Deposition of mimics of planktonic invertebrate larvae on simple and complex substrata in flume flows

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ABSTRACT: The purpose of this study was to compare the distribution of inert particles on polyvinylchloride (PVC) panels with earlier results from field studies. The panels were prepared in order to test heterogeneity (crevices similar in shape, but differing in size) and complexity (combination of crevices of different sizes) effects. The experiments were carried out using PVC particles and pre-served *Placopecten magellanicus* larvae in a flume under controlled flow conditions (mean velocities of 3, 5 and 10 cm s^{-1}) and using silicon-coated panels. The heterogeneous panels had different combina-tions of flat surfaces and 1, 10 and 100 mm crevices. The density of particles per unit surface area adhering to the panels was higher at 3 and 5 cm s^{-1} than at 10 cm s^{-1} for all experiments. The density of adhering particles decreased with increasing panel complexity. Within panels with only 1 mm crevices, the density of particles was significantly higher inside the crevices than on smooth surfaces. However the density of particles was significantly lower in 10 and 100 mm crevices than on adjacent flat surfaces within panels with only 10 and 100 mm crevices, respectively. Furthermore, the 1 and 10 mm crevices nested inside 100 mm crevices collected fewer particles than those outside 100 mm crevices within panels with many scales of crevices. The patterns of distribution for dead larvae on heterogeneous panels in the flume corresponded to those of the inert PVC particles. However, the distribution patterns of inert particles in the flume did not correspond to those of living bivalve spat observed in an earlier field study. This suggests that larval behaviour contributed to the selection of settlement location for these bivalve larvae, though flume hydrodynamical conditions may differ from those in the field. The results also indicate that the hydrodynamic processes affecting settlement on heterogeneous substrates are scale-dependent and that processes occurring at scales of 10 and 100 mm influence processes occurring at smaller, 1 mm, scales.

KEY WORDS: Planktonic invertebrate larvae · Substratum heterogenity · Substratum complexity · Flume · Micro-habitat selection

INTRODUCTION

The distribution patterns of many sessile inverte-brates are influenced by settlement site selection (Bourget 1988) which is evident from the aggregation of individuals on a substratum (Jensen & Morse 1984) These patterns reflect the various factors that influence sessile invertebrate larval settlement. Factors which play a role in larval settlement include: light, gravity, hydrostatic pressure (Crisp 1974), larval concentration (Gaines et al. 1985), bacterial films (Mihm et al. 1981,

Kirchmann et al. 1982), organic matter (Crisp 1974), inorganic matter (Mullineaux & Butman 1990), sub-strate type (Rittschof et al. 1984), conspecifics (Wethey 1984, Chabot & Bourget 1988), and hydrodynamic processes (Havenhand & Svane 1991, Pawlik & But-man 1993, Mullineaux & Garland 1993). Substratum heterogeneity plays an important role, particularly for cirripede settlement (Le Tourneux & Bourget 1988, Chabot & Bourget 1988, Bourget et al. 1994). However, the distribution of settlers and some aggregate pat-terns may be limited by substrate availability.

There is evidence of larval preference under labora-tory conditions; cirripede larvae prefer pitted over smooth surfaces (Crisp 1974). The interaction between

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hydrodynamic processes and substratum heterogeneity at scales <10 cm on larval settlement has been the focus of several studies. Snelgrove et al. (1993) showed that circular depressions (3.8 cm in diameter) increased the number of bivalve and polychaete larvae settling on a given substratum. The effect of depressions appeared to be scale-dependent with larger depressions enhancing settlement.

More recently, Bourget et al. (1994) carried out a field study using panels with many scales of heterogeneity (crevices of similar shape but of different sizes) and complexity (combinations of different scales of heterogeneity). The 1 and 10 mm crevices collected higher densities of larvae of different bivalve species compared to larger crevices, but for more complex panels only 1 mm crevices showed enhanced settlement. The 'influence of heterogeneity' on settlement comprises several factors, including active larval behaviour during settlement and local hydrodynamic influences near or within crevices and adjacent surfaces (Bourget et al. 1994). However, the hydrodynamic influence was not explicitly investigated in Bourget et al.'s study.

Within the bottom boundary layer, flow velocity is reduced and competent larvae of some species may swim freely while selecting a settlement site (Pawlik & Butman 1993). For other species, the first contact with the substratum is controlled by hydrodynamic processes (Mullineaux & Butman 1990, 1991, Harvey et al. 1995).

Enhanced turbulence and advection towards the substratum should increase the contact rate of particles with the surface. Whereas reduced shear stress should increase particle residence time on the surface, for larvae that are passively transported by currents, increased contact or retention on the surface would occur under conditions of any combination of high advection towards the substratum, enhanced turbulence or reduced shear stress (see Mullineaux & Garland 1993).

Studies of settlement in relation to small-scale hydrodynamic processes have been carried out with smooth and more recently on heterogeneous surfaces (see Snelgrove et al. 1993). However, natural marine topography is complex; thus, settlement needs to be understood in reference to both these parameters. In the present study we examined the influence of substratum heterogeneity and complexity on the settlement of inert particles using panels of known heterogeneity and complexity. These panels have previously been used in field settlement studies (Bourget et al. 1994, Lemire & Bourget 1996 in this issue). We used polyvinylchloride (PVC) particles and dead larvae as models to eliminate the effect of active larval behaviour The hypotheses tested were (1) that larvae and inert particles settle more abundantly on substrata of increasing heterogeneity and complexity and (2) that current velocity influences the density and distribution of inert particles.

MATERIAL AND METHODS

Flume design. Passive settlement experiments were carried out using a 0.6 × 0.6 × 13 m (width × height × length) single-passage flume at the Université Laval Département de génie civil. Details of the flume are described in Harvey et al. (1995). A 0.6 × 8.9 m false bottom was installed and tightly fixed 12 cm above the bottom of the flume. This false bottom was made of 4 PVC sheets (1.25 cm thick) of equal length. The furthest upstream and downstream sheets were slightly inclined, ~4°, and the 2 central sheets were horizontal. The 2 central parts were placed 0.3 m apart. This gap allowed the installation of the 0.3 × 0.3 m interchangeable experimental panels which, when fixed in the center, were flush with the false bottom (see 'Experimental panels' section). Water temperature was maintained at 10°C and salinity at 25‰. The working section, 3.6 m downstream of the entrance of the flume, was characterized by a uni-directional average flow. Three flow velocities, 3, 5 and 10 cm s⁻¹, calculated as the vertically integrated mean velocity over the central 2.75 m section of the flume were used for the experiments. In these experiments, we were testing a generic case for a developing boundary layer over panel surfaces in slow flows and not trying to mimic a particular field environment.

The evaluation of Reynolds number indicates a turbulent flow. This was also confirmed by visual observation. The experiments conducted with low velocities were at low turbulent regime ($Re \approx 5 \times 10^3$).

Boundary shear velocity (u_*, Schlichting 1962) near the wall was estimated using:

$$u_* = u \, (f/8)^{0.5} \tag{1}$$

where u is the velocity and f is the friction factor (related to Darcy-Weisbach equation); the equation assumes an equilibrium boundary layer, a condition which may not entirely have been met. The estimated values of u_* for velocities of 3, 5 and 10 cm s⁻¹ were 0.2, 0.3 and 0.6 cm s⁻¹ respectively.

Experimental panels. The term 'scale of heterogeneity' has been defined as the size of equilateral grooves with sides of 1, 10 and 100 mm, on PVC panels (Bourget et al. 1994). 'Complexity', 1st to 4th order, refers to the number of scales of heterogeneity represented on a given panel. The crevices were oriented normal to the flow.

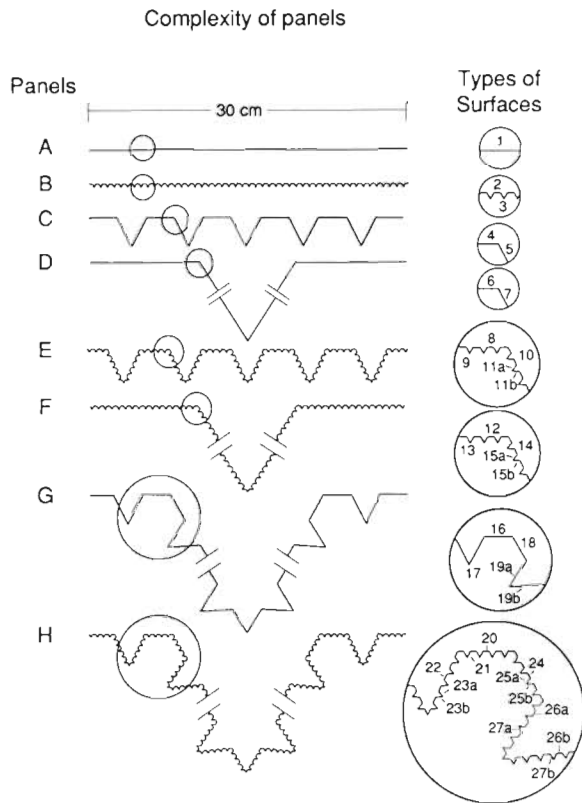A total of 8 different panel types were used (Fig. 1) corresponding to those used in field studies by Bour-

Complexity of panels

Fig. 1. Types of panels and surfaces used during the experiments with inert particles. Crevice angle is illustrated in Fig. 2
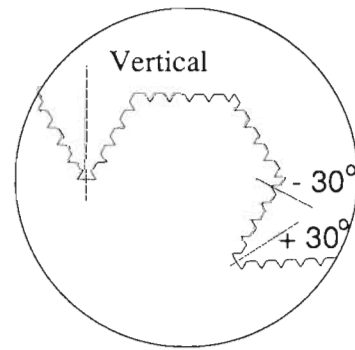

Fig. 2. Crevice angles observed on the panels. Fig. 1 presents an overall view of panels

thickness of the laminar sublayer, the wall is said to be hydrodynamically smooth. On the contrary, when the height of the roughness is much larger (~100) than the thickness of the laminar sublayer, the wall is said to be hydrodynamically rough. Obviously, the transition is not sharp and there is a transition zone (5 < $k_s u./\upsilon$ < 70) where the wall is said to be semi-rough. In our experiments, it is rather difficult to evaluate the value of the average roughness heights since we have few repetitions and the roughness (crevices) only spans a small proportion of the bottom. The 1 and 10 mm crevices are repeated many times, so we can determine the average roughness heights for these crevices. The 100 mm crevices occur only once per panel, so it is difficult to determine any realistic average height of the roughness elements. Table 1 gives the average roughness heights for the 1 and 10 mm crevices for the 3 flow velocities.

Inert particles. PVC microparticles (PVC 'GEON 103EPF76', BF Goodrich, USA; density = 1400 kg m^{-3}) between 150 and 250 μm, the size of larvae of many invertebrate species, were obtained using calibrated sieves. The fall velocity (~4.18 mm s^{-1}) of the particles was assumed to be the same as that of similar PVC particles used by Lindegarth et al. (1991). The particles were stained using a thin fluorescent dye ('DAY-GLO

get et al. (1994) and Lemire & Bourget (1996). These included. one of 1st order complexity, smooth, panel A; three of 2nd order complexity, smooth + crevice sizes, 0 + 1, 0 + 10 and 0 + 100 mm for panels B, C and D, respectively; three of 3rd order complexity, smooth + nested crevice size + crevice sizes, 0 + 1 + 10, 0 + 1 + 100, 0 + 10 + 100 mm for panels E, F and G, respectively and one of 4th order complexity, smooth + 2 orders of nested crevices + crevice size: 0 + 1 + 10 + 100 mm, panel H. Thus, panels of 1st, 2nd, 3rd and 4th order complexity displayed 1, 2, 5 and 12 different types of surfaces, respectively (Fig 1). Panels of 3rd and 4th order complexity contained crevices with different orientations: +30° and −30° to horizontal and 90° vertical crevices, whereas panels of the 1st and 2nd order complexity had vertical crevices only (Fig. 2).

Classification of rough or smooth walls is made by comparison of the reduced thickness of the laminar sublayer expressed by $\delta' u./\upsilon \approx 12$ with the average height of roughness expressed under the reduced form $k_s u./\upsilon$ (δ' is the absolute thickness of the laminar sublayer and k_s is the absolute height of roughness). When the height of roughness is smaller (~5) than the

Table 1 Average roughness heights ($k_s u./\upsilon$) for the different combinations of crevice sizes and flow velocities

Flow velocity	Crevice size	
	1 mm	10 mm
	Average crevice depth (k_s)	
	0.86 mm	8.66 mm
3 cm s^{-1}	1.7	17.3
5 cm s^{-1}	2.6	26.0
10 cm s^{-1}	5.2	52.0

No. A-17', Color Corp.) and counted on the substratum using a UV lamp (Lindegarth et al. 1991). The panels were covered with a thin uniform layer of silicone High-Vacuum Grease (Dow Corning, USA) to ensure particle adhesion at first contact (Walters 1992, Harvey et al. 1995)

Experimental procedure. For each trial, experimental panels were installed in the dry flume. The flume was then filled with water 40 cm above the central portion of the false-bottom. The flow was started and the experimental panel was exposed to particles for 10 min. The particles were maintained in a 10 g l^{-1} solution and continually mixed by a rotor at 5000 rpm. A uniform distribution of particles was achieved by pumping a constant rate of this mixture (3.5 ml min^{-1}) through a series of 16 evenly spaced releasing tygon tubes placed 4 m upstream from the target panels (Harvey et al. 1995). The flow was shut off and the panel removed. Particles that had settled on the false bottom of the flume during the experiment were removed with a shop-vac vacuum cleaner and a new panel installed for the next run. The order in which the experimental panels were tested and the flow velocity were randomly determined at the start of each day. In total, 5 replicates for each panel type × water velocity combination were run.

Whether deviations from 1-dimensionality in the flume flow field significantly affected distributions of particles within the test section was examined by comparing the density of particles across the panels for both panels A and C at flow velocities of 3, 5 and 10 cm s^{-1}. The number of particles observed in ten 1 × 200 mm quadrats (oriented across the crevices parallel to the flow) was determined for each of the six 5 cm wide zones (oriented parallel to the flow) and covered the 30 cm width of each panel. These data were compared by ANOVA. Distribution of particles across the flume showed significant differences among zones but close examination of the results showed no systematic bias among trials (n = 5) within or among current velocities. When comparisons were made among 4 successive sections of 5 × 20 cm in the downstream direction along the surface of smooth panels (type A, 5 replicates), no significant differences were observed among sections, indicating uniform distribution of particles in the downstream direction. Vertical rods inserted into smooth panels (type A) were used to verify the cross-stream distribution of particles in the 1st cm of water above the panel. The rods (0.3 cm in diameter, 2 cm high) were evenly spaced (3 cm apart) across the central part (30 cm wide) of the flume. No significant differences in particle abundance were observed among rods which had been inserted to verify cross-stream particle distribution at flow velocities of 3 and 10 cm s^{-1}; only 1 rod collected more than the others at

5 cm s^{-1}, but this rod was outside the section where samples were taken for the heterogeneity and complexity experiments.

Sampling. Two scales of observation were used to investigate particle distribution on the panels: (1) the scale of the entire panel and (2) the scale of a crevice, either 1, 10 or 100 mm. Particle abundance was determined first for the entire panel and second for each surface type within the panel. To minimize contour (border of panels) effects (Brault & Bourget 1985), only the central zone (200 × 200 mm) of the panels was sampled.

We sampled the panels following a hierarchical method such that 20% of the total surface area (TSA) of each surface was sampled. Randomly chosen 1 × 200 mm quadrats parallel to the crevices (i.e. normal to the flow) allowed a minimum of 5 samples to be taken for any given surface type. Each type of panel was tested 5 times. The increase in TSA for panels of 2nd, 3rd and 4th order complexity increased by factors of 1.5, 2.25 and 3.375, respectively, over that of the smooth panel (1st order complexity). Since each 200 mm length quadrat covered the entire width of the experimental area on the panels, this compensated for any lateral variation in particle density.

Statistical analyses. The number of settled particles was compared among types of panels using particle density (number of particles cm^{-2}) for each panel. Density data were analysed using the following model for a 2-way nested ANOVA:

$$y = \mu + Velocity + Day\,(Velocity) +$$
$$Panel + Velocity \times Panel + Error \qquad (2)$$

where μ is a constant, *Velocity* is the mean flow velocity (3, 5 or 10 cm s^{-1}), *Day* is the day of the experiments (1, 2, 3, ... 15) which is nested into the *Velocity* term and *Panel* refers to the type of panels used (A, B, C, ... H). There were 5 replicates for each condition (see Kirk 1982). The *Day (Velocity)* term was calculated to be used as an error term for *Velocity*. When the ANOVA was significant, LS Means multiple comparisons were used in order to find out which means differed (Milliken & Johnson 1992). *Day (Velocity)* is not meaningful for our interpretation, other than serving as an error term, and will not be considered further.

Density data among surface types were compared for each type of panel using the following nested crossed ANOVA model:

$$y = \mu + Velocity + Day\,(Velocity) + Surface +$$
$$Velocity \times Surface + Day\,(Velocity) \times Surface$$
$$+ Error \qquad (3)$$

where μ is a constant, *Velocity* is as defined previously, *Day* is the day of the experiments (1, 2, 3, ... 15) which is nested into the *Velocity* term, and *Surface* refers to the type of surfaces used (see Fig. 1). *Day (Velocity)*

was calculated to serve as error term for *Velocity* and *Surface*, and *Day (Velocity)* × *Surface* was calculated to serve as error term for *Velocity* × *Surface*, and will not be considered further. There were no significant interactions between velocity and types of panels (*Surface* × *Velocity*), hence these interactions will not be considered further.

The statistical analyses were carried out on the details of surface orientation. LS Means tests revealed that the 2 sides of a crevice were rarely significantly different, irrespective of the size of the crevice. The axes of the crevices were oriented with 3 distinct possibilities: the axis could be vertical, +30° to horizontal or −30° to horizontal (see Fig. 2). When the axis of the crevice was vertical or −30° to horizontal, densities of particles on both sides of the crevices were not significantly different from one another. However, when the axis of the crevice was +30° to horizontal, densities of particles on both sides of the crevices were significantly different. Thus, we separately considered the 2 sides of a crevice only when the axis of the crevice was +30° to horizontal. We ran the ANOVAs and the LS Means tests over again with the data containing less types of surfaces. The results from the pooled approach are shown in the next section instead of the results with the original unpooled approach. One ANOVA was carried out for each type of panel instead of one ANOVA for all types of panels because of the model complexity. All analyses were carried out on data transformed to the two-third power ($x^{0.66}$) to reduce heteroscedascity (Montgomery 1991). Sign tests for matched pairs (Conover 1980) were used to examine the null hypothesis of uniform distribution of particles, regardless of the presence of crevices.

Experiments with preserved larvae. Experiments were conducted using preserved *Placopecten magellanicus* larvae to determine if distribution patterns were similar to the PVC particles on the panels. Because of the few larvae available, this experiment was performed using only panel H. Panel H was selected because it contained all heterogeneity types (4th order complexity). Data analyses were performed using an ANOVA model similar to that used for PVC particles. The distribution of *P. magellanicus* larvae was compared to that of PVC particles by Kendall's coefficient of concordance (Conover 1980)

RESULTS

Comparisons among types of panels

There were significant *Panel* and *Velocity* effects on particle density (Table 2a). The density of particles decreased significantly with increasing complexity,

with panel types A and B consistently collecting more and G and H fewer particles cm^{-2} for each flow velocity (Table 3). For a given level of complexity, panels with 1 mm crevices tended to collect the highest density (Table 3), but this effect was never significant. The density of particles collected at 3 and 5 cm s^{-1} was significantly higher than for 10 cm s^{-1} for all experiments (Fig. 3). The ANOVA showed that the *Velocity* × *Panel* term was not significant (Table 2a).

Comparisons among types of surfaces within panels at all scales

Significant surface effects were observed for all types of panels (Table 2b to i). For panels with 2nd order complexity, particle density was higher inside 1 mm crevices than on adjacent flat surfaces of panel type B, whereas the converse was true for 10 and 100 mm crevices, panel types C and D, respectively (Table 4). Panels with 3rd and 4th order complexity showed variable and complex effects.

Nesting of crevices resulted in the axis of the smallest crevices being inclined at −30° instead of vertical (90°). In this case, the density of particles on the lower side (closest to the horizontal) was consistently higher than that on the upper side (Tables 4 & 5). For the panel with 4th order complexity (panel H), the scale of heterogeneity also influenced the magnitude of differences between the 2 sides of the +30° crevices. For 1 mm crevices the 2 sides had high but different densities of particles (Fig. 4, panel H, types of surface 25a and 25b) whereas the lower side of the 10 mm crevices
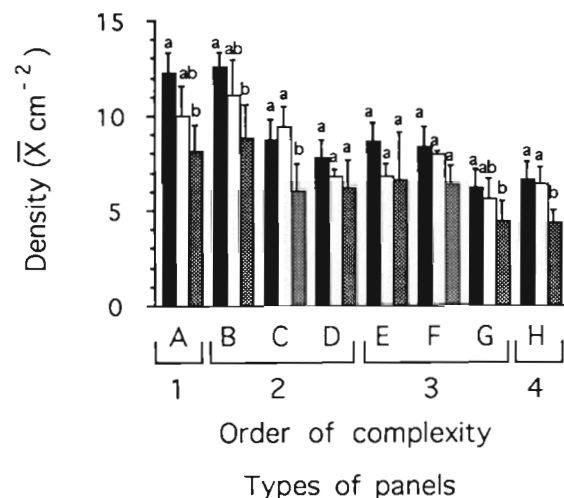

Fig. 3. Density of inert particles (±SE) on all types of panels. Flow velocity: ■ = 0.03, □ = 0.05, ▨ = 0.10 m s^{-1}, respectively. Letters above histograms indicate means that are not significantly different between flow velocities

Table 2. Crossed nested ANOVAs showing (a) the effects of *Velocity*, *Day (Velocity)* and types of *Panels* on particle density, (b to i) the effects of *Velocity*, *Day (Velocity)* and types of *Surfaces* on number of particles for every type of panels, and (j) on total number of preserved *Placopecten magellanicus* larvae on panel H. The effects of *Velocity* were evaluated using *Day (Velocity)* as an error term. The effects of *Surface* and *Surface × Velocity* were evaluated using *Surface × Day (Velocity)* as an error term. (•) Not computable since only 1 type of surface was present

Source of variation	df	Sum of squares	F-value	p	Source of variation	df	Sum of squares	F-value	p
(a) Among panels					**(f) Panel E**				
Velocity	2	8.69	12.52	0.0012	Velocity	2	358.75	2.74	0.1049
Day (Velocity)	12	4.16	4.74	0.0001	Day (Velocity)	12	775.54	50.81	0.0001
Panel	7	33.38	65.14	0.0001	Surface	4	1948.17	62.17	0.0001
Panel × Velocity	14	1.85	1.80	0.0514	Surface × Velocity	8	89.02	1.45	0.2021
Error	84	6.15			Surface × Day (Velocity)	48	369.29	6.05	0.0001
Corrected total	119				Error	1275	1624.71		
(b) Panel A					Corrected total	1349			
Velocity	2	391.36	11.44	0.0017	**(g) Panel F**				
Day (Velocity)	12	205.22	16.56	0.0001	Velocity	2	316.64	7.51	0.0077
Surface	0	0.00	•	•	Day (Velocity)	12	262.97	17.02	0.0001
Surface × Velocity	0	0.00	•	•	Surface	4	2862.98	92.36	0.0001
Surface × Day (Velocity)	0	0.00	•	•	Surface × Velocity	8	91.99	1.48	0.1881
Error	585	604.27			Surface × Day (Velocity)	48	371.99	6.26	0.0001
Corrected total	599				Error	1275	1579.30		
(c) Panel B					Corrected total	1349			
Velocity	2	498.61	7.21	0.0088	**(h) Panel G**				
Day (Velocity)	12	410.82	32.96	0.0001	Velocity	2	249.78	3.54	0.0619
Surface	1	389.03	57.37	0.0001	Day (Velocity)	12	428.31	14.79	0.0001
Surface × Velocity	2	60.02	4.23	0.0406	Surface	4	5685.50	262.03	0.0001
Surface × Day (Velocity)	12	70.91	5.69	0.0001	Surface × Velocity	8	76.18	1.76	0.1098
Error	870	903.68			Surface × Day (Velocity)	48	260.38	2.27	0.0001
Corrected total	899				Error	1275	3041.67		
(d) Panel C					Corrected total	1349			
Velocity	2	609.82	12.68	0.0011	**(i) Panel H**				
Day (Velocity)	12	288.60	18.80	0.0001	Velocity	2	727.85	13.87	0.0008
Surface	1	1021.99	269.74	0.0001	Day (Velocity)	12	314.89	23.64	0.0001
Surface × Velocity	2	80.42	10.61	0.0022	Surface	11	11823.78	427.92	0.0001
Surface × Day (Velocity)	12	45.47	2.96	0.0005	Surface × Velocity	22	373.27	6.75	0.0001
Error	870	1112.85			Surface × Day (Velocity)	132	331.57	2.26	0.0001
Corrected total	899				Error	1845	2048.44		
(e) Panel D					Corrected Total	2024			
Velocity	2	109.90	2.78	0.1020	**(j) Panel H (*Placopecten magellanicus*)**				
Day (Velocity)	12	237.36	20.23	0.0001	Velocity	2	21.70	2.01	0.1893
Surface	1	1132.90	663.88	0.0001	Day (Velocity)	9	48.53	4.74	0.0001
Surface × Velocity	2	7.72	2.26	0.1467	Surface	11	546.44	43.69	0.0001
Surface × Day (Velocity)	12	20.48	1.75	0.0532	Surface × Velocity	22	57.54	2.30	0.0009
Error	870	850.60			Error	366	409.37		
Corrected total	899				Corrected total	404			

had a density roughly an order of magnitude higher than that of the upper side (Fig 4, panel H, types of surface 26a and 26b).

For vertical (90°) crevices on 3rd and 4th order complexity panels, both 10 and 100 mm crevices showed the same trends in particle density seen in the simpler, 2nd order complexity panels; particle density was always lower inside than outside of crevices (Table 5). Vertical (90°) crevices of 1 mm, however, did not follow the pattern observed for the 2nd order complexity panel of highest density within crevices. Rather, density did not differ between the inside and outside of crevices when they were nested within 10 mm crevices (Table 4, Fig. 5 panels E, 10 and 11a).

Table 3. Summary of LS Means multiple comparison tests on density of particles; horizontal bars connect means that were not significantly different. Means used for LS Means tests were from transformed data ($x^{0.66}$). Significance level was adjusted to 0.0018 (Bonferroni's correction). Type of panels were ranked in increasing order of density of inert particles on panels. Type of panel A is of the first order of complexity, types of panel B, C and D are of the second order, types of panels E, F and G are of the third and type of panel H is of the fourth

3 cm s⁻¹		G	H	D	F	E	C	A	B
5 cm s⁻¹		G	H	D	E	F	C	A	B
10 cm s⁻¹		H	G	C	D	F	E	A	B

Table 4. Summary of LS Means multiple comparison tests on density of particles among types of surfaces at all flow velocities and types of panels. Horizontal bars connect means that were not significantly different. Means used for LS Means tests were on transformed data ($x^{0.66}$). Significance level was adjusted to 0.005 on types of panels E, F and G and to 0.0008 on type of panel H (Bonferroni's correction). Types of surfaces were ranked in increasing order of density of inert particles

	B	C	D	E	F	G
3 cm s⁻¹	2<3	5<4	7<6	10 11a 11b 9 8	14 15a 15b 12 13	19a 19b 18 17 16
5 cm s⁻¹	2<3	5<4	7<6	10 11a 11b 9 8	14 15a 12 15b 13	19a 19b 18 17 16
10 cm s⁻¹	2<3	5<4	7<6	10 11a 11b 8 9	14 15a 12 15b 13	19a 18 17 19b 16

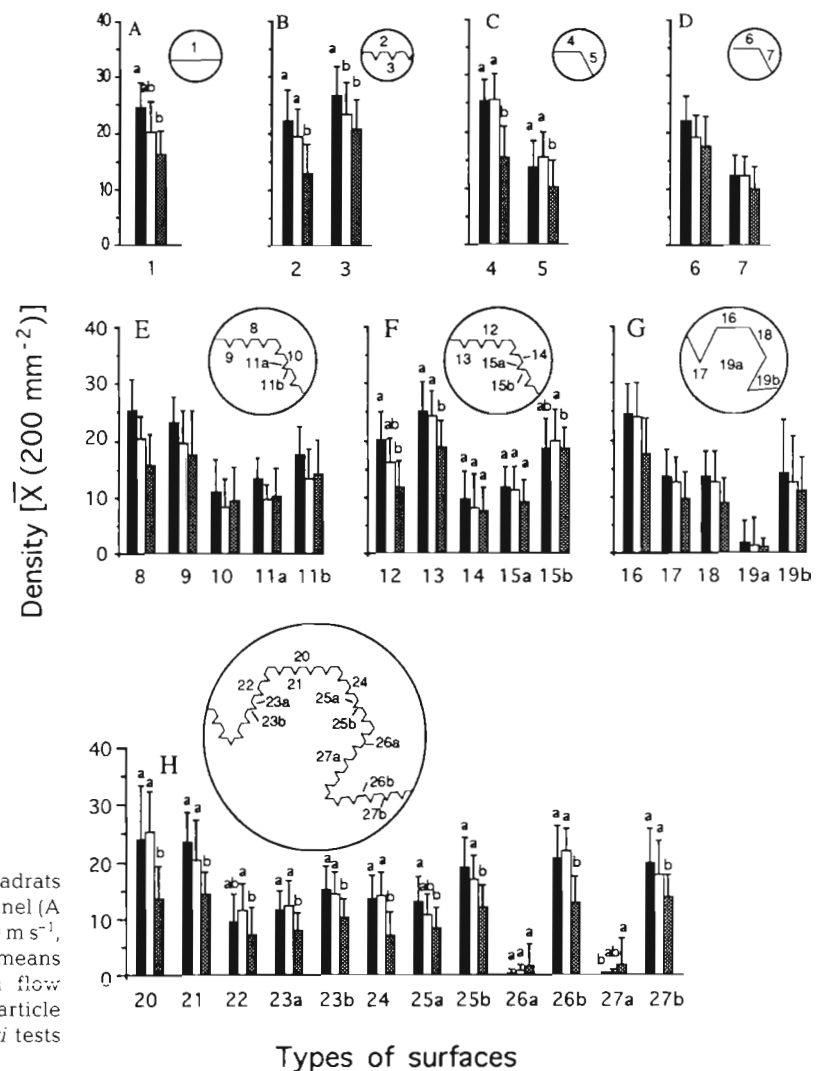|	H
3 cm s⁻¹	27a 26a 22 23a 25a 24 23b 25b 27b 26b 21 20
5 cm s⁻¹	27a 26a 25a 22 23a 24 23b 25b 27b 21 26b 20
10 cm s⁻¹	27a 26a 22 24 23a 25a 23b 25b 26b 20 27b 21

Fig. 4. Density of inert particles in 200 mm² quadrats (±SE) on all types of surfaces for every type of panel (A to H). Flow velocity: ■ = 0.03, □ = 0.05, ▨ = 0.10 m s⁻¹, respectively. Letters above histograms indicate means that are not significantly different between flow velocities. Since velocity had no effect on particle density for panels D, E and G, no *a posteriori* tests were carried out

Types of surfaces

Table 5. Summary of LS Means multiple comparison tests on density of particles among types of surfaces at 10 and 100 mm scales at every flow velocitiy for types of panels E, F, G and H. Horizontal bars connect means that are not significantly different. Means used for LS Means tests were transformed data ($x^{0.66}$). Significance level was adjusted to 0.005 on type of panel H at the 10 mm scale (Bonferroni's correction). Groups of types of surfaces are ranked in increasing order of number of inert particles

	E (10 mm)	F (100 mm)	G (100 mm)
3 cm s^{-1}	(10–11) < (8–9)	(14–15) < (12–13)	(18–19) < (16–17)
5 cm s^{-1}	(10–11) < (8–9)	(14–15) < (12–13)	(18–19) < (16–17)
10 cm s^{-1}	(10–11) < (8–9)	(14–15) < (12–13)	(18–19) < (16–17)
	H (10 mm)		H (100 mm)
3 cm s^{-1}	(26a–27a) < (22–23) < (24–25) < (26b–27b) < (20–21)		(24–25–26–27) < (20–21–22–23)
5 cm s^{-1}	(26a–27a) < (22–23) (24–25) < (26b–27b) (20–21)		(24–25–26–27) < (20–21–22–23)
10 cm s^{-1}	(26a–27a) < (22–23) (24–25) < (26b–27b) (20–21)		(24–25–26–27) < (20–21–22–23)

In summary, density was higher within 1 mm crevices than on adjacent smooth surfaces while the converse was true of 10 and 100 mm crevices. On panels of 3rd and 4th order complexity, the density of particles was higher on the lower side of inclined (+30°) crevices while no differences between sides were observed on panels of 2nd order complexity.

Multiple sign tests were performed to examine the null hypothesis (uniform distribution of particles), regardless of the presence of crevices. In 16 out of 18 tests, 1 mm crevices collected significantly more particles than expected whereas only the inclined (–30°) 1 mm crevices collected less. The 10 and 100 mm crevices also collected more particles than expected, but not as often as 1 mm crevices. Fourteen out of thirty 10 mm crevices and seven out of twelve 100 mm crevices collected significantly more particles than expected. On the upper side of the +30°, 10 mm crevices collected significantly fewer particles than expected.
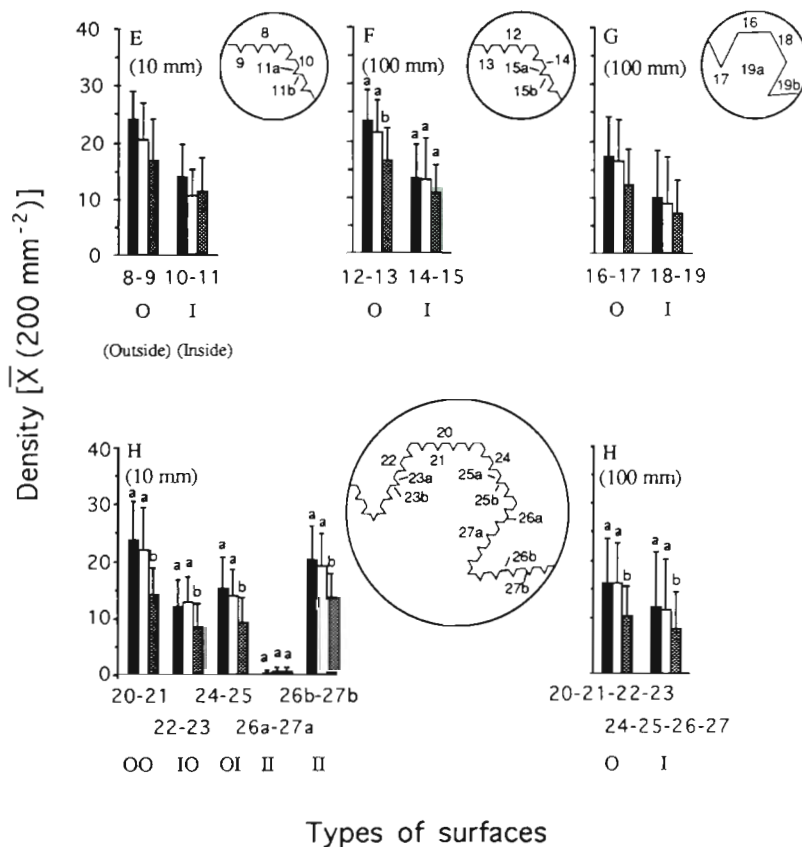

Fig. 5. Density of inert particles in 200 mm^2 quadrats (±SE) on all types of surfaces and scales (10 and 100 mm) of observation for panels E, F, G and H. Flow velocity: ■ = 0.03, □ = 0.05, ■ = 0.10 m s^{-1}, respectively. Letters above histograms indicate means that are not significantly different between flow velocities. Since velocity had no effect on particle density for panels E and G, no a posteriori tests were carried out. For panel E to G, O: outside, I: inside. For panel H at 10 mm, types of surfaces are OO: outside 10 and 100 mm crevices, IO: inside 10 mm but outside 100 mm crevices, OI: outside 10 mm but inside 100 mm crevices, II: inside 10 and 100 mm crevices
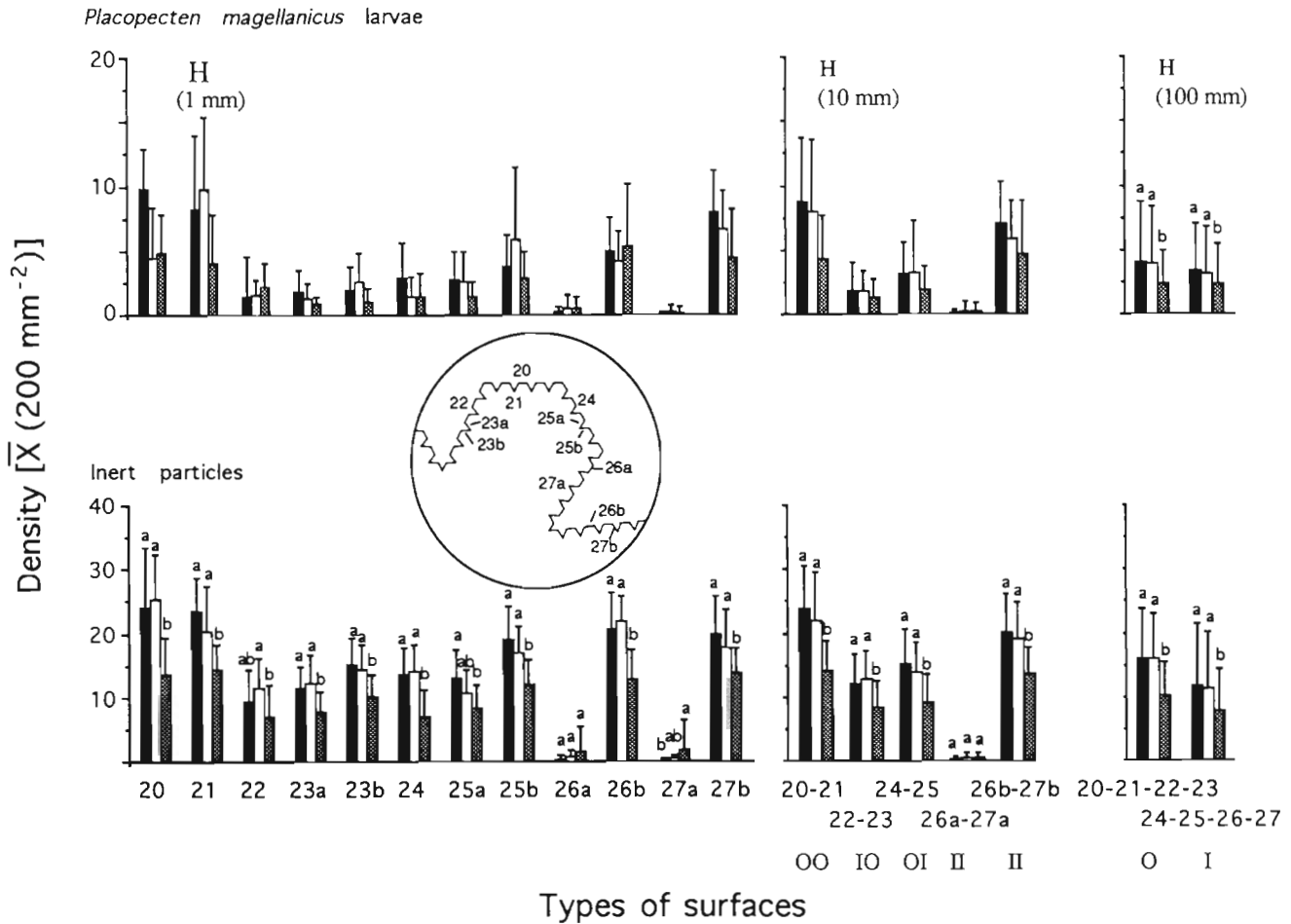
Placopecten magellanicus larvae

Types of surfaces

Fig. 6. Density of preserved larvae and inert particles in quadrats (±SE) for every type of surface and scale (1, 10, 100 mm) of observation on panel H. Flow velocity: ■ = 0.03, □ = 0.05, ▨ = 0.10 m s⁻¹, respectively. Letters above histograms indicate means that are not significantly different between flow velocities. For more details, see Fig. 5

Passive larval accumulation

Dead larvae distribution differed significantly among surface types on panel type H (Table 2j). On a scale of 1 mm, higher densities of larvae were generally observed in vertical crevices and on the lower part of crevices inclined at +30° compared to other surface types (Table 6, Fig. 6). On a 10 mm scale, the lower side of the +30° crevices had higher densities than that of the upper side and no difference was observed on a 100 mm scale (Table 6). Density of larvae did not differ among flow velocities (Table 2j, Fig. 6).

Kendall's coefficient of concordance between distribution patterns of larvae and inert particles at 3 cm s⁻¹ was 0.97, indicating significant concordance (p < 0.05). The coefficients of concordance between distribution patterns of larvae and inert particles at 5 and 10 cm s⁻¹ were high (0.91 and 0.91, respectively), but not significant at 0.05.

DISCUSSION

Influence of scales of heterogeneity

In general, particle density was higher (by ~29%) inside 1 mm crevices than on adjacent smooth surfaces. In contrast, particle density was lower (by ~40%) inside 10 and 100 mm crevices compared to adjacent smooth surfaces. This indicates that particle collection was enhanced by small-scale heterogeneity. These differences due to the scale of heterogeneity might be explained by hydrodynamic processes.

The density of particles in 10 and 100 mm crevices was 40% lower than the density of particles on adjacent smooth surfaces. Given that the crevices have a TSA twice that of flat surfaces, the a priori prediction is that the density of particles in crevices should be half that of flat surfaces, if particles fall uniformly over the panel surface. However, if turbulence or advection toward the

Table 6. Summary of LS Means multiple comparison tests on number of preserved larvae among types of surfaces at scales of 1, 10 and 100 mm for every flow velocity on panel H. Horizontal bars connect means that were not significantly different. Means used for LS Means tests are transformed data ($x^{0.66}$). Significance levels were adjusted to 0.0008 and 0.005 at 1 and 10 mm scales respectively (Bonferroni's correction). Types of surfaces (1 mm) and groups of types of surfaces (10 and 100 mm) are ranked in increasing order of number of inert particles

	H (1 mm)
3 cm s^{-1}	27a 26a 22 23a 23b 24 25a 25b 26b 21 27b 20
5 cm s^{-1}	27a 26a 23a 24 22 25a 23b 26b 20 25b 27b 21
10 cm s^{-1}	27a 26a 23b 23a 24 25a 22 25b 21 20 27b 26b

	H (10 mm)
3 cm s^{-1}	(26a–27a) < (22–23) (24–25) < (26b–27b) (20–21)
5 cm s^{-1}	(26a–27a) < (22–23) (24–25) < (26b–27b) (20=21)
10 cm s^{-1}	(26a–27a) < (22–23) (24–25) < (26b–27b) (20–21)

	H (100 mm)
3 cm s^{-1}	(24–25–26–27) (20–21–22–23)
5 cm s^{-1}	(24–25–26–27) (20–21–22–23)
10 cm s^{-1}	(24–25–26–27) (20–21–22–23)

panel was enhanced by substratum heterogeneity, the density of particles inside would be enhanced. The 1 mm crevices collected significantly more particles than expected indicating that substratum heterogeneity had an influence on hydrodynamic processes which in turn resulted in increased particle collection within these crevices. The 10 and 100 mm crevices collected significantly more particles than expected in only half of the situations indicating that substratum heterogeneity had less influence on hydrodynamical processes and particle collection at these scales.

Our results may be explained by 2 mechanisms. The apparent scale-dependent collection of particles can be linked to average roughness heights (see Table 1). We observe that 1 mm crevices at every flow velocity have an average roughness height below or equal to 5, the upper limit for smooth regime. In the smooth regime, the laminar sublayer is larger than the average roughness (crevice) height, and particles within the sublayer have a strong tendency to fall. Furthermore, the values of average roughness heights for 10 mm crevices all fall into the transition regime (between 5 and 70). The size of the laminar sublayer relative to the one of the crevices does not allow the particles to fall anymore.

The flow velocity also had an effect on particle density. In general, higher densities were collected at lower velocities, 3 and 5 cm s^{-1}, compared to 10 cm s^{-1}. As described before, the experiments were conducted near the lower limit of turbulence, so the particles may have a tendency to settle at low velocities.

Influence of complexity

The increased density of particles in 1 mm crevices was detected inside large crevices. The particle density inside 1 mm crevices was limited by the number of particles entering the larger crevices. This indicates that the hydrodynamic processes occuring on a large scale (10 and 100 mm) influenced the outcome on a smaller scale (1 mm).

Particle versus larval settlement

The experiments with preserved larvae were carried out in order to examine whether the PVC particles used simulated passive larval movement. Kendall's coefficient of concordance (W), varies from 0 to 1, 0 indicating no concordance and 1 perfect concordance. Significant concordance ($W > 0.95$) was observed between larval and inert particle collection at a flow velocity of 3 cm s^{-1} (Kendall's $W = 0.97$) but concordance decreased with flow velocities of 5 and 10 cm s^{-1} (0.90 and 0.91, respectively). These results indicated that the PVC particles 'behaved' as simulated larvae for flow velocities used in the experiments.

Comparisons between field and flume distribution

The patterns of inert PVC particles and of dead larvae accumulating on laboratory panels with 100 mm crevices (panel D) were similar to those found using identical panels for *Mytilus edulis*, *Hiatella arctica* and *Obelia longissima* in the field (Bourget et al. 1994). Panels B or C, with 1 or 10 mm crevices, had a higher abundance of larvae in the field, compared to inert particles in the present study.

The combination of different scales of heterogeneity resulted in different patterns of distribution for larvae in the field and particles in the laboratory. Results from the field study showed that the combination of scales

had little effect on bivalve abundance during early colonization, whereas laboratory results showed that density of particles decreased with increasing complexity.

By comparing the settlement patterns of *Balanus* sp. and *Tubularia crocea* larvae on silicon-treated panels and untreated panels, Lemire & Bourget (1996) suggested that larvae are (1) capable of short distance movements prior to settlement, and (2) capable of movements on the substratum after initial contact. The differences between the patterns of distributions of particles seen in laboratory study and those of larvae in the field (Bourget et al. 1994) support this suggestion.

The results presented in this study apply to hydraulically smooth flow. The hydrodynamical conditions encountered in the field range from hydrodynamically smooth to rough even including supercritical flow. All these flow conditions will likely be encountered by most littoral organisms during their lifespan. The panels used for the experiments are representative of the rocky littoral sites in the St. Lawrence estuary, Canada, which feature crevices of varying sizes and complexity (see Bergeron & Bourget 1986).

The results show that heterogeneity (1, 10 and 100 mm) influenced particle distribution and that the patterns observed were modified with current velocity. The differences observed between larval distributions in the field and particles in the laboratory could be due to movements of larvae on the substrata, avoidance of the substrata by the larvae or differential mortality. Many studies have also suggested that larval distribution resulted from a combination of passive deposition followed by active exploration (Mullineaux & Butman 1991, Walters 1992, Mullineaux & Garland 1993). Further studies with larvae in flumes should be carried out to fully understand the detailed mechanisms involved in larval settlement on complex substrata.

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This article was submitted to the editor