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Effect of turbulence on the mortality of zebra mussel veligers

C.R. Rehmann, J.A. Stoeckel, and D.W. Schneider

Abstract: Small-scale turbulence can increase the mortality of zebra mussel (*Dreissena polymorpha*) veligers. Laboratory experiments were conducted in which veligers were subjected to turbulence due to a bubble plume and the rate of dissipation of turbulent kinetic energy was measured directly. The ratio $d*$ of the shell size and the Kolmogorov length, the size of the smallest eddy in the velocity field, is introduced to quantitatively assess whether turbulence can affect larvae. The laboratory experiments show that mortality increases when $d*$ exceeds 0.9, that is, when the size of the larvae is comparable with or larger than the smallest eddy. The laboratory results are used to show that turbulence can increase veliger mortality in streams and to evaluate the possibility of using bubble screens as a dispersal barrier to control zebra mussels in rivers. If the mortality is due to acute effects of turbulence (taken to be exposure on the order of minutes), the control scheme would work, but if the mortality is due to longer-term exposure, using bubble screens would not be practical.

Résumé : La turbulence à petite échelle peut accroître la mortalité des larves véligères de la moule zébrée (*Dreissena polymorpha*). Dans des expériences de laboratoire, des larves véligères ont été exposées à une turbulence produite par un panache de bulles et la dissipation de l'énergie cinétique turbulente a pu être mesurée directement. Le rapport $d*$ de la taille de la coquille et la longueur de Kolmogorov, la taille du plus petit tourbillon dans le champ de vitesses, permet de déterminer quantitativement si la turbulence peut affecter les larves. Les expériences de laboratoire démontrent que la mortalité augmente lorsque $d*$ dépasse 0,9; c'est-à-dire lorsque la taille de la larve est comparable à celle du plus petit tourbillon ou alors lorsqu'elle est plus grande. Les résultats de laboratoire indiquent que la turbulence peut faire augmenter la mortalité de larves véligères dans les cours d'eau et ils permettent d'évaluer la possibilité d'utiliser des écrans de bulles comme barrières contre la dispersion de la moule zébrée dans les rivières. Si la mortalité est due aux effets aigus de la turbulence (soit une exposition d'une durée de quelques minutes), le système de contrôle pourrait fonctionner, mais si la mortalité est due à une exposition plus longue, l'utilisation d'écrans de bulles ne serait pas pratique.

[Traduit par la Rédaction]

Introduction

Since its accidental introduction into North American waterways, the zebra mussel (*Dreissena polymorpha*) has spread rapidly, threatened native species, and required increased maintenance at hydropower plants, sewage treatment plants, and water supply facilities. Although control measures have been proposed for individual facilities, there have been few attempts to control zebra mussels in an entire ecosystem. Stoeckel et al. (1997) suggested an approach that

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may lead to ecosystem-wide control of zebra mussels. This approach relies on the observation that zebra mussel populations in large rivers like the Illinois River are structured as metapopulations that require a supply of larvae from upstream to survive. If the larval supply can be blocked with a dispersal barrier, downstream populations can be controlled. Because typical control strategies used at facilities, including chlorination, chemical treatment, and electroshock, cannot be used in canals and rivers, we investigate the effect of turbulence on the mortality of zebra mussel veligers and evaluate the possibility of using a series of bubble screens as a dispersal barrier.

Previous work suggests that turbulence can affect the larvae of several organisms. In a review of several laboratory experiments, Peters and Marrasé (2000) concluded that in general, turbulence decreases growth rates, increases energy expenditures, and increases ingestion rates, especially at low and moderate turbulence levels. Quantities describing small-scale turbulence, the kinematic viscosity ν of the fluid and the dissipation rate ε of turbulent kinetic energy (or simply "dissipation"), are important because the sizes of the organisms studied were comparable with or smaller than the Kolmogorov length scale $L_K = (\nu^3/\varepsilon)^{1/4}$, the smallest scale in the velocity field.

Direct effects of turbulence on larval mortality are less clear. In experiments with Couette cells, high shear stress,

which is related to the rotation rate and geometry of the cell, increases the mortality of *Morone saxatilis* and *Morone americana* (Morgan et al. 1976). Turbulence is stated to increase the mortality of the larvae of *Mysis relicta* (Gregg and Bergersen 1980) and *Polyodon spathula* (Killgore et al. 1987); however, in these two studies, the turbulence was not quantified as precisely as in many of the later studies reviewed by Peters and Marrasé (2000). For zebra mussels, Baddour (1998) used bubble screens to prevent veligers from entering water intakes, but the role of the bubbles was to break up vortices and block, rather than kill, the veligers. Horvath and Lamberti (1999) observed that the percentage of live veligers in a stream decreased exponentially with distance. They ruled out starvation, temperature effects, lack of suitable settlement substrata, predation by zooplankton, and upstream settlement as sources of mortality. Because they found empty shells in their samples, they suggested that turbulence and shear might have pulled the veligers apart, possibly during feeding.

We conducted laboratory experiments in which we measured the mortality of zebra mussel larvae of various sizes exposed to different levels of turbulence. To explain the effect of turbulence on zebra mussel veligers, we define the ratio of the shell size d and the Kolmogorov scale:

$$[1] \qquad d^* = \frac{d}{L_K} = \frac{d}{(v^3/\varepsilon)^{1/4}}$$

and hypothesize that turbulence will affect mortality when $d^* \gtrsim 1$. If $d^* \ll 1$, turbulent eddies are too big to affect the larvae. In this case, the turbulence merely transports the larvae, although they will be subjected to shear and straining at the Kolmogorov strain rate $(\varepsilon/v)^{1/2}$ (Thomas and Gibson 1990). If $d^* \sim 1$, however, turbulence could increase mortality, since velocity gradients exist on a scale small enough to affect the larvae. Thus, smaller larvae would require more intense turbulence for an effect. The ability to control the turbulence level and directly measure the dissipation allowed us to test the hypothesis that turbulence increases the mortality when $d^* \gtrsim 1$. We use the experimental results to estimate the effects of turbulence on veligers in streams, and we discuss the implications of the results for a dispersal barrier to control zebra mussels in rivers.

Materials and methods

Turbulence generation and measurement

Veligers were subjected to turbulence generated by air bubble plumes in 4-L Nalgene beakers. The water depth H was 17.5 cm and the mean diameter was 17 cm. A blower pushed room air through plastic tubing and a 2.5 cm long, 1.5 cm diameter aquarium stone to create the bubble plume (Fig. 1). The aquarium stone was fixed to the side of the beaker bottom so that the bubbles would not interfere with the velocity measurements, described below. Airflow rates Q, measured with Gilmont No. 13 flowmeters, ranged from 0 to 5 std. L/min (0–0.3 m³/s). The unit std. L/min refers to airflow measured at standard pressure and temperature, 1 atm (101.325 kPa) and 20°C, respectively.

The turbulence was quantified with velocity measurements before larval mortality experiments were conducted.

Fig. 1. Schematic of the experimental setup to test for the effect of turbulence on the mortality of zebra mussel (*Dreissena polymorpha*) veligers.
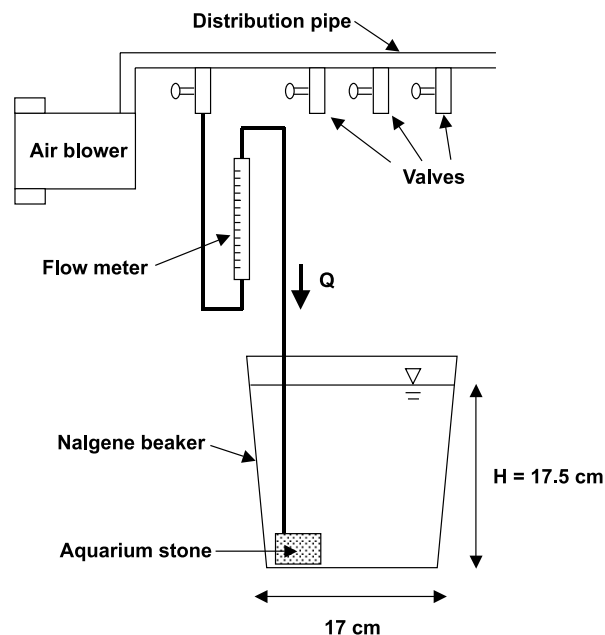
Time series of velocity were measured with an acoustic Doppler velocimeter (Sontek MicroADV), which has a cylindrical sampling volume with a diameter of 4.5 mm and a height of 5.6 mm. Velocities were measured at 5 and 10 cm above the bottom on a vertical line 12.7 cm away from the wall to which the aquarium stone was attached. The flow was seeded with neutrally buoyant, hollow glass spheres with a mean size of about 8–10 μm. At each point, the velocity was sampled at 25 Hz for 5 min, which was long enough for means and variances to converge. Five minutes was allowed for the flow to become steady after the airflow was changed, and 1 min was allowed when the ADV was moved. Dissipation was computed by fitting the inertial subrange of the energy spectrum of the vertical (i.e., streamwise) velocity component. Values at the two depths were averaged to characterize the dissipation at each flow rate. These direct measurements of dissipation allowed us to develop a quantitative relationship between mortality and the intensity of the turbulence, measured by d^*.

Larval culture

Zebra mussels in good spawning condition were collected from the Bark River in Wisconsin and transported to the Illinois River Biological Station. A zebra mussel stock population was then maintained in the laboratory at $10 \pm 1°C$ and fed *Isochrysis galbana* (T-ISO) at 3×10^5 cells/mL of water daily. All mussels were cultured in artificial fresh water, which consists of 10 mL of Artificial SeaWater (28–30 ppt, Instant Ocean), 990 mL of deionized water, 200 mg of $CaCl_2$, and 100 mg of $Na(CO_3)_2$. The artificial fresh water had a final pH between 7.7 and 8.2 and salinity between 0.5 and 1 ppt.

To initiate experiments, adults were removed from culture tanks, allowed to acclimate to room temperature (~21°C)

Table 1. Experimental design to test for the effect of turbulence on the mortality of zebra mussel (*Dreissena polymorpha*) veligers.

Experiment	Initial mean (±SE) larval size (μm)	Initial age (days)	Stage	Initial density (no./L)	Airflow rates (std. L/min)
1	101 ± 1.1	3	D	150	0, 0.5, 2.5, 5.0
2	84 ± 0.8	1	D	150	0, 2.5, 5.0
	126 ± 1.3	11	Umbonal	80	0, 2.5, 5.0

overnight, and then induced to spawn using serotonin and water temperature according to the protocols of Wright et al. (1996) and Ram et al. (1993). Larval culture followed the procedures of Wright et al. (1996) with modifications. Larvae were cultured in a dedicated, embryologically clean room, maintained at a constant temperature of 25°C. Larvae were maintained in artificial freshwater in culture vessels (2–4 L depending on number of larvae required) with loose-fitting lids to reduce dust contamination. Culture water was changed by gently filtering off 80% of the water through a 50-μm filter and then individually pipetting larvae into the new culture water and container. Stock larvae were fed daily (1.5 × 10^5 of *I. galbana* cells/mL of water) and culture water and containers were changed daily. Initial densities in the stock cultures ranged from 300 to 2000 veligers/L depending on the age of larvae required for each experiment.

Mortality experiments

The effects of turbulence on three size classes of larvae were evaluated in two experiments (Table 1). Larvae were subjected to turbulence for 24 h and allowed to feed for an additional 24 h before survival was measured. This procedure incorporates acute effects of turbulence (which we take to be due to exposure on the order of minutes), chronic effects, and delayed effects due to exhaustion and starvation. All treatments were held in a 25°C water bath. Larvae from stock cultures were individually pipetted into replicate chambers. Approximately one third of the total number of larvae were added to each chamber in turn to avoid differences in age of larvae among treatments. Food (1.5 × 10^5 of *I. galbana* cells/mL of water) was added to each chamber, and larvae were allowed to feed for 2.5 h with no airflow before the initiation of the experiment. Chambers were randomly assigned to a turbulence treatment and turbulence maintained for 24 h. With the cessation of turbulence, 90% of the culture water was changed and larvae were again fed. The following day, live larvae remaining in each chamber were counted and measured. Larvae were considered live if they were swimming or exhibited ciliary action within the shell. For Experiment 2, the two cohorts of larvae were easily distinguished and assigned to a cohort on the basis of size and developmental stage (Ackerman et al. 1994). Only larvae in the D or umbonal stages, which have shells, were used.

Effects of turbulence were evaluated using single-factor ANOVA. Survival data were transformed as $\arcsin(p^{0.5})$, where p is the proportion surviving. Individual treatments were compared with controls using a one-tailed Dunnet test. All analyses were performed using Systat statistical software (Systat Software Inc., Richmond, Calif.).

Fig. 2. Rate of dissipation of turbulent kinetic energy as a function of airflow. Solid circles denote the measurements, and the line is a power law fit to the data: $\varepsilon = (3.5 \times 10^{-4})Q^{1.63}$ ($R^2 = 0.995$), where Q is the airflow rate and ε is the dissipation.
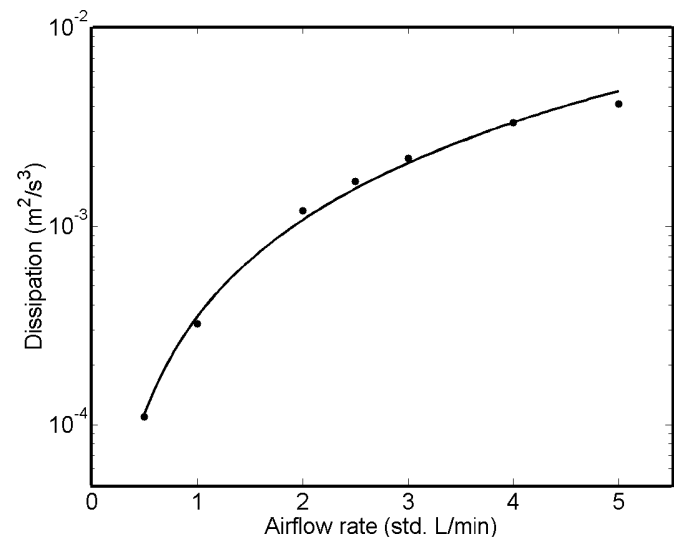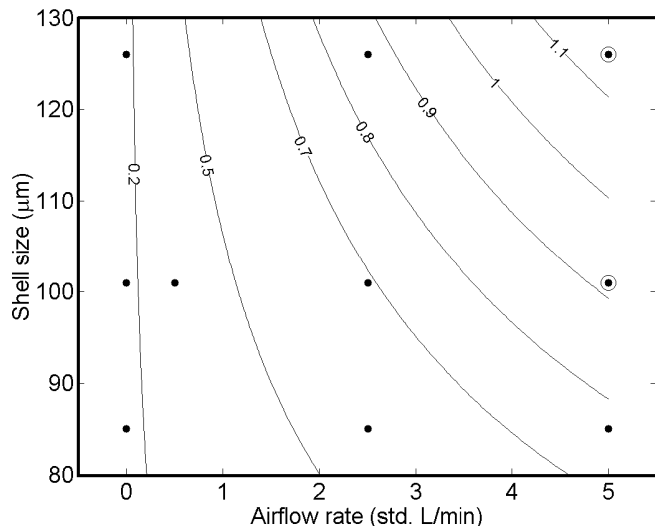

Results

Turbulence was stronger for higher airflow rates. The dissipation of turbulent kinetic energy increased with the flow rate to the 1.6 power (Fig. 2). The rate of work $\dot{W}$ (per unit mass) required to produce the bubble plume also increases as the flow rate increases; assuming isothermal compression (Schladow 1992), the rate of work is

[2] $$\dot{W} = \frac{gQh_a}{V} \ln\left(1 + \frac{H}{h_a}\right)$$

where g is the acceleration of gravity, $h_a = 10.2$ m is the atmospheric pressure head, and V is the fluid volume. The dissipation measured in the experiments represented between 3 and 13% of the rate of work given by eq. 2, with higher fractions occurring for higher airflows. The relationship between airflow rate and dissipation was used to compute d^* as a function of shell size and airflow rate. Values of d^* ranged from 0 (no airflow) to 1.14 (Fig. 3).

Survival of zebra mussel larvae depended on the strength of the turbulence and the mean size of the mussels (Fig. 4a, Table 2). Small mussels (84 μm), which had recently made the transition to shelled larvae from the trochophore stage, were unaffected by turbulence at any of the airflow rates tested. In contrast, both 101-μm mussels ($P = 0.012$), which

Fig. 3. Experimental parameters (●) and contours of the length scale ratio $d^* = d/L_K$. Circled ●s denote the cases in which the mortality was significantly greater than that of the control.

Fig. 4. Survival of zebra mussel larvae under different turbulence conditions (●, initial size of 84 µm, D stage; □, initial size of 101 µm, D stage; ▲, initial size of 126 µm, umbonal stage). Error bars denote 1 SE. Asterisks denote significantly lower survival than that of the control using a one-tailed test. (*a*) Dependence on airflow rate. The abscissae are offset slightly for clarity. (*b*) Dependence on d^*. The measurement for 84-µm larvae at $d^* = 0$ has been offset slightly for clarity.
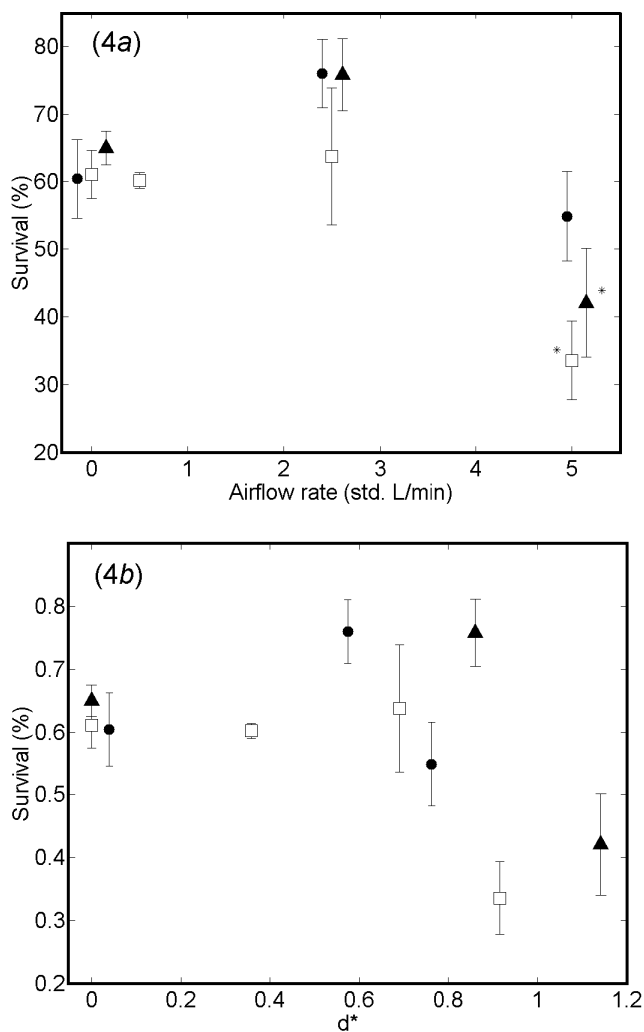

were in the D stage, and 126-µm mussels ($P = 0.034$), which were mostly in the umbonal stage, had significantly higher mortality at the highest flow rate. In the treatments with weaker turbulence, however, there was no effect for mussels of either size. Strong turbulence increased larval mortality by 45% for 101-µm mussels and 35% for 126-µm mussels.

Discussion

Effect of turbulence on mortality

The data support the hypothesis that mortality increases when $d^* \gtrsim 1$. Larval stage does not appear to be a factor because the effect of turbulence on larvae of a particular stage depends on airflow. Mortality increased significantly only for the largest larvae at the highest airflow rate. In terms of the length ratio, turbulence increased mortality when $d^* > 0.9$ (Figs. 3 and 4*b*) or when the shell size was 90% of the size of the smallest eddy in the flow. The survival dropped sharply from a mean of 65% when $d^* < 0.9$ to a mean of 38% when $d^* > 0.9$. Although $d^* \approx 0.85$ for the 126-mm veligers subjected to $Q = 2.5$ std. L/min, the survival did not differ significantly from that of the control. Since d^* depends weakly on the dissipation ($d^* \propto \varepsilon^{1/4}$), the range of d^* is limited, that is, large changes in dissipation correspond to relatively small changes in d^*. For example, the dissipation at $Q = 5$ std. L/min is a factor of 3 larger than that at $Q = 2.5$ std. L/min, but the values of d^* differ by only 6%. Further experiments are required to define the dependence of survival on d^* more precisely.

Other issues to be examined in future experiments include a possible increase in survival for moderate turbulence and the behavior of survival at high d^*. Experiments with other organisms showed beneficial effects of moderate stirring (Peters and Marrasé 2000), and for veligers, medium airflows would keep food suspended and prevent a film of dust and bacterial particles from fouling the veligers. However, the survival for $Q = 2.5$ std. L/min for the smallest and largest larvae is not significantly higher than that of the control. Another question is whether survival continues to decrease

Table 2. ANOVA of the effect of turbulence on survival of zebra mussel larvae.

	SS	df	MS	*F*	*P*
Initial size of 84 µm					
Treatment	0.084	2	0.042	3.594	0.094
Error	0.070	6	0.012		
Initial size of 101 µm					
Treatment	0.188	3	0.063	6.170	0.018
Error	0.081	8	0.010		
Initial size of 126 µm					
Treatment	0.200	2	0.100	8.363	0.018
Error	0.072	6	0.012		

Table 3. Computation of d^* for the field study of Horvath and Lamberti (1999).

Quantity	Upstream reach	Downstream reach
Length (km)	1.8	16.2
Mean depth (m)	0.8	0.4
Width (m)	15	15
Slope	1×10^{-4}	5×10^{-4}
Shear velocity (m/s)	2.7×10^{-2}	4.3×10^{-2}
Mixing time T_z (h)	0.13	0.04
Travel time (h)	0.8	15.2
Max. dissipation (m²/s³)	2.2×10^{-3}	1.9×10^{-2}
Mean dissipation (m²/s³)	1.9×10^{-4}	1.6×10^{-3}
Range of d^* based on mean ε	0.30–0.74	0.51–1.27
Range of d^* based on max. ε	0.55–1.38	0.94–2.35
Min. affected size (µm) based on mean ε	>200	131
Min. affected size (µm) based on max. ε	142	77

Note: The range of d^* is computed for larvae between 80 and 200 µm.

as d^* increases. If the increased mortality is due to damage once the smallest scale of the turbulence is small enough, we expect that a further reduction in scale will have little effect and survival will remain nearly constant as d^* increases further.

Because the mortality increased at the highest flow rate only, an important factor aside from the scale of the turbulence may be the force exerted by the turbulence on the veligers. The shear stress at scales comparable with or smaller than the Kolmogorov scale is $\tau = \mu(\varepsilon/\nu)^{1/2}$ (e.g., Thomas and Gibson 1990), and the force on the veligers would scale as $\mu(\varepsilon/\nu)^{1/2}d^*$. Like d^*, the force increases with dissipation, or flow rate; in fact, for constant viscosity the force is proportional to d^{*2}. One difference between criteria for increased mortality based on eddy sizes and forces is that the critical value of d^* is likely to be nearly constant for all larvae, while the force required to kill larvae probably increases with shell size. Our data suggest that the eddy size, or d^* criterion, is more important because the mortality of the larger larvae increases at the highest airflow rate but the smallest larvae are not significantly affected.

Another reason for increased mortality at higher airflow rates could be abrasion on the walls. Gregg and Bergersen (1980) attributed the increased mortality of *Mysis relicta* at high airflow rates to abrasion and exhaustion due to continuous swimming and an inability to feed. We expect the larger larvae to withstand abrasion better than less-developed larvae, but at the highest airflow the mortality increased for the two cohorts with the larger larvae rather than the cohort with the smallest larvae.

Mortality in streams

Our laboratory results can be used to evaluate the potential for turbulence effects on mortality in streams. To quantify the proposition of Horvath and Lamberti (1999) that turbulence and hydrodynamic stresses can limit the dispersal of zebra mussels in streams, we estimate values of d^* from their data and models of turbulence in rivers. Because Horvath and Lamberti (1999) did not report veliger sizes, we use a typical range of $80 < d < 200$ µm. Nezu and Nakagawa (1993, pp. 77–78) fit dissipation measurements in open channels over the range $0.01 < z/H < 1$ with

$$[3] \qquad \frac{\varepsilon H}{u_*^3} = E_1 \left(\frac{z}{H} \right)^{-\frac{1}{2}} e^{-3z/H}$$

where z is the distance from the channel bottom, H is the depth, $E_1 \approx 9.8$, and u_* is the shear velocity, which is related to the shear stress on the river bottom. A force balance for steady, uniform flow allows the shear velocity to be estimated with

$$[4] \qquad u_* = (gRS_0)^{\frac{1}{2}}$$

where g is the acceleration of gravity, S_0 is the channel slope, and R is the hydraulic radius, or the ratio of the cross-sectional area to the wetted perimeter. Lacking a description of the channel cross section, we take it to be rectangular.

Equation 3 shows that the dissipation varies considerably over the depth; the dissipation near the free surface is a factor of about 200 smaller than the dissipation near the bottom. Larvae in the stream studied by Horvath and Lamberti (1999) will experience the depth-averaged value of dissipation because turbulence will transport larvae over the entire water column many times during downstream transport; the time for mixing over the depth, $T_z \approx 15H/u_*$ (Fischer et al. 1979), is much smaller than the mean travel time. Thus, values of d^* are estimated with the value of the dissipation averaged over $0.01 < z/H < 1$:

$$[5] \qquad \bar{\varepsilon} \approx 8 \frac{u_*^3}{H}$$

Values of d^* computed from the maximum dissipation (i.e., at $z = 0.01H$) are also reported, since our experiments do not distinguish between acute and chronic effects of turbulence, that is, veligers exposed to intense turbulence may be pulled apart and killed, as Horvath and Lamberti (1999) suggested, or they may have increased mortality only after long exposure.

Our experimental results suggest that turbulence increased mortality in the stream, although the magnitude of the effect depends on the size distribution of the larvae and the relative importance of acute and chronic exposure (Table 3). If chronic effects dominate, relatively few larvae would be af-

fected; in the low-gradient, upstream portion of the creek, $d*$ computed with the depth-averaged dissipation never exceeds 0.9, while in the steeper, downstream portion, it exceeds 0.9 only for larvae larger than about 140 μm. These larger larvae probably make up a relatively small fraction of the total. However, if mortality is determined by acute exposure to the maximum dissipation, then in the upstream portion, larvae larger than about 130 μm would be affected and in the downstream portion, all larvae would be affected.

The measurements of Horvath and Lamberti (1999) allow the mortality rate to be estimated and compared with rates measured in systems with little or no turbulence. Horvath and Lamberti (1999) fit an exponential function of downstream distance x to their survival measurements. This spatial dependence would result from the solution of a transport model in which larvae are subjected to advection at mean velocity U and mortality, modeled as a first-order reaction with constant rate λ. This simplified model assumes steady conditions and negligible longitudinal dispersion; the former assumption requires changes over time scales comparable with the travel time to be small, while the latter can be justified with dispersion estimates from Seo and Cheong (1998). Then, the larval abundance N is governed by

$$[6] \qquad U\frac{dN}{dx} = -\lambda N$$

which has the solution

$$[7] \qquad N(x) = N_0 e^{-\lambda x/U}$$

where N_0 is the abundance at $x = 0$. From the measurements of Horvath and Lamberti (1999), we estimate[3] that $\lambda = 1.1$/day, corresponding to a daily survival of 34%. This mortality should be compared with intrinsic mortality that veligers would experience under field conditions with weak turbulence. For example, Sprung's (1989) measurements of the survival of zebra mussel larvae in a lake yield a daily survival of 76–80%. Compared with this value, a daily survival of 34% measured in the stream indicates greater mortality.

Implications for control

The motivation of our work was to assess the possibility of using bubble screens in the Chicago Sanitary and Ship Canal to block zebra mussel larvae from entering the Illinois River. The dispersal barrier would consist of one or more lines of air diffusers spaced evenly across the canal, which has a depth of about 8 m and a width of about 50 m (Thomas 1958). The experimental results allow this design to be assessed. The airflow rate of each diffuser would be determined by setting $d* \sim 1$, since smaller values would not increase mortality and significantly larger values might increase mortality but waste energy. The measurements and analysis of Soga and Rehmann (2003)[4] can be used to relate the airflow rate to dissipation. They used the numerical simulations of Sahai and Guthrie (1982) to find that in tanks of 3–4 m depth, the volume-averaged dissipation is about 40% of that given by eq. 2, somewhat larger than the 3–13% mea-

sured in the present experiments. Soga and Rehmann also measured ensemble-averaged dissipation profiles in a 7 m deep tank and found that the fraction is closer to 1%. They attributed the smaller fraction to the inability to sample near the bubble plume, where the dissipation is highest, and the lack of surface wave generation in the simulations, which would put more energy into the turbulence to be dissipated. Taking a compromise value of 10%, a minimum larval size of 80 μm, and a diffuser spacing of 1 m, we estimate that each diffuser would need to have an airflow rate of about 6 L/s (measured at atmospheric pressure) to affect mortality. A more precise estimate of the flow rate requires further study of the relation between $d*$ and survival, but airflow rates of 5–10 times higher have been used in lakes (e.g., Lemckert and Imberger 1995).

Although the airflow rate for a single diffuser is reasonable, the number of diffusers needed, both across and along the canal, may be impractical. The diffuser spacing of 1 m across the canal was chosen because the numerical simulation results of Sahai and Guthrie (1982) show that the dissipation reaches a peak on the plume axis and decreases by a factor of between 10 and 100 within a radial distance of 1 m. Thus, about 50 diffusers would be needed for each bubble screen. The number of bubble screens along the channel depends on whether mortality occurs by acute or chronic exposure. If the mortality is due to larvae being pulled apart by intense turbulent bursts, fewer screens would be required. If the mortality is due to a day's exposure, bubble screens over the whole length of the canal would be required, since the travel time is about 19 h (Thomas 1958).

Summary

Our laboratory experiments, in which the parameters of the turbulence relevant for larval development were measured directly, show that turbulence can increase mortality if the turbulence is strong enough, i.e., $d* > 0.9$. The dimensionless ratio $d*$ provides a quantitative way to assess whether turbulence can affect larvae in natural water bodies. As a scheme to control zebra mussels, using turbulence could work if the mortality is due to acute effects, due to exposure on the order of minutes, but it would be impractical if longer-term effects are more important. Temporal effects of turbulence on zebra mussel veligers remain to be examined.

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