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The influence of pre-settlement and early post-settlement processes on the adult distribution and relative dominance of two invasive mussel species

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SUMMARY

1. The structure of a community is governed by a complex combination of processes whose relative importance varies over time and space. Larval dynamics, settlement and recruitment are thought to be important processes limiting adult abundance and distribution of benthic invertebrates with planktonic larvae.
2. Two invasive molluscs with similar morphology and resource needs, the Eurasian zebra mussel *Dreissena polymorpha* and the quagga mussel *Dreissena rostriformis bugensis*, co-occur in several North American lakes and rivers but often differ in their adult distribution over depth. Following establishment, the quagga mussel typically replaces the zebra mussel in abundance, particularly in deeper waters. A field sampling programme conducted over 3 years in a lotic system (the Soulanges Canal connected to the St. Lawrence River) examined the extent to which adult distribution and the differential dominance of these two species are determined by larval supply (i.e. larval abundance near settlement sites), settlement and recruitment.
3. Total dreissenid larval abundance in the water column at two depths was determined weekly, and larval competence (size) and species-specific larval composition was estimated, during the main settlement period over three consecutive years. The pattern of total dreissenid settlement over the depth gradient was determined by deployment of settlement plates at both depths. Total abundance and proportional abundance of zebra mussel and quagga mussel juveniles and adults in each depth zone were determined monthly from July to September each year.
4. Mean dreissenid larval size did not differ between depths and the supply of late-stage larvae was generally low, but total larval abundance was consistently greater in deeper water. This differential larval abundance established settlement and recruitment patterns in the canal but contrasted predictions based on total adult dreissenid abundance – which was higher in the shallow zone. Therefore, the significant factor dictating the abundance of adult mussels in these two depth zones must be post-recruitment mortality, rather than larval supply, settlement or recruitment.
5. Despite a strong species-specific adult depth zonation, larvae and juveniles showed no consistent differences in species proportions over the depth gradient. In fact, zebra mussels dominated larval abundance at both depths for *c.* 50% of the sampling dates and dominated juvenile abundance at both depths throughout most of the sampling period. In contrast, the proportional abundance of zebra mussels in the adult dreissenid community was consistently 4–5 times higher in the shallow zone.
6. These results indicate that larval supply, settlement and recruitment processes are not responsible for determining total adult dreissenid distribution or species dominance. Rather, these patterns appear to be governed by post-recruitment factors that manifest themselves in later stages of mussel development and growth.

Keywords: community structure, *Dreissena*, larval supply, recruitment, settlement

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Introduction

The structure of a community – that is, the distribution and relative abundance of its members – is dependent on processes that vary in importance over time and space such that even mature communities are not static. Thus, while community structure is limited by the regional species pool and the relative abundance of these species (Cornell & Lawton, 1992), subsequent processes such as colonisation and recruitment can further shape community structure. Some of these processes can involve priority effects that determine the temporal sequence of establishment, whereas others involve physiological tolerances of different life stages, as well as species-specific traits and local species interactions (Wellborn, Skelly & Werner, 1996; Sait *et al*., 2000; Gamarra *et al*., 2005). Such manifold processes are further complicated as they are susceptible to stochastic forces and environmental filtering (Drake, 1991; Todd, 1998), all of which pose a challenge for disentangling the relative importance of processes driving community structure.

Variation in larval supply, settlement and recruitment can have a major influence on the community structure of benthic invertebrates with sessile adults that reproduce with dispersive planktonic larvae (e.g. Gaines & Roughgarden, 1985; Menge, 1991; Jenkins, 2005; Sams & Keough, 2012). Temporal and spatial variation in pre-settlement and settlement processes has been attributed to physical and biological factors such as currents, predation and larval behaviour, including phototaxis, geotaxis and substratum selection (Rodríguez, Ojeda & Inestrosa, 1993). Post-settlement or early recruitment factors include migration, disturbance, physical gradients, predation and competition (Hunt & Scheibling, 1997; Todd, 1998). Here, recruitment is defined as the number of newly settled individuals (settlers) that have survived to a specified size following settlement, the event in which a planktonic larva becomes attached to the substratum (Rodríguez *et al*., 1993). Variability in recruitment is therefore inherently linked to pre-settlement and settlement processes, just as settlement is affected by larval dynamics. Thus, while many studies have addressed only post-settlement mechanisms, especially competition, variability in one or more of these processes and their associated mechanisms can mediate adult spatial distribution and dominance patterns. For example, settlement patterns generated from differential larval behaviour were found to dictate the adult distributions of two barnacle species, whereas post-settlement mortality merely accentuated the pattern set at settlement (Jenkins, 2005). Earlier factors influencing larval abundance and distribution in the water column may also be of greater relative importance than post-settlement factors, particularly in demographically 'open' communities where settlement is limited (Rodríguez *et al*., 1993). Indeed, larval orientation in the water column has been found to influence settlement patterns and subsequent distributions of sessile invertebrates such as barnacles, corals and sponges (Minchinton & Scheibling, 1991; Carlon, 2002; Ettinger-Epstein *et al*., 2008). However, adult community structure may be decoupled from local patterns of larval supply or settlement through post-settlement events occurring over different time scales, particularly if settlement or post-settlement mortality rates are high (Rodríguez *et al*., 1993; Todd, 1998; McQuaid & Phillips, 2006). Consequently, the relative importance of any one of these processes is often obscured. Attempts to understand how the abundance and distribution of adult benthic invertebrate populations are established and maintained will therefore be incomplete unless larval supply, settlement and recruitment are considered.

The zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena rostriformis bugensis*) are Eurasian bivalves that have had significant impacts within invaded freshwater systems in North America (Vanderploeg *et al*., 2002; Ward & Ricciardi, 2007; Nalepa, Fanslow & Lang, 2009). Their marine-like life cycle involves prolific gamete release and external fertilisation in the water column multiple times per season. After fertilisation, planktonic larvae may remain in the water column for several weeks (Sprung, 1989). During this time, shelled larvae in a straight-hinged (D-stage) or umbonal form, from different locations and species, can mix and be transported over long distances, such that larval supply to a given site may not reflect the local species composition. At the time of settlement, competent larvae metamorphose and attach to substrata by secreting byssal threads, which is unusual behaviour for freshwater molluscs (Ackerman *et al*., 1994).

The shelled larval stage is largely responsible for the subsequent spread of both species after their initial establishment within an invaded system. The zebra mussel tends to spread and attain peak abundance rapidly, particularly in shallow waters, whereas the quagga mussel spreads and builds populations more slowly (Karatayev *et al*., 2011). Their contrasting rates of spread have been attributed to differences in their reproductive, dispersal and colonisation capacities; the zebra mussel tends to invest more energy into reproduction, whereas the quagga mussel devotes more to somatic

growth (Stoeckmann, 2003). Intriguingly, in many areas of the Great Lakes in which the species co-occur, the quagga mussel has replaced the zebra mussel as the dominant dreissenid, often directionally: first in deeper water and subsequently in shallower waters (Patterson, Ciborowski & Barton, 2005; Wilson, Howell & Jackson, 2006; Nalepa *et al*., 2009).

This spatiotemporal replacement pattern has been attributed to species differences in life history strategies, competition–colonisation trade-offs and physiological tolerances, mediated by the invaded environment (reviewed in Ram *et al*., 2012); all these are factors that potentially affect post-settlement survival and recruitment. However, within riverine systems where space is rarely a limiting resource, dreissenid populations typically form a patchy mosaic and the adult population structure may be dependent primarily upon larval supply and subsequent settlement (Stoeckel *et al*., 1997). Like marine systems, riverine systems can be considered 'open', but in a directional context, with larval supply limited by upstream source populations (Schneider *et al*., 2003; Stoeckel *et al*., 2004). Thus, the relative composition of the dreissenid community may be driven by population dynamics at upstream sites, whereas local spatial patterns of dreissenid abundance, distribution and dominance may be a function of pre-settlement larval behaviour (e.g. phototaxis), abundance of competent larvae and substratum choice at settlement (e.g. conspecific cues).

The St. Lawrence River drains the Great Lakes from the outflow of Lake Ontario, where dreissenid species replacement has been particularly extensive (Pennuto *et al*., 2012). In the early 1990s, the zebra mussel became abundant in the Soulanges Canal, an abandoned navigational waterway connected to the river. Within a decade, the quagga mussel replaced the zebra mussel as the dominant dreissenid in total abundance (Ricciardi & Whoriskey, 2004). Remarkably, the zebra mussel has largely disappeared from the deeper areas of the canal where the quagga mussel has proliferated, but it remains common at shallow depths on the canal walls (Jones, 2012); such a vertical zonation pattern is surprising given the narrow (*c.* 6 m) depth range of this unstratified waterbody. We hypothesised that, in addition to post-settlement factors such as differential survival and population growth, a combination of biotic factors involving larval supply and settlement governs the contemporary distribution and relative dominance of adult dreissenid mussels in the canal. Here, we present the results of a 3-year field survey in the Soulanges Canal which sought to determine whether (i) the depth patterns of total dreissenid abundance and (ii) the species-specific distributions and relative abundance of adult dreissenid mussels are determined by differential larval supply and settlement, rather than by recruitment.

Methods

Study site

Sampling of dreissenid larvae, settlers, juveniles and adults was conducted during the ice-free seasons of 2007–2009, at each of two depths (shallow = 1.3 m; deep = 5 m) along the vertical canal walls near the entrance to the west section of the Soulanges Canal (SCW; 45°15′ 36″N and 74°11′ 55″W), which receives water from Lake Saint-François. Larval, settler, juvenile and adult samples from each year were obtained from within the same location along the length of the canal. Samples over the years were taken within a 30-m section of the canal wall. The 23-km-long canal is a low-flow system with minimal disturbance and a maximum depth of *c.* 6 m. Stratification does not occur in the canal, as evidenced by weekly temperature and dissolved oxygen measurements taken at each depth which never differed by more than 1.0 °C and 1 μg L^{-1}, respectively, during the study. Weekly chlorophyll *a*, pH and conductivity measurements also did not vary between depth zones during sampling.

Larval supply

In June 2007, larval sampling was initiated to compare larval abundance, mean larval size and the proportional abundance of each species between the shallow and deep zones. Duplicate larval samples were collected weekly at each depth using an 8.2-L horizontal Van Dorn Alpha Water Sampler (Wildlife Supply Company, Florida, U.S.A.). Weekly samples were collected between May/June and October of 2007, 2008 and 2009, for a total of 18 sampling dates each year. This time frame encompassed the main spawning period, as dreissenid larvae generally first appear between May and June when water temperatures exceed 12 °C, with peak larval occurrences in July and August (Mackie *et al*., 1989; Sprung, 1993). To obtain sufficient volume for analysis, a composite of five Van Dorn hauls was used for each sample, which was then filtered through a 63-μm mesh sieve and preserved in 95% ethanol. This mesh size captures both obligate planktonic larval stages (D-shaped and umbonal) and competent larvae (>200 μm) ready for settlement (Stoeckel *et al*., 2004). In the laboratory,

shelled larvae from each sample were counted in a plankton maze under a dissecting microscope at 40× magnification using cross-polarised light microscopy. Empty shells were found frequently, but only those containing soft tissue were considered in estimates of larval density, measured as number of larvae L^{-1}.

To assess any difference in the supply of competent larvae in the water column across the depth gradient, the average larval body size was estimated from two samples (one from each depth zone) taken at mid-month from June to September of each year. Shell size corresponds to the life stages of dreissenid larvae and competency to settle (Ackerman *et al.*, 1994). Using a microscope fitted with an ocular micrometer, shells of 40 individuals from each sample were measured (±10 μm) perpendicular to the axis from the umbo (centre of the hinge) to the opposing margin of the shell (Stoeckel *et al.*, 2004). In the two samples with fewer than 40 larvae (2 of 24 samples), all intact larvae were measured (n = 32 and n = 35 larvae).

To determine any difference in the proportion of each larval species between the depth zones, species composition at each depth zone was estimated by molecular analysis for a subset of samples taken over the 3-year period. For each year, four sampling dates (approximately one per month), each consisting of two replicate samples from each depth zone, were selected and sent to Pisces Molecular LLC for analysis. Prior to DNA extraction, samples were centrifuged at 1000× g for 5 min, the supernatant was drawn off and discarded, and tissue lysis buffer was added. Samples were then incubated at 55 °C for 1 h, vortexed repeatedly and transferred to a new tube with 1 μg of carrier RNA. Total DNA was extracted from the samples using a spin-column DNA purification procedure. All samples were then assayed undiluted for the presence of *D. polymorpha* or *D. r. bugensis* DNA with quantitative, real-time PCR, targeting a 197-bp fragment of the rDNA ITS 2 region (J. Wood, Pisces Molecular LLC, pers. comm.). The percentage of target sequence molecules that each species comprised for an individual sample was calculated by dividing the amount of absolute target copies for each single species by the total quantified number of target sequence molecules in a sample, multiplied by 100. This calculation reflects the relative biomass of each species in a sample and provides an estimate of the relative abundance (density) of each species, assuming they have a similar size distribution – a reasonable assumption given the low variability of larval size measurements within a given sample in this study.

Settlement

To evaluate any spatial variation in dreissenid settlement across the two depth zones, five replicate settlement plates were deployed in each depth zone for 2-week periods between July and September of 2007 and 2008. Settlement plates deployed in 2009 were not assessed, owing to plate loss and minimal settlement on retrieved plates. Each 10 × 10 cm plastic (Plexiglas®, Evonik Industries, ON, Canada) settlement plate was roughened and then soaked in canal water for 8–10 days to allow a biofilm to develop. Plates were separated by 10-cm sections of PVC pipe and arranged along the length of a stainless steel rod that was positioned horizontally in the water column and perpendicular to the canal wall, thereby allowing the plates to have the same orientation as the canal wall. Plates were later retrieved and brought back to the laboratory where new settlers, defined as post-metamorphic larvae up to 2 mm in length, were removed and counted using a dissecting microscope as per methods described previously. In this way, settlers up to a maximum of 2 weeks old were collected from each depth zone during the early, mid- and late times of the main dreissenid settlement season. Species composition was not assessed at this stage given large uncertainty in species identification of mussels of <2 mm length.

Recruitment & adult mussel distribution

Recruitment (juvenile counts) and adult abundance were monitored over the depth gradient between July and September of 2007–2009. Sampling was initiated to determine differences in (i) total dreissenid abundance and (ii) the proportion of each species between the shallow and deep zones for juveniles and adults. Dreissenid mussels were destructively sampled from five replicate quadrats (0.0625 m^{-2}) within each depth zone on the canal wall in July, August and September of each year. All mussels were sorted to species and their shell lengths were measured to the nearest 0.1 mm using digital vernier callipers. Mussels between 4 and 10 mm were considered juveniles (young-of-the-year), whereas those >10 mm were regarded as adults (Mackie, 1991).

Data analysis

To determine spatial variation in total larval abundance, weekly larval densities at each depth were calculated as the mean value of the two samples per depth and weekly paired depth differences for each year were evaluated using a nonparametric Wilcoxon signed-rank

test. A one-way analysis of variance (ANOVA), with percentage change of mean larval abundance in the shallow compared to the deep zone as the response variable, was used to assess whether the magnitude of difference between depths was consistent across years. For each year of larval sampling, a two-way ANOVA was used to examine the consistency of differences in larval shell size between depths, with both factors (Depth and Time) treated as fixed. Two-way ANOVAs were then used to determine whether there was a consistent effect of depth on the total dreissenid abundance of settlers, juveniles and adults, with both factors (Depth and Time) treated as fixed. For settler, juvenile and adult data, the magnitude of difference between depths was tested for consistency over the years using one-way ANOVAs with percentage difference in mean abundance (shallow relative to deep) as the response variable.

For the assessment of variation in species dominance patterns between depths, species-specific abundance data are not given. Owing to limitations of the genetic analysis of larvae for species identification, estimates of absolute abundance of each species were not comparable to other life stages. Furthermore, because of sampling dates with low larval densities and difficulties in identification to species level, high larval density samples were targeted for genetic analysis, thus biasing any estimates of absolute abundance for each species. Instead, and consistent with the aims of this work, analyses of species dominance patterns for larvae, juveniles and adults use the number of zebra mussels (expressed as a percentage of total dreissenid abundance) as the dependent variable. Separate two-way ANOVAs were used to determine the effects of Depth and Time (fixed factors) on the mean percentage abundance of zebra mussels for larvae, juveniles and adults for each year of the sampling programme.

Data were checked for independence, normality and homogeneity of variances and were log-transformed where necessary; all transformations were successful in normalising variances. Significant effects were analysed further with Tukey's honestly significant difference (HSD) post hoc multiple comparisons test. All analyses were performed in R (R Development Core Team, 2011).

Results

Larval supply

Dreissenid larvae were present in the water column from May to October, but were in very low abundance early and late in the season (Fig. 1). Average larval abundance between 2007 and 2009 ranged from 17.6–31.5 larvae L^{-1} in the shallow zone and 20.1–69.6 larvae L^{-1} in the deep zone. However, larval abundance varied considerably over the season. Each year there were 3–4 peaks of larval abundance occurring simultaneously in both depth zones, but the magnitude of these peaks was typically greater in the deep zone. In all 3 years, there was a significant effect of depth, with dreissenid larval abundance greater in the deep than in the shallow zone

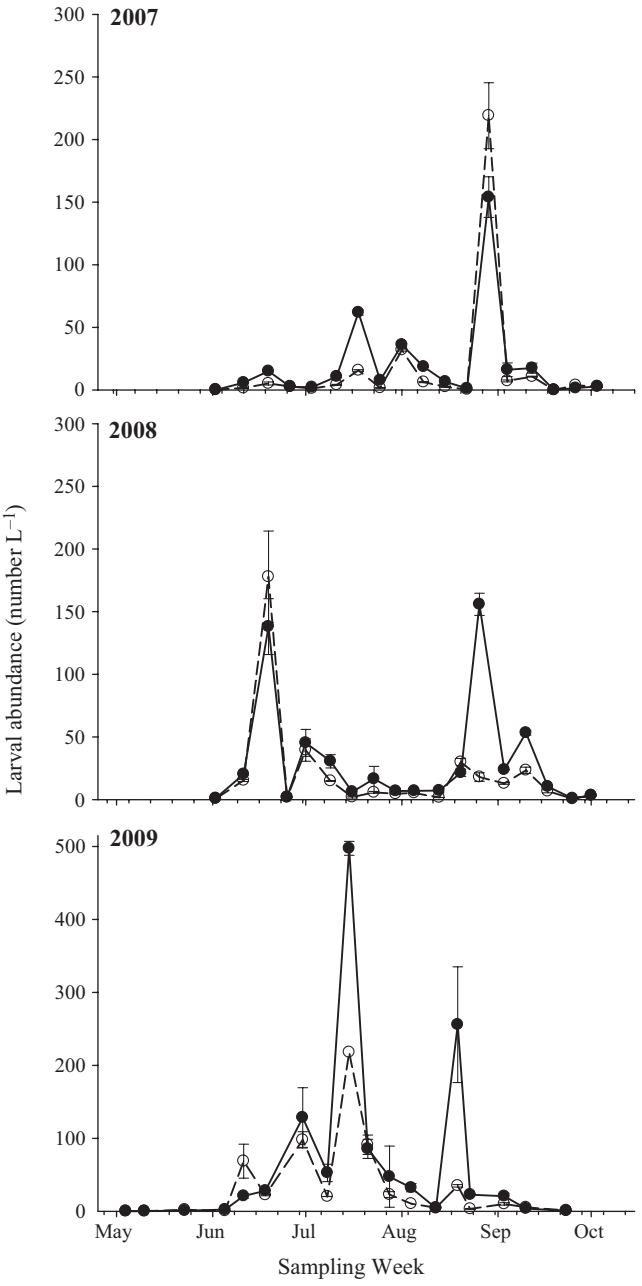

Fig. 1 Variation in dreissenid larval supply for 2007, 2008 and 2009 in the shallow (open symbols, dashed line) and deep (filled symbols, solid line) zones.

(Wilcoxon signed-rank test, $n = 18$: $W_{2007} = 29$, $W_{2008} = 29$, $W_{2009} = 27$, $P = 0.01$). Across all three sampling years, the shallow zone had, on average, 29–33% lower larval abundance than the deep zone, and this percentage difference did not vary significantly over the years (one-way ANOVA, $F_{2,51} = 0.03$, $P = 0.97$).

In all years, the mean larval size increased over the season (two-way ANOVAs, 2007: $F_{3,152} = 28.98$, 2008: $F_{3,52} = 35.83$, 2009: $F_{3,152} = 42.96$, $P < 0.0001$), but did not differ with depth (two-way ANOVAs, 2007: $F_{1,152} = 0.01$, 2008: $F_{1,152} = 0.76$, 2009: $F_{1,152} = 0.06$, $P > 0.05$). For all years, the mean larval size increased from 111–113 μm in June to 155–164 μm in September, with larvae becoming significantly larger in each subsequent month (Tukey's HSD, $P < 0.05$), except between June and July (Tukey's HSD, $P > 0.05$). The increasing abundance of larger larvae over the summer corresponded with an increasing number of new settlers each year. The majority of measured larvae over the season comprised the D-shaped and umbonal larval stages of dreissenid mussels. D-shaped larvae were most abundant earlier in the season, whereas umbonal larvae were more prevalent during July–September. While larger larvae (maximum 225 μm) appeared in August and September in both depth zones for all years, <30% of any given subsample was comprised of larvae of >200 μm (i.e. competent to settle). For each year of the sampling programme, there were an equal number of subsamples that had a greater percentage of competent larvae in the shallow zone as there were in the deep zone.

Zebra mussels constituted >50% of the total dreissenid larval abundance on seven of the 12 sampling dates for the shallow zone and on five of 12 sampling dates for the deep zone. The contribution of the zebra mussel to dreissenid larval abundance did not significantly differ with depth (Fig. 2; Table 1). However, in 2007, there was a significant interaction between depth and sampling date, with a greater percentage abundance of zebra mussels in the shallow zone in June (Table 1). The percentage abundance of zebra mussels changed significantly over time in all years, generally declining towards the end of the sampling season (Fig. 2; Table 1). In 2009, the decline in the mean percentage abundance of zebra

Table 1 Two-way ANOVA results testing variation in the percentage abundance of zebra mussel (*Dreissena polymorpha*) larvae at two depths (Sh = shallow, De = deep) for each of four sampling months in the summer of 2007, 2008 and 2009

Effect	d.f.	MS	*F*	*P*
2007				
Depth	1	1787.78	39.44	**0.0002**
Time	3	3070.47	67.74	**<0.0001**
Depth × Time	3	1615.58	35.64	**<0.0001**
Residual	8	45.33		
Tukey's HSD of Depth × Time:				
June: Sh > De				
July, Aug, Sept: Sh = De				
Shallow: June =				
July > Aug = Sept				
Deep: June =				
Aug = Sept < July				
2008				
Depth	1	54.70	0.17	0.6944
Time	3	3857.40	11.71	**0.0027**
Depth × Time	3	132.30	0.40	0.7558
Residual	8	329.50		
Tukey's HSD of Time:				
June = July = Aug > Sept				
2009				
Depth	1	385.70	2.40	0.1604
Time	3	834.73	5.18	**0.0279**
Depth × Time	3	430.10	2.67	0.1185
Residual	8	161.00		
Tukey's HSD of Time:				
June 11 = June 30 = July > Aug				

Significant effects ($P < 0.05$) are highlighted in boldface.

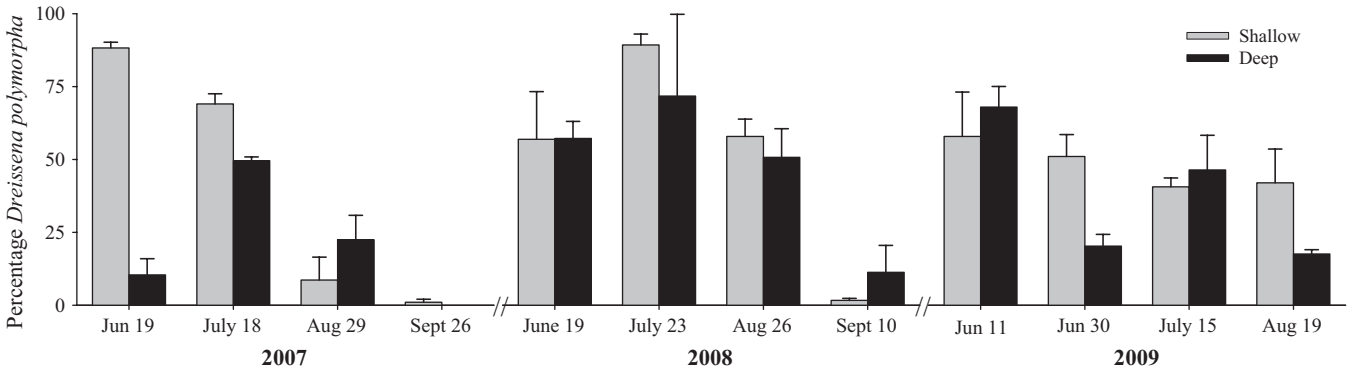

Fig. 2 Mean (±SE) percentage abundance of zebra mussel (*Dreissena polymorpha)* larvae in the shallow and deep zones at four sampling dates during the spawning season of 2007, 2008 and 2009.

mussels over the season was not as significant (Table 1), probably because the last sampling date for which relative species composition was estimated was approximately a month earlier than in previous years (Fig. 2). Overall (pooling over depth), zebra mussels formed greater than 50% (range = 51–81%) of dreissenid larval abundance for six of the 12 selected sampling dates during the 3 years, 2 of 4 in 2007, 3 of 4 in 2008 and 1 of 4 in 2009. As such, quagga mussels also dominated relative abundance for six of the 12 sampling dates (range = 51–93%).

Settlement

In 2007 and 2008, dreissenid settlers were always more abundant in the deep zone (two-way ANOVAs, 2007: $F_{1,24} = 7.62$, 2008: $F_{1,24} = 19.43$, $P < 0.01$; Fig. 3). Over the early, mid- and late settlement periods, the mean abundance of dreissenid settlers was 41 and 53% lower in the shallow zone in 2007 and 2008, respectively; this is nearly identical to the pattern found for juvenile density for these years (see Recruitment, 2007: 49 and 2008: 52%, respectively), but is a greater change than would be expected based solely on the difference in the distribution of larvae between depths (see Larval Supply, 2007: 29% and 2008: 31%, respectively). Settler abundance increased over the main settlement period in both years (two-way ANOVAs, 2007: $F_{2,24} = 33.06$, 2008: $F_{2,24} = 17.06$, $P < 0.0001$), with values 4–6 times as large by the last sampling point (Tukey's HSD, $P < 0.05$).

Recruitment

Mirroring patterns in larval supply and settlement, the mean density of juveniles increased over the season in the summers of 2007 and 2009 (two-way ANOVAs, 2007: $F_{1,24} = 54.98$, 2009: $F_{1,24} = 6.89$, $P < 0.005$), but in 2008 there was a marginally significant opposite trend with the greatest abundance in July (two-way ANOVA, 2008: $F_{1,24} = 9.62$, $P = 0.001$; Tukey's HSD, $P < 0.05$). This early peak in abundance was due to a greater density of zebra mussel juveniles in both depth zones. The abundance of juveniles was consistently higher in the deep than in the shallow zone, for all months in each year (Fig. 4). This effect of depth was significant in 2007 and 2008 (two-way ANOVAs, 2007: $F_{1,24} = 45.88$, 2008: $F_{1,24} = 74.10$, $P < 0.05$); however, in 2009, the difference in density across depths was not significant. Overall, the mean percentage difference in juvenile abundance between depths varied significantly across years (one-way ANOVA: $F_{2,6} = 5.45$, $P = 0.04$). Further analysis revealed that this variation was due to a reduction in the depth effect on percentage abundance in 2009 ($17 \pm 0.08\%$ lower in the shallow zone) compared to 2007 and 2008 (49 and 52% lower in shallow zone, respectively) (Tukey's HSD, $P < 0.05$). In general, the direction and magnitude of the difference in juvenile abundance between the depth zones is similar to that found for larval and settler distributions.

Abundance of juveniles of the two species collected over the summer in each year was clearly unequal, regardless of depth. Zebra mussel juvenile density was higher than that of the quagga mussel in both depth zones, forming greater than 50% of the total juvenile abundance on all but two sampling dates (August and September) in 2009 (Fig. 5). This switch in dominance late in the season in 2009 was driven by an influx of quagga mussel juveniles, particularly in the shallow zone. Across all 3 years, mean zebra mussel juvenile densities were 298 ± 88 m^{-2} and 535 ± 66 m^{-2} in the shallow and deep zones, respectively, while mean quagga mussel juvenile densities were 163 ± 121 m^{-2} and 256 ± 74 m^{-2}, in the

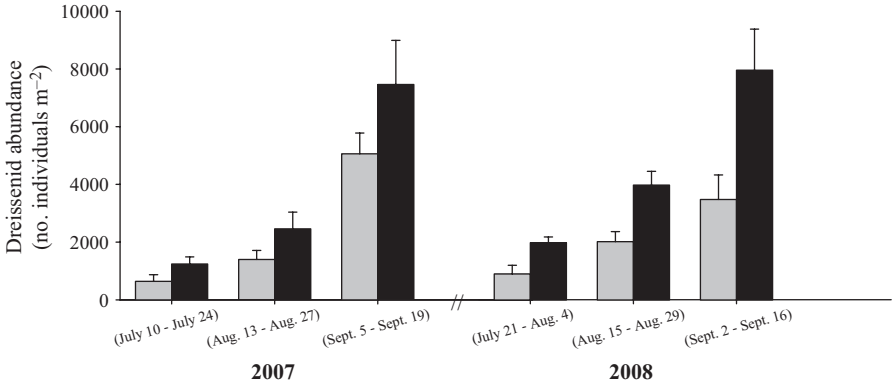

Fig. 3 Mean (±SE) dreissenid settler abundance (number individuals m^{-2}) in the shallow and deep zones in 2007 and 2008 during the early, mid- and late periods of the main settlement season.

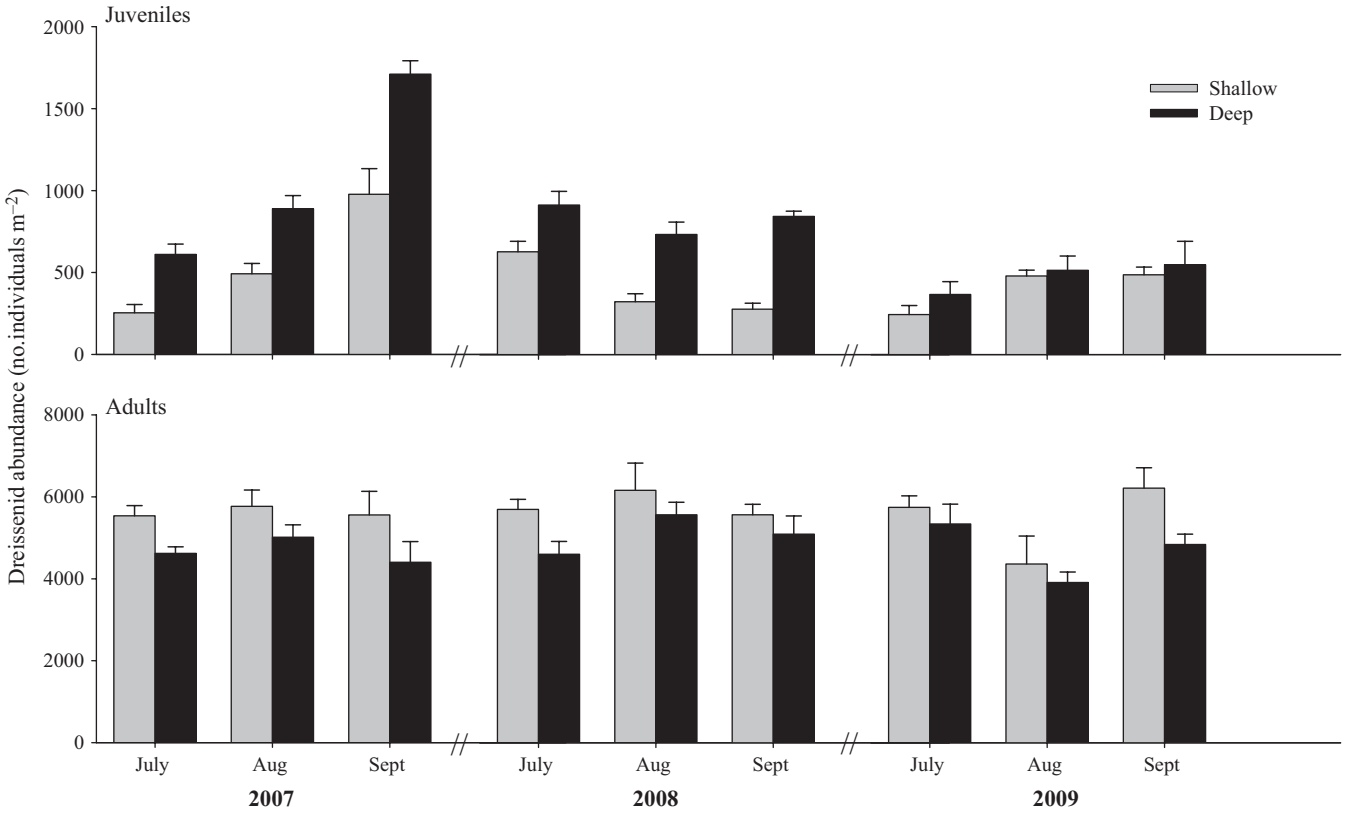

Fig. 4 Mean (±SE) abundance (number of individuals m^{-2}) of dreissenid juveniles and adults in the shallow and deep zones for three sampling dates during the summers of 2007–2009.

shallow and deep zones, respectively. Thus, while both species were more abundant in the deep zone, zebra mussel juveniles dominated both depth zones.

Despite this pattern, the effects of depth and season on the mean percentage abundance of zebra mussels differed among years. In 2007, there was a significant interaction between depth and season (Table 2). The mean percentage abundance of zebra mussel juveniles did not differ with depth, except in September where it was significantly higher in the shallow zone (Fig. 5; Table 2). This was driven by an increase in the density of quagga mussels in the deep zone, until they formed *c.* 50% of the total abundance. In the course of the sampling season, the percentage abundance of zebra mussels declined in both depth zones, but this reduction occurred between July and August in the shallow zone, whereas it occurred between August and September in the deep zone (Table 2). This temporal decline corresponds with a gradual increase in juvenile quagga mussel density from July to September across depth. In 2008, there was no significant difference in relative zebra mussel abundance between depths (Table 2), although the proportion of zebra mussels was always slightly greater in the shallow than in the deep zone (Fig. 5). There was a significant decrease over the season from July to September (Table 2), attributable to a large number of zebra mussel juveniles at the start of the summer of 2008. In 2009, mean percentage abundance of juvenile zebra mussels was actually greater in the deep zone and, as in 2008, was greater in July than in September (Fig. 5; Table 2).

Overall, there was no clear difference in the relative abundance of juvenile stages of the two dreissenid species between the depth zones during the years of the sampling programme. In 2007 and 2008, the percentage abundance of zebra mussels was between 8–12% higher in the shallow zone, but in 2009 it was 41% lower here (Fig. 5). However, within both depth zones, zebra mussels were generally the dominant (>50%) dreissenid at this early life stage.

Adult mussel distribution

In all 3 years, adult dreissenid mussels were consistently more abundant in the shallow zone (two-way ANOVAs, 2007: $F_{1,24} = 8.65$, 2008: $F_{1,24} = 5.10$, 2009: $F_{1,24} = 4.30$, $P < 0.05$), with no significant interaction between depth and sampling month (Fig. 4). Unlike the pattern for settlers and juveniles, there was no overall increase in adult

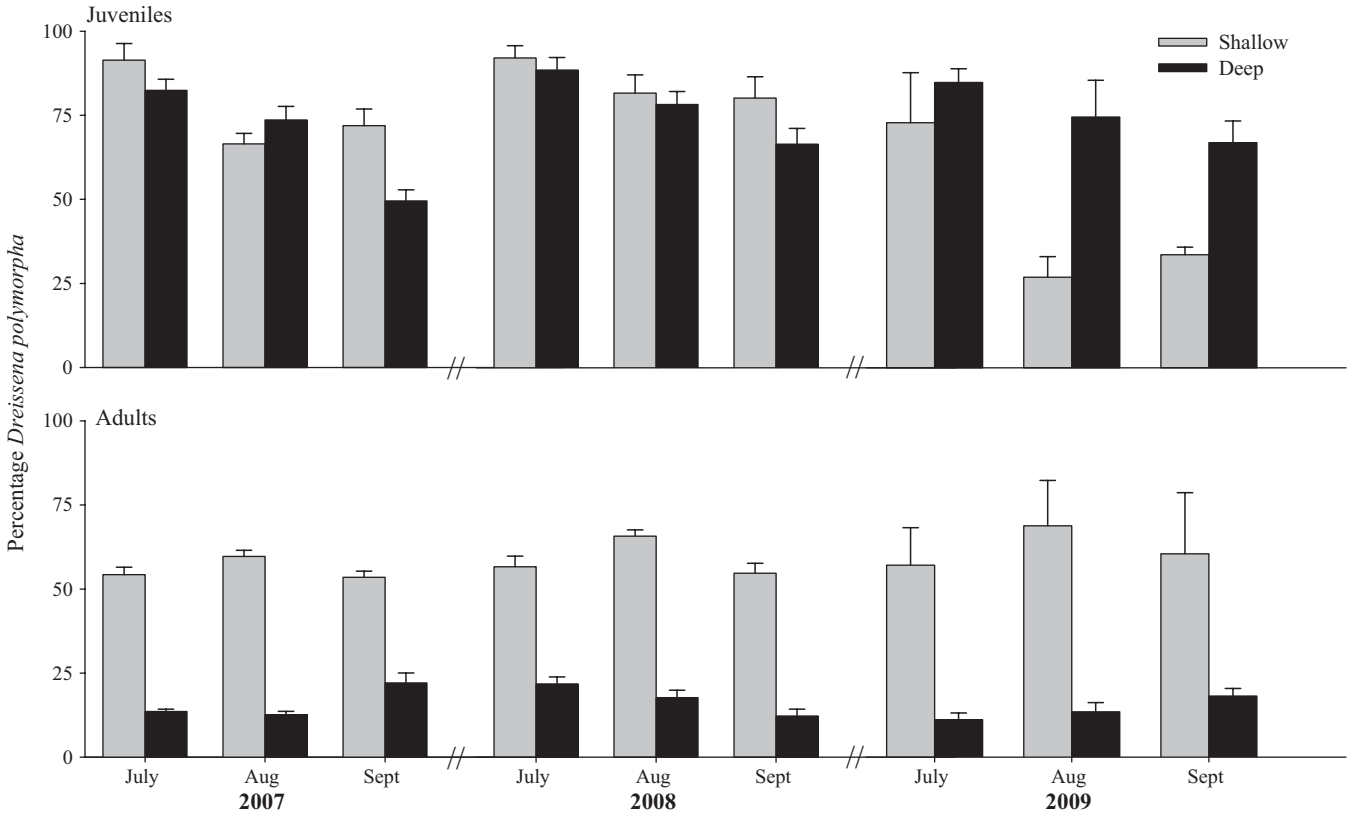

Fig. 5 Mean (±SE) percentage abundance of zebra mussel (*Dreissena polymorpha*) juveniles and adults in the shallow and deep zones at three sampling dates during the summers of 2007–2009.

abundance over the season, but in 2009 there was a significant effect of sampling month (two-way ANOVA, $F_{2,24} = 6.79$, $P = 0.005$) due to a lower mean abundance in August compared to July and September (Tukey's HSD, $P < 0.05$). The mean percentage difference in abundance between depths (shallow relative to deep) did not differ across the 3 years (one-way ANOVA, $F_{2,6} = 0.38$, $P = 0.70$). In contrast to the spatial distribution of previous life stages (larvae, new settlers and juveniles) whose abundance was generally greatest in the deep zone, the mean adult abundance was $17 \pm 0.02\%$ greater in the shallow zone.

The contribution of zebra mussels to overall adult dreissenid abundance showed a remarkably consistent pattern between the two depth zones throughout the study period (Fig. 5). On average, zebra mussels dominated in the shallow zone, forming 55–62% of total abundance, but comprised only 14–17% in the deep zone. Across the 3 years of sampling, the mean density of zebra mussels in the shallow and deep zone was 3299 ± 91 m^{-2} and 767 ± 54 m^{-2}, respectively, whereas for the quagga mussel it was 2302 ± 128 m^{-2} and 4093 ± 66 m^{-2}, respectively. In 2007, there was a significant interaction between depth and month of sampling, as the mean percentage abundance of zebra mussels in the deep zone was greater in September than it was in either July or August, while it did not change across months in the shallow zone (Table 3). A significant interaction was also found in 2008, in which the percentage abundance of zebra mussels in the shallow zone in August was slightly greater than in either July or September, although there was no difference over the season in the deep zone (Table 3). In 2009, the effects of depth did not vary over time, but both main effects were significant (Table 3); percentage abundance of zebra mussels was consistently greater in the shallow zone, and abundance was greater later in the season (Fig. 5). In general, the percentage abundance of adult zebra mussels in both depth zones was consistent over the season in each year and between years, with 3–4 times greater percentage abundance in the shallow zone – a pattern that was not observed for either the larval or juvenile stages.

Discussion

Benthic invertebrate communities are structured, in part, by spatiotemporal variation in larval supply, settlement and recruitment (Underwood & Fairweather, 1989;

Table 2 Results of two-way ANOVAs testing variation in the percentage abundance of zebra mussel (*Dreissena polymorpha*) juveniles at two depths (Sh = shallow, De = deep) for each of 3 months in the summer of 2007, 2008 and 2009

Effect	d.f.	MS	*F*	*P*
2007				
Depth	1	490.0	6.08	**0.0211**
Time	2	1761.9	21.88	**<0.0001**
Depth × Time	2	544.9	6.76	**0.0050**
Residual	24	80.6		
Tukey's HSD of Depth x Time:				
July, Aug: Sh = De; Sept: Sh > De				
Shallow: July > Aug = Sept				
Deep: July = Aug > Sept				
2008				
Depth	1	356.4	3.19	0.0868
Time	2	730.9	6.54	**0.0054**
Depth × Time	2	87.1	0.78	0.4697
Residual	24	111.7		
Tukey's HSD of Time:				
July = Aug, Aug = Sept, July > Sept				
2009				
Depth	1	4606.5	19.56	**0.0034**
Time	2	1716.9	7.29	**0.0002**
Depth × Time	2	514.6	2.19	0.1343
Residual	24	235.5		
Tukey's HSD of Depth:				
July, Sept: Sh = De; Aug: Sh < De				
Tukey's HSD of Time:				
July > Aug = Sept				

Significant effects ($P < 0.05$) are highlighted in boldface.

Table 3 Two-way ANOVA results testing variation in the percentage abundance of adult zebra mussels (*Dreissena polymorpha*) at two depths (Sh = shallow, De = deep) for each of 3 months in the summer of 2007, 2008 and 2009

Effect	d.f.	MS	*F*	*P*
2007				
Depth	1	11837.3	652.63	**<0.0001**
Time	2	37.7	2.08	0.1467
Depth × Time	2	154.5	8.52	**0.0016**
Residual	24	18.1		
Tukey's HSD of Depth × Time:				
July, Aug, Sept: Sh > De				
Shallow: July = Aug = Sept				
Deep: July = Aug < Sept				
2008				
Depth	1	13078.2	437.93	**<0.0001**
Time	2	177.9	5.96	**0.0080**
Depth × Time	2	108.9	0.04	**0.0414**
Residual	24	29.9		
Tukey's HSD of Depth x Time:				
July, Aug, Sept: Sh > De				
Shallow: July = Sept < Aug				
Deep: July = Aug = Sept				
2009				
Depth	1	17185.2	461.54	**<0.0001**
Time	2	133.3	3.58	**0.0436**
Depth × Time	2	112.4	3.02	0.0676
Residual	24	37.2		
Tukey's HSD of Depth:				
July, Aug, Sept: Sh > De				
Tukey's HSD of Time:				
July < Aug = Sept				

Significant effects ($P < 0.05$) are highlighted in boldface.

Rodríguez *et al.*, 1993; Todd, 1998). The evaluation of any of these processes is incomplete unless its contribution to adult patterns is assessed relative to the other stages. The results of this study reveal that pre- or early post-settlement processes (larval supply, settlement and recruitment) do not account for the distribution and abundance of adult dreissenid mussels, and neither does larval supply or recruitment explain the differential dominance pattern of the two species between depths. Rather, these patterns emerge following the first year of establishment (mussels >10 mm).

Dreissenid (combined zebra and quagga mussel) distribution

Larval supply often explains variability in settlement and recruitment (e.g. Gaines & Roughgarden, 1985; Minchinton & Scheibling, 1991; Jonsson, Berntsson & Larsson, 2004); daily settlement rates of the zebra mussel can be strongly correlated with larval abundance (Fraleigh *et al.*, 1993; Martel *et al.*, 1994). Indeed, greater larval abundance in the deep zone of the Soulanges Canal was associated with higher local settlement and recruitment. The distribution and relative abundance of larvae in the water column can be influenced by numerous factors, such as temperature, wind, hydrodynamics, food availability, predation and pre-settlement larval behaviour (e.g. phototaxis, geotaxis) (Mackie *et al.*, 1989; Rodríguez *et al.*, 1993; Dobretsov & Miron, 2001; Barnard, Frenette & Vincent, 2003). In central Lake Erie, for example, densities of zebra mussel larvae increased with depth, but were uniformly distributed when wind speed was high (Fraleigh *et al.*, 1993). Dreissenid larvae swim by means of a velum and may retract the velum to sink (Mackie *et al.*, 1989). Bivalve larvae in general exhibit a modal distribution in the water column, often located above the thermocline; maximal dreissenid larval abundance typically occurs at 4–7 m depth in lacustrine environments (Mackie & Schloesser, 1996). However, given the narrow depth range of the Soulanges Canal and the lack of depth gradients in temperature, oxygen and chlorophyll *a*, the greater abundance of larvae near

the bottom of the canal might be attributable to negative phototactic or positive geotactic behaviour (Rodríguez *et al*., 1993). Indeed, diurnal movement of dreissenid larvae has been reported elsewhere, with maximum densities occurring near the surface during early morning (Mackie *et al*., 1989). Furthermore, there is some evidence of preferential settlement of post-larval mussels in shaded areas (Marsden & Lansky, 2000). Regardless of the factor(s) responsible for the vertical distribution of dreissenid larvae, this spatial variation is reflected in the distribution of both settlers and juveniles.

The difference in abundance between the shallow and deep zones was even greater for settlers than it was for larvae. The supply–settlement relationship may be explained by the filtration effect of the relatively larger population of adult dreissenid mussels in the shallow zone. Adult bivalves of many different species have been found to consume bivalve larvae, including larvae of their own species (Lehane & Davenport, 2004; Alfaro, 2006; Porri, Jordaan & McQuaid, 2008). Cannibalism by adults may be a significant source of larval mortality (MacIsaac, Sprules & Leach, 1991) and might alter the relationship between larval supply and settlement (cf. Pineda *et al*., 2010).

The fraction of competent larvae (those large enough to settle), rather than total larval abundance, probably provides a more accurate coupling between settlement and recruitment (Martel *et al*., 1994; Pineda *et al*., 2010). However, differential larval competency does not appear to be an important factor in explaining depth zonation patterns in the canal. We found no depth difference with respect to larval size (which correlates with life stages) and no apparent differences in the number of samples containing a greater proportion of competent larvae in the shallow or deep zones. It is of note, however, that few larvae of >200 μm were present at either depth, which suggests that significant mortality occurs from the umbonal to the pediveliger (settling) stage, as has been observed in other riverine systems (Sprung, 1989; Schneider *et al*., 2003). The significance of differential competency remains unclear, as the sample sizes available for estimates of larval size differences between depths were small.

Regardless of what factors drive the larval depth zonation pattern, these results demonstrate that settlement and recruitment patterns in the canal are established by spatial variation in larval supply. However, the relative abundance of adult mussels in these two depth zones does not appear to be determined by larval supply, settlement or recruitment. While there was a consistent depth difference through successive stages (larvae, settler and juvenile), it was surprisingly in the direction opposite to that of the adult pattern. The depth pattern of adult dreissenid density was consistent over the 3-yr sampling period, but adult density in the shallow zone was 17% greater, on average, than that in the deep zone. In contrast, larval supply was 31% lower in the shallow zone, while settlers and juveniles were 47 and 39% lower, respectively. However, we note that the 2007 adult community largely resulted from larvae and settlers not measured in this study. Nevertheless, the general adult distribution pattern is maintained throughout the study, despite the consistent but opposite pattern of earlier life stages measured during this study that should contribute, at least in part, to the 2008 and 2009 adult community (based on dreissenid growth rates and their estimated longevity of 2–3 years in this system; Jones, 2012). Thus, it is unlikely that the adult distribution was established by larvae and settlers from the 2 years prior to this study. Adult abundance and distribution must therefore be established by factors operating subsequent to recruitment. Differential post-recruitment mortality (of mussels >10 mm) due to predation, competition or abiotic stress, represents the most likely factor dictating the relative abundance of adult mussels in these two depth zones. Indeed, while larval supply, settlement and recruitment are often strong determinants of adult abundance, the magnitude of the relationship can be strongly modified by post-recruitment processes (Menge, 2000).

Species-specific depth zonation

The differential dominance pattern of adult zebra mussels and quagga mussels between depths was remarkably consistent over the 3 years. Adult zebra mussels represented a significantly higher proportion of the total adult abundance in the shallow zone, while forming only 14–17% of dreissenid abundance in the deep zone. This pattern of adult distribution may be a direct result of one or more factors including differential larval supply, differential larval behaviour (pre-settlement and at settlement) and differential mortality occurring within weeks to months after initial settlement. Our study points to post-recruitment mortality as the most significant factor driving the dominance pattern of adult zebra and quagga mussels over the depth gradient.

If larval supply alone controlled adult distribution, then quagga mussel larvae should dominate in the deep zone and zebra mussel larvae should be most common in the shallow zone. However, in all 3 years, differences in larval abundance of the two species between depths

did not reflect the pattern of adult distribution. Rather, the dominance of zebra mussel larvae fluctuated between the shallow and deep zones at different times throughout the season each sampling year. The net effect therefore resulted in no overall difference in the mean proportion of zebra mussel larvae between depths. This suggests that the spatial dominance pattern of the two species in the adult population is independent of the larval distribution pattern of these two co-occurring mussels. However, we note that the 2007 adult species composition, like the adult dreissenid distribution, largely resulted from larvae not measured in this study. Nevertheless, the species-specific adult depth pattern was also maintained throughout the study, despite the variation in species dominance of the larval stage measured during this study that should contribute, at least in part, to the 2008 and 2009 adult community. Thus, it is unlikely that the species-specific adult depth zonation was set by larvae from the 2 years prior to this study. Furthermore, despite the low flow in the canal, the difference in larvae and adult patterns suggests that the larval supply is 'open' and not dependent on self-recruitment.

Like marine systems, recruitment into riverine populations of mussels with free-swimming planktonic larvae relies heavily upon immigration of larvae produced externally. Most larvae produced by riverine populations are flushed downstream and do not contribute to recruitment within the population that produced them (Schneider *et al.*, 2003). While it is possible that riverine populations are maintained by upstream sources within the river as components of a linear metapopulation, these upstream populations are themselves ultimately dependent on a headwater lake (Stoeckel *et al.*, 1997, 2004). As such, and given that the most abundant dreissenid in Lake Ontario (the source of the St. Lawrence River) has been the quagga mussel for at least 5 years prior to this study (Mills *et al.*, 1999; Wilson *et al.*, 2006; Pennuto *et al.*, 2012), it could be expected that quagga mussels should dominate the larval supply in the river and in the Soulanges Canal, assuming sufficient current velocity and travel time. Clearly this is not the case, suggesting that larval supply in the canal is perhaps influenced more by the input from proximate populations in upstream fluvial lakes, where the zebra mussel remains abundant (Jones & Ricciardi, 2005). Regardless of factors mediating larval supply, there is no consistent differential depth distribution of larvae in the water column for these two species, and so larval supply does not explain the species-specific adult zonation in the canal.

It is possible that the species-specific adult zonation is set by substratum selection at the time of settlement. Larval supply patterns can be decoupled from settlement patterns and subsequent adult distributions as a consequence of settlement behaviour (Pineda *et al.*, 2010). Substratum selection is an important influence on the local distribution and abundance of recruits and adults and often involves chemical cues from adult conspecifics (Pawlik, 1992; Rodríguez *et al.*, 1993). Dreissenid mussels preferentially settle on conspecific adults (Chase & Bailey, 1996; Jones, 2012), which may act to maintain the adult zonation pattern. However, as juvenile and adult patterns differ, our results suggest that the influence of settlement selection behaviour by itself is not strong enough to drive the adult distribution of these two species.

Post-settlement mortality of juvenile marine invertebrates can be extremely high and thus limit abundance, constrain distribution and shape community structure (Gosselin & Qian, 1997). Zebra mussels similarly exhibit high larval and juvenile mortality (Lewandowski, 1982; Sprung, 1989; Schneider *et al.*, 2003). Yet the zebra mussel comprised a greater percentage abundance at the juvenile stage than it did during the larval stage, contributing >50% of the total juvenile dreissenid abundance for all but two sampling months between 2007 and 2009. The predominance of zebra mussel juveniles compared to larvae at both depths suggests that the quagga mussel suffers higher mortality in the transition from the larva to juvenile stages than does its congener. Furthermore, despite their predominance, the mean proportional abundance of juvenile zebra mussels was only slightly (and not significantly) higher in the shallow zone than in the deep zone in 2007 and 2008, and in 2009, it was actually greater in the deep zone. Hence, variation in the recruitment of these two species does not appear to set the species-specific adult zonation.

Variability in dominance by the zebra mussel during the larval stage, along with its persistent dominance at both depths during the juvenile stage, points to post-recruitment (affecting mussels >10 mm) as the critical period for the establishment of the species-specific adult patterns of dominance. As mussels continue to grow and reproduce, zebra mussels in the deep zone must be increasingly adversely affected by inclement biotic and abiotic conditions, including perhaps interspecific competition; thus, they must suffer differential mortality, unless a substantial number migrate up the canal wall. While mussel movement may play a role, it is unlikely to be the driving factor, given that zebra mussels tend to adhere tightly to substratum, invest a significant amount of

energy into byssal thread production (Peyer, McCarthy & Lee, 2009) and become less mobile as they grow larger (Burks, Tuchman & Call, 2002; Toomey, McCabe & Marsden, 2002).

Jones (2012) hypothesised that the pattern of replacement of dreissenid mussels results, in part, from a competition–colonisation trade-off. The zebra mussel, which produces more gametes than quagga mussels of similar size, is characterised as an *r*-strategist and a superior coloniser, while the quagga mussel is the better competitor (Stoeckmann, 2003). In the Soulanges Canal, the mean proportions of zebra mussel larvae and juveniles in the spawning season were greater earlier (June/July) than later (August/September) and frequently represented a greater proportion of dreissenid abundance than its congener. The predominance of zebra mussel larvae in the canal (despite shifting dreissenid demography upstream) and its greater relative abundance earlier in the season are concordant with an *r*-type strategy. While the zebra mussel may be a superior coloniser (as evident, in part, from its greater contribution to total juvenile abundance), it does not dominate the adult dreissenid population in the deep zone and must therefore suffer a higher post-recruitment mortality there. The importance of post-recruitment mortality has been previously demonstrated for two congeneric marine mussels and was deemed the significant factor determining their adult distributional patterns (Delany *et al*., 2003). Our results support this putative mechanism of replacement, as zebra mussels dominated both larval supply and recruitment, but do not maintain this dominance into the adult life stage where competitive ability and stress tolerance may become limiting factors.

Although these two species are confamilial and have a similar life cycle, morphology and ecology, they exhibit strikingly distinct patterns of adult distribution and abundance in our study system and in other sites (Mills *et al*., 1999; Ricciardi & Whoriskey, 2004). These patterns differ sharply from those observed for earlier life stages. In the Soulanges Canal, larval supply, settlement and recruitment generated greater total dreissenid abundance in the deep zone – the opposite of the spatial pattern of the adult community. Larval supply and recruitment were frequently dominated by the zebra mussel regardless of depth, again in contrast with the adult community. We therefore conclude that the most significant factor determining the dreissenid depth zonation and the relative dominance of these two species in our study site is post-recruitment mortality and suggest that the ongoing displacement of the zebra mussel as the dominant dreissenid may be attributable to differential species survivorship.

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References

Ackerman J.D., Sim B., Nichols S.J. & Claudi R. (1994) A review of the early life history of zebra mussels (*Dreissena polymorpha*): comparisons with marine bivalves. *Canadian Journal of Zoology*, **72**, 1169–1179.

Alfaro A.C. (2006) Evidence of cannibalism and benthopelagic coupling within the life cycle of the mussel, *Perna canaliculus*. *Journal of Experimental Marine Biology and Ecology*, **329**, 206–217.

Barnard C., Frenette J. & Vincent W.F. (2003) Planktonic invaders of the St. Lawrence estuarine transition zone : environmental factors controlling the distribution of zebra mussel veligers. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 1245–1257.

Burks R.L., Tuchman N.C. & Call C.A. (2002) Colonial aggregates: effects of spatial position on zebra mussel responses to vertical gradients in interstitial water quality. *Journal of the North American Benthological Society*, **21**, 64–75.

Carlon D.B. (2002) Production and supply of larvae as determinants of zonation in a brooding tropical coral. *Journal of Experimental Marine Biology and Ecology*, **26**, 33–46.

Chase M.E. & Bailey R.C. (1996) Recruitment of *Dreissena polymorpha*: does the presence and density of conspecifics determine the recruitment density and pattern in a population? *Malacologia*, **38**, 19–31.

Cornell H.V. & Lawton J.H. (1992) Species interactions, local, and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, **61**, 1–12.

Delany J., Myers A., McGrath D., O'Riordan R. & Power A. (2003) Role of post-settlement mortality and "supply-side" ecology in setting patterns of intertidal distribution in the chthamalid barnacles *Chthamalus montagui* and *C. stellatus*. *Marine Ecology Progress Series*, **249**, 207–214.

Dobretsov S. & Miron G. (2001) Larval and post-larval vertical distribution of the mussel *Mytilus edulis* in the White Sea. *Marine Ecology Progress Series*, **218**, 179–187.

Drake J.A. (1991) Community-assembly mechanics and the structure of an experimental species ensemble. *The American Naturalist*, **137**, 1–26.

Ettinger-Epstein P., Whalan S., Battershill C. & de Nys R. (2008) A hierarchy of settlement cues influences larval behaviour in a coral reef sponge. *Marine Ecology Progress Series*, **365**, 103–113.

Fraleigh P.C., Klerks P.L., Gubanich G., Matisoff G. & Stevenson R.C. (1993) Abundance and settling of zebra mussel (*Dreissena polymorpha*) veligers in Western and Central Lake Erie. In: *Zebra Mussels: Biology, Impacts, and Control*. (Eds Nalepa T.F. & Schloesser D.W.), pp. 129–142. Lewis Publishers, Boca Raton, Florida.

Gaines S. & Roughgarden J. (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the National Academy of Sciences, U.S.A.*, **82**, 3707–3711.

Gamarra J.G.P., Montoya J.M., Alonso D. & Solé R.V. (2005) Competition and introduction regime shape exotic bird communities in Hawaii. *Biological Invasions*, **7**, 297–307.

Gosselin L. & Qian P.Y. (1997) Juvenile mortality in benthic marine invertebrates. *Marine Ecology Progress Series*, **146**, 265–282.

Hunt H.L. & Scheibling R.E. (1997) Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Marine Ecology Progress Series*, **155**, 269–301.

Jenkins S.R. (2005) Larval habitat selection, not larval supply, determines settlement patterns and adult distribution in two chthamalid barnacles. *Journal of Animal Ecology*, **74**, 893–904.

Jones L.A. (2012) *The Role of Biotic and Abiotic Factors in Exotic Species Replacement*. PhD Thesis, McGill University, Canada.

Jones L.A. & Ricciardi A. (2005) Influence of physicochemical factors on the distribution and biomass of invasive mussels in the St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 1953–1962.

Jonsson P.R., Berntsson K.M. & Larsson A.I. (2004) Linking larval supply to recruitment: flow mediated control of initial adhesion of barnacle larvae. *Ecology*, **85**, 2850–2859.

Karatayev A.Y., Burlakova L.E., Mastitsky S.E., Padilla D.K. & Mills E.L. (2011) Contrasting rates of spread of two congeners, *Dreissena polymorpha* and *Dreissena rostriformis bugensis*, at different spatial scales. *Journal of Shellfish Research*, **30**, 923–931.

Lehane C. & Davenport J. (2004) Ingestion of bivalve larvae by *Mytilus edulis*: experimental and field demonstrations of larviphagy in farmed blue mussels. *Marine Biology*, **145**, 101–107.

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 number of settled individuals. *Ekol Polska*, **30**, 223–286.

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.

Mackie G., Gibbons W.N., Muncaster B.W. & Gray I.M. (1989) The zebra mussel, *Dreissena polymorpha*: a synthesis of European experiences and a preview for North America. Ontario Ministry of the Environment. Water Resources Branch, Queen's Printer for Ontario, Great Lakes Section, Toronto, ON.

Mackie G.L. (1991) Biology of the exotic zebra mussel, *Dreissena polymorpha*, in relation to native bivalves and its potential impact in Lake St. Clair. *Hydrobiologia*, **219**, 251–268.

Mackie G.L. & Schloesser D.W. (1996) Comparative biology of zebra mussels in Europe and North America: an overview. *American Zoologist*, **36**, 244–258.

Marsden J.E. & Lansky D.M. (2000) Substrate selection by settling zebra mussels, *Dreissena polymorpha*, relative to material, texture, orientation, and sunlight. *Canadian Journal of Zoology*, **78**, 787–793.

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 Science*, **51**, 856–861.

McQuaid C.D. & Phillips T.E. (2006) Mesoscale variation in reproduction, recruitment and population structure of intertidal mussels with low larval input: a bay/open coast comparison. *Marine Ecology Progress Series*, **327**, 193–206.

Menge B.A. (1991) Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology*, **146**, 69–100.

Menge B.A. (2000) Recruitment versus postrecruitment processes as determinants of barnacle population abundance. *Ecological Monographs*, **70**, 265–288.

Mills E.L., Chrisman J.R., Baldwin B., Owens R.W., O'Gorman R., Howell T. *et al.* (1999) Changes in the dreissenid community in the lower Great Lakes with emphasis on southern Lake Ontario. *Journal of Great Lakes Research*, **25**, 187–197.

Minchinton T.E. & Scheibling R.E. (1991) The influence of larval supply and settlement on the population structure of barnacles. *Ecology*, **72**, 1867–1879.

Nalepa T.F., Fanslow D.L. & Lang G.A. (2009) Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. *Freshwater Biology*, **54**, 466–479.

Patterson M.W.R., Ciborowski J.J.H. & Barton D.R. (2005) The distribution and abundance of *Dreissena* Species (Dreissenidae) in Lake Erie, 2002. *Journal of Great Lakes Research*, **31**(Suppl. 2), 223–237.

Pawlik J.R. (1992) Chemical ecology of the settlement of benthic marine invertebrates. *Oceanography and Marine Biology Annual Review*, **30**, 273–335.

Pennuto C.M., Howell E.T., Lewis T.K. & Makarewicz J.C. (2012) *Dreissena* population status in nearshore Lake Ontario. *Journal of Great Lakes Research*, **38**, 161–170.

Peyer S.M., McCarthy A.J. & Lee C.E. (2009) Zebra mussels anchor byssal threads faster and tighter than quagga mussels in flow. *The Journal of Experimental Biology*, **212**, 2027–2036.

Pineda J., Porri F., Starczak V. & Blythe J. (2010) Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity. *Journal of Experimental Marine Biology and Ecology*, **392**, 9–21.

Porri F., Jordaan T. & McQuaid C.D. (2008) Does cannibalism of larvae by adults affect settlement and connectivity of mussel populations? *Estuarine, Coastal and Shelf Science*, **79**, 687–693.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing, Version 2.12.2*. R Foundation for Statistical Computing, Vienna.

Ram J.L., Karim A.S., Banno F. & Kashian D.R. (2012) Invading the invaders: reproductive and other mechanisms mediating the displacement of zebra mussels by quagga mussels. *Invertebrate Reproduction and Development*, **56**, 21–32.

Ricciardi A. & Whoriskey F.G. (2004) Exotic species replacement: shifting dominance of dreissenid mussels in the Soulanges Canal, upper St. Lawrence River, Canada. *Journal of the North American Benthological Society*, **23**, 507–514.

Rodríguez S.R., Ojeda F.P. & Inestrosa N.C. (1993) Settlement of benthic marine invertebrates. *Marine Ecology Progress Series*, **97**, 193–207.

Sait S.M., Liu W.C., Thompson D.J., Godfray H.C.J. & Begon M. (2000) Invasion sequence affects predator-prey dynamics in a multi-species interaction. *Nature*, **405**, 448–450.

Sams M.A. & Keough M.J. (2012) Contrasting effects of variable species recruitment on marine sessile communities. *Ecology*, **93**, 1153–1163.

Schneider D.W., Stoeckel J.A., Blodgett D.K., Sparks R.E. & Padilla D.K. (2003) A developmental bottleneck in dispersing larvae: implications for spatial population dynamics. *Ecology Letters*, **6**, 352–360.

Sprung M. (1989) Field and laboratory observation 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*. In: *Zebra Mussels, Biology, Impacts and Control*. (Eds T.F. Nalepa & D.W. Schloesser), pp. 39–53. Lewis Publishers, Boca Raton, Florida.

Stoeckel J.A., Rehmann C.R., Schneider D.W. & Padilla D.K. (2004) Retention and supply of zebra mussel larvae in a large river system: importance of an upstream lake. *Freshwater Biology*, **49**, 919–930.

Stoeckel J.A., Schneider D.W., Soeken L.A., Blodgett D.K. & 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.

Stoeckmann A. (2003) Physiological energetics of Lake Erie dreissenid mussels: a basis for the displacement of *Dreissena polymorpha* by *Dreissena bugensis*. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 126–134.

Todd C.D. (1998) Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? *Hydrobiologia*, **375/376**, 1–21.

Toomey M.B., McCabe D. & Marsden J.E. (2002) Factors affecting the movement of adult zebra mussels (*Dreissena polymorpha*). *Journal of the North American Benthological Society*, **21**, 468–475.

Underwood A.J. & Fairweather P.G. (1989) Supply-side ecology and benthic marine assemblages. *Trends in Ecology and Evolution*, **4**, 16–20.

Vanderploeg H.A., Nalepa T.F., Jude D.J., Mills E.L., Holeck K.T., Liebig J.R. *et al.* (2002) Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1209–1228.

Ward J.M. & Ricciardi A. (2007) Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: a meta-analysis. *Diversity and Distributions*, **13**, 155–165.

Wellborn G.A., Skelly D.K. & Werner E.E. (1996) Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics*, **27**, 337–363.

Wilson K.A., Howell E.T. & Jackson D. (2006) Replacement of zebra mussels by quagga mussels in the Canadian nearshore of Lake Ontario: the importance of substrate, round goby abundance, and upwelling frequency. *Journal of Great Lakes Research*, **32**, 11–28.

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