

DEPOSITION AND SWIMMING BEHAVIOUR OF *CHICOREUS RAMOSUS* L.
(GASTROPODA: MURICIDAE) LARVAE AT VARYING SUBSTRATE GRAIN
SIZES AND CURRENT VELOCITIES IN A LABORATORY FLUME FLOW

Svend J. Steinfeldt

Department of Marine Ecology, Institute of Biological Sciences, University of Aarhus,
Finlandsgade 14, DK-8200 Århus N, Denmark

ABSTRACT

In a laboratory flume at Phuket Marine Biological Center, Thailand, boundary layer profiles were described above 3 substrate grain sizes 0.5, 3.3, and 5.4 mm at the free stream current velocities 3, 8, and 13 cm sec⁻¹. Shear velocities ranged from 0.22±0.02 cm sec⁻¹ to 0.99±0.24 cm sec⁻¹. Roughness Reynolds numbers were between 1.8±0.1 and 66.7±15.9. At 3 cm sec⁻¹, shear velocity was not correlated to grain size. At 8 cm sec⁻¹ and 13 cm sec⁻¹, shear velocities were correlated to grain size. Roughness Reynolds numbers were correlated to grain size at all free stream velocities. At 3 cm sec⁻¹, there was no correlation between grain size and number of larvae hitting the bottom. At 8 cm sec⁻¹ and 13 cm sec⁻¹, there was a positive correlation between grain size and number of larval bottom encounters. Larvae close to the bottom could be divided into two groups. One group with horizontally oriented velum and one group with tilted velum. A high fraction of larvae with tilted velum were oriented with their velar lobes behind the shell. Most larvae encountering the bottom seemed to be larvae behaving like passive particles with neutral buoyancy.

INTRODUCTION

Most populations of marine benthic invertebrates are non randomly distributed on the sea bottom (André 1992). Even within limited areas a large variation in temporal and spatial distribution is typical (Petersen 1918; Thorson 1966). In benthic species, with a pelagic larval stage, recruitment may play an especially high role, but to what extent the final distribution is a reflection of varying recruitment has not yet been fully understood (Baggerman 1953; Thorson 1956, 1966; Butman 1986, 1987; Butman *et al.* 1988; André 1992; Bachelet *et al.* 1992).

The settling process is central in the evaluation of the role of recruitment in the distribution of benthic invertebrates (Grosberg 1981; Keough & Downes 1982; Connell 1985; Pawlik 1992)

There has been a dramatic increase in laboratory experiments concerning recruitment since the sixties (Young 1990), and by shortening the interval between observations, estimates of recruitment have been approximated to represent settlement. Direct observations of larvae approaching and landing

on substrates are rare.

Larval swimming capabilities are limited, and a combination of passive deposition and active choice of substrate seems to be a likely situation. Larvae are passively transported horizontally over large geographical distances and may check a very limited area by swimming and drifting, after which settling or re-entry of the overlying current system is possible (Thorson 1950; Butman *et al.* 1988).

If *Chicoreus ramosus* (Linnaeus, 1758) larvae, when reaching settling competence, withdraw their velum and start sinking at maximal speed, they would be deposited in areas with a sandy substrate according to correlations between sinking velocities of larvae and sediment grain sizes made by Butman (1986). This seems to contradict the preference of coarse substrates found for larvae in still water (Steenfeldt & Bussarawit 1992), juveniles in laboratory experiments (Bech 1992), and observations from habitats of adult individuals of the species (Jalk 1992).

This paper is based on direct observations of larvae approaching the bottom in a number of near bottom flow situations generated in a laboratory flume tank.

MATERIALS AND METHODS

Supply and culture of C. ramosus larvae

The experiments were conducted at Phuket Marine Biological Center (PMBC), Phuket, Thailand. Egg capsules of *C. ramosus* were kindly provided by Jintana Nugranad, Prachuap Khiri Khan Coastal Aquaculture Development Center, Thailand. The capsules were transferred to PMBC where hatching took place in cylindrical 100 litre polyethylene tanks filled with 1 μ m filtered sea water. Daily, newly hatched larvae were transferred to 200 or 500 litre polyethylene tanks filled with 1 μ m filtered sea water. Microalgae (*Tetrasalmis* sp.) were added to an approximate density of 20,000 cells ml⁻¹. Every 3 days the water was changed.

Detailed descriptions of the culture of *C. ramosus* are found in Nugranad (1992), Nugranad *et al.* (1994) and Steinfeldt & Bussarawit (1992). The protoconch of *C. ramosus* is fully developed after 6-10 days (Steenfeldt & Bussarawit 1992). Larvae used in the experiments were more than 20 days old and competent of settling as described by Steinfeldt & Bussarawit (1992).

Flume experiments

The flume tank at PMBC is an 8 m vertical recirculation flume with a basic design as the one described by Vogel (1981). The flume is 60 cm wide with a double set of collimators placed upstream. After the collimators, water moves 5.2 m before entering the 1 m test section, placed 0.8 m upstream from the exit section. Flow is created by a double set of propellers in the downstream vertical pipe. A 1 HP electric motor fitted with a 1/10 gear, drives the propellers.

The test section and an area 0.5 m upstream in front of the test section were filled with sand, very fine gravel or fine gravel (average grain sizes 0.5 mm, 3.3 mm, and 5.4 mm, respectively). The grain average size of the

sand was found by wet-sieving whereas the grain sizes of the very fine gravel and fine gravel were estimated by measuring minimal and maximal lengths of individual grains with a slide gauge. The mean of these lengths for each grain was calculated for 3 samples (n=50) and the average of these estimates used as the grain size.

The flume was filled with sand filtered sea water to a depth of 10 cm, and run for 1/2 hour with a 60 μ m nylon net in front of the collimators to remove large particles from the water, before larvae were added in the downstream end. Water temperature during the experiments ranged between 28 °C and 30 °C. The experiments were run at 3 free stream velocities separately, beginning with the lowest velocity.

Approximately 5,000 competent larvae were isolated in one culture tank and divided into 3 subgroups. Each subgroup was used with one of the 3 sediment types at one velocity. Totally, 27 experimental runs were performed to test the effects of the 9 velocity/grain size combinations with 3 replicates.

Hydrodynamics

Velocity profiles were made with a thermistor flow probe (LaBarbera & Vogel 1976). The probe was mounted on a micro-manipulator fitted with a stepping motor making it possible to move the probe vertically in steps of 1/50 mm. The stepping motor and sampling of data was controlled by a computer fitted with an A/D-D/A PC lab card. Each profile was made by manually moving the probe down until it touched the sediment surface. The computer programme was activated and the probe would make 50 measurements with a 1 second interval before moving up 0.2 mm where a new set of 50 measurements were made. This was repeated until the probe reached a height of 2 mm. Above 2 mm from the bottom, vertical steps of 1 mm were made to a height of 34 mm above the bottom. For each of the 9 sediment/velocity combinations, 5 profiles were made on a transect parallel to the flow in the centre of the canal. The first profile was made 88 cm from

the upstream edge of the sediment cover, and followed by 4 profiles with a distance of 6 cm downstream.

A clear boundary layer was visually observed in the test section with a logarithmic velocity profile reaching higher than 5 cm above the bottom. Plots of mean velocities against the logarithm of the height above the bottom were made for all profiles using data in the range from 6 mm to 34 mm above the bottom. Bottom shear velocity (u^*) was calculated according to the equation:

$$u^* = du/5.75 \times d \log z$$

where u^* is shear velocity, $du/d \log z$ is the inverse of the slope and 5.75 is a proportionality constant for velocity gradients plotted with \log_{10} on the depth scale (Brown *et al.* 1991). The roughness Reynolds number (Re^*) was calculated using the equation:

$$Re^* = u^* \times D/\nu$$

where D is the grain diameter, u^* is the shear velocity, and ν is the kinematic viscosity of sea water. The estimated values of Re^* makes it possible to differentiate between hydraulically smooth turbulent flows ($Re^* < 3.5$), intermediate turbulent flows ($3.5 < Re^* < 100$) and rough turbulent flows ($Re^* > 100$) (Nowell & Jumars 1984). To ensure homogeneity of the flow in the cross stream direction, a profile was made 10 cm on the left and right side of the 5th profile in the sand sediment, at the two extreme current velocities 3 cm sec^{-1} and 13 cm sec^{-1} . Comparisons of the centre profile and the profile made on the left and right side respectively were made by comparing the respective standard error intervals of the velocity measurements on each of the 29 levels from 6 to 34 mm above the bottom. Overlap of the standard error intervals occurred on all levels at the 13 cm sec^{-1} velocity. Only 1 and 4 non-overlapping standard error intervals at the right and left side, respectively, were found at 3 cm sec^{-1} velocity. This was accepted as a proof of a homogeneous flow in

the cross stream direction.

Effects of light on larval swimming behaviour

An experiment, recording velocities of larvae swimming into an illuminated zone, was made with 22 days old larvae to test whether larval swimming behaviour would be affected by sudden changes in illumination. A 250 ml cylinder was placed in front of a slide projector which illuminated the upper part of the cylinder. First the projector was turned off and individual larvae were pipetted into the cylinder. Swimming velocities of larvae swimming up through the low (shaded) and high (shaded) section were recorded. Some larvae would stay in the same position or move slowly up or down. These were not recorded. The procedure was repeated until 40 records had been made. Then the projector was turned on and swimming velocities of 20 larvae swimming up through the low (shaded) and high (illuminated) section were recorded. A single factor Anova test was used to compare swimming speeds of the larvae.

Larval encounters with the substrate

Larval encounters with the bottom were recorded with a video camera (Procec type 1030 equipped with a macro zoom lens). The camera was placed above the test section pointing down and recording a 5 by 3 cm area of the bottom sediment (5 cm in the direction of the current).

The combination of relatively high flow velocities ($u_\infty = 8 \text{ cm sec}^{-1}$ and 13 cm sec^{-1}) and close up video recording made it difficult to distinguish larvae from the bottom due to blurring of the larval shape. To get an estimate of larval flux, a zonation was made by projecting a beam of light from a slide projector through the observation window of the flume tank horizontally into the water column, illuminating the water between 1 and 2 cm above the bottom. All particles and larvae in this zone of light would be brightly illuminated and could clearly be distinguished from larvae above or below the light. By focusing the camera at 0.5 cm above

the bottom, and adjusting the depth of field, it was possible to see all larvae passing in the lower dark zone (0-1 cm) as well as in the illuminated zone (1-2 cm) and distinguish these from larvae in the upper dark zone (> 2 cm) at the lowest flow velocity. At the two higher velocities larvae passing in the illuminated zone were still clearly visible, as well as larvae slowing down or hitting the bottom in the lower dark zone.

Each experiment took 1 1/2 hour and to minimise effects of local topographic variations 3 camera positions were used. First the camera was placed at a fixed downstream position 110 cm from the edge of the sediment cover. After 30 minutes the camera was moved 7 cm upstream for 1/2 hour and then again moved further 7 cm upstream.

Video recordings were analysed on a Panasonic HS1000 S-VHS video recorder connected to a Sony 15" monitor. Larvae entering the picture in the light zone were counted and used to calculate the flux of larvae over the substrate. A larval bottom encounter was defined as an interruption of larval swimming/drifted. Larvae often rolled over especially on the sand substrate, and these were not registered. To avoid registration of dead larvae, only larvae with visible velar lobes were registered. Statistic comparisons of larval encounters with the various substrates were based on Anova tests on arcsine transformed proportions of larvae.

Larval swimming behaviour

The orientation of larvae entering the area in the illuminated zone were registered. The larvae were divided into a group with approximately horizontally placed velar lobes and a group with tilted velar lobes. A larva was defined as being tilted if the shell protruded beyond an imaginary line between the tip of the velar lobes on each side of the shell (Fig. 1). The orientation of larvae with tilted lobes were registered in degrees (0°-360°). Larvae with the shell pointing upstream were defined as having a 0 degree orientation.

To compare larval orientations the tilted larvae were differentiated into 8 orientation groups each having a 45 degree orientation span (Fig. 1).

RESULTS

Hydrodynamics

A flow profile is illustrated in Fig. 2. At 3 cm sec⁻¹ there was no correlation between grain size and bottom shear velocity u^* ($r = -0.62$, Tab. 1). At higher velocities the shear velocity u^* was correlated to grain size with a minimal $u^* = 0.31 \pm 0.03$ cm sec⁻¹ over the sandy sediment at $u_\infty = 8$ cm sec⁻¹ to a maximal value of 0.99 ± 0.24 over fine gravel at $u_\infty = 13$ cm sec⁻¹ (Tab. 1).

Roughness Reynolds numbers Re^* were correlated to grain size at all velocities from 1.80 ± 0.11 over the sandy sediment at $u_\infty = 3$ cm sec⁻¹ to 66.74 ± 15.88 over the fine gravel at $u_\infty = 13$ cm sec⁻¹ (Tab. 1). Above the two gravel substrates the flow could be characterised as intermediary between smooth and rough turbulent ($3.5 < Re^* < 100$) with a

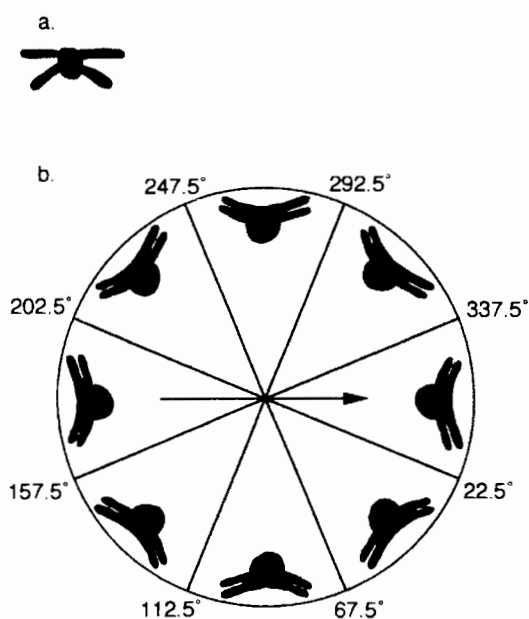


Figure 1. (a) Veliger larvae with horizontally oriented velum seen from above. (b) Illustration of tilted larvae and their separation into 8 groups according to orientation of the larvae.

Table 1. Bottom shear velocity (u^*), roughness Reynolds numbers (Re^*) and correlation coefficients estimated from the flow profiles above the 9 substrate/velocity combinations.

| u_∞ | Substrate type | u^* (cm/s) | r | Re^* | r |
|------------|------------------|--------------|-------|-------------|------|
| 3 cm/s | Sand | 0.29±0.02 | | 1.80±0.11 | |
| | Very fine gravel | 0.22±0.02 | -0.62 | 9.02±0.74 | 0.92 |
| | Fine gravel | 0.25±0.04 | | 16.86±2.93 | |
| 8 cm/s | Sand | 0.31±0.03 | | 1.93±0.17 | |
| | Very fine gravel | 0.42±0.03 | 0.95 | 17.38±1.07 | 0.90 |
| | Fine gravel | 0.70±0.08 | | 47.09±5.21 | |
| 13 cm/s | Sand | 0.36±0.04 | | 2.25±0.24 | |
| | Very fine gravel | 0.62±0.11 | 0.98 | 25.32±4.41 | 0.91 |
| | Fine gravel | 0.99±0.24 | | 66.74±15.88 | |

minimal Re^* at 9.02 ± 0.74 at 8 cm sec^{-1} over very fine gravel to a maximal Re^* at 66.74 ± 15.88 at 13 cm sec^{-1} over fine gravel.

Effects of light on larval swimming behaviour

Swimming behaviour of *C. ramosus* larvae includes periods of active upwards swimming with fully extended velar lobes and periods where the larvae sink towards the bottom. In addition to this there seems to be an intermediate behaviour where gravitational forces are just balanced by a limited swimming effort.

To test whether the use of light to divide the water column had an effect on larvae drifting or swimming into the illuminated zone,

an experiment was made to compare swimming velocities in a dark water column and in the same water column with the upper part illuminated. The swimming speeds did not differ (Tab. 2).

Larval encounters with the substrate

At 3 cm sec^{-1} the number of bottom encounters were highly variable and not correlated to grain size (Fig. 3a). At 13 cm sec^{-1} there was a significant increase in bottom encounters with increasing grain size (Anova test, $F = 20.70$ against $F_{\text{critical}^*} = 10.92$).

At 8 cm sec^{-1} there was a tendency to an effect comparable to the situation at 13 cm sec^{-1} (Fig. 3b). The effects were not strong enough, though, to prove significant at the

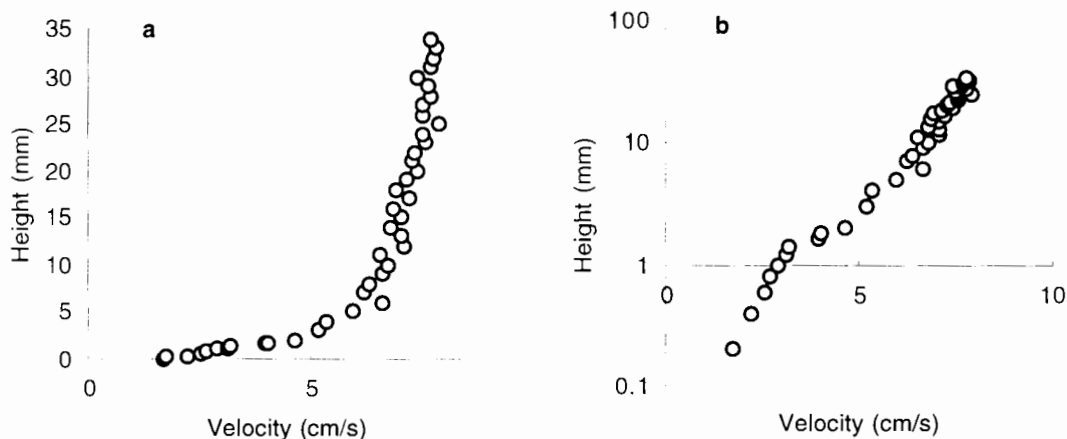


Figure 2. a.) One velocity profile over the very fine gravel substrate at a free stream velocity, 8 cm sec^{-1} . b.) The same velocity profile plotted with a log transformed height above bottom.

Table 2. Single factor Anova comparing swimming speed of 22 days old *C. ramosus* larvae in a water column without illumination (top two rows) and in a water column with the upper part illuminated (bottom two rows).

| Region | Illumination | Swimming velocity | n | F | F-critical |
|--------------|--------------|-------------------|----|------|------------|
| Lower region | Shaded | 0.63±0.17 | 40 | 0.18 | 3.96 |
| Upper region | Shaded | 0.65±0.20 | 40 | | ns |
| Lower region | Shaded | 0.67±0.11 | 20 | 0.96 | 4.10 |
| Upper region | Illuminated | 0.71±0.17 | 20 | | ns |

95 % level of significance (Anova test, $F = 1.18$ against $F_{critical*} = 5.14$). An Anova test between number of bottom encounters on sand compared to number of bottom encounters on fine gravel resulted in $F = 7.67$ against $F_{critical*} = 7.71$). Number of bottom encounters on very fine gravel had an intermediate value of 10.4 ± 4.8 %, not different from either of the 2 extremes (Fig. 3b).

Larval swimming behaviour

Larvae crossing the test section could be separated into several behavioural groups.

Most larvae would pass the test section high in the water column, as described by Steinfeldt (1995). They would bounce off the water surface repeatedly and would orient their velar lobes in a horizontal position.

A limited number of larvae would move from high in the water towards the bottom. They would typically have their velar lobes extended and swim in the direction of the current with an almost vertically oriented velum or would sink passively towards the bottom with the velum partly withdrawn into the shell.

Most larvae crossing the test section close to the bottom seemed to drift horizontally over the substrate without swimming up or down. Their behaviour could best be described as passive drifting with the current and just compensating the gravitational force by a limited

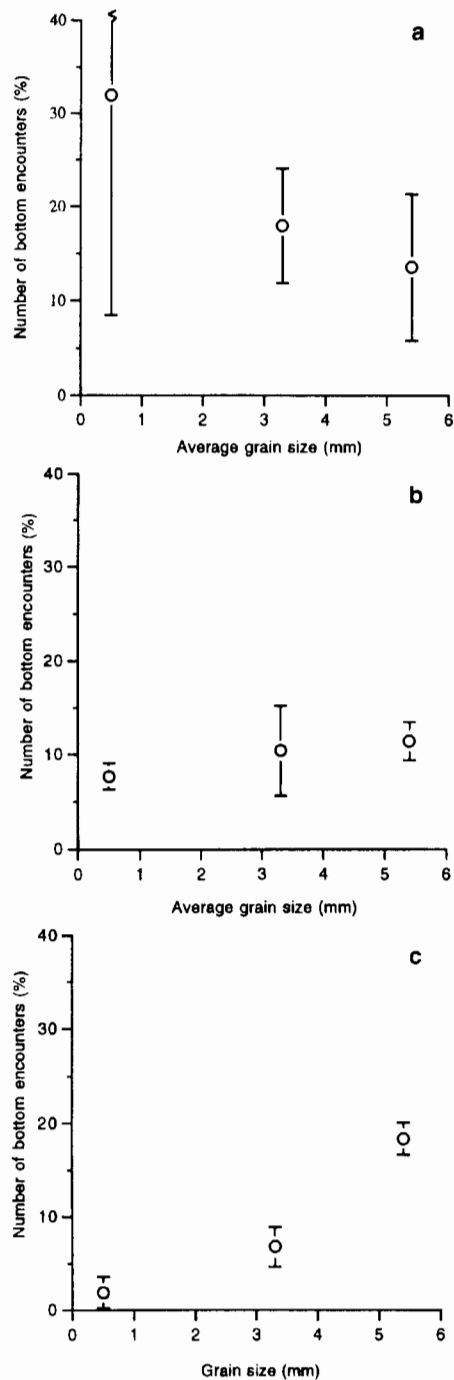


Figure 3. Larval encounters with the 3 substrate grain sizes in percent of number of larvae passing 1-2 cm above the bottom zone at (a) $u_{\infty} = 3 \text{ cm sec}^{-1}$; (b) $u_{\infty} = 8 \text{ cm sec}^{-1}$; (c) $u_{\infty} = 13 \text{ cm sec}^{-1}$.

swimming effort. A high fraction of these larvae would orient their velum in a vertical or half-vertical position hereafter specified as larvae with tilted velum.

The orientation of the velar lobes relative to the shell was analysed for all tilted larvae passing between 1 and 2 cm from the bottom at $u_{\infty} = 3 \text{ cm sec}^{-1}$ (Fig. 4). In all 9 experiments (3 substrate types with 3 replicates), the larvae showed a clear non random orientation relative to the direction of the current (Chi-square-test, $P < 0.01$).

DISCUSSION

Several models have been proposed to explain the non random distribution of benthic invertebrates on the sea bottom. One extensively considered aspect is the possibility of active larval choice contra passive deposition on the bottom. Testing either of these hypotheses demands knowledge concerning

larval swimming behaviour, as well as hydrodynamic properties of the environment. Comparisons of bottom encounters at the different flow velocities have not been made in this study. Different velocity gradients caused by the boundary layers, did not make a correction factor between the 3 flow velocities legible.

The larvae seemed able to orient themselves in the water column. Very few larvae were spiralling through the test section and even these were never observed tumbling when not encountering the bottom. At the maximal current velocity and fine gravel substrate, larvae swimming very close to the bottom were seen to follow bottom contours, and could lose momentum totally in the relatively low mixed still water between grains. The positive correlation between rates of bottom encounters and substrate grain size at 13 cm sec^{-1} (Fig. 3), is by a first glance

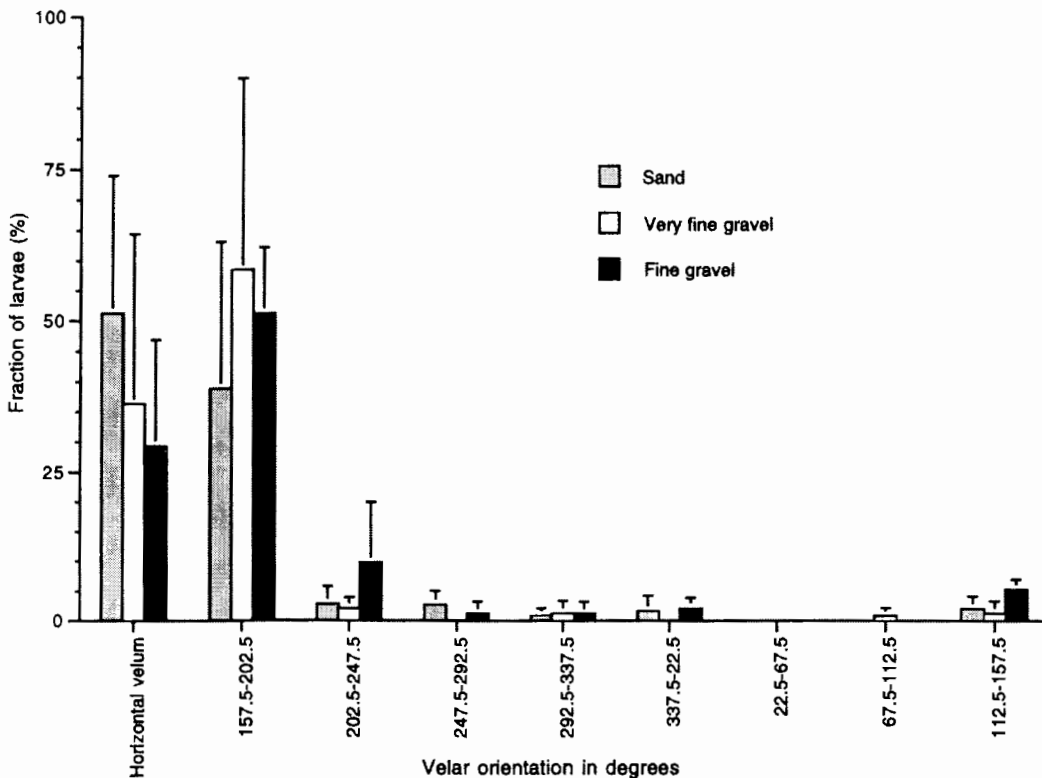


Figure 4. Fraction of larvae passing in the illuminated zone with horizontal velum or tilted velum differentiated into the 8 orientation groups.

contradictory to a theoretical model of larval settlement expecting "a negative relationship between settlement rates and roughness heights" (Eckman 1990). The model assumes that turbulent eddies in the water are able to move the larvae against gravity. The highest effect of grain size is found when the ratio between sinking speed (w) and bottom shear velocity (u^*) is around 0.17 and the effect is negligible at both low (< 0.02) and high (> 0.33) w/u^* ratios. A constant sinking speed is assumed before and during settling, which eliminated active larval swimming. Competent *C. ramosus* larvae have sinking speeds of 1.02 ± 0.35 cm sec⁻¹ (Steenfeldt 1995). This equals w/u^* ratios between 1.0 and 4.6 at the two extreme flow cases ($u^* = 0.22$ and $u^* = 0.99$) in this study. This is clearly above the upper limit of 0.33. The negative correlation between settling and roughness height referred to by Eckman (1990) are based on assumptions which are violated by the high sinking speed and active behaviour of the *C. ramosus* larvae.

Average vertical swimming speeds of 0.75 ± 0.22 cm sec⁻¹ for competent larvae of *C. ramosus* were estimated by Steenfeldt (1995) and are comparable to the velocities found in this study (Tab. 2).

The missing correlation between ratio of bottom encounters and substrate type at the lowest velocity, and the correlation at the highest velocity (Fig. 3) suggests that the observed results were due to passive deposition, but not passive deposition of larvae sinking at maximal speed. By reduced swimming, a veliger larva can simulate all sinking velocities up to a maximal value when the larva is fully withdrawn into the shell. Estimates of ratio between bottom encounters and flux of larvae above the bottom reflected swimming and sinking behaviour of fast rising and falling larvae to some extent. This might to a high degree also have reflected effects of turbulent mixing on larvae just compensating sinking by reduced swimming, in other words, larvae acting like neutral buoyant particles.

The surface grain size in a given area is de-

termined by deposition of particles in that area as well as re-suspension of particles followed by transport away from the area. All sizes of suspended particles will hit the bottom more often when turbulence is increased. But only particles below a given threshold size will be re-suspended and transported away from the area. A gastropod larva can use its foot to adhere to the bottom if conditions for metamorphosis are met and thereby avoid re-suspension.

Much evidence suggests that *C. ramosus* prefer coarse sediments (Bech 1992; Jalk 1992; Steenfeldt & Bussarawit 1992).

Both Shear Velocity and Roughness Reynolds number increase with increased grain size above a given threshold current velocity. A consequence of this may be an increased deposition of *C. ramosus* larvae in hydrodynamic rough turbulent areas. Larvae were often observed rolling over the sandy substrate at the 8 cm sec⁻¹ and 13 cm sec⁻¹ velocities. A phenomenon described by André (1992) concerning *Cerastoderma edule* larvae at 15 cm sec⁻¹ velocity on a finer grained sandy substrate (grain size 170 μ m). This behaviour seemed disadvantageous to the larvae. They were forced to extend their velum in order to get away from the bottom, and would be tilted when trying to take off from the bottom. They were easily rolled over repeatedly before leaving the bottom.

On the gravel sediments, encounters with the substrate seemed more sudden. Larvae would often hit protruding pebbles and fall into crevices between grains. Often the larvae were seen again after a short while, swimming actively in a hole between grains before suddenly being swept up into the overlying water by a turbulent eddy.

CONCLUSION

Due to high possible sinking speeds of *C. ramosus* larvae, they would be deposited within tens of centimetres even in the roughest flow in the flume tank if they withdrew their velar lobes fully into the shell. Only active swimming made the larvae stay in suspension. Most larvae passing the obser-

vation area within the height of registration were larvae swimming suboptimally and acting like particles with neutral buoyancy. No effect of substrate type was seen at a low current velocity where shear velocity did not differ between substrate types. At higher velocities there was an effect of substrate type on shear velocity, and this did have a positive effect on the number of larval bottom encounters.

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