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Algal spore settlement and germling removal as a function of flow speed

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ABSTRACT: The settlement success of zoospores from the green alga *Ulva intestinalis* (syn. *Enteromorpha intestinalis*) was studied in relation to the small-scale hydrodynamic forces acting close to the substratum. In moderate flow speeds (free-stream velocity 20 cm s^{-1}) *U. intestinalis* spore settlement was strongly reduced, with only 5% of spores settled compared with settlement in still water. The decrease in settlement occurred when calculated flow speeds at the height of settling spores exceeded the swimming speed of spores (approximately 0.2 mm s^{-1}). This indicates that the relatively low swimming speed of the spores is important for successful settlement in the viscous sublayer. A possible longer-term effect of flow during settlement was also tested by measuring the removal of 2 wk old germlings exposed to a flow speed of 10 m s^{-1}, which is approximately the maximum speed encountered on a rocky shore. The percentage removal was lower from the less densely populated panels, i.e. panels exposed to 20 cm s^{-1} during settlement. After removal, biomass was nearly equal on all panels regardless of the initial density of settling spores. The footprint of reduced settlement in 20 cm s^{-1} flow speed did not persist, in terms of biomass, after the removal treatment. Even though rough surfaces and stochastic variations in hydrodynamic forces are likely to affect spores and germlings in nature, the results from this study can give an estimate of flow effects for tested conditions.

KEY WORDS: Algal spores · Settlement in flow · Small-scale hydrodynamic forces · Germling removal · *Ulva* · *Enteromorpha*

INTRODUCTION

Flow velocity has been demonstrated to have significant effects on settlement of invertebrate larvae (e.g. Eckman & Duggins 1998). Successful establishment of marine macroalgae is dependent on the dispersal and attachment of propagules, and most species rely on release of spores that find and establish contact with a suitable surface. The spores are often microscopic and, owing to their small size, will experience the environment differently compared with the adult algae from which they are released. The size and shape of spores vary among algal species, and many are dispersed as passive particles with sinking speeds between 0.01 and 0.1 mm s^{-1} (Coon et al. 1970, Vogel 1994). However, some brown and green algae have motile spores with maximum swimming speeds of 0.08 to 0.3 mm s^{-1} (Norton 1992). These speeds are very low compared with water velocities in the field, which in the surf zone are typically in the range of 1 to 10 m s^{-1} (Denny 1988, Norton 1992). However, close to solid surfaces like rocks, the local water velocity is substantially slower. The gradient of decreasing flow velocity close to any surface is known as the boundary layer. Within this approximately 1 to 10 mm thick layer, water velocities are reduced. Further down, very close to a solid surface in a 10 to 150 µm thin layer called the viscous sublayer, water velocities are estimated to range from 1 to 10 mm s^{-1} (Denny 1988). In this layer, the small-sized spore (≤10 µm in diameter) can be protected from hydrodynamic forces (Charters et al. 1970). The most important process for bringing propagules to the substratum is thought to be turbulence, as opposed to the much slower process of sedimentation (Norton & Fetter 1981, Vogel 1994). Swimming ability in general is not considered necessary for successful settlement (Amsler

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et al. 1992), but motility might play a role in location of the substratum by spores in the viscous sublayer (Vogel 1994, Abelson & Denny 1997). The distribution of macroalgae is highly dependent on flow conditions. The number of propagules that settle has been seen to decrease with increasing water velocities over the range of 22 to 55 cm s^{-1} (Norton & Fetter 1981). For some species, like the brown alga *Ascophyllum nodosum*, water movement is found to be the primary factor controlling recruitment and distribution, and a relatively low-energy wave could remove up to 99% of newly settled zygotes (Vadas et al. 1990).

Ulva spp. (syn. *Enteromorpha* spp. Hayden et al. 2003), hereafter referred to as *Ulva*, are common green algae that are present on rocky shores world-wide and are well-known fouling organisms on ship hulls and other submerged substrata. Upon release, the majority of *Ulva* zoospores settle within minutes (Callow et al. 1997), though they are viable for up to 8 d (Jones & Babb 1968). The zoospores of *Ulva* are negatively phototactic and swim towards areas of low light intensity (Callow et al. 1997). When zoospores are ready to settle, the spore becomes positioned in relation to the substratum with the anterior end pointed downward (Callow & Callow 2000). Moreover, spores show a characteristic spinning behaviour and withdraw their flagella when settling (Callow et al. 1997). Spores from the green alga *Ulva* were reported to settle in flow speeds as high as 9 knots (5 m s^{-1}) (Houghton et al. 1972). Here we present results on the effect of flow on early life stages of *U. intestinalis*. First, spore settling was studied in moderate flow speeds (0 to 20 cm s^{-1}) under defined oscillatory flow conditions. Second, the risk of hydrodynamic removal to *U. intestinalis* germlings was tested under flow conditions simulating maximum flow speeds in breaking waves. Finally, the net effect of flow on new *U. intestinalis* biomass was measured by following germling growth.

MATERIALS AND METHODS

Spore swimming speed and settlement at different flow speeds. Spore swimming speed was measured using a horizontally oriented stereomicroscope looking into a transparent Plexiglas aquarium in a setup designed to minimize effects of convection currents. Fiber optic illumination directed against the lens of the microscope was used to maximize the contrast between spores and background. From video recordings of spores swimming in the focal plane, the speeds of 10 zoospores were calculated. Measurements were made at a water temperature of 20°C and salinity of 20 psu. The bottom of polystyrene containers (220 × 170 mm) was covered with standard glass microscope slides (26 × 76 mm). Zoospores of *Ulva intestinalis* were obtained according to the method described by Callow et al. (1997), and a 500 ml spore suspension (1×10^5 spores ml^{-1}) was added to each container. Spores were then allowed to settle for 30 min in filtered 0.2 µm seawater with 20 psu salinity, in darkness and under different flow conditions. Slides were carefully rinsed and stored in stagnant seawater (filtered 0.2 µm). The number of attached spores was counted under the microscope after 24 h, at 20 fields of view for each treatment. Experiments were conducted on 3 dates.

Hydrodynamic regime and flow speed measurements. Close to shore, oscillating flow predominates over stationary currents (Riedl 1964). A shaking table was used to generate an oscillatory flow regime with 4 different mean flow speeds. The free-stream velocities were measured at 4 mm distance from the bottom with a conical (55 R42) hot-film probe (Dantec Dynamics A/S). Measurements were made for 30 s at 100 Hz. The water depth in the experimental plastic containers after adding 500 ml seawater was 1.1 cm. Two of the measured free-stream velocities are shown in Fig. 1. Maximum free-stream velocity and wave frequency both increased with higher shaking table frequency (Fig. 1, see Table 1). Because the hot-film probe measures in only 1 direction, despite the maximal values in the oscillating flow occurring in both directions, the measured frequency was multiplied by 2.

Calculated boundary layer flow velocity at spore height. The local flow acting on a spore at settlement will be very different from bulk flow because of the declining flow speed towards the substrate surface. This gradient in flow speed is known as the boundary layer (Schlichting 1979). Under field conditions, most boundary layers on rocky shores are turbulent with a

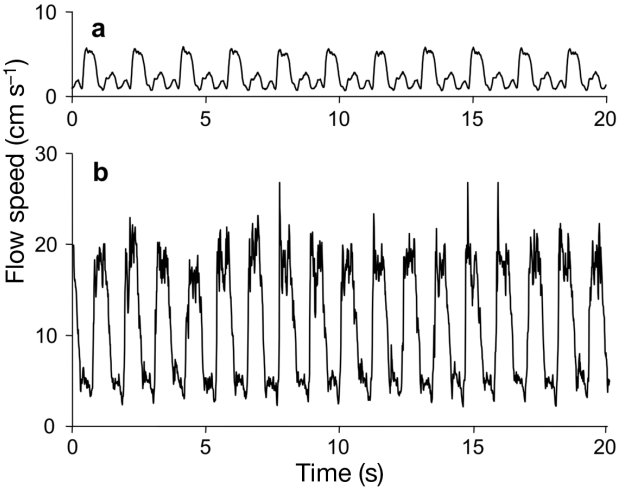

Fig. 1. Flow speed measured with a hot-film probe 4 mm above the container bottom, placed on a shaking table generating free-stream velocities of (a) 5.6 cm s^{-1} and (b) 20.8 cm s^{-1}

logarithmic velocity gradient. However, close to the boundary, viscous forces dominate and flow in this sublayer is laminar with speed increasing linearly with boundary distance. It is within this viscous sublayer that the 10 µm *Ulva* spores settle. The thickness of the viscous sublayer (δ_v) following Vogel (1994) is estimated as:

$$\delta_v = 11.6\nu/u_* \quad (1)$$

where ν is kinematic viscosity of water and u_* is friction velocity. Friction velocity is assumed to be 10% of free-stream velocity (Denny 1988). Flow speed in a turbulent boundary layer will fluctuate around the mean on short time scales. The speed within the viscous sublayer will also fluctuate in phase with the lower part of the turbulent boundary layer. We here use the maximum flow speed at the height of the settling spore to define the flow conditions where spore swimming speed may affect settlement. Following Denny (1988), the rationale is that the time interval between flow peaks (τ) is in the order:

$$\tau = \frac{6\delta}{U} \quad (2)$$

where δ is the thickness of the turbulent boundary layer and U is mean free-stream velocity, and τ is considerably shorter than the time for the settlement process (Callow et al. 1997). The maximum flow speed at height z within the viscous boundary layer is estimated using the empirical finding that maximum flow speed in the lower part of the turbulent boundary layer is approximately equal to mean free-stream velocity (Johansson & Alfredsson 1982). Local flow speed in the viscous sublayer (u_z) was estimated from linear interpolation from the bed ($z = 0$), where local flow speed is zero, to the height of the viscous sublayer (δ_v), where maximum flow speed is set equal to mean bulk speed (the free-stream velocity):

$$u_z = zU/\delta_v \quad (3)$$

Germling cultivation and removal. Germlings were cultivated on standard glass microscope slides in f/2 medium at 20°C with a 16:8 h light:dark cycle. Biomass was estimated after 14 d by extraction of chlorophyll *a* (chl *a*). Germlings were removed from half of each slide and chl *a* extracted in dimethyl sulphoxide (DMSO) (Shoaf & Lium 1976). The concentration of chl *a* was determined spectrophotometrically using equations of Jeffrey & Humphrey (1975) and data expressed as chl *a* per unit area of test surface. To assess the capability to withstand removal for the different spore densities (achieved from settlement under different flow conditions), the slides with the second half of the germlings attached were mounted onto the hull of a 4.55 m long boat and driven at 10 m s^{-1} (20 knots) for 30 s (for a detailed description of the boat see Granhag 2005). This was done to simulate a common but rapid flow speed that a germling is likely to encounter on a rocky shore (Denny 1988). The remaining biomass was manually removed and the chl *a* content determined as above. For each treatment (settling flow speed) 3 slides were used. The density of the 14 d old germlings (8 transects counted for each treatment) and size (height and width) of germlings were measured.

Statistical analysis. The effect of flow speed on the number of settled spores was analysed using linear regression. The percentage of settled spores in the different flow treatments was used as the dependent variable after setting settlement in still water to 100%. The effect of flow speed on the number of grown up germlings and total biomass was also analysed using linear regression. Percentage removal of 2 wk old germlings was tested using a 1-way ANOVA with flow speed during settlement as a fixed factor. Prior to ANOVA, homogeneity of variances was tested using Cochran's test of homoscedasticity (Winer et al. 1991). Percentage removal (dependent variable) was calculated from estimated biomass (chl *a* content) before and after high flow treatment. Biomass (chl *a* content) after the removal treatment was analysed with linear regression. A Type I error rate of 0.05 was used. Differences in height and width of 2 wk old germlings settled under different flow conditions were investigated with a 1-way ANOVA with height/width as dependent variable.

RESULTS

Swimming speed and settlement of spores

The swimming speed of *Ulva intestinalis* zoospores was found to be 0.2 ± 0.03 mm s^{-1} (mean ± SD, n = 10). Settlement (% of settled spores compared with still water) decreased with increasing flow speed (linear regression, $r^2 = 0.96$, $F_{1,5} = 115$, $p = 0.00012$). At 20.8 cm

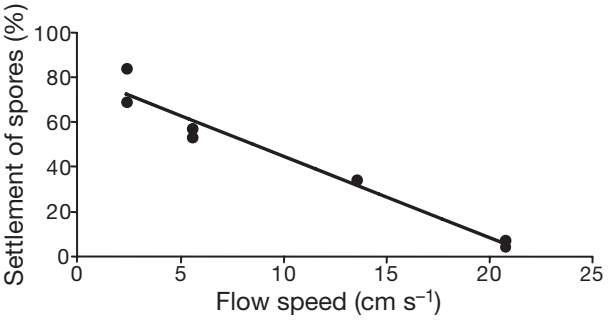

Fig. 2. Effect of flow speeds on spore settlement, where settlement in still water was set to 100%

s^{-1}, settlement was only 5% compared with settlement in still water (Fig. 2). At free-stream velocities higher than approximately 5 cm s^{-1}, the local flow speed at the height of settling spores (10 µm) is expected to exceed the swimming speed of the spores (0.2 mm s^{-1}) (Fig. 3, Table 1).

Germling growth and removal of germlings in high flow speeds

Both germling density (linear regression, $r^2 = 0.61$, $F_{1,30} = 47$, $p = 1.3 \times 10^{-7}$) and biomass after 2 wk (linear regression, $r^2 = 0.45$, $F_{1,10} = 8$, $p = 0.017$) decreased with flowspeed. The height of 2 wk old germlings of spores settled in the highest flow speed (20.8 cm s^{-1}) was significantly higher (1.9 ± 0.2 mm, mean ± SD, n = 10) than that of germlings in all other groups settled in lower speeds (1.0 ± 0.2 mm, mean ± SD, n = 10) (1-way ANOVA, $F_{4,10} = 42$, $p = 0.0001$). However, the width of the germlings did not differ among groups (0.5 ± 0.02 mm, mean ± SD, n = 10; $F_{4,10} = 1.25$, $p = 0.3$).

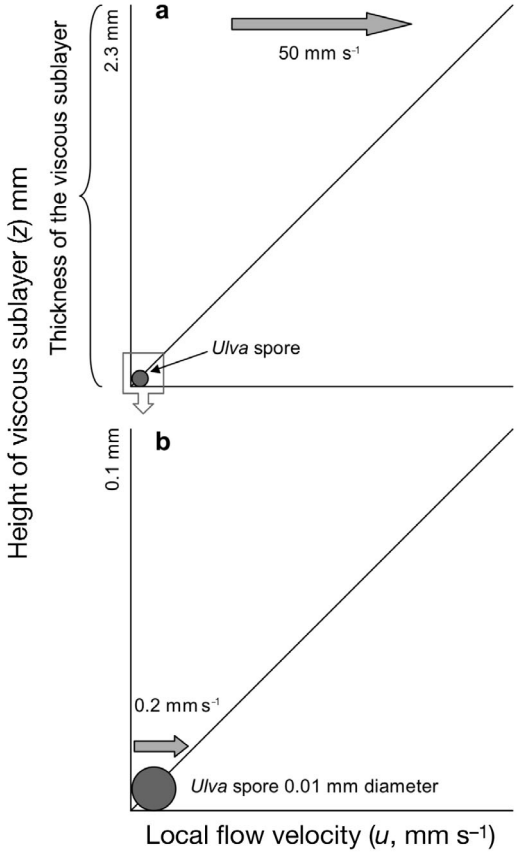

Fig. 3. A free-stream velocity of 50 mm s^{-1} gives a (a) viscous sublayer thickness of 2.3 mm (Eq. 1) and (b) maximum flow speed of 0.2 mm s^{-1} at a spore height of 10 µm (0.01 mm) (Eq. 3). Diagonal line is the increase in local flow velocity with increasing height of the viscous sublayer

Table 1. Free-stream velocities and frequency for 4 shaking table speeds used in the experiment, and calculations of viscous sublayer thickness (δ_v) and local flow velocity at 10 µm spore height (u_z) (from Eqs. 1 & 3 respectively)

Free-stream velocity (cm s^{-1})	Frequency (s^{-1})	δ_v (mm)	u_z (mm s^{-1})
2.4	0.7	4.8	0.05
5.6	1.1	2.1	0.26
13.6	1.4	0.9	1.51
20.8	1.8	0.6	3.46

Removal (%) of 2 wk old germlings after exposure to high flow speed (10 m s^{-1}) was significantly lower for germlings grown from spores that settled in the highest flow speed (20.8 cm s^{-1}; 1-way ANOVA, $F_{4,10} = 11.2$, $p = 0.001$). There was no relationship between the chl *a* content of germlings after boat exposure and flow speed at settlement (linear regression, $r^2 = 0.08$, $F_{1,10} = 0.9$, $p = 0.37$).

DISCUSSION

We found that many *Ulva intestinalis* spores failed to settle even in moderate free-stream flow speeds (<20 cm s^{-1}). Spores were able to settle to a greater extent (more than 50% settlement compared with still water) when flow speed at spore height was lower than or equal to the swimming speed of the spores. Sufficient periods of velocities low enough for settlement ('settling windows') are more likely at low flow speeds because both the maximum speed and frequency of high flow speeds are lower, and a gradual decline in settlement is seen with increasing flow speed (Crimaldi et al. 2002). An alternative explanation for the settlement of fewer spores in the high flow speed could be that newly settled spores are detached. We believe this to be rather unlikely, however, since spore adhesive cures within minutes after attachment (Callow et al. 1997). At the highest free-stream velocity used in the experiment (20.8 cm s^{-1}), local velocity at spore height was estimated to be approximately an order of magnitude higher than spore swimming speed, and spore settlement was highly reduced. Owing to a lack of accessible theory for oscillatory flow that would be applicable to the experimental system, we used expressions for stationary flow when predicting local flow speed in the viscous sublayer. It is possible that the viscous sublayer will become thinner with steeper velocity gradients during oscillatory flow, resulting in underestimates of local flow speed.

The results might also have been altered if germlings were grown under shaking conditions, rather than being simply exposed to shaking during settlement. Our results contrast with the findings of Houghton et al. (1972), who reported settlement at a 10-fold higher flow speed. However, the flow regime will differ among experimental systems, e.g. in terms of boundary layer thickness and bed roughness (Nowell & Jumars 1987, Jonsson et al. 2006a). The small size of spores probably makes the bed roughness an essential factor for predicting settlement as a function of free-stream velocity. Even small elements of roughness may create local micro-environments with reduced flow suitable for settlement (Callow et al. 2002). In our experimental system, the glass slides used as the settlement substrate were also smooth on the scale of the spores, and the effect of flow presented here should be regarded as the more sensitive end of a spectrum of combinations of flow regime and bed roughness. Indeed, it may be speculated that very small propagules, like green algal spores, are particularly suited for settlement in high flow environments because they may exploit the roughness of even water-polished rocky shores. Our finding that settlement decreased when local flow speed was higher than spore swimming speed suggests that active spore motility is involved in successful settlement. It may be speculated that the swimming motion is necessary for proper orientation of the spore after surface contact, leading to the spinning phase preceding successful adhesion (Callow et al. 1997). Spores spin with the anterior end pointed down, and the adhesive vesicles are found in the anterior end prior to secretion (Callow & Callow 2000). The fixation process involves adhesive release together with withdrawal of flagella and takes place within minutes (Callow et al. 1997), securing zoospores to the substratum.

In our study, the high flow treatment (10 m s^{-1}) removed 40 to 85% of the 2 wk old germlings from glass. In a study by Schultz et al. (2003), 30% or less of a 6 d old germling biofilm was removed from glass slides with a flume generating 5 m s^{-1}. In our experiment, removal in high flow was lower for germlings grown from spores that settled in a free-stream velocity of 20 cm s^{-1}, in which germlings constituted a less dense mat. Higher loss in dense assemblages could be explained by a shared risk of peeling and detachment for dense germling mats (Chaudhury et al. 2005). This is probably because dense populations may increase the drag on the whole consortium of germlings, leading to removal of the whole mat. The initial difference in spore settlement caused by settlement in different moderate flow speeds was no longer evident in our experiments when the 2 wk old germlings were exposed to a flow of 10 m s^{-1}. There was a density-dependent effect on the growth rate of germlings, which decreased the initial effect of reduced settlement at higher flow speeds. Possible explanations for density-dependent growth include competition for nutrients and light, and this can even out the difference in biomass among the various settlement treatments. Quantifying germling removal solely from chl *a* measurement calls for some caution because this does not separate density and size of germlings. The difference in geometry of individual germlings is likely to influence the hydrodynamic drag force. However, it is hard to predict the risk of dislodgement as a function of flow speed owing to the flexible morphology of the algae. Nonetheless, we believe that width (which did not differ among treatments in our experiment) is of major importance for creating drag force, while height (which did differ) is of minor importance. This is because bending of germlings in flow will give a similar projected area regardless of total height. Variation in the width of germlings may thus be important when trying to account for why some germlings are removed while others are not. For a more thorough understanding of which factors are important for germling detachment, the rhizoids of the germlings should be studied to reveal if they differ among different flow regimes and if their shape influences detachment. For example, it has been shown that materials with different surface energies influence the shape of algal rhizoids (Fletcher & Baier 1984)

Finally, does flow matter? It is well known that factors other than flow may have considerable effects on the settlement of algal spores. Conditioning (i.e. the development of a biofilm) of the surface affects settlement of algal spores, and Joint et al. (2002) showed that zoospores of *Ulva* spp. respond to biofilms by way of chemoperception of diffusible signal molecules. In our study, the panels were not conditioned prior to the experiment; therefore, spores at the surface could not respond to cues or be trapped in a sticky biofilm, which may happen in the field. Other factors that also affect settlement are chemistry and roughness (microtopography) of the substrate (Callow et al. 2002). As Amsler et al. (1992) pointed out, factors such as behaviour, chemistry, flow and roughness must all be considered together when interpreting their possible role in spore settlement. However, our aim here was to specifically test the effects of flow on spore settlement and germling removal. In our experiments it was seen that more spores settled on the surface when velocity in the viscous sublayer was low.

On the one hand, slow flow conditions may have negative effects on other parts of the life cycle. For example, calm conditions may prevent spore release from the plant and hence lead to germling growth from the tip of the plant instead of to dispersal. An increase

in water motion increased zoospore release from *Ulva lactuca* (Gordon & Brawley 2004). On the shore, *Ulva* colonizes surfaces where average flow is high (Jonsson et al. 2006b). This is possible because *Ulva* spores can utilize periods of low flow conditions. *Ulva* has a high propagule release, and the spores are able to settle quickly under calm conditions. On the other hand, high flow conditions may perhaps limit the tissue biomass and reproductive output because algal plants may be pruned by high flow speeds (or by grazers). The reproductive parts of *Ulva* are in the upper margins of the thalli and could be the most easily torn off. However, the effect of this pruning is not clear because free-floating fragments can continue to grow and release spores, and parts of thalli can survive passage through digestive systems of grazers (Santelices & Paya 1989). Furthermore, thalli that detach can leave small rhizoidal parts from which new thalli regenerate (Fletcher 1976).

In conclusion, our results indicate that flow constrains settlement in the viscous sublayer to velocities that do not exceed spore swimming speed. However, density-dependent growth and risk of removal during extreme events of high flow speeds was seen to reduce the effects of initial flow during settlement. To be able to further predict scenarios likely to occur in the field, factors such as surface roughness and stochastic variation in hydrodynamic regime should also be investigated.

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