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Macrofouling in unidirectional flow: miniature pipes as experimental models for studying the effects of hydrodynamics on invertebrate larval settlement

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ABSTRACT: Intake pipes are unique habitats that provide an experimental environment for studying the role of hydrodynamics and larval settlement in community development. In this study, we used 5 and 10 mm (inner diameter) tubes as experimental models to mimic intake pipe environments to study the settlement patterns at different flow rates of the bryozoan *Bugula neritina*, the polychaete *Hydroides elegans*, and barnacles of the genus *Balanus*. Clean, unfilmed PVC tubes were used to examine settlement of *B. neritina*. PVC tubes, on which biofilm had been allowed to develop for 48 h, were used for studying attachment of *H. elegans*, while clean tubes were used for investigating settlement of *Balanus* spp. In all but very low flows, the flow velocity and Reynolds number were poorly correlated with patterns of larval settlement. A hydrodynamic measure, which is theoretically independent of the size of the tube, the so called 'velocity gradient', was well correlated with the highest settlement for all 3 species. Comparisons of results from field and laboratory experiments reveal slight differences. Settlement of the small elongate larvae of *H. elegans* was offset to higher shear values in the tubes of smaller diameters. Flow velocities for the highest settlement were from 1 to 3 cm s^{-1} for *B. neritina* and *H. elegans*, and from 3 to 15 cm s^{-1} for barnacles. Velocity gradients for the highest settlement of tubeworms and bryozoans ranged from 8 to 25 s^{-1}, while those for barnacles ranged from 50 to 120 s^{-1}. Barnacles, as reported previously by other authors, did not settle in high numbers when velocity gradients were too low or too high. Barnacles did not settle at <30 s^{-1} velocity gradients. Although the optimal velocity gradient (approx. 20 s^{-1}) for settlement of *B. neritina* was much lower than that for barnacles, some *B. neritina* settled at velocity gradients of >400 s^{-1}. *H. elegans* had the narrowest range of settlement in relation to flow as settlement of this species was the highest from 8 to 20 s^{-1} and hardly occurred above 200 s^{-1}. In general, larval settlement in response to flow is species specific. We suggest that this species specificity is related to larval morphology, swimming ability, and behavior.

KEY WORDS: Fouling · Hydrodynamics · Barnacles · Bryozoans · Tubeworms · *Balanus* · *Bugula* · *Hydroides*

INTRODUCTION

Estuarine and marine sessile invertebrates rapidly colonize (foul) on any submerged surface in their planktonic dispersal stages. The rate of colonization is dependent upon the physical and chemical characteristics of the surface (review by Crisp 1984, Roberts et al. 1991, Holm et al. 1997), the presence of micro- and macrofauna (Knight-Jones 1951, Scheltema et al. 1981, Kirchman et al. 1982, Maki et al. 1989, 1992, 1994, Toonen & Pawlik 1994, Keough & Raimondi 1995), hydrodynamics (Butman 1986, 1987, Wethey 1986, Mullineaux & Butman 1990, 1991, Walters 1992a,b, Mullineaux & Garland 1993, Pawlik & Butman 1993, Walters et al. 1997), larval density (Clare et al. 1992), and larval age (Rittschof et al. 1984). Initial colonization by foul-

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ing organisms plays an important role in the structuring of marine communities (Sutherland 1978, Underwood & Fairweather 1989) and alters the performance and efficiency of manmade installations (Costlow & Tipper 1984, Sasikumar et al. 1989, Alberte et al. 1992, Rittschof & Holm 1997).

Fouling of cooling water intakes and heat exchangers by marine invertebrates has become a prominent technical and economic issue in recent years (Stewart & de Mora 1990). In addition to the classic fouling problems associated with water intakes of ships, seawater is increasingly used along the coasts of the world's oceans for waste disposal, cooling of domestic and commercial buildings, and heat exchange in power plants.

The unidirectional flow environment of water intakes provides a unique habitat in which to study the development of the community structure of marine invertebrates. These pipe systems are ideal fouling environments. The intake flow provides attached filter-feeding organisms with a continuous supply of food and means of waste removal, and the defined nature of the flow provides a controlled environment in which to study community development. Studies on the influence of flow on the settlement of macrofoulers have demonstrated that their settlement patterns are strongly related to characteristics of boundary-layer flow (shear stress) (Wethey 1986). Experiments using tubes to examine the effects of defined flow on settlement patterns have focused on barnacles and have not been performed on other macrofouling organisms.

Experiments using flumes and flat plates in the field have revealed the complex nature of flow (e.g. Wethey 1986, Walters 1992a, b, Mullineaux & Garland 1993, Walters et al. 1997). The surface of a flat plate, however, differs from the surface inside a pipe in terms of light availability, characteristics of the velocity gradient, and consistency of the flow pattern. Inside pipes, darkness prevents survival of autotrophic organisms (e.g. diatoms), whereas such organisms often settle on plates or in flumes. Velocity gradients inside a circular pipe do not change along the length of the pipe, whereas velocity gradients become complicated on the surface of a plate in the field or in a flume (Vogel 1994). Therefore, settlement in a flume system or on flat plates may differ from that inside a pipe.

The objective of the present study was to determine the parameters of colonization in pipe systems for 3 cosmopolitan fouling organisms, the barnacle *Balanus amphitrite* Darwin, the bryozoan *Bugula neritina* (L), and the calcareous tube-building polychaete *Hydroides elegans* (Haswell). Our goal was to provide baseline information useful in future studies in which small pipes and empirical approaches are used to probe community development in well-defined hydrodynamic conditions. We envision practical application of our results in testing procedures for control of fouling in seawater intakes.

METHODS

Our studies were conducted in the laboratory, with larvae that were competent to settle, and in the field, during the times when competent larvae were available in the water column. The life history and larval settlement biology are well known for *Balanus amphitrite* (Walton-Smith 1946, Crisp 1955, Branscomb & Rittschof 1984, Costlow & Tipper 1984, Rittschof et al. 1984, Standing et al. 1984, Rittschof et al. 1985, Rittschof & Costlow 1987, Tegtmeyer & Rittschof 1989, Eckman et al. 1990, Holm 1990, Qiu & Qian 1997a, Qiu et al. 1997), *Bugula neritina* (Maki et al. 1989, Walters 1992a, b, Bryan et al. 1997b), and *Hydroides elegans* (Hadfield et al. 1994, Bryan et al. 1997a, Gosselin & Qian 1997, Lau & Qian 1997, Qiu & Qian 1997b, 1998, Walters et al. 1997, Bryan et al. 1998, Pechenik & Qian 1998, Qian & Pechenik 1998, Harder & Qian 1999). Settlement stage larvae of *H. elegans* (Bryan et al. 1997a) and *B. amphitrite* (Rittschof et al. 1984) can be readily mass cultured in the laboratory and used for settlement studies. *Bugula neritina* broods lecithotrophic larvae. The procedures for laboratory experimentation with larvae of *B. neritina* are also well established (Rittschof & Bonaventura 1986, Maki et al. 1989, Gosselin & Qian 1997, Bryan et al. 1997b, 1998).

Larval cultures for laboratory experiments. ***Hydroides elegans:*** Larvae of *H. elegans* were obtained through laboratory culture by following the methods described in Bryan et al. (1997a). Briefly, adult *H. elegans* were obtained from glass panels that were submerged at a fish farm in Port Shelter, near the Hong Kong University of Science and Technology, or from a laboratory broodstock. Adult worms were placed individually in Petri dishes containing filtered seawater (FSW) and their tubes were gently broken to induce the release of eggs and sperms. Eggs of several females were combined in 1 dish and were treated with a diluted sperm solution collected from 2 to 3 males. Eggs were fertilized within 15 min, and the fertilized eggs were carefully washed 2 times with FSW to remove the excess sperm, then transferred to a 4 l Nalgene beaker containing FSW. Larvae were fed daily with *Isochrysis galbana* (Tahitian strain) at a concentration of approximately 1 to 2×10^5 cell ml^{-1} for 4 to 5 d until they reached a state of metamorphic competence. Cultures were maintained at 24°C under a 15 h light: 9 h dark photoperiod, and aerated (Qiu & Qian 1997b). Larval competence to settle and metamorphose was assessed by pipetting a subsample of larvae into a

solution of 10^{-4} M IBMX in seawater, following the method described in Qian & Pechenik (1998). All settlement experiments were performed with 5 to 6 d-old competent larvae.

Bugula neritina: Adult colonies of *B. neritina* were collected from ropes hanging from a floating dock in a fish farm and transported to the laboratory. These colonies were placed in a beaker containing aerated seawater and kept in the dark overnight. The next morning, colonies were transferred to a beaker containing FSW and placed directly under an artificial light. Adults released larvae in response to the light shock. Larvae were attracted to the light source and within 10 min were pipetted into a clean container of FSW for use in settlement experiments. Feeding was not necessary as *B. neritina* larvae are lecithotrophic and settle within 2 to 3 h of being released (Bryan et al. 1998).

Balanus amphitrite: Broodstocks of the barnacle *B. amphitrite* were collected from an intertidal mud flat in Marina Cove (22° 19' N, 114° 16' E), Hong Kong. These stocks were kept in the laboratory in aerated seawater. Newly hatched *Artemia* sp. larvae were offered daily as food. Broodstock were induced to release nauplii by changing the water and exposing them to a light shock (Qiu & Qian 1997a). Nauplius I larvae were attracted to a point light source and transferred to a 4 l culture container by pipette. These nauplii were kept in a beaker containing FSW at 28°C. Planktotrophic Nauplii II were fed the diatom *Skeletonema costatum* at a concentration of 2×10^6 cells ml^{-1}. Streptomycin and penicillin at final concentrations of 2.50×10^{-4} M and 6×10^{-5} M were respectively added to the culture to suppress bacterial growth. The culture was kept at 28°C on a cycle of 15 h light:9 h dark and examined for the presence of cyprids after 4 d. Larval stages were identified according to Kurata (1962). Cyprids were separated from late stage nauplii by filtration through 250 and 125 µm mesh. Cyprids that were retained by the 125 µm mesh were stored at 6°C in FSW. Cyprids in storage conditions were inactive and did not settle on the container. Three-day-old cyprids were used in experiments. Low temperature storage for 3 days leads to predictable larval settling rates (Rittschof et al. 1984) which have been used in many previous studies (Rittschof & Costlow 1987, Maki et al. 1989, Qiu & Qian 1997a, Qiu et al. 1997).

Experimental setup. A seawater flow system was developed in the laboratory for conducting the experiments (Fig. 1). Seawater was pumped through a submersible pump from the bottom tank to the side tank. A second pump in the side tank pumped seawater from there to the head tank. The water level of the head tank was kept constant throughout the experiments. Volume of water was 4 l in the head tank and 6 l in the side and bottom tanks. A separate study indicated that most larvae of the 3 species settled within the first 50 cm of the tube opening (Qian et al. unpubl. data). Plastic tubes (PVC), 2 m long and 5 or 10 mm in internal diameter, were connected to the bottom of the head tank (9 tubes, 3 replicates per flow) for observing the

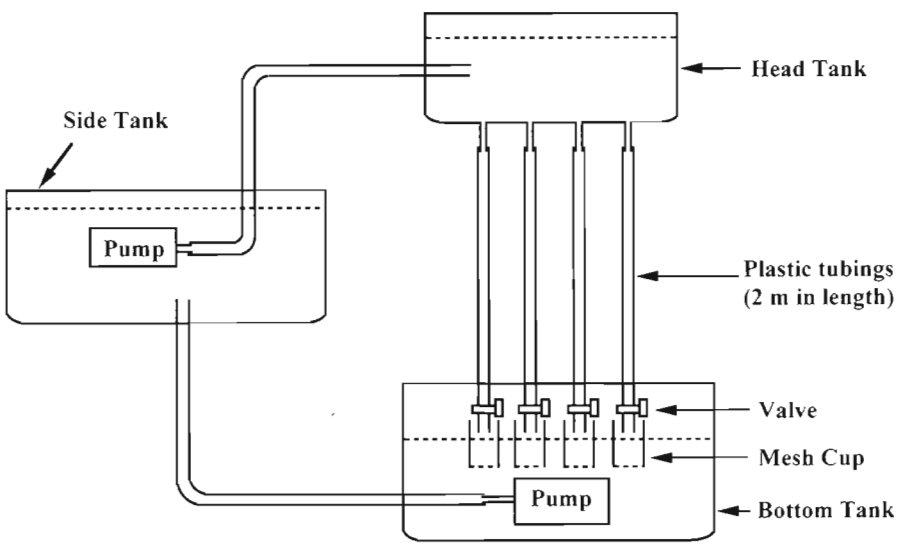

Fig. 1. Illustration of laboratory apparatus used to determine larval settlement in response to specific flow rates. Seawater was pumped through a submersible pump from the bottom tank to the side tank; a second pump in the side tank pumped seawater from there to the head tank. The water level in the head tank was kept constant throughout the experiments. The volume of water was 4 l in the head tank and 6 l in the side and bottom tanks. Plastic tubes (PVC), 2 m long by 5 or 10 mm in internal diameter, were connected to the bottom of the head tank for observing the settlement of *Hydroides elegans* and *Bugula neritina* larvae, whereas clean glass tubes, 30 cm long by 5 mm or 10 mm in diameter, were used for *Balanus amphitrite* larvae (3 replicates per flow). Mesh cups were used to collect the larvae that passed through the tubes

settlement of larvae of *Hydroides elegans* and *Bugula neritina*. For the experiments with *H. elegans*, the tubes were pre-soaked in seawater for 48 h to allow a biofilm to develop on the tube walls. For the experiments with *B. neritina*, clean tubes were used. Settlement experiments with the barnacle larvae were conducted in clean glass tubes (30 cm long and 5 or 10 mm internal diameter), as little or no settlement of barnacles was observed on PVC tubes over 72 h in prior trials. The flow rate in each tube was regulated with an adjustable valve placed at the discharge end of the tube and measured with a volumetric cylinder at the outlet. After adjusting the flow rate, competent larvae were released to the side tank. The larval concentration in the system was 1 larva ml^{-1}. The larvae that did not settle on the tubes were collected by nylon mesh cups (90 µm) kept at the outlets of each tube.

The tubes were removed from the head tank after 12 h for both barnacles and *Hydroides elegans* and after 1 h for *Bugula neritina* larvae. They were filled with FSW and sealed at both ends. The settled larvae were enumerated with a dissecting microscope. The percentage of larval settlement was calculated as the ratio of settled larvae to the larvae that were collected on the mesh plus the settled larvae.

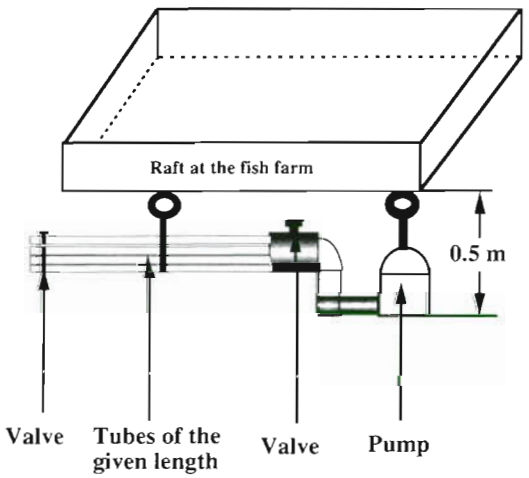

Fig. 2. Illustration of field apparatus used to determine larval settlement in response to specific flow rates. A submersible pump supplied seawater from 1 m depth to the tubes connected to the pump by a connector. Again, PVC tubes, 2 m long by 5 mm or 10 mm in internal diameter, were used for observing *Hydroides elegans* and *Bugula neritina* settlement, whereas glass tubes, 30 cm long by 5 or 10 mm in internal diameter, were used for barnacle settlement. Tubes were suspended horizontally from a floating raft and placed in parallel alignment in a single row in total darkness by fitting all the tubes in larger, black rubber tubes. The rate of flow through each tube was regulated with adjustable valves at the intake and discharge ends of the tubes. Flow rates were checked daily by volumetric measurement at the outlet. Each set of experiments lasted 3 d

Field experiments. Field experiments were conducted at the fish farm where the adult *Hydroides elegans* and *Bugula neritina* were collected for the laboratory experiments. Each set of experiments lasted 3 d. A submersible pump supplied seawater from 1 m depth to the tubes (Fig. 2). Again, PVC tubes, 2 m in length and 5 or 10 mm in internal diameter, were used for observing settlement of larvae of *H. elegans* and *B. neritina*, whereas glass tubes, 30 cm length with internal diameter of 5 or 10 mm, were used for observing barnacle settlement. The tubes were suspended horizontally from a floating raft and placed in parallel alignment in a single row. They were kept in total darkness by fitting all the tubes into larger, black rubber tubes.

Ten flow rates (4 replicated tubes per flow rate) for each tube diameter, ranging from laminar to turbulent flows (Vogel 1994) were tested. Two of the 10 flows for the 5 mm diameter tubes were turbulent, whereas 5 of the 10 flow rates for the 10 mm diameter tubes were turbulent. The rate of flow through each tube was regulated with adjustable valves at the intake and discharge ends of the tubes. Flow rates were checked daily by volumetric measurement at the outlet.

Temperature and salinity of the seawater were measured daily during the experiments with a thermometer and a portable refractometer (ATAGO S/Mill). The abundance of settlement-stage larvae was estimated from 4 l samples of seawater collected daily from a depth of 1.0 m. The experiments were conducted under the same hydrobiological conditions in order to avoid fluctuations in parameters that might affect the settlement rates of larvae.

After each deployment, the tubes were removed from the experimental apparatus and plumed. The settled larvae were enumerated under a dissecting microscope. Since a fine mesh is required to collect larvae that are passing through the tubes and since this mesh is always jammed by plankton and debris within 4 to 6 h, it was technically impossible for us to quantify the total number of larvae that passed through the tubes over 72 h. Therefore, we could not determine the percentage of larvae that settled in the tubes. We report only the total number of larvae settled in the tubes under different flows.

Reynolds number and velocity gradient. The Reynolds number (R_e) and velocity gradient (V_g) can be used to characterize flow properties of any pipe. The Reynolds number of flowing seawater inside a tube was obtained according to Vogel (1994):

$$R_e = 2r\rho/\nu$$

where ν is the kinematic viscosity (0.01 $cm^2\ s^{-1}$) of seawater, r is the radius (cm) of the tube, and ρ is the average flow velocity (cm s^{-1}) inside the tube, which was

the volume flow or flow rate ($cm^3\ s^{-1}$ or $ml\ s^{-1}$) divided by the cross-sectional area (cm^2). The flow shifts from laminar to turbulent when R_e exceeds 2000 (Vogel 1994).

The velocity gradient $(\partial \upsilon/\partial r)_0$ at the internal surface of a tube was calculated according to Crisp (1955):

$$(\partial \upsilon/\partial r)_0 = 4q/\pi r^3$$

where q is the flow rate through the tube and r is the radius (cm). The velocity gradient was determined 500 µm off the surface of the tube.

It should be pointed out that since different species responded to different flow rates and were in tubes with different diameters, different flow rates as well as different flow treatments were thus used in this study of 3 different species.

RESULTS

Field experiments with *Bugula neritina*

The plots in Fig. 3 showed that settlement with respect to mean flow velocity and the Reynolds number was dependent upon the diameter of the tube (Fig. 3). While larval settlement of *B. neritina* decreased as the mean flow increased in the 2 diameters of tubes, settlement in relation to mean flow was higher at the same velocity in the larger diameter tubes. Settlement in relation to the Reynolds number was also dependent upon tube diameter. In the small diameter tubes, settlement decreased to 0 in laminar flow, at a Reynolds number of 1000. In the larger tubes, settlement continued well into regions of turbulent flow.

The velocity gradient (Crisp 1955) reflects the velocity of the fluid stream as the larva approaches the surface. Unlike mean flow velocity and the Reynolds number, the velocity gradient reflects the hydrodynamics near the surface of all sizes of tubes and allows direct comparison of responses of larvae to flow in tubes of different diameters. The velocity gradient is the best descriptor of settlement in the 2 diameters of tubes. When number of larval settlement is plotted in relation to velocity gradient, the data for both sized tubes are in close agreement (Fig. 3). Larvae in both diameters of tubes settled most frequently at a velocity gradient of 15 to 25 s^{-1}.

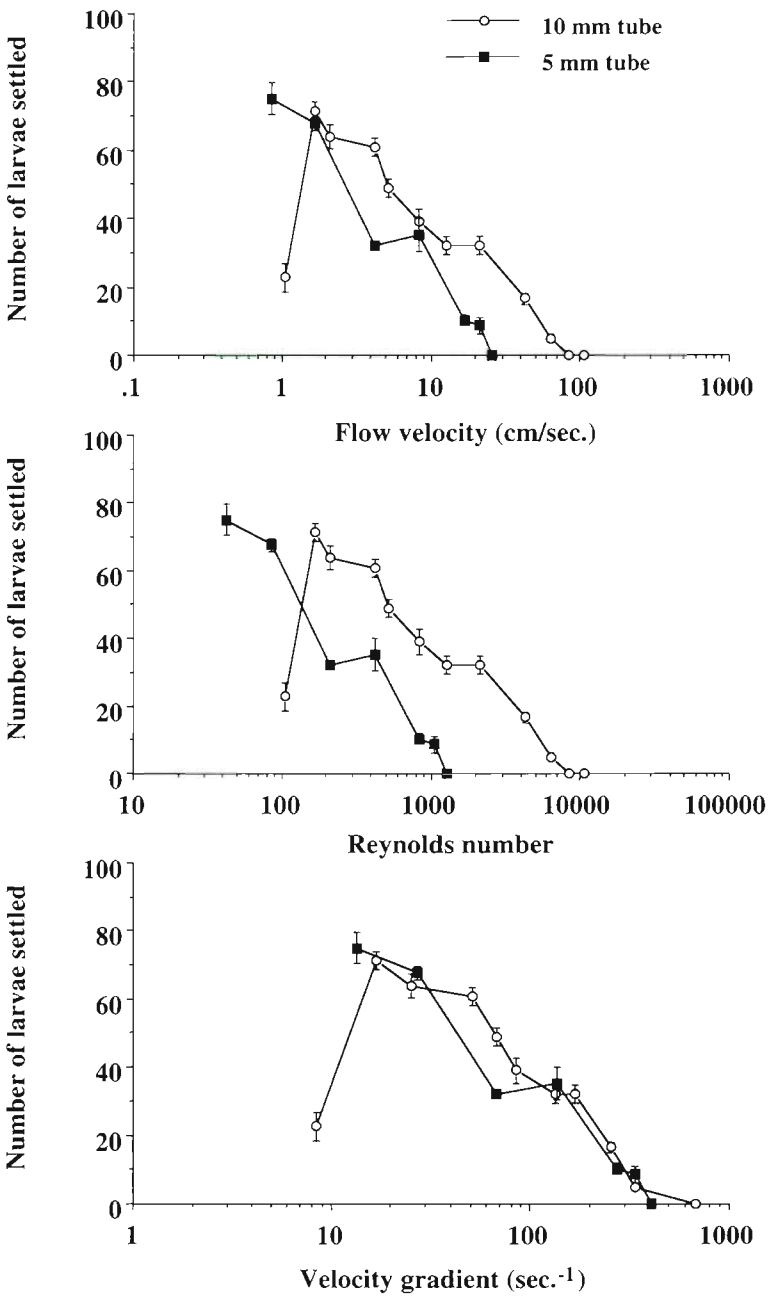

Fig. 3. *Bugula neritina*. Settlement in 5 and 10 mm diameter tubes in the field. Mean number of larvae ±SD is plotted against mean flow velocity (upper panel), Reynolds number (middle panel), and velocity gradient (lower panel)

Laboratory experiments with *Bugula neritina*

Data from laboratory experiments using 10 mm diameter tubes agreed closely with data from the field experiments (Fig. 4). Settlement of *B. neritina* was the highest at low mean flow velocity and continued well into turbulent flow. Settlement was the highest at velocity gradients between 10 and 20 s^{-1}.

It should be pointed out that larval settlement of this species in 5 mm diameter tubes of different flows was investigated previously in the laboratory. Trends were similar to those observed in 10 mm tubes but within a narrower flow regime. However, the data were collected by a different research staff at different times and with a much higher larval density (10 times higher). We therefore feel that it is not appropriate to include this earlier data set in the present study because the experimental conditions were different.

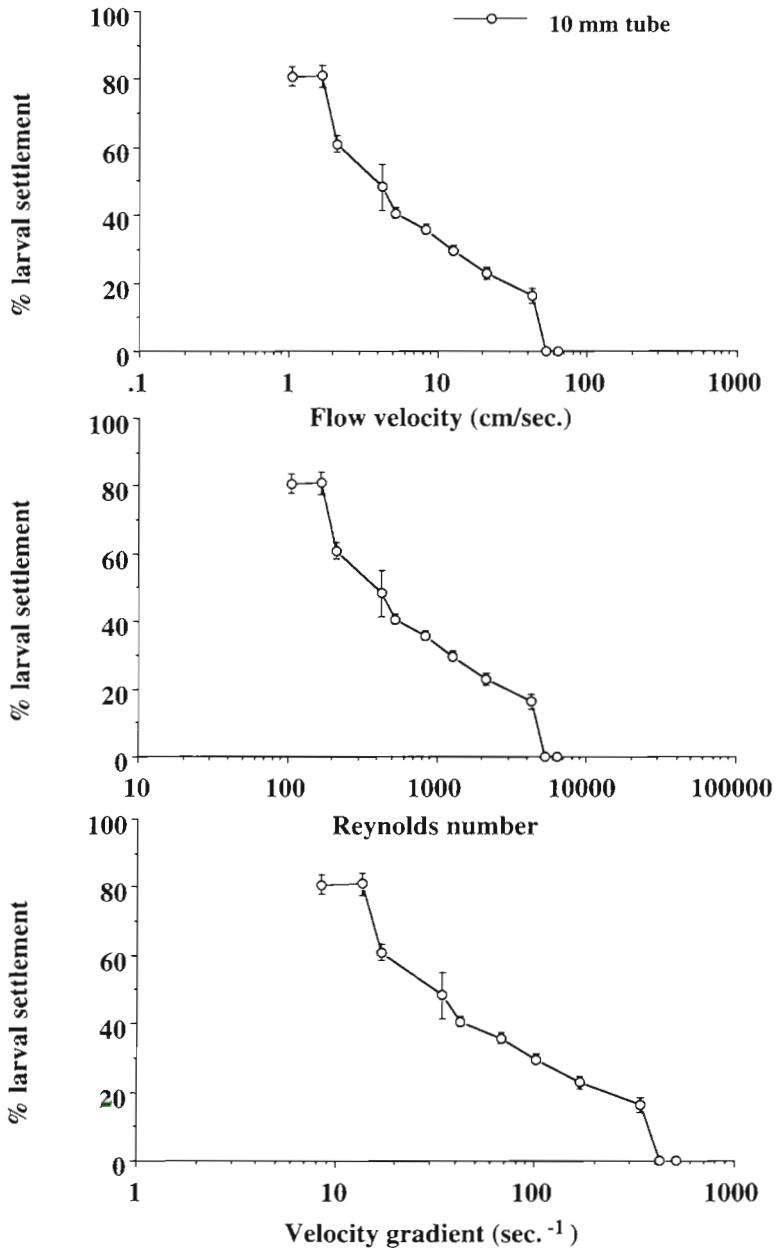

Fig. 4. *Bugula neritina*. Settlement in 10 mm diameter tubes in the laboratory, with laboratory-reared larvae. Mean percentage settlement ±SD is plotted against mean flow velocity (upper panel), Reynolds number (middle panel), and velocity gradient (lower panel)

Laboratory experiments with *Hydroides elegans*

Results of experiments using laboratory-reared larvae of *Hydroides elegans* were similar but not identical to the results of experiments with larvae of *Bugula neritina* (Fig. 5). *H. elegans* settled preferentially in very low mean flow velocities. The highest settlement was at flow velocities from 0.3 to 2 cm s^{-1} in 5 mm diameter tubes and 1 to 2 cm s^{-1} in 10 mm diameter tubes. At low flow velocities, the differences between large and small diameter tubes were minimized and the settlement data for both tube sizes were similar. Although the Reynolds numbers were always in the laminar range, settlement in relation to the Reynolds number depended strongly on tube diameter.

Settlement of *Hydroides elegans* larvae was the highest at velocity gradients from 8 to 20 s^{-1}. There was a clear difference in the relationship between settlement and velocity gradient for the 5 mm diameter tubes as compared with the 10 mm diameter tubes. Settlement was higher in higher velocity gradients in the smaller diameter tube.

Field experiments with *Balanus* spp.

We do not know with certainty the species identity of the balanoid barnacles that settled in the field flow experiments. Most balanoid barnacles have very similar cypris and early juvenile stages and can only be identified with certainty after they have grown. The field data reveal dramatic effects of the tube size on the settlement of barnacles (Fig. 6). Flow velocities and Reynolds numbers for the highest settlement differed greatly between the 5 and 10 mm tubes. The differences in flow velocities and Reynolds numbers associated with the highest settlement values were approximately 6-fold. Velocity gradients for the highest settlement in the different sized tubes were in close agreement, between 90 and 120 s^{-1}.

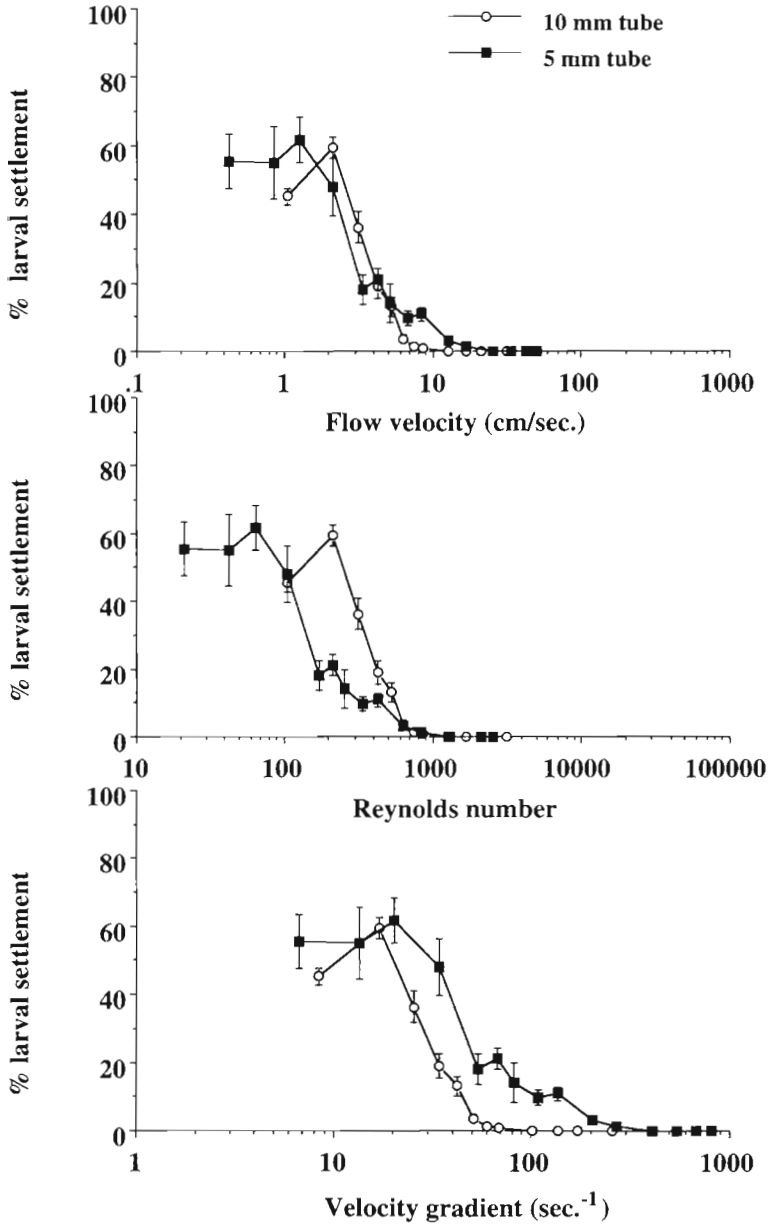

Fig. 5. *Hydroides elegans*. Settlement in 5 and 10 mm diameter tubes in the laboratory, with laboratory-reared larvae. Mean percentage settlement ±SD is plotted against mean flow velocity (upper panel), Reynolds number (middle panel), and velocity gradient (lower panel)

Laboratory experiments with *Balanus amphitrite*

Results of laboratory experiments using mass-cultured larvae of *Balanus amphitrite* show a pattern similar to that observed in the field experiments (Fig. 7). Flow velocities and Reynolds numbers associated with the highest settlement differed by a factor of approximately 6. Again, there was close agreement between the tubes of different diameters with respect to the velocity gradient associated with maximum settlement. The highest settlement of laboratory barnacles in the range of 50 to 100 s^{-1} was slightly lower than the velocity gradients associated with the highest settlement in the field.

Comparisons between the groups

Larvae of the 3 organisms all responded differentially to the flow conditions presented. *Bugula neritina* settled maximally in low flow conditions but settled over a wide range of flows, while *Hydroides elegans* settled maximally in very low flow conditions and settled over a relatively narrow range of flows. Both bryozoans and tubeworms settled maximally at velocity gradients of 8 to 25 s^{-1}. In contrast, barnacles settled over a relatively narrow range of higher flow velocities and maximally in velocity gradients 3 to 5 times higher than were optimal for the other 2 groups.

DISCUSSION

Laboratory and field settlement experiments using 3 major fouling species, barnacles *Balanus amphitrite*, bryozoans *Bugula neritina*, and tubeworms *Hydroides elegans*, were conducted to quantify larval settlement in tubes of different diameters with unidirectional flows that ranged from laminar to turbulent. In all but the cases of very low flow, the Reynolds numbers correlated poorly with patterns of settlement because settlement at a given Reynolds number differed between the tubes of different diameters. The velocity gradient (Crisp 1955) correlated well with the highest settlement for all 3 species in both diameters of tubes, as settlement at a given velocity gradient of a given species was similar in tubes of different diameters. Flow velocity for the highest settlement for all 3 fouling species in the tubes used ranged from 1 to 3 cm s^{-1} for both bryozoans and tubeworms and 3 to 15 cm s^{-1} for barnacles. Velocity gradients for the highest settlement of tubeworms and bryozoans ranged from 8 to 25 s^{-1}, while those for barnacles were 75 to 120 s^{-1}. Settlement of barnacles, as reported previously (Walton-Smith 1946, Crisp 1955), was lower when velocity gradients were too low or too high. Barnacles

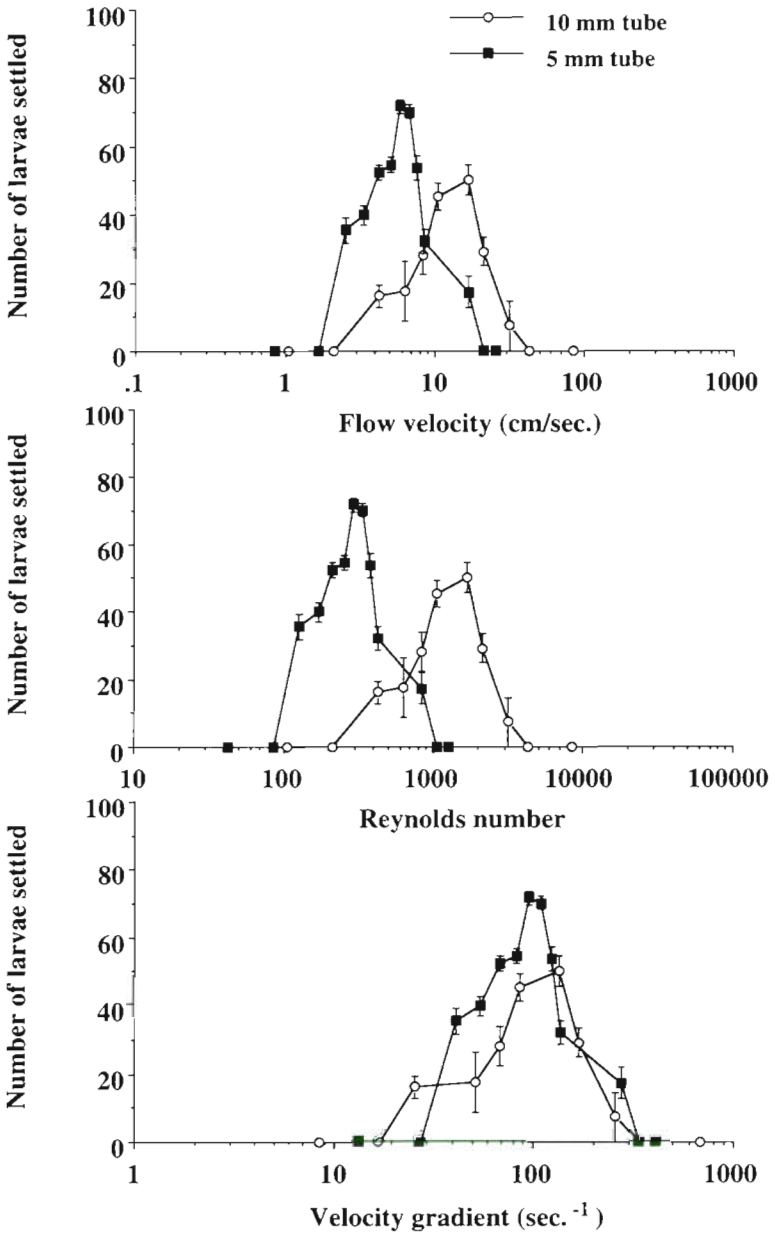

Fig. 6. *Balanus* spp. Settlement in 5 and 10 mm diameter tubes in the field. Mean number of larvae ±SD is plotted against mean flow velocity (upper panel), Reynolds number (middle panel), and velocity gradient (lower panel)

did not settle in velocity gradients $<20\ s^{-1}$. In contrast, although settlement of bryozoans was the highest at a velocity gradient of approximately $20\ s^{-1}$, some *B. neritina* settled at velocity gradients of $>400\ s^{-1}$. Tubeworms had the narrowest range of settlement in relation to flow. Settlement for tubeworms was greatest from 8 to $20\ s^{-1}$ and hardly occurred above $200\ s^{-1}$.

In the field barnacles, bryozoans, and tubeworms settled in the same habitat (Sutherland 1978, Roberts et al. 1991, Walters 1992a, Gosselin & Qian 1996). Differential responses to velocity gradients may aid in partitioning the heterogeneous microenvironment and may reflect differences in the phase of the tide when larvae settle. Our data, though generated by entirely different experiments, are consistent with conclusions of field studies of larval settlement of congeneric bryozoans that different species responded differentially to different flow characteristics (Mullineaux & Garland 1993). A comparison of the larval swimming ability of *Bugula neritina* and *Balanus amphitrite* shows that the ciliated bryozoan larvae are very weak swimmers. The fact that some bryozoan larvae settle over a wide range of velocity gradients is consistent with their dispersal biology in which competent larvae are apparently released by light cues regardless of the stage of the tide. They settle rapidly (Roberts et al. 1991). Similar to *B. neritina*, larvae of *Hydroides elegans* avoid or are incapable of settling in high shear and are routinely found in low flow habitats. Our results are consistent with reports of tubeworm settlement on flat plates with differing hydrodynamics (Mullineaux & Garland 1993).

Crisp (1955) argued convincingly that settlement behavior could best be explained by the velocity gradient. When our barnacle settlement data were plotted based upon velocity gradients, data for the different diameter tubes were in close agreement. Our data are also consistent with those of Walton-Smith (1946) (recalculated by Crisp 1955), who used even larger diameter tubes, and with those of Rittschof et al. (1984), who quantified only behavior of *Balanus amphitrite* in response to flow. This suggests that large tubes and large flows can be modeled in many respects like small tubes and relatively low flows. Previous studies used *B. amphitrite* from the Atlantic ocean. Moreover, maternal and dietary effects on attachment behavior of *B. amphitrite* have been documented (Holm 1990) and may explain the differences we observed between laboratory and field experiments with barnacle larvae.

Larval shape, swimming ability, and behavior that results in settlement in optimal conditions for adult feeding are likely explanations for deviations from expected results based solely upon hydrodynamics. Results for *Bugula neritina* did not deviate dramatically from what would be expected if larvae were simply

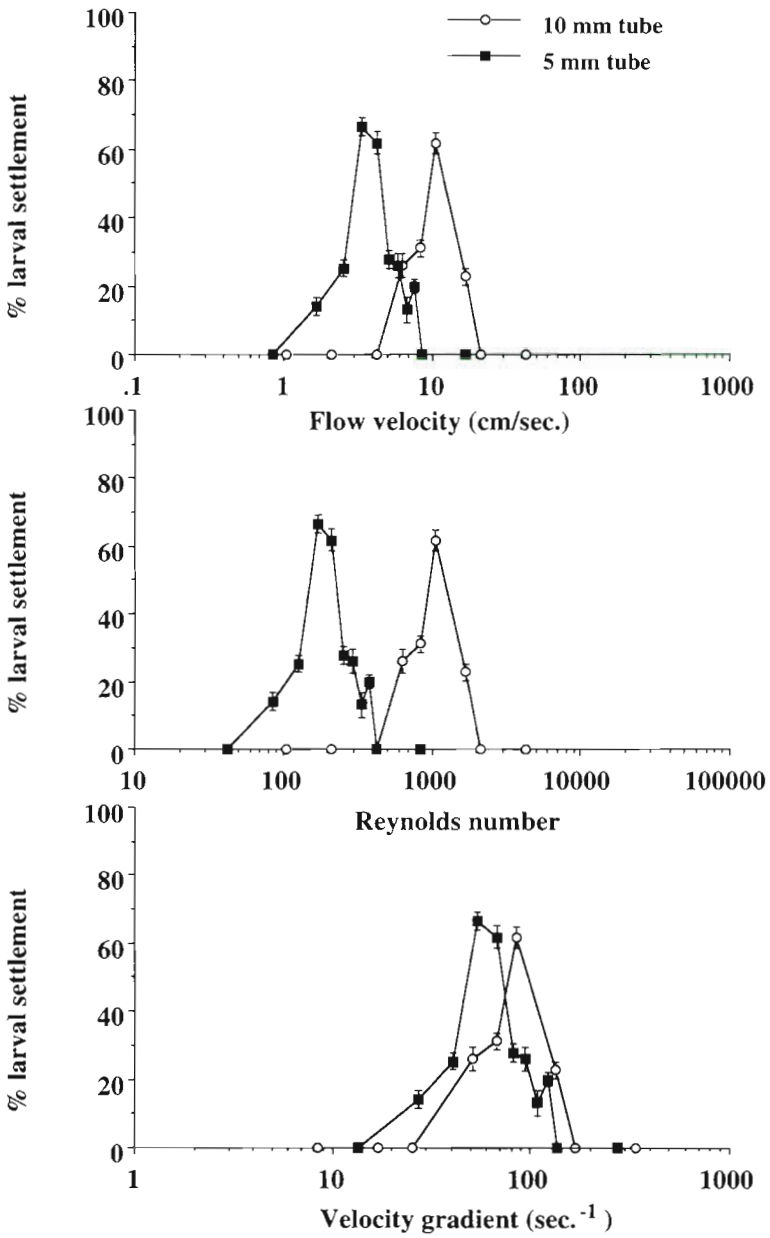

Fig. 7. *Balanus amphitrite*. Settlement in 5 and 10 mm diameter tubes in the laboratory, with laboratory-reared larvae. Mean percentage settlement ±SD is plotted against mean flow velocity (upper panel), Reynolds number (middle panel), and velocity gradient (lower panel)

acting as passive particles. *B. neritina* larvae are relatively large (600 µm spherical), swim very poorly, and are released and settle in the morning. They are capable of swimming at a rate of approximately 0.5 mm s^{-1} in a straight line. Their feeding structures are small and they lack skeletal elements. *B. neritina* adults are found in a huge variety of flow regimes from quiescent areas to areas with tidally driven 6 knot currents, indicating that larvae of this species can settle in the flows of a wide velocity range.

The prediction by Crisp (1955) that velocity gradient should best describe the responses of larvae in tubes holds for barnacle and bryozoan larvae, but it does not hold for *Hydroides elegans* larvae. *H. elegans* larvae are elongated, approximately 275 µm long (Walters et al. 1997) and 125 µm wide. Compared to *Bugula neritina*, *H. elegans* larvae are strong swimmers and can swim at a rate of approximately 1.5 cm s^{-1} (Qian unpubl. data). The adult form is a recumbent tube that eventually grows several centimeters off the substrate. Larval swimming behavior in the laminar flow of the smaller diameter tube may account for the deviation from the expected agreement for data from the large and small diameter tubes.

Barnacle larvae are very strong swimmers for short distances (Crisp 1955) and can swim as fast as 10 cm s^{-1}. Settlement is gregarious and mediated by several pheromones (Crisp & Meadows 1962, Yule & Crisp 1983, Rittschof et al. 1984, Rittschof 1985). The adults are volcano shaped. The feeding structures of juvenile and adult barnacles are relatively large and are reinforced with skeletal elements. Barnacle data may fit the expected positive relation of velocity gradient to settlement response well because their swimming capabilities perpendicular to flow are well beyond the dimensions of the tubes.

In unidirectional flowing seawater intakes, all 3 species should readily colonize surfaces with velocity gradients of <120 s^{-1}. Even if the velocity gradient is considerably above 120 s^{-1}, it is likely that all 3 species would successfully colonize the surface due to the ability of *Bugula neritina* and *Balanus amphitrite* to settle in velocity gradients approaching 300 s^{-1}. Once some larvae settle and grow, the local flow regime will be altered, resulting in areas of low shear stress becoming available for colonization (Wethey 1986, Walters 1992b, Walters et al. 1997). Although far from the physical complexity of a natural community, artificial communities can help our understanding of the importance of hydrodynamics in community development in less well-defined environments. The use of multiply replicated small pipes with defined flow meets many of the criteria for effective ecological study of the role of hydrodynamics and larval recruitment in community development (Mullineaux & Garland 1993).

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