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Mortality of zebra mussel, *Dreissena polymorpha*, veligers during downstream transport

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SUMMARY

1. Streams flowing from lakes which contain zebra mussels, *Dreissena polymorpha*, provide apparently suitable habitats for mussel colonization and downstream range expansion, yet most such streams contain few adult mussels. We postulated that mussel veligers experience high mortality during dispersal via downstream transport. They tested this hypothesis in Christiana Creek, a lake-outlet stream in south-western Michigan, U.S.A., in which adult mussel density declined exponentially with distance downstream.
2. A staining technique using neutral red was developed and tested to distinguish quickly live and dead veligers. Live and dead veligers were distinguishable after an exposure of fresh samples to 13.3 mg L^{-1} of neutral red for 3 h.
3. Neutral red was used to determine the proportion of live veligers in samples taken longitudinally along Christiana Creek. The proportion of live veligers (mean ± SE) declined from 90 ± 3% at the lake outlet to 40 ± 8% 18 km downstream.
4. Veligers appear to be highly susceptible to damage by physical forces (e.g. shear), and therefore, mortality in turbulent streams could be an important mechanism limiting zebra mussel dispersal to downstream reaches. Predictions of zebra mussel spread and population growth should consider lake-stream linkages and high mortality in running waters.

Keywords: dispersal, *Dreissena polymorpha*, mortality, streams, veligers

Introduction

Zebra mussels, *Dreissena polymorpha* (Pallas), are among a few freshwater molluscs which produce truly planktonic larvae called veligers. The veliger lasts for about 2–4 weeks (Sprung, 1989), during which the larvae can be carried long distances by water currents. The rapid spread of zebra mussels in the Laurentian Great Lakes and their colonization of large rivers in Europe and North America have been attributed largely to the dispersal abilities of veligers (Griffiths *et al*., 1991; Kern, Borcherding & Neumann, 1994; Stoeckel *et al*., 1997; but see also Carlton, 1993). However, successful invasion may be impeded by high veliger mortality in some habitats.

In marine ecosystems, where planktonic larvae are more common, methods for directly determining larval mortality have proved difficult, and mathematical models are normally used to estimate an instantaneous mortality rate based on changes in larval density over time (Jackson & Strathmann, 1981; Connell, 1985; Rumrill, 1990). However, changes in larval density could be caused by other factors such as advection, diffusion and mechanical factors associated with wind and internal waves (Rumrill, 1990). Difficulties in distinguishing between overlapping cohorts of larvae also complicate mortality estimates (Sprung, 1989).

Mortality in zebra mussel veligers is believed to vary from 30% to 100% in lakes (Stanczykowska, 1977; Lewandowski, 1982; Sprung, 1989). These estimates were based mostly on differences between veliger abundance and settlement, and only Sprung (1989)

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distinguished cohorts. In lakes, dead veligers probably settle out of the water column, and thus, would not be included in plankton counts. In rivers and streams, dead veligers may remain suspended in the water column and would be included in density estimates. Because recruitment is partly a function of the number of live veligers in the water column, including dead veligers in the counts will overestimate the pool of recruits and give false indications of invasion potential.

It is difficult to distinguish live and dead zebra mussel veligers at present. An obvious approach would be to observe individual veligers under a compound microscope to verify swimming or filtering activity, but this method is impractical because each sample would need to be viewed immediately after collection. Staining provides the potential advantage of being able to determine at a glance the physiological condition of larvae at the time of sampling. Dressel, Heinle & Grote (1972) used neutral red to differentiate between live and dead marine calanoid copepods, but cyclopoid copepods, amphipods and cladocerans did not stain successfully. Crippen & Perrier (1974), using a method slightly modified from that of Dressel *et al*. (1972), were able to differentiate between live and dead marine zooplankton, although some species produced inconsistent results. We tested a staining technique, similar to that of Crippen & Perrier (1974), to differentiate live and dead zebra mussel veligers.

In many streams, colonization by zebra mussels is linked to populations in upstream lakes (Horvath *et al*., 1996). Lake populations produce veligers which can eventually found mussel populations in outflowing streams. However, adult zebra mussel density in streams tends to decline rapidly with distance downstream from the source population of mussels in the lake (Horvath *et al*., 1996). The mechanisms responsible for such downstream patterns have not been determined, but habitat and food resources do not appear to limit zebra mussels in lake-outlet streams (Horvath & Lamberti, 1999). We hypothesized that veligers experience high mortality during transport, and thus, the proportion of live veligers in the water column would decrease with distance downstream of a lake outlet. To test this hypothesis, we used the staining method to quantify veliger mortality at sites along 19 km of stream running from a lake in south-western Michigan, U.S.A.

Methods and materials

Description of study site

Christiana Creek drains the Eagle and Christiana lakes in south-western Michigan (Fig. 1). The Eagle and Christiana lakes were first colonized by zebra mussels in 1991, probably by contaminated boats, and Christiana Creek was colonized in 1993. Veligers are present in the lakes and stream from May to September (Horvath, 1997). A low-head dam (height = 2.5 m) is located 1.8 km downstream of the lake outlet (Fig. 1), upstream of which the stream has a gradient of 0.1 m km^{-1} (derived from topographic maps), stream width is about 15 m and mid-channel depth ranges from 0.5 to 1.2 m. The stream bottom consists of small gravel, sand and mud with dense macrophytes [*Potamogeton* spp., *Vallisneria americana* (Michx.) and the macroalga *Chara* sp.]. Downstream of the dam, the stream gradient increases to 0.5 m km^{-1}, stream width remains about 15 m and mid-channel depth ranges from 0.15 to 0.60 m. The stream bottom

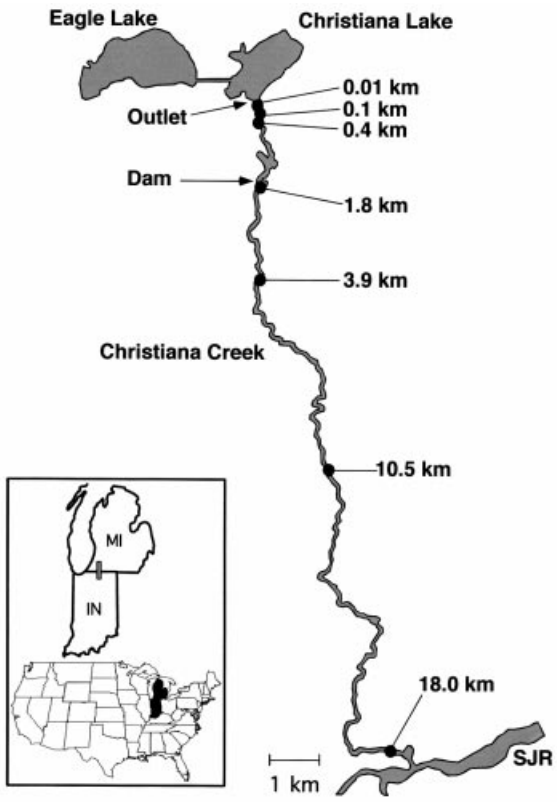

Fig. 1 Map of Christiana Creek showing the sampling points along the stream. Distances are in kilometres downstream of the lake outlet. Water flows from Eagle Lake into Christiana Lake and then into Christiana Creek: (SJR) St Joseph River.

consists mostly of sand and gravel with occasional macrophyte patches. Normal discharge for Christiana Creek is about 2–3 $m^3 s^{-1}$ and water velocity at mid-channel (measured at 0.6 depth) rarely exceeds 0.5 m s^{-1}. However, discharge increased to >6 $m^3 s^{-1}$ in early June 1996 and we recorded water velocities >1.0 m s^{-1} downstream of the dam during this spate. Discharge returned to normal by July.

Staining technique

Zebra mussel veligers were collected from Eagle Lake by towing a plankton net (63-μm mesh) through the epilimnion in the pelagic zone of the lake and transferred to the laboratory in open sterile plastic bags. In a pilot experiment, three concentrations of neutral red and four exposure times were tested for their effectiveness in staining veligers. We applied stain to two, 300-mL samples in concentrations of 10, 13.3 and 20 mg L^{-1} for periods of 1, 3, 6 and 12 h (after Crippen & Perrier, 1974). To determine if stain was assimilated by dead veligers, veligers were killed in one of the samples at each concentration–time combination by rapidly heating a sample to 50 °C and allowing it to stand for 1 h prior to staining (after Crippen & Perrier, 1974). At the end of the exposure, the samples were rinsed with distilled water in a 63-μm-mesh plankton bucket un-til the sample water was clear. Samples were concentrated to ≈ 50 mL and then transferred to clean bags. A minimum of 100 veligers from each sample were located under cross-polarized light (Johnson, 1995) using a dissecting microscope at × 20 power. The polarized light was then removed to determine if the veligers were stained. We distinguished between larvae with tissue in the shell and empty shells; empty shells were not considered in the stain assessment. In contrast to Crippen & Perrier (1974), we did not attempt to fix the stain and preserve the samples; rather, we examined the samples immediately after rinsing the stain.

The optimal staining condition (concentration and time) determined from the pilot experiment was used in two separate, replicated (n = 10) experiments (experiments I and II) comparing untreated and heat-killed veligers. Subsamples of veligers from these replicates were viewed under a compound microscope (×200 magnification) to verify that un-stained veligers were dead and stained veligers were alive as determined by beating cilia. At least ten veligers were viewed from each subsample. To test the effectiveness of the staining procedure, a one-way analysis of variance (ANOVA) was used to examine differences in the percentage-stained veligers between heat-treated and untreated samples. Proportional data were normalized by an arc-sine square-root transformation.

In situ *sampling*

Veliger samples were collected from Christiana Creek at distances of 0.01, 0.1, 0.4, 1.8 (separate samples immediately up- and downstream of the dam), 3.9, 10.5 and 18.0 km downstream of the lake outlet about once every 2 weeks from May to August 1996 (n = 3 samples per site and date). A 63-μm-mesh plankton net was suspended at mid-depth in the current in mid-channel for 5 min and the plankton collected was rinsed into sterile plastic sample bags and brought up to 300 mL with stream water. Neutral red stain was added in the field at a concentration of 13.3 mg L^{-1}. Samples were transported to the laboratory in open sample bags and temperature was maintained at about ambient stream temperature by suspending the bags in a water bath during transport. After 3 h of exposure to stain, samples were rinsed with distilled water, veligers were immediately observed under a dissecting microscope and between fifty and 100 individuals were counted to determine the proportion of stained individuals. More veligers could not be counted because of low density in samples. Veligers were not separated by development stage during counting.

Using late-stage veliger (distinguished as a pediveliger with well-developed umbo; see Conn *et al.*, 1993) density (Horvath & Lamberti, in press) and proportion of all live veligers (no distinctions were made based on developmental stage), we calculated the flux of potential settlers in transport along Christiana Creek. The number of potential settlers was calculated as: daily potential settlers = flux in late-stage veligers per day × proportion of live veligers, where flux is determined from veliger density and stream discharge. The percentage survival and flux of veligers were regressed separately on distance downstream using an exponential decay model:

where y = percentage survival or flux, a = constant, k = slope and x = distance downstream.

$$y = ae^{-kx}$$

Results

Staining technique

The pilot staining experiment indicated that live (untreated) veligers were distinguishable from dead (heat-treated) veligers at all combinations of stain concentration and exposure time. Live veligers were all stained pink to red, whereas no dead veligers were stained at any concentration–time combination. Increasing the stain concentration or exposure time generally resulted in more darkly stained veligers, but only slightly improved our ability to differentiate live from dead veligers. From these treatment combinations, an 'optimal' staining concentration and time of 13.3 mg L^{-1} for 3 h for distinguishing live and dead veligers was chosen. Using this protocol in experiments I and II, we found a significant difference in the percentage of stained veligers between untreated and heat-treated samples (Table 1). All stained individuals were alive as determined by the presence of moving cilia, whereas unstained veligers showed no signs of movement and were apparently dead.

In situ sampling

In Christiana Creek, the percentage of live veligers declined exponentially with distance downstream (x) (percentage live = $80.1e^{-0.5x}$; $R^2 = 0.99$; $P < 0.001$; Fig. 2). The daily flux of potential settlers (i.e. live late-stage veligers) in Christiana Creek also declined exponentially with distance downstream (flux = $5.69 \times 10^8\ e^{-2.62x}$; $R^2 = 0.46$; $P = 0.001$; Fig. 3), but at a higher rate than veliger survival.

Discussion

Utility of staining technique

Using a moderate stain concentration (13.3 mg L^{-1}) and a short exposure time (3 h), the neutral red staining technique distinguished live and dead veligers. Live veligers ranging from young, straight-hinged veligers to pediveligers competent to settle were stained, whereas dead veligers were not stained.

Table 1 Percentage of veligers stained with neutral red in untreated and heat-killed samples of lake water ($n = 10$). Differences between treatments were analysed with a one-way analysis of variance (ANOVA)

Experiment	Treatment	Percentage stained (±1 SE)	$F_{1,18}$	P-value
I	Untreated	97.3 ± 1.1	216.3	<0.001
	Heat-killed	0.7 ± 0.2	–	–
II	Untreated	100.0 ± 0.0	2075.1	<0.001
	Heat-killed	0.2 ± 0.2	–	–

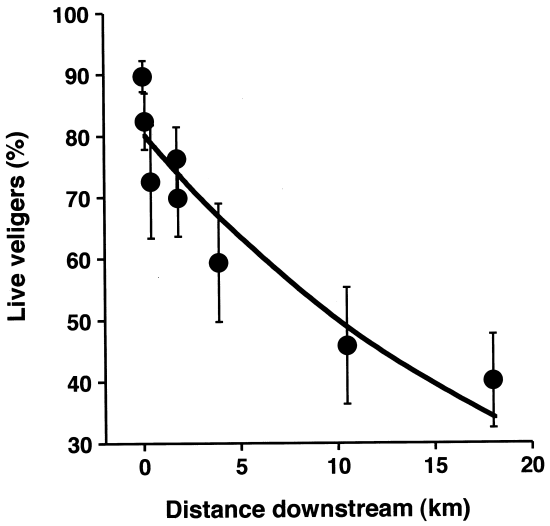

Fig. 2 Proportion of live veligers along Christiana Creek, starting at the lake outlet. Live veligers were determined using a vital stain (neutral red) which coloured only live individuals. The data points are the means of eight sampling dates from May through August (error bars are ± 1 SE).

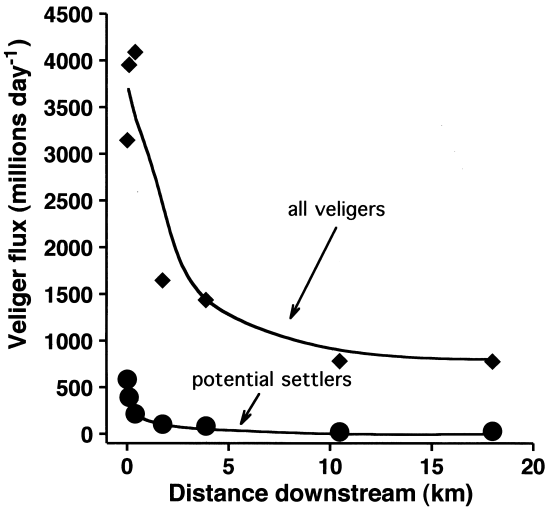

Fig. 3 Daily flux of all veligers (◆) (including all veligers from quantitative samples) and potential settlers (●) along Christiana Creek, starting at the lake outlet. Daily potential settlers = flux in late-stage veligers per day × proportion of live veligers.

Thus, the developmental stage and larval size did not appear to affect staining success. However, the intensity of staining varied among individual veligers. Some veligers were stained only in a centralized area within the digestive tract, whereas all tissues were stained in other veligers. The reason for such variation in staining is unknown, but is consistent with that observed for other bivalves (Loosanoff & Davis, 1947).

It is unclear how long the stain will persist in veligers. Crippen & Perrier (1974) achieved limited shelf lives of about a month by fixing their stained samples with an acetic acid-sodium acetate solution and then preserving these in formalin and methylated ethanol. We added 70% ethanol to a stained sample and found that the stain was washed out of all previously stained veligers. However, we were still able to differentiate live from dead veligers in unpreserved samples for up to 2 days following staining. In general, we recommend that samples be analysed within 24 h of staining.

Sources of veliger mortality

Veligers exhibited a significant increase in mortality during downstream transport in Christiana Creek. Welker & Walz (1998) also noted mortality of *Dreissena* veligers in the Spree River, but they did not directly determine dead veligers as in the present study. Rather, high mortality was estimated from size distribution and disappearance of veligers from the water column. Mortality in the Spree River was attributed to predation by the benthic bivalves Unionidae and *Dreissena* (Welker & Walz, 1998). Although we could not identify a specific cause of mortality in Christiana Creek, there are several possibilities.

In marine systems, planktonic larvae are subject to high mortality resulting from suboptimal temperature, lack of adequate settlement substrata, transport of larvae away from suitable habitat, starvation and predation (Thorson, 1950). Mortality of zebra mussel veligers can result from similar mechanisms in freshwater systems. For example, veligers do not develop successfully at a temperature above 24 °C or below 10 °C (Sprung, 1987), and will eventually die if suitable substratum is not found (Lewandowski, 1982; Sprung, 1989). These factors probably contribute little to veliger mortality in Christiana Creek because water rarely reaches lethal temperature and the availability of suitable substratum actually increases at downstream sites (Horvath *et al.*, 1996; Horvath & Lamberti, 1999). Veligers could starve if suitably sized food particles are not present in the plankton (Sprung, 1989) or if they are not able to feed in turbulent flow. However, veligers can survive for 1–2 weeks without food (Sprung, 1989) and the average transport time through Christiana Creek was estimated to be 16 h based on dye releases (Horvath & Lamberti, 1999). Thus, veligers are likely to be transported out of Christiana Creek before they can die from starvation.

Predation on veligers by zooplankton (reviewed by Stanczykowska, 1977) and by adult zebra mussels (MacIsaac, Sprules & Leach, 1991) has been documented. We have no data on the density of zooplankton, other than *Dreissena*, in Christiana Creek, but benthic predators, such as *Hydra* or adult zebra mussels, are present (Horvath *et al.*, 1996; Horvath, 1997). However, these predators ingest their prey whole and it is unknown if they selectively capture only live veligers. Thus, these predators may reduce the total abundance of veligers by consuming live and dead veligers, but not affect the proportion of live veligers. Some proportion of veligers may escape contact with *Hydra*, but die as a result of damage from their nematocysts.

Alternatively, an increase in veliger mortality could occur if live veligers settled in the upper reaches of the stream, thereby reducing the proportion of live veligers downstream. However, this explanation is unlikely because only late-staged veligers are capable of settlement (Sprung, 1993) and high numbers of these veligers were collected along the entire stream length (Horvath & Lamberti, 1999).

Hydrodynamic forces have not been investigated previously as a possible source of mortality. Exposure to high shear stress can damage planktonic species such as the dinoflagellate *Gonyaulax polyedra* Stein (Thomas & Gibson, 1990) and larvae of the sea urchin *Strongylocentrotus purpuratus* Stimpson (Mead & Denny, 1995). In a lake-outlet stream, phytoplankton showed signs of physiological damage caused by exposure to physical stresses associated with turbulence (Uehlinger, 1993).

We did not measure turbulence directly, but they attempted to qualify flow con-ditions in Christi-

ana Creek by computing whole-channel Reynolds numbers. Flow is considered turbulent at a Reynolds number above 2000 (Davis & Barmuta, 1989); Reynolds numbers throughout the stream (130 000–200 000) exceeded this value by nearly two orders of magnitude. Thus, veligers were exposed to continuous turbulence during transport and progressively increasing mortality could have resulted.

Individual veligers probably experience low Reynolds number during transport because of their short body length (Vogel, 1994). However, the appearance of veligers collected from Christiana Creek suggests that mechanical forces may also have contributed to veliger mortality. Empty but unbroken veliger shells were frequently observed in samples from Christiana Creek (e.g. 41% at the 18 km site), whereas empty shells were rarely observed (e.g. 8% at lake outlet) in source lakes or at the lake outlet, suggesting that veligers were pulled open during transport. Veligers may be particularly susceptible to shell separation while feeding because the shell must be open to allow the velum to sweep food particles into the food groove (Sprung, 1993). An open shell may provide greater surface area and exposed tissue over which shearing forces could act.

Consequences of veliger transport for stream mussel populations

Flowing water poses special problems for benthic animals which produce planktonic larvae since the unidirectional flow of water in streams carries propagules (gametes and developing larvae) away from the parent population. Since there is no upstream migration in zebra mussels, recruits to stream populations must originate upstream (e.g. colonized lakes) and then survive downstream transport (Horvath *et al*., 1996).

Recruitment of zebra mussels in streams may be influenced by the abundance of competent veligers. Martel *et al*. (1994) reported a positive relationship between the number of competent veligers and daily settlement rates in Lake Erie, but they considered all late-stage veligers to be competent. The viability of veligers is an integral component in determining the pool of potential settlers. When we corrected for dead veligers in their calculation of the flux of potential settlers in Christiana Creek, the flux declined substantially at all distances downstream (Fig. 3). Such a decline in the abundance of potential settlers could partly explain the longitudinal decline in adult mussels observed in small streams (e.g. Horvath *et al*., 1996; Miller & Haynes, 1997).

Neutral red staining could be a useful tool in future studies of invasion by zebra mussel and of their population dynamics. For example, accurate quantification of larval mortality could lead to better estimates of population growth (Rumrill, 1990), provide insight to the susceptibility of new habitats to invasion (Horvath *et al*., 1996) and help to identify factors causing larval mortality.

Our field observations strongly suggest that exposure to turbulence or shear during transport in streams can negatively affect the survival of zebra mussel veligers. Veliger mortality induced by prolonged exposure to hydrodynamic stresses could be the key factor limiting the distribution of mussels in streams. Because streams provide corridors through which zebra mussels can invade new eco-systems, determining the limiting factors for mussels can lead to better predictions of future range expansions and ecological effects.

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References

Carlton J.T. (1993) Dispersal mechanisms of the zebra mussel (*Dreissena polymorpha*). *Zebra Mussels: Biology, Impacts, and Control* (eds T. F. Nalepa and D. W. Schloesser), pp. 677–697. Lewis Publishers, Boca Raton, FL.

Conn D.B., Lutz R.A., Hu Y. & Kennedy V.S. (1993) *Guide to the Identification of Larval and Postlarval Stages of Zebra*

Mussels Dreissena *spp. and the Dark False Mussel,* Mytilopsis Leucophaeata. New York Sea Grant, Stoney Brook, NY.

Connell J.H. (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology*, **93**, 11–45.

Crippen R.W. & Perrier J.L. (1974) The use of neutral red and Evans blue for live-dead determinations of marine plankton. *Stain Technology*, **49**, 97–104.

Davis J.A. & Barmuta L.A. (1989) An ecologically useful classification of mean and near-bed flows in streams and rivers. *Freshwater Biology*, **21**, 271–282.

Dressel D.M., Heinle D.R. & Grote M.C. (1972) Vital staining to sort dead and live copepods. *Chesapeake Science*, **13**, 156–159.

Griffiths R.W., Schloesser D.W., Leach J.H. & Novalak W.P. (1991) Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1381–1388.

Horvath T.G. (1997) *Dispersal and ecological impact of zebra mussels,* Dreissena polymorpha *(Pallas) in coupled lake-stream ecosystems.* Ph.D. Thesis, University of Notre Dame, Notre Dame, IN.

Horvath T.G. & Lamberti G.A. (1999) Recruitment and growth of zebra mussels (*Dreissena polymorpha*) in a coupled lake-stream system. *Archiv für Hydrobiologie*, **145**, 197–217.

Horvath T.G., Lamberti G.A., Lodge D.M. & Perry W.L. (1996) Zebra mussel dispersal in lake-stream systems: source-sink dynamics? *Journal of the North American Benthological Society*, **15**, 564–575.

Jackson G.A. & Strathmann R.R. (1981) Larval mortality from offshore mixing as a link between precompetent and competent periods of development. *American Naturalist*, **118**, 16–26.

Johnson L.E. (1995) Enhanced early detection and enumeration of zebra mussel (*Dreissena* spp.) veligers using cross-polarized light microscopy. *Hydrobiologia*, **32**, 139–146.

Kern R., Borcherding J. & Neumann D. (1994) Recruitment of freshwater mussel with a planktonic life-stage in running waters-studies on *Dreissena polymorpha* in the River Rhine. *Archiv für Hydrobiologie*, **131**, 385–400.

Lewandowski K. (1982) The role of early developmental stages in the dynamics of *Dreissena polymorpha* (Pall.) (Bivalvia) populations in lakes. II. Settling of larvae and the dynamics of numbers of settled individuals. *Ekologia Polska*, **30**, 223–286.

Loosanoff V.L. & Davis H.C. (1947) Staining of oyster larvae as a method for studies of their movements and distribution. *Science*, **106**, 597–598.

MacIsaac H.J., Sprules W.G. & Leach J.H. (1991) Ingestion of small-bodied zooplankton by zebra mussels (*Dreissena polymorpha*): Can cannibalism on larvae influence population dynamics? *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 2051–2060.

Martel A., Mathieu A.F., Findlay C.S., Nepszy S.J. & Leach J.H. (1994) Daily settlement rates of the zebra mussel, *Dreissena polymorpha*, on an artificial substrate correlate with veliger abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 856–861.

Mead K.S. & Denny M.W. (1995) The effects of hydrodynamic shear stress on fertilization and early development of the purple sea urchin *Strongylocentrotus purpuratus*. *Biological Bulletin*, **188**, 46–56.

Miller S.J. & Haynes J.M. (1997) Factors limiting colonization of western New York creeks by the zebra mussel (*Dreissena polymorpha*). *Journal of Freshwater Ecology*, **12**, 81–88.

Rumrill S.S. (1990) Natural mortality of marine invertebrate larvae. *Ophelia*, **32**, 163–198.

Sprung M. (1987) Ecological requirements of developing *Dreissena polymorpha* eggs. *Archiv für Hydrobiologie*, **79** (Suppl.), 69–89.

Sprung M. (1989) Field and laboratory observations of *Dreissena polymorpha* larvae: abundance, growth, mortality and food demands. *Archiv für Hydrobiologie*, **115**, 537–561.

Sprung M. (1993) The other life: an account of present knowledge of the larval phase of *Dreissena polymorpha*. *Zebra Mussels: Biology, Impacts, and Control* (eds T. F. Nalepa and D. W. Schloesser), pp. 39–53. Lewis Publishers, Boca Raton, FL.

Stanczykowska A. (1977) Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. *Polskie Archiwum Hydrobiologh*, **24**, 461–530.

Stoeckel J.A., Schneider D.W., Soeken L.A., Blodgett K.D. & Sparks R.E. (1997) Larval dynamics of a riverine metapopulation: implications for zebra mussel recruitment, dispersal, and control in a large-river system. *Journal of the North American Benthological Society*, **16**, 586–601.

Thomas W.H. & Gibson C.H. (1990) Effects of small-scale turbulence on microalgae. *Journal of Applied Phycology*, **2**, 71–77.

Thorson G. (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biological Review*, **25**, 1–45.

Uehlinger U. (1993) Primary production and respiration in the outlet of an eutrophic lake (River Glatt, Switzerland). *Archiv für Hydrobiologie*, **128**, 39–55.

Vogel S. (1994) *Life in Moving Fluids: The Physical Biology of Flow*, 2nd edn. Princeton University Press, Princeton, NJ.

Welker M. & Walz N. (1998) Can mussels control the plankton in rivers? A planktological approach applying a Lagrangian sampling strategy. *Limnology and Oceanography*, **43**, 753–762.

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