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Physical and numerical modeling of the role of hydrodynamic processes on adult-larval interactions of a suspension-feeding bivalve

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ABSTRACT

The importance of hydrodynamic processes for adult-larval interactions in the cockle, *Cerastoderma edule*, was examined through physical and numerical modeling. A set of physical experiments in a flow-tank using adult cockles and larval mimics showed that the settlement of particles was affected by adult cockles. Settlement was reduced by 20% in an area of 2.5 cm² surrounding the siphons, and the most marked decrease occurred near the inhalant siphon. On a larger spatial scale downstream of the siphons, settlement was more heterogeneous compared to surfaces without cockles. The experimental results near individual cockles were compared with numerical models of settlement dynamics in conditions with no horizontal flow. The models suggest that the vertical position of the siphon orifice determines whether any small-scale reduction in larval settlement should be expected near suspension-feeding benthic invertebrates. The results are compared qualitatively and quantitatively with previous observations of small-scale patterns (≈ 1 cm) around individual *C. edule* and with observations of larger-scale (1–10 m) differences among patches with varying densities of cockles. These comparisons indicate that passive hydrodynamic processes can explain patterns around individual cockles, whereas a combination of active and passive processes are necessary to explain differences among patches. Such hydrodynamic modification of larval behavior has previously been reported to greatly increase rates of mortality for settling bivalve larvae.

1. Introduction

Settlement of larvae and survival of juveniles are vital components for the persistence and growth of benthic marine invertebrate populations (e.g. Thorson, 1950; Eckman, 1996). Nevertheless, the extent to which temporal and spatial variability in settlement and early survival are responsible for observed patterns in adult populations is a matter for much debate, but clearly their relative importance is likely to vary among places, times, habitats, species, scales, etc. (Underwood and Denley, 1984; Connell, 1985; Butman, 1987; Olafsson *et al.*, 1994). For animals with a sessile adult stage, the settlement and metamorphosis are events which put irreversible constraints on future survival and reproduction. Therefore, much emphasis has been put on the evolutionary significance and

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role of settlement for structuring populations and assemblages of benthic animals (e.g. Thorson, 1950; Young, 1990a).

Many empirical observations have demonstrated that settlement of larvae often is highly variable in space and time (e.g. Muus, 1973; Raimondi, 1990). The magnitude of this variability typically differs among scales and it is often suggested that different physical and ecological processes are responsible for causing variability at different scales (e.g. Butman, 1987; Lindegarh *et al.*, 1995; Hewitt *et al.*, 1997). Because planktonic larvae swim at speeds slower than 1 cm s^{-1} , coastal and ocean currents are believed to be increasingly important in generating patterns of settlement at larger scales. Thus, these large-scale patterns of larval supply set the scene for biological processes to shape the distribution of settlement and recruitment at smaller scales (Underwood and Fairweather, 1989; Gaines and Bertness, 1992). In particular, observations of small-scale patterns of benthic organisms have spawned ideas that settling larvae actively choose where to settle. Such active choices of micro-habitats have been observed in numerous empirical studies (e.g. Meadows and Campbell, 1972; Woodin, 1986; Pawlik, 1992). Nevertheless, there is also growing evidence that physical forces generated by hydrodynamic processes can affect larval behavior and thus be important in the formation of small-scale patterns of larval settlement (Butman, 1987; Eckman *et al.*, 1990; Jonsson *et al.*, 1991; Gross *et al.*, 1992; Snelgrove and Butman, 1994; Abelson and Denny, 1997; Bouma *et al.*, 2001).

Small-scale hydrodynamic processes are thought to be of great significance for mediating interactions between settling larvae and established assemblages of animals. These, 'adult-larval interactions' are among the most powerful models for explaining patterns of assemblages in soft sediment habitats (e.g. Rhoads and Young, 1970; Woodin, 1976; Young, 1990b; Constable, 1999). Adult macrofauna may modify hydrodynamic conditions at the sediment surface by adding structural complexity which cause heterogeneity in near-bed flow (Eckman and Nowell, 1984; Nowell and Jumars, 1984). This may cause small-scale heterogeneity in settlement of larvae coupled to a net increase or decrease in settlement (Eckman, 1979; Gallagher *et al.*, 1983; Peterson, 1986; Young, 1990b; Snelgrove, 1994). Adult macrofauna may also alter the hydrodynamic conditions by generating feeding-currents (Ertman and Jumars, 1988; Monismith *et al.*, 1990; Young, 1990b). It has, for example, been shown that feeding-currents generated by bivalves interact with horizontal flow near the sediment surface and affect settlement in the vicinity of individual bivalves (Ertman and Jumars, 1988; André *et al.*, 1993). Although, such small-scale effects are not always detected as larger scale patterns (Young, 1990b; Hewitt *et al.*, 1997), experimental evidence has often suggested that filter-feeding bivalves cause decreased intensities of settlement in larger areas with dense populations of bivalves (Williams, 1980; Möller, 1986; André and Rosenberg, 1991).

The common cockle, *Cerastoderma edule* (Linnaeus, 1758), is abundant on shallow sediment bottoms along the European Atlantic coast. It may reach densities up to several hundreds per square meter but is usually found at densities of $1\text{--}100 \text{ m}^{-2}$ on the Swedish west coast. Observations of year-class distributions and variability in recruitment have also

been made which suggest that adult-larval interactions may affect the recruitment of cockles (Brock, 1980; Möller and Rosenberg, 1983; Lindegarth *et al.*, 1995). These observations have been verified in manipulative experiments. André and Rosenberg (1991) observed a 40% reduction in settlement of bivalve larvae at densities of 400 *C. edule* m⁻² compared to areas with no cockles. Subsequent experiments in laboratory flow tank have shown that the average time of survival for settling larvae is only about 1 minute at a similar density of adult cockles (André *et al.*, 1993) and is strongly affected by the interaction between larval behavior and horizontal flow (Jonsson *et al.*, 1991). Despite this large rate of mortality, the area of decreased settlement extends only 1–1.5 cm away from individual siphons of *C. edule*. In this area the density of settled larvae was reduced by approximately 30% (André *et al.*, 1993).

The aim of this study was to test hypotheses about the extent to which (1) observed decreases in settlement around bivalve siphons (André and Rosenberg, 1991; André *et al.*, 1993) and (2) increased heterogeneity in settlement downstream of filter-feeders (Eckman and Nowell, 1984; Ertman and Jumars, 1988) can be explained by passive hydrodynamic processes. The first hypothesis was investigated by physical modeling in two sets of experiments in a flow tank and in numerical simulations using two different hydrodynamic models. In the physical modeling we predicted that if larval mimics, i.e. inert particles with sinking velocities similar to those of bivalve larvae, are released in a dense population of cockles, patterns of settlement will be similar to those of settling larvae. Such a pattern would indicate that hydrodynamic processes are primarily responsible for creating patterns of settling larvae rather than larval behavior. Numerical modeling was then used to investigate the importance of position of cockle siphons and sinking velocity for creating the observed patterns at no flow. The second hypothesis was tested using physical modeling using inert particles in a set of flow tank experiments. Here we predicted that the presence of filter-feeding cockles would interact with horizontal flow and cause a settlement of particles which was more heterogeneous than in the absence of cockles.

2. Methods and materials

a. Physical modeling in flow tank

Unidirectional, boundary-layer flow was generated using a 3.5 m long, 0.5 m wide and 0.4 m deep recirculating flow tank (Vogel, 1981; for further details see also Jonsson *et al.*, 1991). The test section was 0.5 × 0.4 m with a 0.2 m deep sediment box with an upstream edge 2.2 m away from the water inlet. Sediment to be used in the experiments was sieved through a 0.5 mm mesh to exclude potential roughness elements. The median grain diameter was determined to be 170 μm by size-fractionating (Buchanan, 1971).

Before the experiments, vertical velocity profiles were measured in undisturbed flow, for 3 free-stream velocities ($U_{\infty} = 2, 10$ and 15 cm s^{-1}). Flow velocity was measured with a heated thermistor probe connected to a pen-recorder (Vogel, 1981). Boundary shear velocity (u_*) was calculated from the velocity profiles according to:

$$u(z) = \frac{u_*^*}{\kappa} \ln(z/z_0)$$

where $u(z)$ is the flow velocity at height z above the bed, u_* is boundary shear velocity, z_0 is the roughness parameter and κ is the von Karman's constant (≈ 0.4). Calculated shear velocities in our experiments were 0.19 ± 0.010 ($n = 12$), 0.36 ± 0.031 ($n = 17$) and 0.57 ± 0.062 ($n = 11$) cm s^{-1} (mean \pm 95% CI) for the free-stream velocities 2, 10 and 15 cm s^{-1} , respectively. In addition, experiments in still water were also done in the flow tank. Water depth in the tank was 0.35 m during the experiments. This depth was chosen to allow good mixing of particles before settlement, and to avoid interactions between the exhalant jet, produced by cockles, and the water surface. Nevertheless, this ratio of width:depth may result in secondary flow (i.e. flow which is not strictly parallel to the main current). Visual inspection of flow fields using dye had previously shown that the exclusion of a 5 cm strip near each of the walls was sufficient to ensure that vertical profiles of mean horizontal velocities were homogeneous (see Jonsson *et al.*, 1991), and that any cockle used in the experiments would be exposed to equally strong flow. This notion was further strengthened by initial observations of settlement in undisturbed flow (see below).

Patterns of settlement were studied using fluorescent PVC-microparticles ($149 \pm 36 \mu\text{m}$, mean \pm SD, $n = 2000$) with mean sinking velocity of $4.2 \pm 0.57 \text{ mm s}^{-1}$ (mean \pm SD, $n = 22$) (Lindgarth *et al.*, 1991). This is within the range of observed sinking velocities for invertebrate larvae (Chia *et al.*, 1984). Before use, the particles were suspended in 250 ml water from the flow tank (salinity = 33‰) with a few droplets of detergent (Tween 20). The number of particles added varied between 100,000 and 200,000 in each experimental run. To ensure an even distribution in the cross-stream direction, 30–50 portions of suspended particles were introduced in different parts of the tank below the surface upstream the working area using a Pasteur-pipette. When few particles remained in suspension, after 5–10 min, settlement patterns were documented by photographing the sediment surface (Olympus OM-2, 50 mm macro lens with a yellow filter, and Kodak TMAX 400 ASA monochrome film). Particles were made visible by illumination using a harmless blue light source (Philips TLD 18 W/08 fluorescent tube; peak wavelength 370 nm). The camera was mounted vertically 0.4 m over the sediment surface, and a complete picture of the working section was constructed from 9 photos taken at fixed positions. This method allowed spatial resolution of all settled particles around the cockle siphons. The negative photos were projected on a wall ($4.2 \times$ magnification) where all analyses of spatial patterns were carried out.

Although appropriate replication with respect to individual cockles and experimental runs ensures that any heterogeneity in settlement will not affect conclusions about effects of experimental treatments, the patterns of settlement in undisturbed flow were studied in separate runs with no cockles present. Settlement patterns were tested for heterogeneity in two different ways. At the scale of the whole working section, settlement intensity was tested for goodness-of-fit to a Poisson-distribution by 30 ($1 \times 1 \text{ cm}$) random samples from

Table 1. Test for goodness-of-fit on sedimentation patterns in the working section against a Poisson-distribution.

Flow speed (cm s^{-1})	df	χ^2	p
0	4	23	0.0001
2	3	3.8	0.28
10	3	4.9	0.18
15	3	2.2	0.54

each run. These analyses revealed that particles were heterogeneously distributed in 0 cm s^{-1} (Table 1), whereas in the other flow regimes the Poisson-distribution could not be rejected. Additionally, we performed nearest-neighbor analyses (Pielou's α ; Andrew and Mapstone, 1987) at the scale of the individual cockles. Fifty nearest-neighbor distances were measured in 3 randomly chosen areas ($3 \times 3 \text{ cm}$) from each of the runs. If particles are randomly distributed, $2n\alpha$ will be distributed as χ_{2n}^2 , where n is the number of distances measured and $\alpha = \pi d\omega$, where d is the density of particles and ω is the mean squared distances between particles. At this scale particles were randomly distributed ($\chi_{100}^2 < 124.3$) in all flows except in one of the areas in the 2 cm s^{-1} treatment ($\chi_{100}^2 = 136.7$). In summary, these tests show that for the purposes of the following experiments the settlement can essentially be considered random within the working section. Nevertheless, they also suggested that to avoid unnecessary heterogeneity of particles, which reduces the power of future statistical tests, extra caution was appropriate when particles were added at weak flow speeds.

Naturally occurring specimens of *Cerastoderma edule* burrow just beneath the sediment surface in shallow soft bottoms, with the short in- and exhalant siphons protruding to the sediment surface. Evenly sized cockles were selected for the experiments (length $36 \pm 2.5 \text{ mm}$, mean \pm SD, $n = 30$). The cockles buried readily into the sediment, keeping the original position and orientation (with the inhalent siphon upstream). New individuals were used for each separate run. Two sets of experiments were designed to estimate and test how siphonal flow and ambient currents interact to create patterns of settlement around individual cockles. First, experiments were run with 3 individual cockles placed 10 cm apart in a row perpendicular to the water flow. These experiments were run at $0, 2, 10$ and 15 cm s^{-1} and duplicated within each flow speed. To examine the spatial extent of any decrease in settlement rate around siphons, the number of particles around individual cockles were counted in a series of concentric circles with increasing radius (Fig. 2a). This was done for one experimental run only for each of the flow speeds. This information was examined graphically and used in the design of the subsequent set of experiments. Furthermore, to test for increased heterogeneity in settlement downstream of individual cockles, the number of particles were counted in a $8 \times 3 \text{ cm}$ grid (Fig. 1a), and the variance in number of particles were used as a measure of heterogeneity. This was done for duplicate runs at 10 and 15 cm s^{-1} .

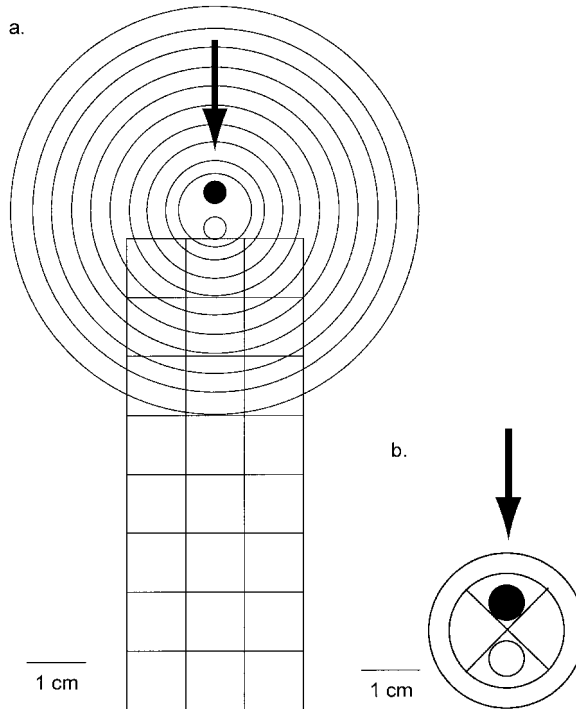


Figure 1. Grids used to sample the deposition intensity in: (a) the preliminary experiments, and (b) in the main experiments. Flow direction is indicated by arrows, and empty and filled siphons represent inhalant and exhalant siphons, respectively.

Second, duplicate experiments at flow speeds of 0, 2, 10 and 15 cm s^{-1} were done with 76 cockles per run (corresponding to 380 m^{-2}). Individuals that did not bury or feed actively; i.e. generated siphonal currents, were replaced prior to the experiments. The number of particles around individual cockles were counted using a grid consisting of two circles with radii corresponding to 0.88 and 1.24 cm, creating two separate sub-areas of equal sizes = 2.4 cm^2 (Fig. 1b). The central area was divided into 4 sectors to allow resolution of the effects of the inhalant and the exhalant siphons. The intensity of settlement as functions of distance and direction relative to the siphons was analyzed in two separate tests. The number of particles in each sub-area was standardized with respect to area (including subtraction of the areas occupied by the siphons inhalant = 0.11 and exhalant = 0.095 cm^2) and total number of particles. This was to minimize variability due to inconsistencies in the addition of particles. In summary, these standardizations resulted in predicted proportions of 0.5 for the two distances and 0.25 for the four sectors if there were no effects of the siphons on settlement.

Effects of cockles on heterogeneity in settlement downstream and in the vicinity of cockles as described above was analyzed using analysis of variance (ANOVA). All

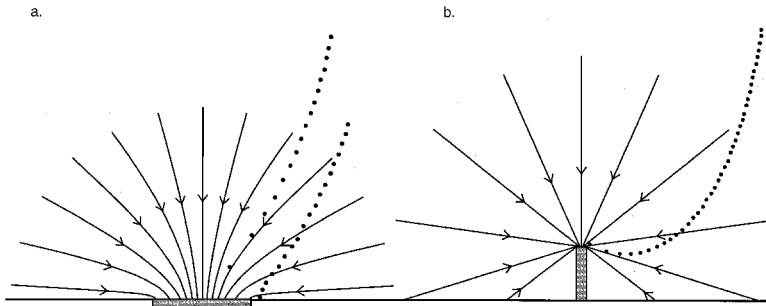


Figure 2. Alternative hydrodynamic models of inhalant siphonal currents on settling particles in still water. (a) Model with siphon orifice flush with the substratum surface, (b) model with a protruding point sink. Example particle trajectories are indicated with dots separated by a constant time interval.

analyses were done with balanced data. In the second set of experiments, this was achieved by randomly excluding data from some experimental runs. Heterogeneity of variances were tested for using Cochran's test and comparisons among individual means were done *a posteriori* using Student-Newman-Keuls test (Underwood, 1997). Standard procedures were initially attempted to remove heterogeneity of variances (e.g. arcsine for proportions). If this was not successful, we used the 'omnibus'-procedure described by Legendre and Legendre (1998). The procedure replaces the data with random numbers (normal distribution with mean = 0 and standard deviation 1) and ranks them in the same way as the original data. This removes heterogeneity of variances for all types of data.

b. Numerical modeling

Two different hydrodynamic models were used in an attempt to investigate potential processes that could generate the observed settlement patterns around the cockles when there is no horizontal flow (Fig. 2). The first model considers the effect of the inhalant flow combined with particle sinking velocity and unidirectional horizontal flow. This model does not account for patterns created by exhalant flow and its interaction with the horizontal flow (e.g. Monismith *et al.*, 1990). For an inhalant siphon, flush with the sediment, flow was modeled as laminar flow through a circular aperture (derived from Happel and Brenner, 1983; p. 153) for which there exists the stream function:

$$\psi = \frac{q}{2\pi} (1 - 8^{1/2}(z^2 + r^2 + c^2 + (z^2 + r^2 + c^2)^2 + 4c^2z^2)^{-3/2})$$

expressed in circular, cylindrical coordinates (ρ , ϕ , z) and where q is the volumetric flow rate ($= 1 \text{ cm}^3 \text{ s}^{-1}$, André *et al.*, 1993) through the aperture with radius c (1.9 mm, pers. obs.). The velocity components $V(\rho)$ and $V(z)$ for a point in the flow field are found by derivation of the stream function with respect to ρ and z as (note that $V(\phi) = 0$):

$$V(\rho) = \frac{1}{\rho} \frac{\delta \psi}{\delta z}$$

and

$$V(z) = -\frac{1}{\rho} \frac{\delta \psi}{\delta \rho}.$$

During the experiments and in the field, we often observed that siphons were protruding slightly into the water column (pers. obs.). This was also observed by Monismith *et al.* (1990) for 3 other bivalve infaunal species. The vertical position of the feeding structure has previously been suggested to affect the likelihood of observing small-scale patterns of settlement in the vicinity of filter-feeding benthic animals (Young, 1990b). If the inhalant siphon is located slightly above the sediment, there will be a current with a vertical component directed upwards (Fig. 2b). This causes a decrease in the net sinking velocity, which could lead to a decrease in the intensity of settlement. The boundary conditions of the first model do not allow simulation of a protruding siphon. To specifically investigate the effect of a protruding siphon a simpler model was therefore applied. In the second numeric model the siphon is modeled as a point sink with radial flow lines, i.e. the orifice has no spatial extension and the effect of the no slip condition on the internal siphon wall is ignored (Happel and Brenner, 1983; p. 140). The velocity at radial distance r from the siphon is calculated as:

$$V(r) = \frac{q}{4\pi r^2}$$

The velocity vectors from inhalant flow and settlement were used to generate trajectories of settling particles by finite time difference simulation (time step = 0.1 s). This was done for 6,400 particles. Sinking velocities were set to 1 and 4 mm s⁻¹. The former corresponds to that of descending larvae of *C. edule* (Jonsson *et al.*, 1991) and the latter corresponds to those of the particles used in the physical model. Particles were initially released with starting coordinates in a regular 2 × 2 cm grid 3 cm above the inhalant siphon. The second model was run with the siphon 0 and 3 mm above the surface. The resulting settlement intensity as a function of distance to siphon opening was then plotted to illustrate differences in particle density at different distances from the siphon.

3. Results

a. Physical model

The fact that particles were visible during the experiments provided a means to observe the feeding activity of *Cerastoderma edule* in flowing water. Entrainment of particles both in the inhalant and in the exhalant siphonal currents could be observed. During the experiments we observed that cockles readily inhaled particles without any signs of

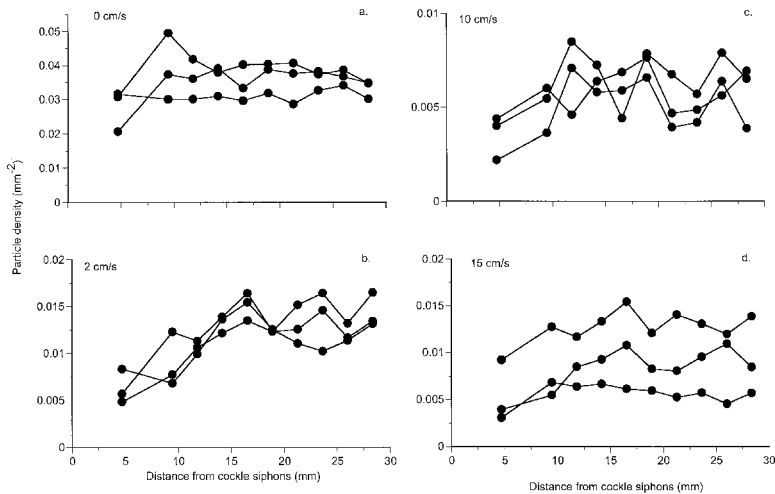


Figure 3. Settlement intensity as a function of distance from a central point between the inhalant and the exhalant siphons for three replicate individuals in four different flow regimes.

immediate rejection. After one experiment a few cockles were collected, and inspection of the digestive tracts showed that particles entered the gut.

Patterns of settlement around the individual cockles in the first set of experiments are shown in Figure 3a–d. The graphical analysis indicated a tendency of reduced settlement within a radius of less than 1 cm from a central point between the two siphons. The decrease in settlement appeared relatively consistent in all flow regimes. Based on this information it was decided that subsequent analyses should be done using a grid consisting of two circles with radii corresponding to 0.88 and 1.24 cm, creating two separate sub-areas of equal sizes ($=2.4 \text{ cm}^2$; Fig. 2b).

In combination with replicate experimental runs without cockles, the same set of experiments was used to test for increased heterogeneity (measured as variance in the number of particles) in settlement downstream of cockles at free-stream velocities of 10 and 15 cm s^{-1} (Table 2). One missing value due to photographic error (15 cm s^{-1} replicate 2 with cockles) was replaced by the mean of the other values in that replicate to make the

Table 2. Three-factor nested ANOVA on estimated variances (s^2) of settlement intensity downstream of siphons. Cochran's test for homogeneity of variances: $p > 0.05$, $C = 0.25$, $df = 8, 2$.

Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Presence/absence	1	44.14	8.1	0.047
Flow	1	0.097	0.018	0.90
Presence/absence \times flow	1	52.59	9.6	0.036
Run (presence/absence \times flow)	4	5.47	1.5	0.22
Residual	15	3.58		

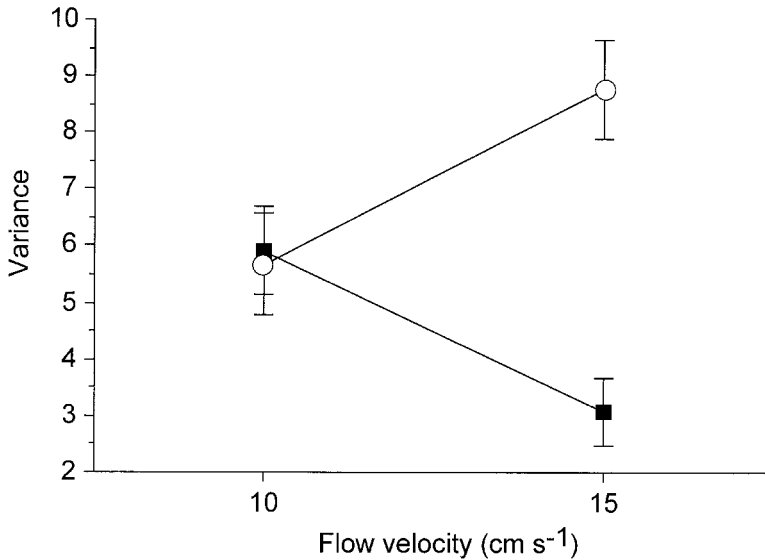


Figure 4. Heterogeneity of settlement of particles downstream of filter-feeding cockles (mean \pm SE). ○: cockles present, ■: no cockles present.

analyses balanced, and one degree of freedom was accordingly subtracted from the residual degrees of freedom (Underwood, 1997). The analysis showed that the effect of the presence of a filter-feeding cockle differed between flow-speeds. SNK-tests revealed that the predicted increase in heterogeneity was observed at 15 cm s⁻¹, while there was no difference at 10 cm s⁻¹ (Fig. 4).

In the second set of experiments, analysis of the intensity of settlement as a function of distance from the siphons resulted in a complex pattern. In general, there was a tendency for a decrease in settlement closest to the siphons (Fig. 5a), but the difference in proportions between distances varied among experimental runs within flow-speeds

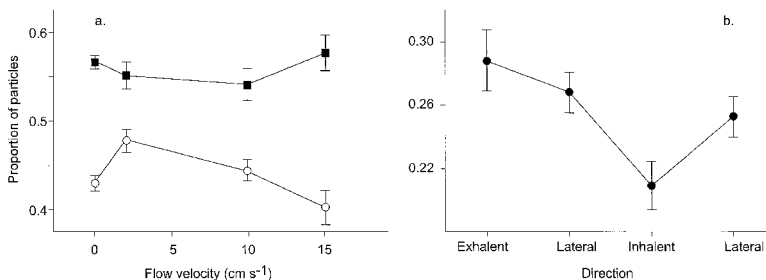


Figure 5. Proportions of settled particles in (a) the inner and outer area (○ and ■, respectively) at different flow velocities and (b) in quadrants containing the inhalant and the exhalant siphon, and 2 quadrants located laterally of the inhalant-exhalantaxis (mean \pm SE).

Table 3. Analyses of variance on proportions of total number of particles at different (a) distances and (b) directions in relation to siphons of the cockle, *Cerastoderma edule*. Data on proportions in different directions are transformed using the 'omibus'-procedure (see text). Cochran's test: distance data: $p > 0.05$, $C = 0.14$, $df = 16, 10$; direction data: $p > 0.05$, $C = 0.11$, $df = 32, 4$.

a.					b.				
	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>		<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Flow	3	0.005	0.46	0.72	Flow	3	0.372	1.98	0.259
Run (flow)	4	0.011	2.6	0.040	Run (flow)	4	0.188	0.24	0.916
Distance	1	0.640	29	0.006	Direction	3	4.051	3.76	0.041
Flow \times distance	3	0.022	1.0	0.48	Flow \times direction	9	0.895	0.83	0.602
Distance \times run (flow)	4	0.022	5.1	0.001	Direction \times run (flow)	12	1.078	1.37	0.187
Residual	160	0.004			Residual	128	0.785		

(Table 3a). SNK-tests showed that the inner area had significantly smaller proportions in both experimental runs at 0 and 15 cm s⁻¹. At 2 and 10 cm s⁻¹ there was a significant decrease only in one of the experimental runs. On average there was a 20% reduction of settlement in the inner area as compared to the outer area.

The analysis of the proportions of particles in different sectors close to the siphons showed significant differences among directions (Table 3b). The smallest proportions were found upstream of the cockles, near the inhalant siphon while the largest proportions were found near the exhalant siphon (Fig. 5b). SNK-tests revealed significant differences between these two sectors but none of them differed significantly from the two lateral sectors which had intermediate levels of settlement. The difference among sectors did not change significantly as a function of flow speed. The presence of a pattern also in still water indicates that differences in settlement among directions near the siphons were mainly caused by currents generated by the siphons and not primarily an effect of interactions with the horizontal flow.

b. Numerical model

Results of runs of both models showed that a large proportion of the particles would have been inhaled by a cockle. For example in the first model at 1 mm s⁻¹, 52% of the particles were inhaled. Not surprisingly, a smaller proportion of particles were inhaled at larger sinking velocities (17%) and consequently the density of settled particles was higher at a sinking velocity of 4 mm s⁻¹. Nevertheless, this substantial inhalation of particles did not cause any reduction in settlement intensity near the modeled siphon (Fig. 6). Thus, the hydrodynamic flows involved in this model does not explain the qualitative patterns of settlement of larvae observed in this study, those observed by André *et al.* (1993) or those of inert particles observed from the physical model above.

The second model run with a sink (inhalant siphon) flush with the surface produced patterns of settlement which was similar to those observed from the first model at similar flow speeds and sinking velocities (Fig. 7a). This pattern of settlement near the sink changed radically when the sink was located 3 mm above the surface. The new configura-

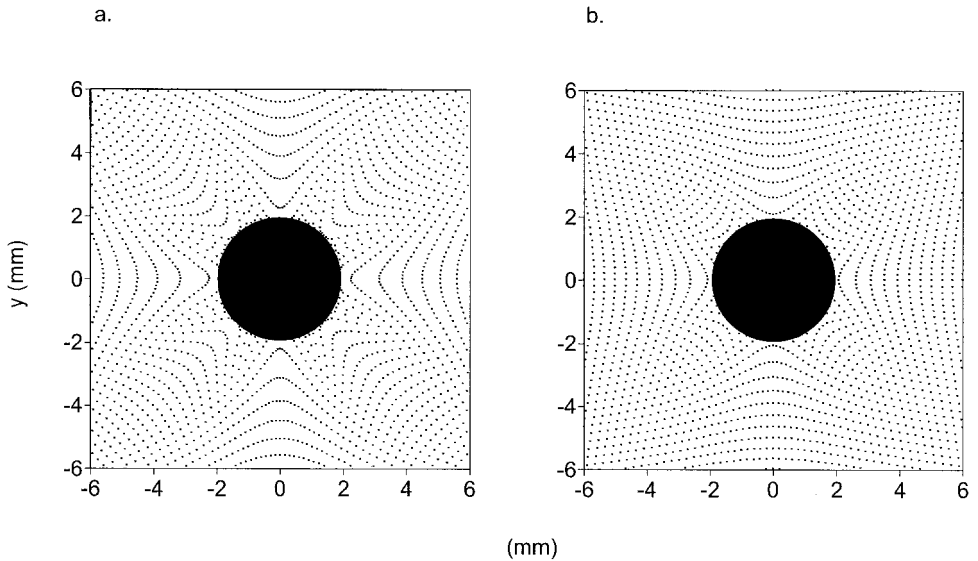


Figure 6. Simulated sedimentation patterns, using the complex hydrodynamic model, in still water with particle sinking velocities of (a) 1 mm s^{-1} and (b) 4 mm s^{-1} . The black circle represents the orifice of the inhalant siphon.

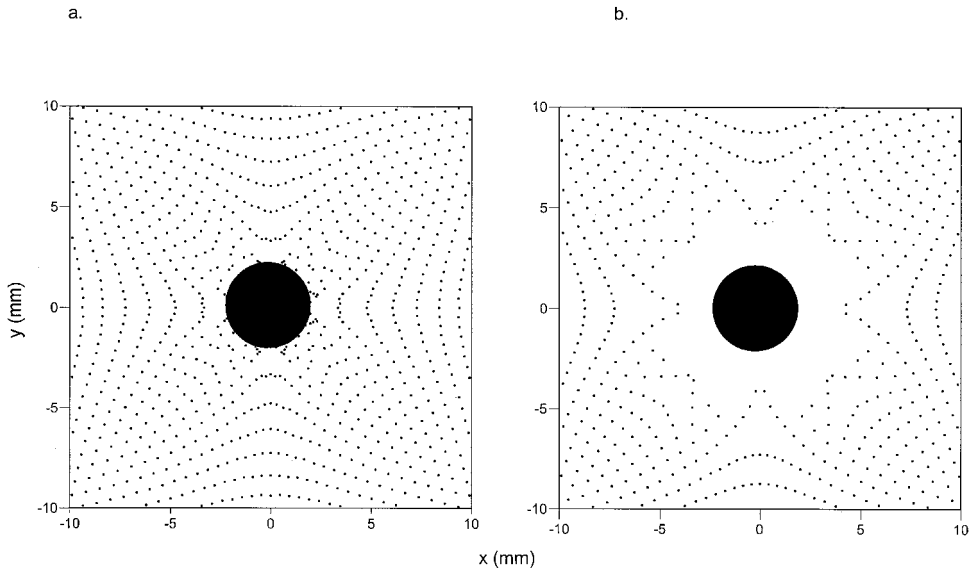


Figure 7. Simulated sedimentation patterns, using the simple hydrodynamic model, in still water with particle sinking velocities of (a) 1 mm s^{-1} and (b) 4 mm s^{-1} .

tion produced a decrease in settlement near the model siphon (Fig. 7b). The extent of the decrease in settlement roughly coincides with the patterns observed in the physical experiments and by André *et al.* (1993). Thus, the physical flows included in the second model was more successful in explaining the observed qualitative and quantitative patterns around siphons.

4. Discussion

In these laboratory flow tank experiments we have found statistical evidence of reduced settlement of inert particles around individual cockles, *Cerastoderma edule*. There was an increased heterogeneity in settlement downstream of cockle siphons at fast flow speeds (15 cm s^{-1}). Visual observations during the experiments indicate that increased variability was a result of entrainment of particles in the exhalant siphonal current and the induction of turbulent eddies that interfere with settling particles. These observations are in agreement with predictions from previous studies of small-scale flow-fields and shear stresses downstream of different types of animal mimics (e.g. Eckman and Nowell, 1984; Monismith *et al.*, 1990; Young, 1990b). Furthermore, there was a decrease in settlement rate by 20% in an area of about 2.5 cm^2 surrounding the siphons. These patterns correspond roughly to those observed for bivalve larvae with similar sinking velocities (cf. André *et al.*, 1993). Thus, the physical modeling suggest that small-scale patterns of larval settlement around individual filter-feeding bivalves can be explained by passive deposition of larvae and that mechanisms invoking larval behavior are not necessary to explain these patterns. Although the statistical tests did not reveal any significant effects of flow on the differences between distances of among directions, it is possible that such exist but that they were not detected due to lack of statistical power. Nevertheless, it is clear that differences between distances occur at no flow and that differences are qualitatively consistent among flows (Fig. 5a).

The observed small-scale settlement patterns around cockle siphons could not be reproduced by the complex hydrodynamic model of flow through an orifice flush with the surface. The analytically simpler model with a radial point sink and a variable vertical position, however, resulted in settlement patterns which were consistent with those observed in the experiments. The numerical models thus indicate that the vertical position of siphons may have profound effects on the types of settlement patterns which may be expected around bivalves and possibly other types of filter-feeding benthic animals. This does, however, not conclusively demonstrate that the decreased settlement around cockles were caused by the vertical location of the inhalant siphon. One reason for caution against such an interpretation may be that the numerical models did not include the effects of exhalant siphons. The rationale for this simplification was that, in the physical modeling, the exhalant siphon was always oriented downstream of the inhalant and therefore would not interact substantially with incurrent flow. This assumption was based on previous studies of flow around siphons of *C. edule* (André *et al.*, 1993), which showed that there were distinct areas of influence from the two separate siphons. Flow around the inhalant

siphon was largely symmetrical while the jet from the exhalent siphon was directed in an angle away from the inhalent siphon. Importantly, this argument was also supported by the empirical results from the physical modeling presented here. The decrease in sedimentation observed here occurred mainly in the vicinity of the inhalant siphon and not near the exhalant (Fig. 5b). With this information at hand, the simplified model to investigate effects on settlement in the immediate vicinity of the siphons is arguable reasonable. Nevertheless, it is possible that the exhalent siphon may cause heterogeneity in larger-scale patterns of settlement. Explanations of such patterns are obviously beyond the scope of the numerical models.

Apart from models involving hydrodynamic processes, other alternative explanations based on, for example, physical disturbance due to bioturbation are theoretically possible (Lindström Swamberg, 1991). Nevertheless, direct (but unquantified) observations during the experiments indicate that the patterns really were caused by siphonal flow. Young (1990) noted that small-scale patterns of settlement can only be expected to occur around individual filter-feeders if feeding-currents reach the surrounding substrate. This suggests that the effect will increase if the distance between the structure used for feeding and the substratum is decreased. Our results indicate that interaction between feeding current and substratum is necessary but not sufficient to create a zone of decreased settlement around filter-feeders. For this to occur, it appears necessary that there is an upward component of the feeding-current which will counteract the net sinking velocity. This can only happen if the siphon's orifice is located slightly above the substratum. However, if the siphon is further removed from the substratum the feeding-current will no longer affect the probability of settlement near the base of the siphon.

In view of these data we thus predict that entrainment of larvae in the inhalant current and subsequent ingestion will reduce the probability of settlement close to adult cockles. Even at high densities of cockles, however, extrapolation to larger plots using these estimates of small-scale effects near individual cockles will lead to underestimates of rates of predation and of large-scale reduction in settlement. As an example, naive calculations based on this experiment show that the settlement would decrease roughly by 2% at the large density of 400 adults m^{-2} and predation would reduce settlement substantially in 10% of the substratum area (affected area = $400 \times 0.00025 \text{ m}^2 / 1 \text{ m}^2 = 0.1 \text{ m}^2$, proportional settlement = $0.1 \text{ m}^2 \times 0.8 + 0.9 \text{ m}^2 \times 1.0 = 0.98$). This is consistent with calculations based on the settlement patterns of larvae of *Cerastoderma edule* near filter-feeding adults which would have decreased in approximately 5% of the area and with a total reduction of 1.5% (using data from Fig. 5 in André *et al.*, 1993). Although these calculations do not allow a formal comparison, these estimates are substantially smaller than previously observed reductions by 20–40% in a field-experiment where 0.5 m^2 plots containing 400 cockles m^{-2} were compared to those with no cockles (André and Rosenberg, 1991). Similarly, the relatively small reduction in settlement which have been inferred from the small-scale patterns in flow tank experiments appears to be in contradiction to the large rate of mortality which was observed by André *et al.* (1993). This apparent

discrepancy clearly illustrates the difficulties associated with extrapolation of effects of ecological processes from one spatial scale to another (Peterson and Black, 1987; Young, 1990b; Schneider *et al.*, 1997). Inferences about large-scale effects of predation based on patterns observed around individual cockles are bound to be underestimates because settling larvae may encounter several filter-feeding cockles during the process of settlement. This means that the probability of settlement near one individual cockle depends on events further away. Comparisons of average settlement rates among plots with different densities of adults will incorporate small-scale local effects as well as effects of surrounding individuals while comparisons around individual cockles will incorporate differences caused by local processes only. Young (1990) predicted that effects of larval predation would be larger at small (around individual filter-feeders) and large scales compared to those at intermediate scales. On the other hand he concluded that large-scale effects would be more difficult to detect due to large-scale variability caused by other processes than adult-larval interaction. The results presented here are consistent with these conclusions. Nevertheless, it is important to realize that observations of patterns around individual cockles can not be used to evaluate the importance of adult-larval interactions for patterns at larger spatial scales.

This study is an experimental and analytical attempt to examine the importance of passive processes in larval settlement in the vicinity of, i.e. <5 cm away from, individual adult suspension-feeding bivalves. It is clear that larvae of bivalves and other benthic invertebrates are capable of influencing their position during settlement in flow (Butman *et al.*, 1988; Pawlik *et al.*, 1991), but that hydrodynamic forcing may modify the behavior of settling larvae (Jonsson *et al.*, 1991; Pawlik *et al.*, 1991). Thus, settlement patterns at different spatial scales will be a result of a combination of active and passive processes. We concluded that passive processes are sufficient to explain observed patterns around individual filter-feeders. This is largely in agreement with direct observations of settling larvae made by André *et al.* (1993), which did not observe any successful, active avoidance by larvae. Failure of larvae to actively influence settlement patterns at such small scales is in contrast to general models of larval settlement. If anything, these predict that active behavior is increasingly important at smaller scales. Our results suggest that this might not be the case near adult, filter-feeding bivalves.

Similarly, it can not be assumed that patterns of larval settlement in larger-scale patches (10^1 – 10^2 m) of *Cerastoderma edule* (e.g. André and Rosenberg, 1991; Lindegarh *et al.*, 1995) are entirely generated by passive processes. Jonsson *et al.* (1991) and André *et al.* (1993) observed that settling larvae of *C. edule* were confined to a few mm above the sediment surface when exposed to flow. Analytical modeling by Jonsson *et al.* (1991) suggested that this phenomenon could be explained by active swimming and physical forces acting on various parts of the larvae. The behavior greatly enhanced the risk of predation and thus the potential for adult bivalves to cause large-scale patterns of settlement. Thus, at larger scales patterns of settlement are also likely to be strongly influenced by a combination of active and passive processes. These results indicate the

complex role and need for a clear focus on spatial scales in future models of larval settlement and recruitment of invertebrate larvae.

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