis of the activity patterns. Thus, a minimum time is required to get information on the dynamics of the sediment analysed. This may be appreciated by observation of the dynamics of the response of the benthic assemblage. In this study a time of 4 h was appropriate to obtain good estimates of activity, which was selected after 5 trials with 15 h recordings.

Records of the activity show that there was an overlap of the areas exploited by some species. The activity of benthic animals may be a result of search for food or territorial behaviour (Levin 1981). In the present study it was shown that part of the sediment surface was continuously searched even when no or little particulate food settled on the bottom. This was visible from individual activity patterns extracted from the cumulated signal. Competition evolves when 2 species seek the same food resource, especially if food is limited. Thus, species try to spread out to optimise feeding conditions, which have been shown for *Amphiura filiformis* (Rosenberg et al. 1997). This is also illustrated for *Amphiura* spp. in this study (Fig. 1B), where their arms searched the bottom in a circle with the arms protruding from the sediment in the centre. *A. filiformis* seems to have 2 arms active at the sediment surface (Loo et al. 1996). Given that *A. filiformis* was about 2.7 times

more abundant than *A. chiajei*, most of their combined activity can probably be attributed to *A. filiformis*. The presence of *Melinna cristata* tubes may be a hindrance for that circular activity, as shown on the left side of Fig. 1B close to the white shell. When animals are closely situated, they may disturb each other by antagonistic behaviour. Intraspecific aggressive behaviour has been shown for, e.g., the spionid *Pseudopolydora paucibranchiata* (Levin 1981) and for *A. filiformis* (Rosenberg et al. 1997). Such disturbance may induce changed activity patterns both within and between species.

The water supplying the experiments was pumped from a 35 m depth through 1 mm filters, which probably resulted in negligible particulate food in the food supply. When food was added to the box-cores, animal activity was concentrated in the same areas that were searched before. This activity pattern suggests that it may be an advantage to be active when food suddenly appears on the sediment. Particularly the *Amphiura* species were active, and when food appeared they cleared the surface from the visible green phytodetritus within minutes. As seen in Fig. 4 and Table 2, *Amphiura* spp. were very active for about 25 min after food had been added, but after that period the activity declined to a low level. This decline in activity was lower than the total activity (Fig. 3), indicating that species other than *Amphiura* spp. were active at that time. The behaviour of the *Amphiura* species suggests that they remove food from the surface that cannot be ingested immediately and probably process that food in the sediment. Thus, that excess food may be stored within the sediment for later use. Food detection was sometimes followed by displacement of the burrow openings to improve food collection, which was observed in the video recordings. A similar behaviour of subsurface feeders to drag down food from the surface has been reported by Blair (1996) and Levin et al. (1997). *Melinna cristata* did not respond immediately to the food supply and can probably not record a sudden change in food availability. However, when the food was found, the feeding activity increased and was maintained at a level higher than before food was added.

The mean sediment surface area covered by infaunal activity over 4 h recordings was 24% and when food was added 41% (Fig. 2). Thus, the benthic animals were active over a large area for a few hours only. Many of the species recorded here have been classified as sessile or weakly mobile. However, the probably most active species in this study, *Amphiura filiformis*, has been shown to be able to move more or less continuously within the sediment (Rosenberg et al. 1997). Thus, the areas where no activity was recorded in this study would most probably have shown animal

activity within the next hours, particularly if food were still available. Consequently, the length of recording animal activity is crucial for the results. In benthic communities with a species composition similar to the one studied here, it is likely that most of the sediment surface may be used for animal activity every 24 h and most parts much more frequently.

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