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Suspension-feeding Activity of a Dense *Ophiothrix fragilis* (Abildgaard) Population at the Water–Sediment Interface: Time Coupling of Food Availability and Feeding Behaviour of the Species

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Ophiothrix fragilis is a suspension-feeder which forms dense aggregations (up to 2000 individuals m^{-2}) in the Dover Strait. Its optimal suspension-feeding activity is expressed when currents are less than 20 cm s^{-1}. Thus, the duration of this behaviour over a tidal cycle depends on the tidal velocity, and can be very short during spring tides.

During neap tides, suspension-feeding is almost continuous but the flux of nutrients (phytoplankton, organic carbon and nitrogen) remains low because current increases slowly after slack water, and resuspension phenomena do not occur. In contrast, during spring tides, the current speed rapidly increases and induces an important resuspension of particles. Thus, the flux of nutrients is very important during the short duration of suspension-feeding of the *O. fragilis* population. Minimum gut contents were observed 3 h before slack current and maximum gut contents were observed about 1 h after slack water.

Introduction

The Dover Strait (Figure 1) is subjected to strong tidal currents which determine the distribution of benthic communities (Prygiel *et al.*, 1988). These alternating and long-shore currents attain velocities of more than 1·5 m s^{-1} during an average spring tide (S.H.O.M., 1968), limit the diffusion phenomena and keep terrigenous inputs close to the coast (Brylinski *et al.*, 1984). These tidal currents combined with other forcings, such as winds, generate an important average water residual drift from the English Channel to the North Sea which has been estimated at 5 km day^{-1} (Pingree & Maddock, 1977), i.e. a flow through the Dover Strait estimated between 87 000 m^3 s^{-1} (Prandle, 1993) and 114 000 m^3 s^{-1} (Salomon *et al.*, 1993).

The ‘ pebbles with sessile epifauna ’ community colonizes the area with highest tidal current (Prygiel *et al.*, 1988). Typically, the biomass of the community is higher close to

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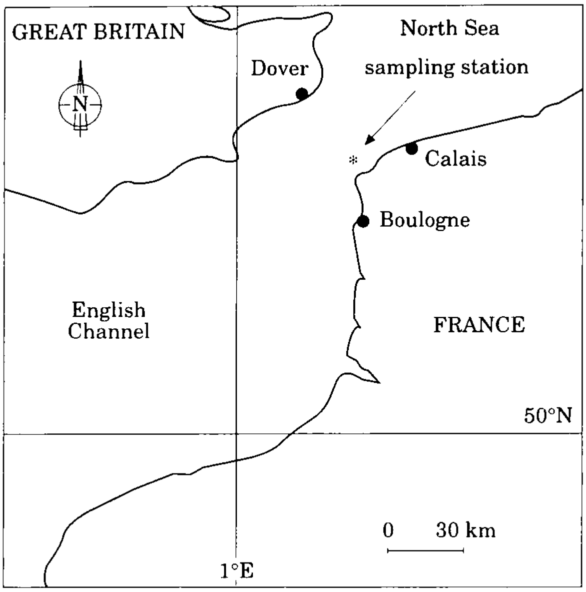

Figure 1. Location of the sampling station.

shore than offshore and that is particularly the case of suspension-feeders. The ophiuroid *Ophiothrix fragilis* is the main species of the coastal part of the community: its mean density is about 1500 individuals m $^{-2}$ and its average biomass is 210 g m $^{-2}$ (ash-free dry weight) (Davoult, 1989).

The suspension-feeding behaviour of *O. fragilis* (Vevers, 1952; Cabioch, 1968; Warner, 1971) and its method of catching food (Warner & Woodley, 1975) have already been described. The relationship between the location and density of these ophiuroids and the hydrological characteristics is still not well known. Direct interception is the most common particle capture mechanism among marine suspension-feeders (Rubenstein & Koehl, 1977) and is commonly used by ophiuroids (LaBarbera, 1984) and crinoids (Meyer, 1973). Previous studies showed seasonal changes in the diet of ophiuroids and crinoids but phytoplankton appears to be the main part of the diet (Rutman & Fishelson, 1969; Warner & Woodley, 1975). Meyer (1973) suggested that population densities may be related to the primary productivity of the area.

Available data which describe the hydrological gradient from the coast to the offshore in the Dover Strait, deal with the water column between the surface and about 1 m above the sea floor (Brylinski *et al.*, 1984; Quisthoudt, 1987; Quisthoudt *et al.*, 1987). Several authors (e.g. Smaal *et al.*, 1986; Muschenheim, 1987; Fréchette *et al.*, 1989) have demonstrated that significant variations of seston occur near the sediment surface. Off Cap Gris-Nez, the hydrological gradient is very pronounced: coastal and offshore waters are well individualized and separated by a mixing area (Quisthoudt *et al.*, 1987). Water–sediment interface characteristics (resuspension, tidal currents and turbulence, nutrient concentrations) which directly influence benthic suspension-feeding (Fegley *et al.*, 1992) have so far not been dealt with.

In spite of the great variability of environmental conditions, the *O. fragilis* population has remained stable, i.e. always dense (>1000 individuals m $^{-2}$) and with a precise and

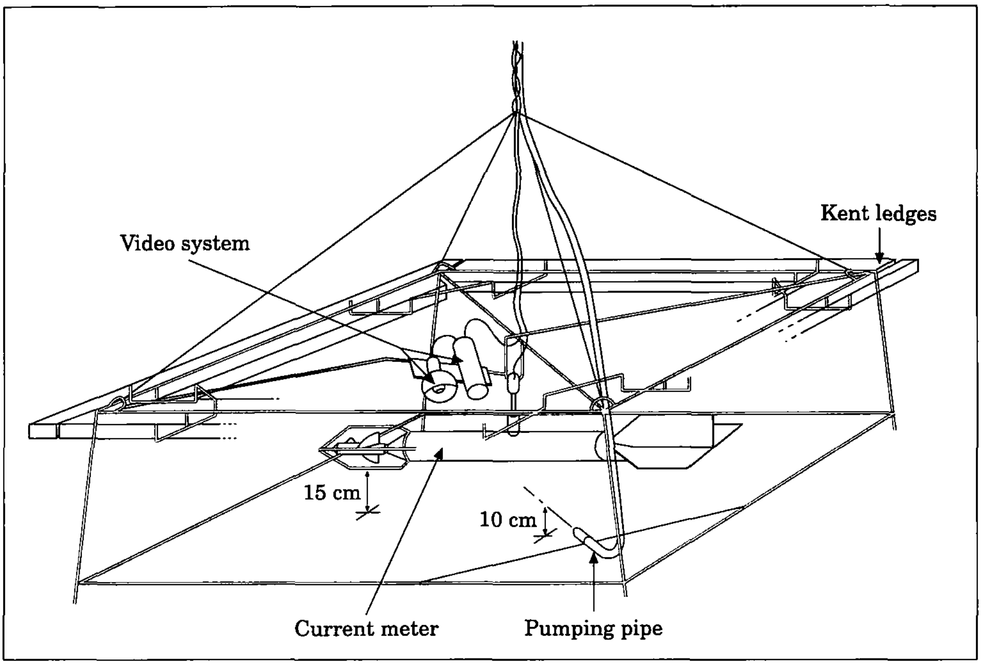

Figure 2. Sampling system.

unchanged location for several years (Cabioch & Glaçon, 1975; Gounin, 1993). In this study, the relationship between near bottom hydrological conditions, food availability, the suspension-feeding activity and gut content of *O. fragilis*, will be examined and discussed.

Materials and methods

Observations were made and samples collected from the area of highest *O. fragilis* density (Figure 1). The water depth of the study site was 36 m.

The system used (Figure 2) allowed water sampling between 10–15 cm from the sea bottom. Current speed was measured with a Braystoke BFM008 flowmeter located about 15 cm from the sea bottom. An Osprey video camera (light sensitivity 5×10^{-4}lux) enabled checking the quality of samples and monitoring for artifacts (e.g. picking up suspension caused by the movement of the system). It also enabled checking of the exact time of slack current and observing changes in behaviour of the ophiuroid population.

Parameters monitored during this study include turbidity, salinity, suspended matter (SM), particulate organic carbon and nitrogen (POC, PON) and chlorophyll *a* (Chl. *a*). These parameters provide information on the food quality and concentration available for suspension-feeders and allowed estimation of the flux of nutrients according to visual observations or measurements of current speed variations.

Turbidity and salinity were measured respectively with a nephelometer and a Beckman salinometer. Suspended matter was weighed after filtering 1 l of seawater through a Whatman GF/C filter (two replicates). A CHN analyser (Carlo Erba 1106) was used to measure POC and PON. Both POC and PON were decarbonated through

Current speed (cm s^{-1})	*Ophiothrix fragilis* behaviour	Symbol used in figures
Speed ≤ 20	 Typical suspension-feeding behaviour	Solid plot
20 < Speed < 30	 Changing behaviour	Striped plot
30 ≤ Speed	 No suspension-feeding behaviour	Open plot

Figure 3. Variations of the suspension-feeding behaviour of *Ophiothrix fragilis* in relation to current speed.

concentrated hydrochloric acid (two replicates). The Chl. *a* concentration (two replicates) was obtained by acetone extraction and spectrophotometric measurement (Scor-Unesco, 1966) after filtering 1 l of seawater. Standard deviations were generally very low: only the higher values are indicated on the figures.

Twenty adult ophiuroids (8 mm<disc diameter<10 mm) were sampled at different times of the tidal cycle with a Van Veen grab and immediately fixed in Carnoy liquid. After dissection, gut contents were drawn off with a pipette, settled on Whatman GF/C filters, weighed and analysed (POC, PON).

During the dissection, an arbitrary scale was established to roughly evaluate the gut content:

0: Empty or nearly empty gut;
1: Gut with a thick spread out film;
2: Full gut (thick spread out film, occurrence of several food boluses and/or diatoms).

Results

Suspension-feeding behaviour

The relationship between suspension-feeding behaviour of *O. fragilis* and current speed is indicated in Figure 3. When current was less than 20 cm s^{-1}, *O. fragilis* generally raised two or three arms (up to four), orienting them vertically into the oncoming current. At slack water, ophiuroids moved and seemed to seek the water movement by raising their arms alternately. As current speed increased (between 20–30 cm s^{-1}), the number of raised arms decreased as described by Cabioch (1968) and Warner (1971). When current speed was more than 30 cm s^{-1}, no raised arms could be seen and individuals remained motionless.

The duration of the suspension-feeding behaviour of *O. fragilis* changed with tidal conditions. Video observations showed that suspension-feeding activity was almost continuous during neap tides (tidal height=4·75 m, Figure 4), taking place for about 86% of the tidal cycle. It only stopped when current speed was maximum. When tidal strength increased (tidal height=6·30 m, Figure 4), the duration of this activity was shorter, only for about 37% of the time.

After slack water, the current speed increased more rapidly in spring tides than in neap tides (Figure 5), and resulted in a shorter optimal feeding period. In the two observations, suspension-feeding behaviour occurred up to 28 cm s^{-1}, but this behaviour continued for about 95 and 70 min after the slack current in spring tides and neap tides, respectively.

Food availability

Hydrological characteristics near the sea-floor were very different during neap tides and medium or spring tides.

During neap tides (tidal height=3·20 m, Figure 6), most of the parameters were close to their minimum around slack water. Little variation occurred during the suspension-feeding activity of *O. fragilis* (values given as mean ± SD, SM=28·3 ± 4·2 mg l^{-1}; Chl. *a*=2·1 ± 0·4 μg l^{-1}; POC=711 ± 216 μg l^{-1}; PON=95 ± 32 μg l^{-1}). Results obtained during another neap tide (Figure 4) also indicated few variations of any parameters except one unexplained value of POC (SM=10·0 ± 3·6 mg l^{-1}; Chl. *a*=1·3 ± 0·2 μg l^{-1}; POC=224 ± 94 μg l^{-1}; PON=58 ± 36 μg l^{-1}). In this case, the slack-water period did not always correspond with a minimum in turbidity. There was little particle resuspension when current speed increased. Variations of suspended matter, POC and PON did not occur simultaneously and could not be related to the tidal cycle.

When tidal height was greater (Figure 4), a turbidity minimum occurred at slack water. Particle resuspension was noticeable at the beginning of the flood current, but not at the beginning of the ebb current. This increase of suspended matter occurred while the *O. fragilis* population was still showing typical suspension-feeding behaviour. Other measurements (Gounin, 1993) made during a tidal cycle with higher intensity (tidal height=6·40 m) confirmed the resuspension at the beginning of the flood tide current (turbidity 3–5 times higher than before). Data for POC, PON and Chl. *a* showed that suspended matter was made up of a large proportion of organic matter and phytoplankton, and thus was potential food for *O. fragilis*. So, during the flood current, food availability was greater during the suspension-feeding activity of *O. fragilis* (SM=74·2 ± 130·9 mg l^{-1}; Chl. *a*=5·2 ± 6·0 μg l^{-1}; POC=2648 ± 3194 μg l^{-1}; PON=162 ± 131 μg l^{-1}) than during its non-feeding activity (SM=21·4 ± 5·2 mg l^{-1}; Chl. *a*=3·3 ± 0·9 μg l^{-1}; POC=1685 ± 455 μg l^{-1}; PON=113 ± 39 μg l^{-1}).

Few variations of salinity (S) were measured during this tidal cycle (S=34·64 ± 0·04), which indicated that the water mass near the sea bottom was homogeneous. So, fluctuations detected in the evolution of the different parameters (Figure 4) were simply a consequence of a vertical change in the dynamic balance of particles in the same water mass (sedimentation, turbulence, resuspension).

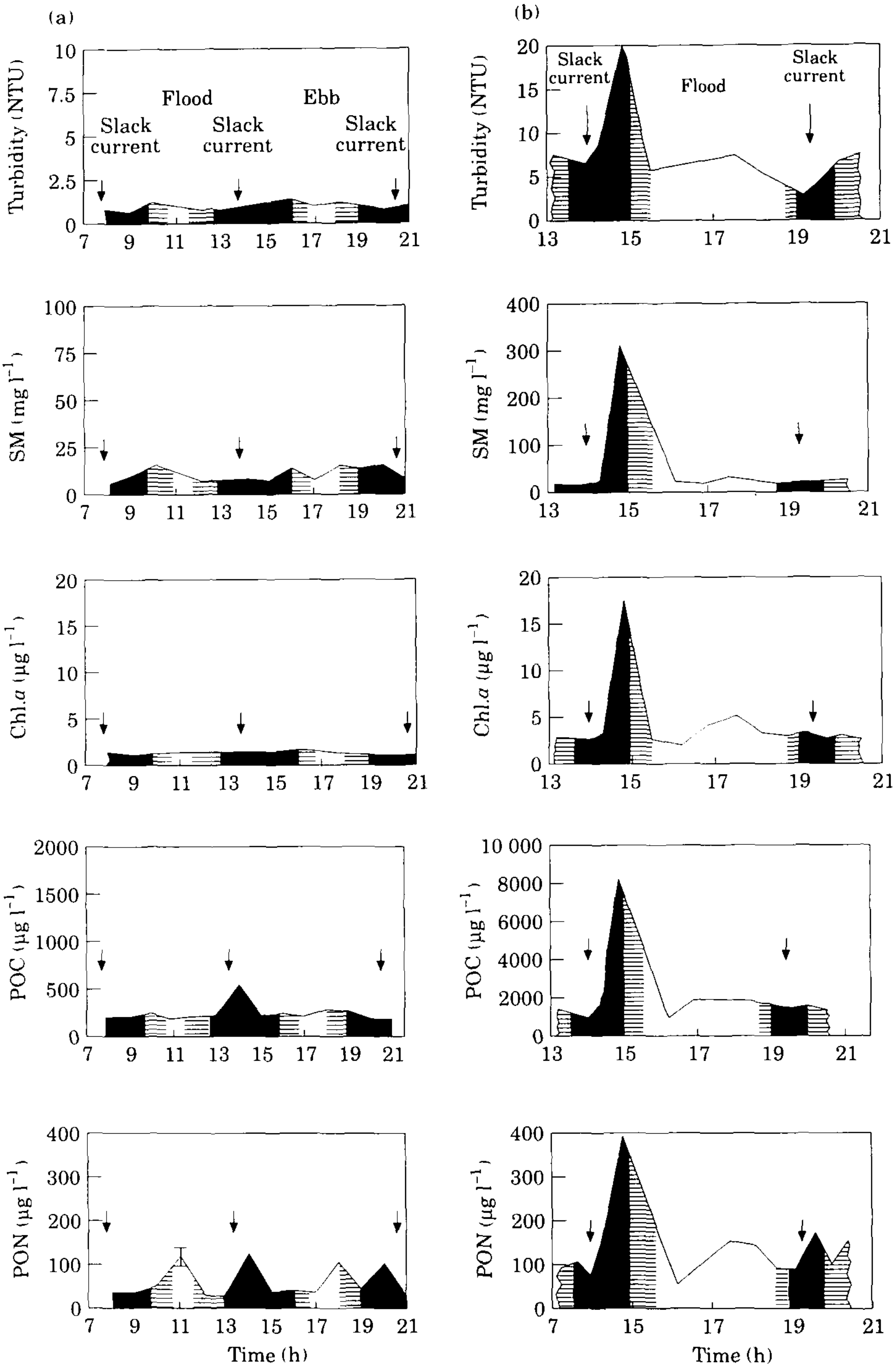

Figure 4. Temporal variations of turbidity, suspended matter (SM), chlorophyll *a* (Chl. *a*), particulate organic carbon (POC) and nitrogen (PON) during (a) a neap tide (15 June 1989, tidal height=4·75 m and (b) a spring tide (25 May 1989, tidal height=6·30 m) in relation with the suspension-feeding behaviour of *Ophiothrix fragilis* (Solid plot: typical behaviour; striped plot: change of behaviour; open plot: no suspension-feeding behaviour).

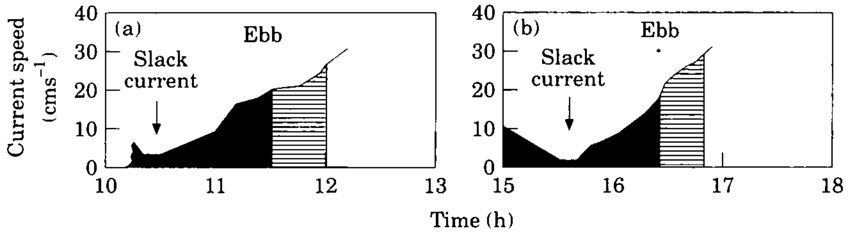

Figure 5. Duration of the suspension-feeding behaviour of *Ophiothrix fragilis* in relation to the tidal current speed during (a) a neap tide (21 May 1991, tidal height=5·55 m) and (b) a spring tide (10 July 1991, tidal height=6·65 m). Same symbols as in Figure 4.

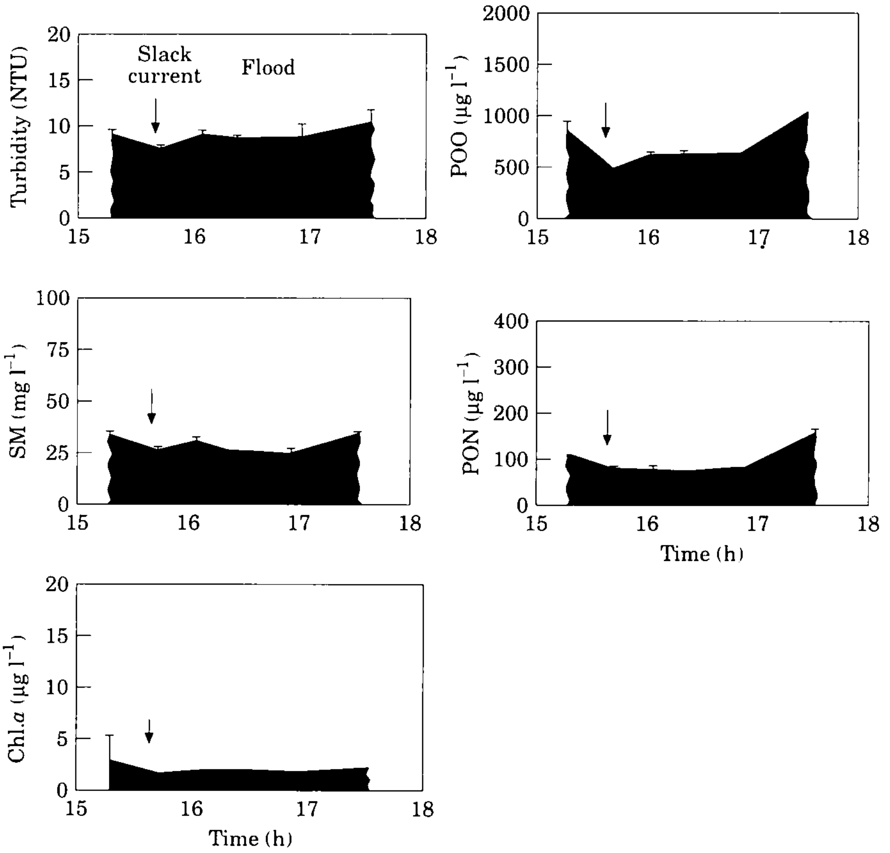

Figure 6. Temporal variations of turbidity, suspended matter (SM), chlorophyll *a* (Chl. *a*), particulate organic carbon (POC) and nitrogen (PON) during a neap tide (27 September 1990, tidal height=3·20 m) in relation to the suspension-feeding behaviour of *Ophiothrix fragilis* (same symbols as in Figure 4).

Gut contents

Gut contents were analysed to confirm the feeding period of the species. Gut contents increased when current speed decreased up to the slack-water period. At the beginning of the flood current, gut contents continued to increase while *O. fragilis* kept its typical suspension-feeding behaviour (Figure 7). Maximum gut contents (1·7) occurred 1 h

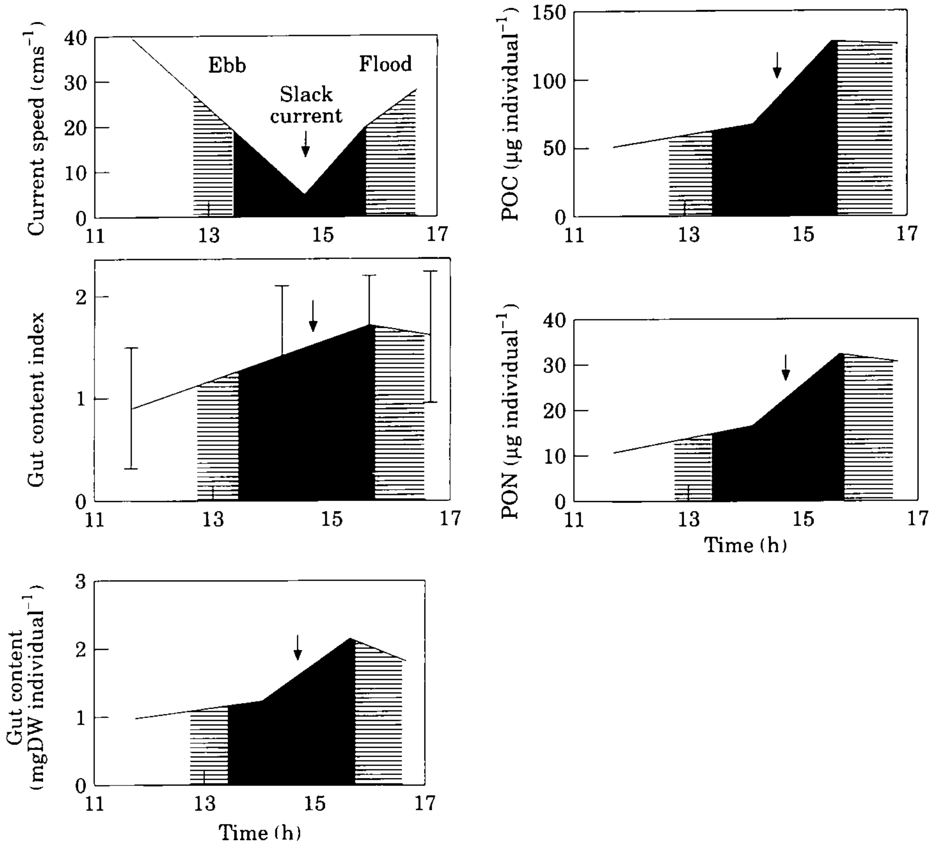

Figure 7. Temporal variations of tidal current speed and gut content of *Ophiothrix fragilis*: arbitrary scale, dry weight (DW), particulate organic carbon (POC) and nitrogen (PON). Taken on 21 September 1989 (tidal height = 6 m) (same symbols as in Figure 4).

after slack water (current speed = 18·5 cm s^{-1}). This value remained almost constant during the next hour. In the middle of the ebb current, guts were not empty but no bolus or diatoms could be seen.

The temporal sequences of both qualitative and quantitative analyses (Figure 7) were quite similar. The maximum gut contents noted 1 h after slack water indicated a mean weight of 2·1 mg individual^{-1}. The increase of gut contents involved an enrichment of POC and PON whose maxima were also found to occur 1 h after slack water (POC = 138·1 µg individual^{-1}; PON = 31·9 µg individual^{-1}).

Discussion

These observations confirmed that the duration of *O. fragilis* suspension-feeding behaviour changes with tidal conditions. The current speed maximum for optimal filter feeding (20 cm s^{-1}) is near that given by Warner (1971, no indication of the level of measurement above the sea-floor) and Warner and Woodley (1975, measurements taken at about 3 cm above the bottom). These authors described a typical feeding posture for a current speed of 15 cm s^{-1}, then a decrease of the number of raised arms and the angle formed with the sea bottom, up to a 25 cm s^{-1} current speed limit (individual flattened on the floor). Other ophiuroids filter up to a current speed between 15–30 cm s^{-1} (Warner, 1982). Leonard (1989) stated that 'the feeding activity of the crinoid *Antedon mediterranea* is not a function of the rate at which particles approach the filter but depends only on the ambient particle concentration and current speed'.

Such variations in the duration of suspension-feeding according to current conditions suggest that food supply would be lower during spring tides than during neap tides because of variations in tidal currents if other environmental conditions, such as nutrient concentrations, did not change. However, hydrological conditions change near the sea floor according to the tidal strength. During spring tides, the current speed rapidly increases after slack water, especially during the flood current, inducing a resuspension of particles settled just before and during slack tide. This very large increase of suspended matter allows the *O. fragilis* population to filter during higher food availability; during this period, POC and Chl. *a* concentrations can be eight times higher than previously (Figure 4).

In the upper water column, turbidity varies throughout the year between 1–6 NTU, suspended matter varies between 18–32 mg l^{-1} and particulate organic carbon is always lower than 500 µg l^{-1} (Maillard-Quisthoudt, 1988). Chlorophyll *a* concentration always remains lower in the upper water column than near the sea floor during resuspension: from less than 2 µg l^{-1} (June–March) to about 12 µg l^{-1} during the phytoplanktonic spring bloom (Quisthoudt, 1987).

During the ebb current, resuspension seems to be strongly attenuated because of the smaller increase in current speed. In the Dover Strait, the flood tide current is of shorter duration but stronger than the ebb tide current, which is responsible for an important part of the residual drift of water towards the North Sea (S.H.O.M., 1968; Clabaut, 1988; Prandle, 1993; Salomon *et al.*, 1993). This could explain why resuspension phenomena are generally observed at the beginning of the flood tide current. Other observations, however, showed that important resuspension occurs at the beginning of the ebb tide current when particular conditions prevail, such as the wind blowing in the same direction as the current.

Quantities of nutritive elements available for the ophiuroid population remain high even when suspension-feeding behaviour of *O. fragilis* is of short duration. Indeed, current speed rapidly increases after slack current and the population is still filtering when resuspension occurs.

During neap tides, fluxes of nutrients are low (no resuspension, low current speed after slack water) but the suspension-feeding behaviour of *O. fragilis* is almost constant. In contrast, during stronger tides, higher food supply occurs during the short duration of the suspension-feeding activity.

Chlorophyll *a* and particulate organic matter are always higher above the ophiuroid population than offshore (Quisthoudt, 1987). The growth of the *O. fragilis* population is maximal in April and May as is its state of sexual maturity (Davoult *et al.*, 1990) when the phytoplanktonic bloom occurs. Knowledge of the hydrological gradient from the coast to the offshore area, estimated on the whole water column, can partially explain the location of dense ophiuroid beds to be due to the enrichment of the area due to passive sedimentation of nutritive particles. However, the phenomena at the water–sediment interface (turbulence, resuspension) appear to be essential in understanding the richness of suspension-feeders in this community.

The examination of gut contents confirms that feeding occurs mainly on either side of slack water when current speed is low, and that *O. fragilis* is mainly a suspension-feeder. The deposit-feeding behaviour observed in aquaria (Nagabushanam & Colman, 1959), as well as the fragments of benthic organisms collected in the guts of very few individuals (Warner & Woodley, 1975; Davoult, 1988), could be opportunistic and infrequent *in situ* behaviour: in the area studied, *O. fragilis* does not move when it is not filtering because of the current speed, as observed on video, so how could it find deposited food? These observations appear to be partly in contradiction with the hypothesis of Hily *et al.* (1988) who suggested that *O. fragilis* feeds using almost the total length of its arms during low currents, and may only use its arm tips during strong currents and so could maintain the efficiency of nutrition during the tidal cycle. Experimental observations under controlled hydrodynamic conditions (unpubl. data) confirm our *in situ* video observations. The presence of a minimum gut content during maximum current speed probably corresponds to material collected previously and in the process of digestion. Measurements of the ammonium excretion of *O. fragilis* (Davoult *et al.*, 1991) also showed a higher metabolism 90 min after slack water, compared with 90 min before slack water.

In this area, water movement and turbulence near the bottom do not favour passive deposition of particles, except during short periods of slack current. The very low proportions of sand and mud in the sediment (Davoult, 1990) precludes the abundance of deposit-feeders which would recycle the organic matter. The richness of the benthic compartment of the ecosystem is due to the collecting of exogenous organic matter by suspension-feeders, mainly *O. fragilis*. So, suspension-feeders appear to be important components in the functioning of coastal ecosystems because they remove large quantities of particulate organic matter from the water and excrete abundant amounts of reactive nutrients. It is assumed that this dynamic process mainly explains why, in the Eastern English Channel and the Dover Strait, the epifaunal pebbles community is richer than other communities settled in fine sediments and low currents areas which are dominated by deposit-feeders.

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