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RECRUITMENT**

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EFFECTS OF INDIVIDUAL BEHAVIORS, INTER-INDIVIDUAL INTERACTIONS WITH ADULT *PECTINARIA KORENI* AND *OWENIA FUSIFORMIS* (ANNELIDA, POLYCHAETA), AND HYDRODYNAMISM ON *PECTINARIA KORENI* RECRUITMENT

Nicolas Desroy, Frédéric Olivier and Christian Retière

ABSTRACT

The English Channel is a megatidal sea characterized by large tidal currents in which the larvae of *Pectinaria koreni* are dispersed on a large spatial scale by tidal currents. They settle abundantly on a wide edaphic spectrum, but the populations of adults are confined to bays and estuaries. Laboratory experiments under still water and flume flows showed that post-larvae of *P. koreni* were able to actively select a suitable substrate i) on a macrospatial scale by resuspending themselves in the water column; ii) on a microspatial scale by crawling at the sediment surface. Adults also influenced the post-larvae habitat selection. When post-larvae settle on a suitable sediment in presence of adults, they resuspend themselves immediately. This resuspension phenomenon is a consequence of bioturbation by the adults (sub-surface deposit feeders) whose vertical movement and feeding activity are mainly dependent on hydrodynamic conditions. However, in the presence of *Owenia fusiformis* adults (deposit/filter feeders), resuspension rates were weak. This recruitment facilitation might be interpreted as a limitation of post-larval resuspension abilities, tubes in a gregarious distribution stabilizing the sediment and resembling particle traps. The feeding behavior of *O. fusiformis*, which exhibited high plasticity in relation to hydrodynamism, also influenced the post-larvae response.

The spatio-temporal variability of species with benthopelagic life cycles is initially dependent upon the success of larval recruitment although post-settlement changes in abundance may subsequently be significant (Bachelet, 1990). Physical parameters such as hydrodynamism or sediment composition (Thorson, 1957; Rhoads and Young, 1971; Butman, 1987; Butman et al., 1988; Bhaud, 1990; Armonies, 1992) and biological factors such as predation or competition (Levinton and Lopez, 1977; Andre et al., 1993) have been shown to influence the distribution and density of intertidal infaunal invertebrates. Coupling of aforementioned factors, acting on newly metamorphosed recruits, may also be a major determinant of structure in subtidal infaunal communities, but few direct tests of this hypothesis exist. The megatidal regime which characterizes the English Channel is particularly favorable to study influences of both physical and biological factors.

Adult populations of *Pectinaria koreni* (Malmgren) and *Owenia fusiformis* (Delle Chiaje) are largely confined to the shallow waters of bays and estuaries in the English Channel. Larval dispersal of these two species is, however, dominated by the large tidal movements and reflects the residual circulation pattern. As a result, the larvae may settle in abundance over a large edaphic spectrum regardless of substrate suitability for adults (Lagadeuc, 1990; 1992; Thiebaut, 1994).

During the first weeks of benthic life, densities of recruited *P. koreni* decrease rapidly (Lambert, 1991). It is not known whether this is due to mortality or, as found for juveniles of some intertidal species (Beukema and De Vlas, 1989; Armonies, 1992; Armonies and Hellwig-Armonies, 1992; Armonies, 1994a, 1994b) to transport to more suitable habitats through resuspension-deposition mechanisms. In the latter case, the relative importance of physical and biological processes acting on the emigration of recruits must be studied. In addition, it is not yet known how recruits, established on a favorable substrate, react to physical

constraints (in particular to hydrodynamism) and therefore how individual behavior and inter-individual interactions are involved in the regulation of recruitment.

To address the above questions, experiments were carried out with adults of *P. koreni* and *O. fusiformis* and post-larvae of *P. koreni*. These two species were chosen because of their high abundances in the field and their eco-ethological characteristics.

The objectives of the present study were to: i) study the mobility and feeding behavior of adults of the two species in relation to lighting and hydrodynamic conditions; ii) test the sediment selection abilities of *P. koreni* post-larvae; iii) assess effects of *P. koreni*/*O. fusiformis* adults feeding and mobility on the fate of post-larvae under different hydrodynamic conditions.

MATERIAL AND METHODS

Biological Models.—The tubicolous polychaetes *P. koreni* and *O. fusiformis* are two of the most common species on the *Abra alba* muddy fine sand community (2–15 m depth) in the eastern part of the Bay of Seine, France. *P. koreni* and *O. fusiformis*, which respectively behave as sub-surface deposit and surface deposit or filter feeders, both exhibit a benthopelagic life cycle. *P. koreni* lives 15 to 18 months and *O. fusiformis* 3 to 5 years in the Bay of Seine.

Worms were collected from the eastern Bay of Seine during May and June reproductive period in 1990–1994. Adults were obtained using a Rallier du Bathy dredge or Smith Mac-Intyre grab whereas post-larvae and juveniles were collected using Reineck and Rouvillois corers. Sediments were sieved through i) a 2-mm mesh to exclude original macrofauna and coarse particles when fated to experiments; ii) a 0.5-mm mesh when used for organism maintaining. Biological material was passed through a 1-mm (adults) or a 0.5-mm (post-larvae) sieve and put into isothermal boxes containing sandy mud and seawater. Adults were transferred to running water aquaria in the laboratory and post-larvae were sorted/counted under a dissecting microscope, kept in dishes filled with sandy mud and held at 13°C before use.

Experimental Devices, Procedures and Data Analysis.—Sediment types used were: mud (median diameter less than 40 μm), sandy mud (median diameter: 50 μm), fine muddy sand (median diameter: 140 μm) and clean fine sand (median diameter: 200 μm). These sediments corresponded to substrates on which adults of both species live or *P. koreni* larvae may settle.

Adult *P. koreni* Responses to Lighting Conditions.—STILL WATER CONDITIONS. Experiments were carried out during spring 1992 in 0.1-m² tanks filled with a 15 cm layer of mud divided into three sections. Individuals were maintained under continuous immersion with a seawater drip, either under continuous light or natural dark/light conditions. Each section was filled with 20 individuals so as to minimize variation from natural populations. Over a continuous 24-h period, observations were made every hour on the vertical positions of all individuals. Two groups were defined: i) individuals that had the distal part of their tube extending more than 5 mm above the sediment; ii) all others. A Wilcoxon-Mann-Whitney nonparametric test was performed to determine any significant differences in the number of individuals of each group under dark and light conditions.

UNDER CONTROLLED HYDRODYNAMIC CONDITIONS. Experiments were conducted in the racetrack-design recirculating laboratory flume of Dinard which general characteristics have been described by Lambert (1991). In the experimental section of the flume, one compartment (0.166 m³) was filled with a 5-cm-deep layer of muddy sand, collected from the sampling site. 200 individuals (1,200 ind · m⁻²; tube mean length: 39.0 \pm 6.2 mm) were placed on the sediment. Dark/light conditions were maintained at a ratio of 9 to 15 h. Throughout the experiment, salinity was constant and temperature ranged between 19.0°C and 21.0°C; current velocity was adjusted gradually. Adult vertical positions were noted at the beginning of the experiment, after 1.5 h of 20 cm · s⁻¹ flow regime and after 1.5 h of still water conditions. The above observations were repeated six times over a total period of 21 h. All results were statistically analyzed for significant differences using a nonparametric *U*-test.

***O. fusiformis* Behaviors in Response to Hydrodynamism.**—ADULT FEEDING BEHAVIORS. In the experimental section of the flume, three compartments were filled with a 10-cm-deep layer of muddy sand. Each compartment contained 15 regularly spaced individuals (body mean length: 34.8 \pm 7.5 mm). Observations were made under still water conditions and at the following flow velocities: 5, 10 and 20 cm · s⁻¹. Feeding activities were monitored between 14:00–15:00 for 4 days, salinity was constant and temperature varied from 14.0°C to 16.8°C. Two replicates were used for each treatment. A Kruskal-Wallis nonparametric test was used to determine any correlation between a particular feeding act and current velocity.

JUVENILE FEEDING BEHAVIORS. Juvenile and adult feeding activities were compared under still water conditions. The three enclosures, filled with a 3-cm-deep layer of muddy sand, had a density of 15 juveniles (body mean length: 1.9 ± 0.3 mm) and each worm was observed every 2 min for a 30-min period.

***P. koreni* Post-larva Mobility and Habitat Selection.**—STILL WATER CONDITIONS. Experiments were carried out in four circular enclosures measuring 5.3 cm in diameter: one half of each circular enclosure was filled with a 2-cm-deep layer of sandy mud favorable for adults and represented a control. The other halves were filled with mud, sandy mud, muddy fine sand and clean fine sand. To avoid a crowding, 10 post-larvae ($4,500 \text{ ind} \cdot \text{m}^{-2}$; cephalic diameter: 0.86 ± 0.21 mm) were placed on the border line which allowed a choice of the two different sediment types. Individuals were counted after 10 days, and each experiment was repeated 15 times. Differences among treatments were assessed using a Kolmogorov-Smirnov test.

The distances covered by *P. koreni* post-larvae were quantified with experiments carried out in rectangular enclosures measuring $1 \text{ m} \times 3.6 \text{ cm}$ and filled with the control sediment to a depth of 1.5 cm. Sowing areas of 0.001-m^2 had densities of 12, 50 and 100 individuals (12d, 50d and 100d) to correspond to field observations. Each experiment was repeated three times. Post-larvae were placed at one end of the compartment and the progressive increase in area occupied was measured each day over a 16-day period.

IN THE FLUME FLOW. Two experiments were carried out in the flume to assess the ability of *P. koreni* post-larvae to select a suitable sediment under flow conditions. In both experiments, the experimental area was divided into five sections measuring $1 \text{ m} \times 10 \text{ cm}$ and 5 cm in depth. In the first experiment, the central compartment was filled with a fine sand unsuitable to adults with a density of 932 post-larvae which had a mean tube length of 4.73 ± 1.2 mm. Post-larvae were given a choice of two different substrates on either side of the central compartment: a suitable organic rich mud and a bare flat PVC surface. In the second experiment, 911 post-larvae were placed on mud suitable to adults and were given the same choice as above. Flow velocity was maintained at the constant speed of $15 \text{ cm} \cdot \text{s}^{-1}$ for a 24-h period. Experimental results were statistically analyzed using a χ^2 conformity test.

Inter and Intraspecific Adult Influences on *P. koreni* Post-larval Settlement.—Two experiments were carried out in the flume to quantify the effects of *P. koreni* and *O. fusiformis* adults on the resuspension of *P. koreni* post-larvae. Both studies were performed under identical conditions (Fig. 1). Animals were placed on a sandy mud suitable for *P. koreni* adults on the fourth experimental upstream section at densities determined by field observations. Resuspended post-larvae were collected using a filter system of 0.5-mm mesh sieve situated downstream from the experimental area. To avoid the clogging of meshes and to assess rates of post-larvae resuspension, the filter was replaced every 4 h over the 44 h of the experiment period. Prior to use, post-larvae were sieved through a 0.5-mm mesh to make sure the tube would be retained on the filter. Then, 175 post-larvae ($8,413 \text{ ind} \cdot \text{m}^{-2}$, mean cephalic diameter in experiment 1: $700 \pm 110 \mu\text{m}$; mean cephalic diameter in experiment 2: $440 \pm 100 \mu\text{m}$) were placed in each of the six experimental cells of compartments A, B, C, D, E and F with or without i) 38 *P. koreni* adults ($1,824 \text{ ind} \cdot \text{m}^{-2}$; mean cephalic diameter: 5.49 ± 0.45 mm); ii) 40 *O. fusiformis* adults ($2,000 \text{ ind} \cdot \text{m}^{-2}$; mean body length: 41.7 ± 6.7 mm). All results were statistically analyzed using a G test.

RESULTS AND DISCUSSION

Mobility and Feeding Behavior of Adults.—**P. KORENI**—STILL WATER CONDITIONS. Under still water conditions, recently introduced adults immediately bioturbated, moved vertically and, as a result of sediment ejection, produced graded mounds of 1–2 cm high. Results showed that the number of *P. koreni* adults buried under the sediment was significantly higher ($P < 0.001$) during periods of illumination. Under the same experimental conditions, Nicolaidou (1988) noted that individuals buried themselves during periods of illumination while, in the dark, the distal part of the tube rose approximately 10 mm above the sediment surface. Although our results agree with this rhythmic activity, it did not seem so apparent as stated by Nicolaidou (1988).

P. KORENI—IN THE FLUME. When exposed to the flow regime of $20 \text{ cm} \cdot \text{s}^{-1}$, the proportion of buried individuals progressively rising to the sediment surface did not exceed 40%, and the results were not significantly different during the diurnal cycle. It is interesting to note that during still water conditions in the flume the percentage of risen individuals was not significantly different between dark

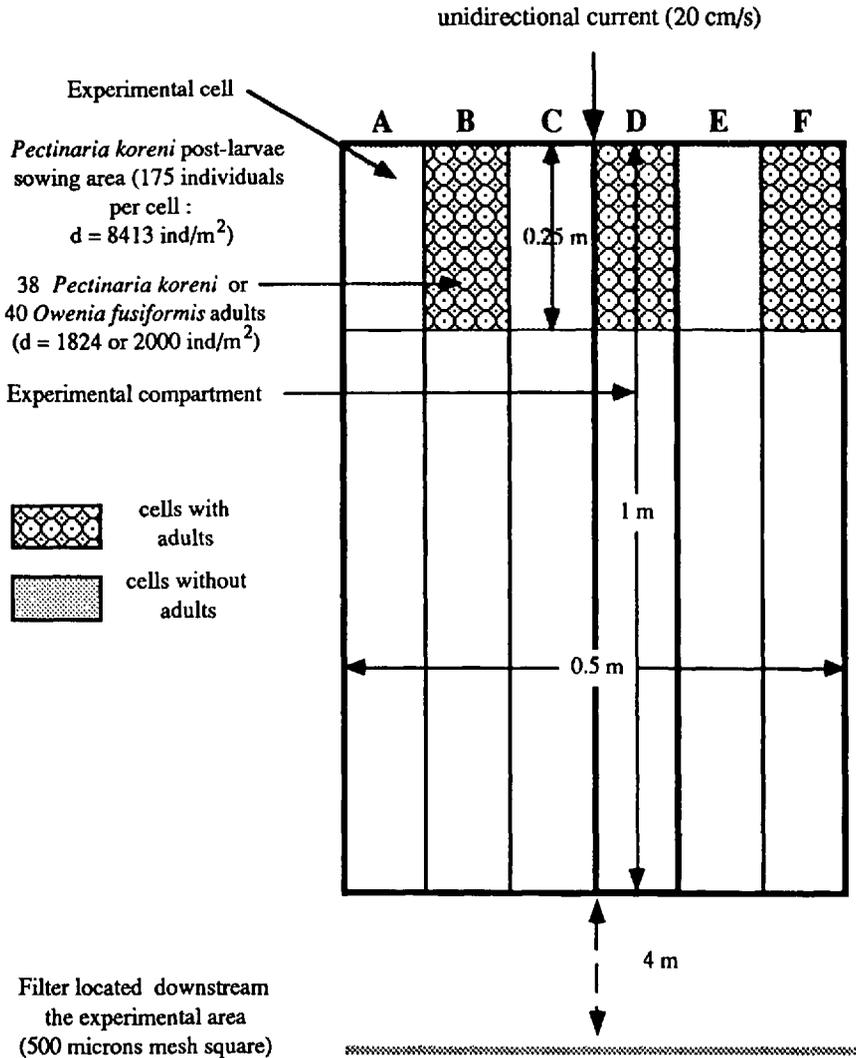
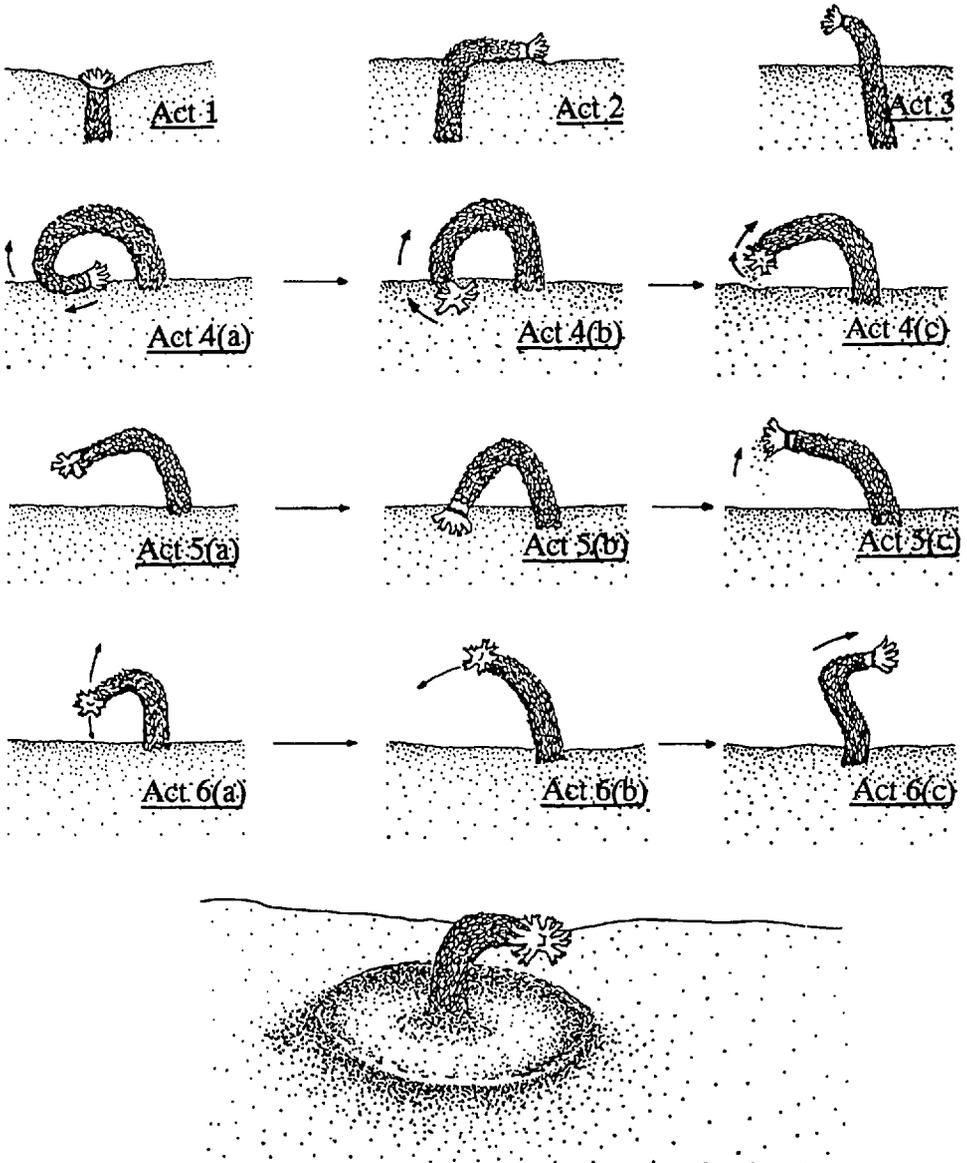


Figure 1. Experimental design used to quantify the effects of *Pectinaria koreni* and *Owenia fusiformis* adults on *Pectinaria koreni* post-larval resuspension.

and light periods but was lower than in permanent flow conditions. Moreover, it was noticed that a plume of watery sediment was ejected every 3–4 min instead of 25–35 min as observed by Davies (1993) under still water conditions. It appears that, under still water conditions, adult *P. koreni* react to light and move vertically within the sediment as opposed to an absence of such rhythmic activity under conditions of water flow. Sediment resuspension also increased during flow speed variations. Increase in egestion rhythm directly intensified the disturbance of the sediment surface layer and influenced conditions on which post-larvae will settle.

O. FUSIFORMIS—IN THE FLUME. Two new feeding acts (1 and 2, Fig. 2), not described by Gambi (1989), appeared dominant with a mean frequency exceeding 90% and independent of flow speed. In act 1, the worm moved vertically up and down and entrained sand grains around its tube which lead to the formation of a



Micro-crater generated by the surface deposit feeding behavior of *Owenia fusiformis* (act 4)

Figure 2. Feeding behaviors of *Owenia fusiformis* modified from Gambi, 1989.

microdepression. The tentacular crown was above the sediment surface, and it behaved as a filter feeder. In act 2, the anterior part of the tube and the branchial crown laid across the sediment surface. The worm may behave as a deposit or filter feeder in this position.

Gambi (1989) described four major feeding acts (3, 4, 5 and 6, Fig. 2). According to her observations, under still water or weak current conditions, *O. fusiformis* behaves as a deposit feeder by i) picking up the sediment around the tube with its branchial crown and forming a crater in the bottom (act 4, Fig. 2); ii)

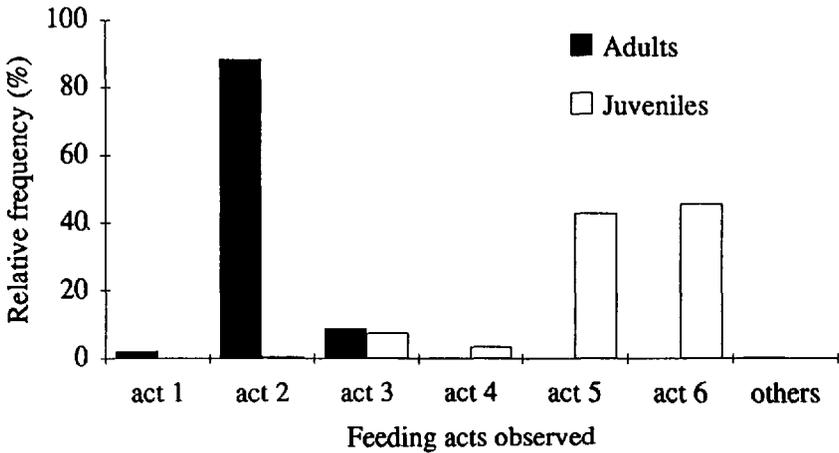


Figure 3. Relative frequencies of *Owenia fusiformis* juvenile and adult feeding behaviors under still water conditions.

resuspending sediment particles with its branchial crown (act 5, Fig. 2) or as a filter feeder (act 6, Fig. 2). The worms become filter feeders at higher flow velocities, orientating their crowns in the direction of the current with their tube held slightly curved (act 3, Fig. 2). During our experiments, all of these four acts were very rarely observed. None of these feeding acts, including acts 1 and 2, were correlated with the flow intensity in our flume experiments.

In conclusion, although *O. fusiformis* was considered exclusively as a filter feeder (Fauchald and Jumars, 1979), it can also behave as a deposit feeder. It appears however that filter feeding predominates (acts 1, 2 and 3) at the adult population level. Conversely, juveniles alternated between deposit and filter feeding activities (acts 5 and 6) under still water conditions at similar frequencies (Fig. 3). These acts may constitute a "feeding sequence" consisting of the resuspension of sediment particles (act 5) and initiation of filter activity (act 6) in the juveniles. Such behavioral variability between adults and juveniles may be linked to differences in the buccal apparatus morphology.

Substrate Selection by P. koreni Post-larvae.—STILL WATER CONDITIONS. Our laboratory experiments showed that *P. koreni* post-larvae were able to crawl at the sediment surface on a microspatial scale and actively select ($P < 0.001$) sandy muds and muds rather than muddy fine sands or clean fine sands (Fig. 4). Preferential larval settlement in response to a particular substrate has been demonstrated in a number of invertebrates (Wilson, 1952; Butman, 1987; Butman et al., 1988; Butman and Grassle, 1992; Butman et al., 1992; Bhaud and Cha, 1994). Larvae of many species respond chemotactically to a substance released into and retained within the substrate (asteroids, Birkeland et al., 1971; barnacles, Crisp, 1979; sand dollars, Highsmith, 1982). However, no data exists on the capacity of post-larvae to actively select particular sediment types. In the case of substrates devoid of adults, *P. koreni* post-larvae chose their substrate according to its physical characteristics, such as grain size, compaction and organic matter content.

During the selection procedure post-larvae moved by crawling on the sediment surface at estimated rates of a few tens of centimetres over 16 days. Distances covered varied with recruit densities (d): at the 100-d treatment, larvae moved 6 or 7 times more than at the 12-d treatment (Fig. 5). Rate of movement fluctuated between 0.36 and 1.90 cm per day according to recruit densities. It could be sug-

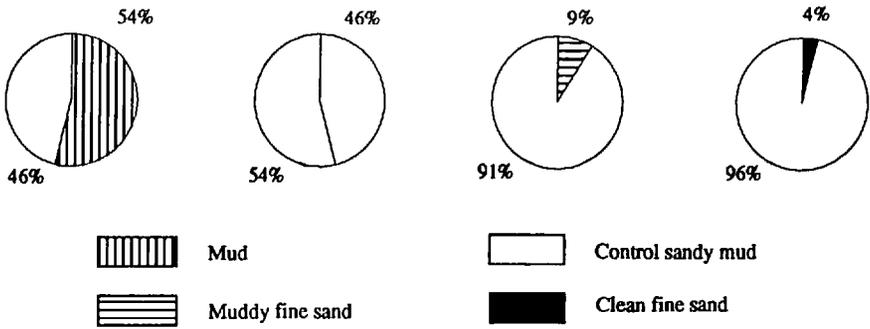


Figure 4. *Pectinaria koreni* post-larval substrate selection under still water conditions. Percentages of recruits recovered in the different sediments tested.

gested that crawling may be involved in the establishment of inter-individual distances and therefore the control of the field population levels.

IN THE FLUME. At the end of the experiment, 85.5% of the recruits introduced to the unsuitable clean fine sand were resuspended and preferentially settled on the mud of the lateral compartments. When they were placed on the suitable sediment, only 1.2% of them were resuspended after 24 h. In the first case, migration was found to be highly significant ($P < 0.005$). These results and those of Lambert (1991) showed that post-larvae and juveniles are capable of leaving an unfavorable sediment and selecting a suitable one. Post-larvae will resuspend them-

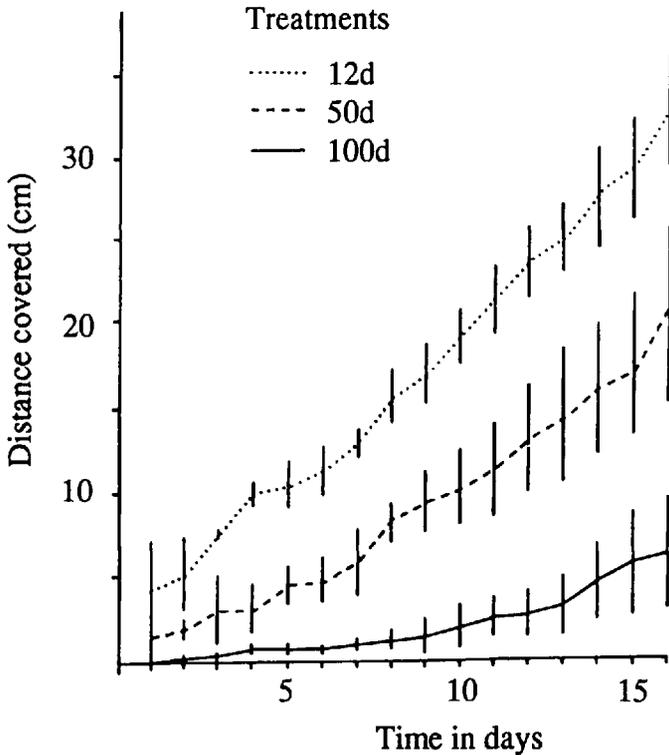


Figure 5. Distances covered by *Pectinaria koreni* by crawling at the sediment surface under still water conditions (cm per day with one standard error). Different densities were tested: 12d (12,000 ind · m⁻²); 50d (50,000 ind · m⁻²) and 100d (100,000 ind · m⁻²).

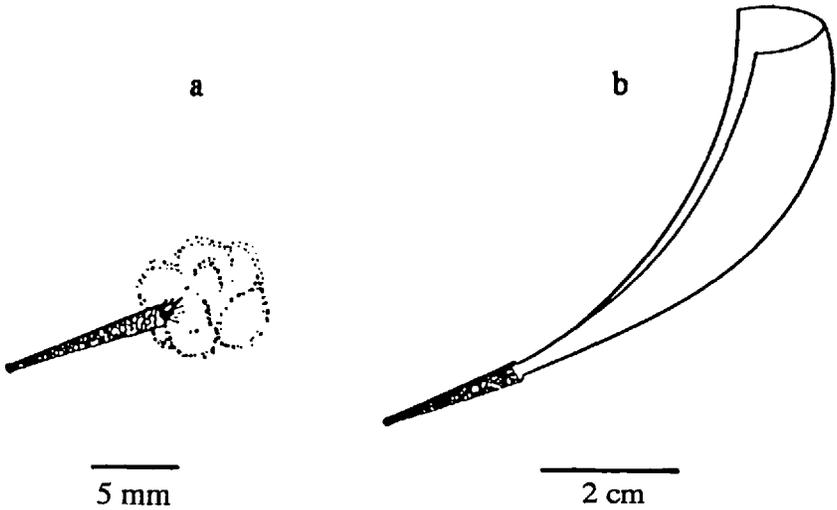


Figure 6. a. Mucus plug secretion by a *Pectinaria koreni* post-larva; b. Extension on a sail-like structure with the water flow.

selves under unfavorable ecological conditions. This process involves the secretion of a mucus bead (Fig. 6a) which is drawn out into a sail-like structure with the flow (Fig. 6b). The post-larva is then drawn across the sediment surface for approximately 10 cm by this structure, resuspended into the boundary layer flow and carried into the water column. In flume experiments, Lambert (1991) observed that a resuspended juvenile could cover more than 60 m in 5 min and Thiebaut (1994) estimated that in the field a post-larva could cover 1,800 m in 1 h. Beukema and De Vlas (1989) thought that the maximum distance covered by *Macoma balthica* juveniles may reach 24 km over several months. Günther (1992) suggested that distances covered in post-larval transport may vary from a few meters to more than 1 km. The coupling of active and passive processes have obviously consequences on the dynamics of natural populations of *P. koreni* with their characteristic localized distributions.

Influence of Adult/Post-larval Interactions on P. koreni Resuspension under Conditions of Flow.—WITH *P. KORENI* ADULTS. After 44 h, 400 post-larvae were collected in the filter. The maximum resuspension of recruits occurred at 4 h with 65% of the vertical migration taking place by 16 h (Fig. 7). Nonparametric testing showed a significant heterogeneity between the A, C, E and B, D, F compartments ($P < 0.05$). Some 84.4% and 27.2% of the recruits from compartments with and without adults, respectively, resuspended themselves. Essentially resuspension took place from compartments with adults.

WITH *O. FUSIFORMIS* ADULTS. The post-larvae resuspension remained low throughout the flume experiment; only 75 of the 1,050 recruits introduced resuspended themselves. The emigration was continuous without any substantial peaks (Fig. 7). In contrast to the experiment carried out with conspecific adults, resuspension took place from control cells: 23% and 48% of the recruits resuspended themselves from cells with and without adults respectively.

DISCUSSION

P. koreni post-larvae are able to move on different spatial scales. On a microspatial scale, they are able to crawl at the sediment surface over tens of centimetres. Such activity could also occur in the natural habitat under the following con-

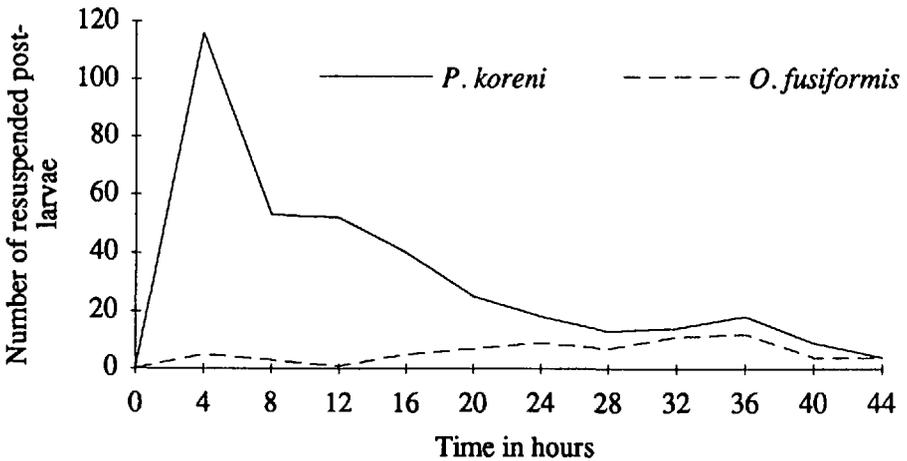


Figure 7. Number of *Pectinaria koreni* post-larvae resuspended in the flume flow, in the presence of adults of i) *Pectinaria koreni*; ii) *Owenia fusiformis*.

ditions: i) Exploration of prospective habitats before commencing burrowing; ii) Consistently selection of substrates of a heterogeneous nature; iii) Spatial separation of individuals; iv) Response to the disturbance generated by a mobile organism. On a macrospatial scale, the post-larvae can actively resuspend themselves in the water column in response to unfavorable ecological conditions and could cover distances of a few hundred to thousand metres. For example, post-larvae initially settling on unsuitable sediments offshore could resuspend themselves and be transported by tidal currents to the suitable muds of the *Abra alba* community of Bay of Seine from which they originated. Recent field observations, using a suprabenthic sledge, have demonstrated the existence of such deposition-resuspension phenomena which may be correlated with the tidal cycle (Olivier et al., 1996).

The presence of adults influences the intensity of post-larval resuspension. In the presence of *P. koreni* adults, post-larval resuspension was massive and immediate, whereas in the presence of *O. fusiformis* adults, the resuspension rate remained low throughout the experiment. Bioturbation of *P. koreni* controlled the intensity of post-larval resuspension of this species.

Bioturbation destabilizes the sediment surface and generates boundary layer flow disturbances (Davies, 1993). It is well known that deposit feeders produce significant alterations in the benthic environment; the most important of which is the production of a fecal surface and a decrease in the compaction of the reworked sediment (Rhoads and Young, 1970). In addition, post-larvae can be passively redistributed through sediment erosion by bedload transport and resuspension. Vertical movement of adults which is dependent on light and hydrodynamic conditions contributes to an increased destabilization of the sediment surface. At the mouth of the Seine estuary, the high water turbidity suggests hydrodynamic factors are probably the major influence on the mobility of *P. koreni*. Egestion rates also increase in response to variations of tidal current intensity and such disturbance effects are more important when densities are up to $5,000 \text{ ind} \cdot \text{m}^{-2}$ in the Bay of Seine. Gordon (1966) derived an estimated time of 15 years for population density of $10 \text{ ind} \cdot \text{m}^{-2}$ of *Pectinaria gouldii* to bioturbate the superficial layer sediment to a depth of 6 cm. It has been estimated by Dobbs and Scholly (1986) that bioturbation by *P. koreni* is approximately five times less than those calculated by Gordon (1966).

Bioturbation leads to the smothering of post-larvae which either are resuspended

and move or die within the sediment. Elmgren et al. (1986) described such an interaction between the amphipod *Pontoporeia affinis* adults and the bivalve *Macoma balthica* juveniles. It was shown experimentally by him that after 12 days of smothering, the *M. balthica* mortality rate was significant and 23 days later 99% had died. Under such conditions, it is surprising that populations of *P. koreni* in the Bay of Seine are stable from 1 year to the next at a high density level. In fact, only the first cohorts of recruits may be affected by such interactions with *P. koreni* adults. The success of the breeding populations is dependent on the arrival of the next cohorts when adult mortality is high in July.

In the case of *O. fusiformis*, the apparent recruitment facilitation might be interpreted as a limitation of post-larval resuspension abilities of *O. fusiformis*. Aggregations of *O. fusiformis* resemble particle traps in which complex patterns of fluid circulation occur. *O. fusiformis* tubes of nearly 8 mm in diameter and the high population density give a stabilizing effect on the sediment (Eckman et al., 1981). As a consequence, post-larvae could be neither passively nor actively resuspended as before. Individual behaviors and feeding activities also influence post-larval responses. In terms of these factors, *O. fusiformis* showed a high behavioral plasticity which is sufficient to explain differences observed between individuals from the Pacific coast studied by Gambi (1989) and those in the present study. The adults of *O. fusiformis* behave almost exclusively as filter feeders in still water and flume flows whereas juveniles behave as deposit feeders in still water conditions. The fate of *P. koreni* post-larvae would be differentially altered according to whether settlement occurred among *O. fusiformis* juveniles or adults. It is not clear whether *P. koreni* post-larvae will resuspend themselves in the presence of *O. fusiformis* juveniles whose small size results in the minimal sediment disturbance.

The parameters influencing the post-larval settlement can be arranged chronologically. Initially, sediment characteristics play a role and with time the biological interactions between recruits and adults increase in importance. As recruits grow and orient themselves spatially with respect to one another, spatial and trophic competition become more important.

Under mega-tidal conditions, which contribute to the wide dispersion of pelagic larvae (Lagadeuc, 1990; Thiebaut, 1994), the regulation of populations with localized distributions depends not only on hydrodynamic conditions; life history characteristics and particularly behavioral features also play an important role. The results presented in this study demonstrate the functional significance of feeding behavior and mobility on different spatial scales of the experimental organisms at different stages of their life cycles. The present study also illustrates the necessity for considering behavioral ontogenesis in studying population biology.

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