

Dispersal limitation of unionid mussels and implications for their conservation

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SUMMARY

1. Freshwater unionid mussels are a highly imperilled group. Their dispersal abilities depend on the availability and the movement of host fish on which their parasitic mussel larvae develop.
2. We examined the relationship between the dispersal abilities of unionid mussels and their conservation status on a regional (SW Ontario) scale and their distribution and abundance on a catchment scale (Sydenham River, SW Ontario) by determining host specificity and estimating the dispersal abilities of mussels on fish from a review of the literature.
3. On the regional scale, we found that mussels with the most precarious conservation status relied on host fish with short movement distances, whereas vulnerable and more secure mussel species had host fish with 2–3 orders of magnitude larger movement distances. We were not able to detect a clear pattern on the catchment scale.
4. Our results suggest that limited dispersal by host fish affects the abundance and distribution of unionid mussels and ultimately their conservation status on a regional scale. Information on dispersal limitations because of differences in host fish communities should be included in conservation and management decisions to ensure connectivity and maintain functioning mussel metacommunities.

Keywords: connectivity, freshwater mussel conservation, host specificity, metacommunity, parasitism

Introduction

Unionid mussels (family: Unionidae) are a highly imperilled group of freshwater organisms with extinction rates similar to those of tropical rainforest communities (Ricciardi & Rasmussen, 1999; Lydeard *et al.*, 2004). Mussel species have gone extinct, and the distributions of the remaining species have often been fragmented through declines or local extinctions (Strayer, 2008). The declines of unionid mussels have been attributed to overharvesting, habitat modifica-

tion (including pollution) and destruction, and the introduction of dreissenid mussels (Williams *et al.*, 1993; Bogan, 2008). In addition, the specialised life history of unionids in which their glochidia larvae parasitise fish makes them vulnerable to factors that affect fish populations (McNichols, Mackie & Ackerman, 2011).

Interestingly, there are pronounced differences in conservation status among unionoid taxa. For example, whereas the majority of the *Epioblasma* species (Lampsilini) have gone extinct, others such as *Pyganodon* and *Anodonta* species (Anodontini) thrive in some areas (Metcalf-Smith *et al.*, 1998a; Strayer, 2008). Such differences in conservation status have been attributed to differences in mussel body size and the number of host fish used, with common mussel

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species being generally larger and having more host fish (Strayer, 2008). In addition to the number of host fish used, the dispersal biology of the host fish is an important component of mussel dispersal (Schwalb, Poos & Ackerman, 2010b), which occurs through the movement of the host fish while glochidia are attached and through the transport of glochidia and juvenile mussels in the water column (Morales *et al.*, 2006; Newton, Woolnough & Strayer, 2008; Schwalb, Garvie & Ackerman, 2010a). Transport on host fish is essential for both upstream and long-distance dispersal, which is necessary for the connectivity among populations and communities in general (i.e. meta-communities, Hanski, 1999; Leibold *et al.*, 2004; Newton *et al.*, 2008). Connectivity may vary widely among mussel populations, since genetic studies indicate that freshwater mussel populations can have low to high levels of genetic differentiation both within and among catchments (Berg *et al.*, 1998; Kelly & Rhymer, 2005; Zanatta & Murphy, 2007). Such differences may be attributed to differences in the mobility of their host fish (Berg, Christian & Guttman, 2007).

Because dispersal via host fish is crucial to the dispersal of mussels, both the number of host fish used, which provides an indication of the overall likelihood for successful dispersal, and the movement behaviour of those hosts, which provides an indication of the potential for large-scale movement, will influence a mussel species' dispersal abilities. Host fish size should also be important as fish home ranges increase exponentially with fish size (Minns, 1995), and movement of small benthic fish, such as darters and sculpins, is typically restricted to a few metres (e.g. Freeman, 1995; Petty & Grossman, 2004). Mussels relying on dispersal via those small benthic fish can be expected to have lower dispersal abilities (Schwalb *et al.*, 2010b).

The distribution and abundance of mussels is probably affected by a hierarchy of scale-dependent constraints, ranging from global climatic factors to local environmental factors (Vaughn & Taylor, 2000; Strayer, 2008). Dispersal via host fish may play a role at the catchment scale and at the regional scale, involving several catchments. For example, positive correlations have been found between the number of mussel species and the number of fishes in a river catchment (Watters, 1992), and some evidence for the importance of dispersal was found in an analysis of distribution patterns of mussels from 16 catchments in the USA (Vaughn, 1997).

In this study, we hypothesise that the dispersal abilities of unionid mussels, as determined by the number and movement distances of their host fish, affect their abundance and distribution on both regional and catchment scales. Specifically, mussel species with low dispersal abilities (fewer hosts, hosts that do not move large distances) should have the most precarious conservation status regionally, whereas mussel species with high dispersal abilities (more hosts, hosts that move large distance) should have higher local abundances and occupy a larger fraction of the occupied sites on a catchment scale.

Methods

For the analysis on a regional scale, we focused on Sydenham River, Thames River, Ausable River and Grand River in south-western Ontario (Canada), because these have the highest diversity of aquatic fauna, including unionid mussels, and are considered 'hotspots' for freshwater species with conservation designations in Canada (Staton & Mandrak, 2006; Hutchings & Festa-Bianchet, 2009). Data for the presence of fish and mussel species were obtained from community inventory surveys conducted in these rivers (Metcalf-Smith *et al.*, 1998b; Angela Van Niekerk, Ausable Bayfield Conservation Authority, pers. comm.; Cudmore, MacKinnon & Madzia, 2004; Poos, Mandrak & McLaughlin, 2007, 2008). We used the provincial conservation ranks developed by the Ontario National Heritage Information Centre to determine the conservation status of mussel species and the national rank for one species that has not been assessed in Ontario (Appendix S1, Ministry of Natural Resources, 2009).

Whenever possible, we gathered data on mussel host fish from studies that identified host fish species based on the transformation of glochidia larvae into juvenile mussels ($n = 26$ species, Cummings & Watters, 2008, K.A. McNichols & J.D. Ackerman, unpubl. data). If these data were lacking, we included results that were based on field observations of glochidia infestations on fish, but where metamorphosis into juvenile mussels had not been observed ($n = 5$). The method used for host fish identification was not stated for two of the mussel species. We found 84 potential host fish species for the 34 unionid mussel species that occur in the studied rivers but only included the 57

fish species that actually occur in these rivers in our analysis (Appendix S2).

We consulted FishMaP (Fish Migration and Passage Knowledgebase, McLaughlin *et al.*, 2008), which includes fish movement and migration data, and ISI Web of Knowledge to compile data on fish movement to determine the average movement distances for each host fish. The use of the terms 'home range', 'movement' and the fish species name in the latter source provided 38, of more than 1000, articles that contained quantitative data on movement distances for 26 fish species (Appendix S2). Many of these articles contained information for several species. We also collected data on fish species in the same genus as host species (Appendix S3).

We restricted the data to studies from rivers, since fish home ranges in lakes can be 19–23 times larger than in rivers (Minns, 1995). We also differentiated between data obtained outside and during seasonal migrations because some fish migrate long distances during winter (Lucas & Baras, 2001) and the glochidia attached to such host fish over winter could disperse over great distances (Watters & O'Dee, 2000). In many cases, the average movement distances were determined or inferred as follows: (i) an average movement distance was calculated if movement was provided as frequency data ($n = 16$); (ii) the midpoint was used if a range in movement distance was provided ($n = 4$); and (iii) the home range size was used if no other information was provided ($n = 12$). Movement data were log-transformed to ensure a more uniform distribution of the data. The average was used when more than one reference was available for a given species. A linear regression of the log-transformed movement data vs. log-transformed average sizes of fish (from Scott & Crossman, 1973) was used to estimate movement distances for host fish species for which no movement data were available ($n = 24$, and $n = 26$ for seasonal migration, Appendix S3). The estimated dispersal abilities for each mussel species were calculated from the average of the log-transformed movement distances of their host fish species (i.e. the geometric mean).

For the catchment-scale analysis, we used mussel and fish survey data from the Sydenham River, Ontario, which has the highest diversity of mussel species in Canada (Staton *et al.*, 2003), to examine the hypothesis that dispersal abilities of mussels affect their abundance and distribution on a catchment scale.

Specifically, data from semi-quantitative surveys of mussels conducted at 17 sites on the Sydenham River in 1997–1998 (Metcalf-Smith *et al.*, 2007) were used. For each mussel species, we computed its average abundance only for the sites where it occurred (i.e. local abundance) and excluded all the sites where it did not occur. Those data were based on timed searches (4.5 person-hour (p-h)), which is an efficient method for detecting rare species (Metcalf-Smith *et al.*, 2000). Data on fish presence were obtained from Poos *et al.* (2007, 2008), who used a variety of sampling methods (e.g. electrofishing, seine netting) at the same sites in 2002 and 2003. The number of host fish and movement estimates for mussels were restricted to species occurring in the Sydenham River (Poos *et al.*, 2007, 2008), and only movement data outside seasonal migrations were used in the analysis.

Statistical analysis

Kolmogorov–Smirnov and Shapiro–Wilk tests for small sample sizes ($n < 20$) were used to determine whether the estimated dispersal abilities and number of host fish data were normally distributed, and the data were log-transformed where necessary. Potential difference in the estimated dispersal abilities, number of host fish and mussel body size (maximum shell length) among critically imperilled (S1), vulnerable (S2–S3) and more secure species (S4–S5) (see Appendix S1) was examined using analysis of variance (ANOVA), and pairwise differences were examined using the Tukey *post hoc* test. A forward multiple linear regression analysis was used to examine the relationship between conservation status and shell length, number of host fish, and estimated dispersal abilities.

Analysis of covariance (ANCOVA) was used to examine whether there was a relationship between the number of host fish and mussel local abundance (or distribution) using conservation status as the covariate. ANCOVA was also used to examine whether there was a relationship between estimated dispersal abilities and mussel local abundance (or distribution) using conservation status as the covariate.

The effort devoted to the identification of host fish varies considerably with mussel species, often with less information (in terms of numbers of studies) available for less-common species. To evaluate the potential bias caused by differences in the number of studies per mussel species, we examined (i) whether the number of

host fish per mussel species increased significantly with the number of studies using linear regression; (ii) the relationship between the residuals of the linear regression from (i) and the conservation status of the mussels; and (iii) whether significant differences in the estimated dispersal abilities would occur if host fish species were assigned randomly to each mussel species, but the number of host fish per mussel species was kept constant. These analyses were undertaken with the software R (Hornik 2010, <http://CRAN.R-project.org/doc/FAQ/R-FAQ.html>, ISBN 3-900051-08-9) by computing the estimated dispersal distance (with and without seasonal migration) for each mussel species while selecting randomly their host fish species and then computed the average fish movement distance for each conservation category. The process was repeated 1000 times and the results compared to the real data (code is available from the authors).

Results

Ten of the 34 unionid mussel species occurring in rivers in south-western Ontario are considered critically imperilled (S1) under the Province of Ontario ranking. However, the host of the critically imperilled mussel *Simpsonaias ambigua* (Say), the Mudpuppy, is an amphibian, and so this mussel was excluded, leaving 33 mussel species in the analysis (Appendix S1). In addition to the nine S1 species, three species are considered 'imperilled' (S2), eight are 'vulnerable' (S3), four are 'apparently secure' (S4) and seven are 'secure' mussel species (S5, Ministry of Natural Resources, 2009, Appendix S1). The rank of two mussel species ranged from S2 to S3, indicating the range of uncertainty about their status (Ministry of Natural Resources, 2009). Owing to this uncertainty and the low sample size for some ranks (i.e. S2 and S4), we grouped imperilled to vulnerable species (category S2–S3) as 'vulnerable' and S4 and S5 as the 'more secure' species. This resulted in three categories with reasonable sample sizes ($n = 9–13$).

A total of 216 host fish relationships were identified involving 57 host fish and 33 mussels, with mussel species often sharing the same hosts; the number of fish hosts ranged between 1 and 32 host fish per mussel (Appendixes S1 and S2). Movement data were obtained for 24 (26 including seasonal migration) of the 57 host fish, 6 of which were smaller than 100-mm total length (TL) and 20 of which were larger than 100-

mm TL (Appendix S2). Movement data for the remaining 33 of the 57 host fish species (21 < 100 mm TL and 12 > 100 mm TL) were estimated for a log–log regression of fish size vs. movement distance ($\log \text{ distance} = (2.4 \pm 0.3) \times \log \text{ size} - (3.1 \pm 0.6)$, $R^2 = 0.77$, $P < 0.001$, $n = 24$; $\log \text{ distance} = (3.1 \pm 0.3) \times \log \text{ size} - (4.6 \pm 0.7)$, $R^2 = 0.80$, $P < 0.001$, $n = 26$ including seasonal migration; Appendix S3).

Conservation status – regional scale

The average estimated dispersal abilities, based on the geometric mean of host fish movement distances, of critically imperilled mussels were on the order of tens of metres, whereas those of vulnerable and more secure species were one to two orders of magnitude higher, and three orders of magnitude higher when seasonal migration was included in the analysis (Fig. 1). Vulnerable species had the largest range of estimated dispersal abilities from a few metres to a few kilometres (or 10^4 m when seasonal migration data were included; Fig. 1). Critically imperilled mussels had significantly lower estimated dispersal abilities compared with vulnerable and more secure species (Fig. 1, ANOVA $F_{2,30} = 10.0$, $P < 0.001$). The same significant pattern was found using only the 26 mussel species for which host fish were identified in laboratory experiments (ANOVA $F_{2,23} = 10.9$, $P < 0.001$).

Estimated dispersal abilities did not differ among conservation statuses when host fish were assigned randomly to each mussel species (solid lines above box plots in Fig. 1). Simulations in R of the estimated dispersal abilities of the critically imperilled mussels were an order of magnitude higher compared with those derived using actual host fish information.

There were 2–6 host fish per mussel for critically imperilled mussel species, 1–10 hosts for vulnerable species, whereas the range was 1–32 hosts for more secure mussel species (Fig. 2a). The number of hosts found for the critically imperilled and vulnerable mussel species (median: 3 and 2 hosts per mussel, respectively) was significantly lower compared with more secure species (median: eight hosts per mussel, ANOVA $F_{2,30} = 5.9$, $P < 0.01$). Critically imperilled and vulnerable mussel species also had significantly lower numbers of hosts compared with more secure species (ANOVA $F_{2,23} = 7.1$, $P = 0.004$) using only the 26 mussel species for which host fish were identified in laboratory experiments.

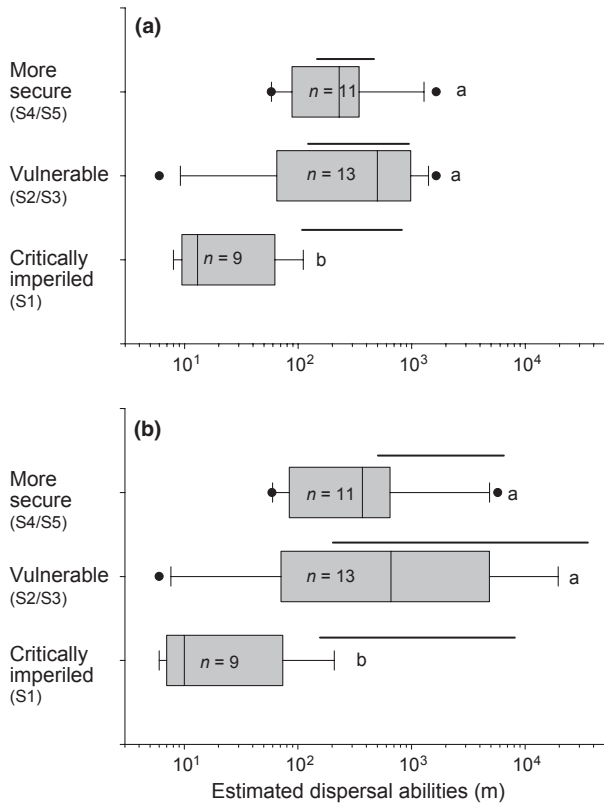


Fig. 1 (a) Average estimated dispersal abilities in relation to conservation status of unionid mussels in south-western Ontario (b) including data for seasonal migration. The boundaries of the box plot indicate the 25th and 75th percentiles, the whiskers the 10th and 90th percentiles, points indicate outliers, and the line in the box marks the median. The solid lines above each box plot indicate the ranges for estimated dispersal abilities from the analysis where host fish were assigned randomly (average of 1000 repetitions). Different letters indicate a significant difference (Tukey test, $P < 0.05$).

Mussel shell length was significantly lower for critically imperiled mussels compared with more secure species (Fig. 2b, ANOVA $F_{2,30} = 6.1$, $P < 0.01$). Shell length, log (number of host fish) and log (estimated dispersal abilities) were significantly related to conservation status and together explained 56% of the variation in conservation status (forward multiple linear regression, $R^2 = 0.56$, $F_{3,29} = 12.1$, $P < 0.001$, $n = 33$). Shell length alone explained 28% of the variation, whereas shell length and log (number of host fish) together explained 41% ($R^2 = 0.28$, $F_{1,31} = 11.8$, $P = 0.002$ and $R^2 = 0.41$, $F_{2,30} = 10.3$, $P < 0.001$, $n = 33$, respectively).

Interestingly, the number of host fish increased significantly with the number of studies ($R^2 = 0.87$, $P < 0.001$, $n = 33$), but there was no significant rela-

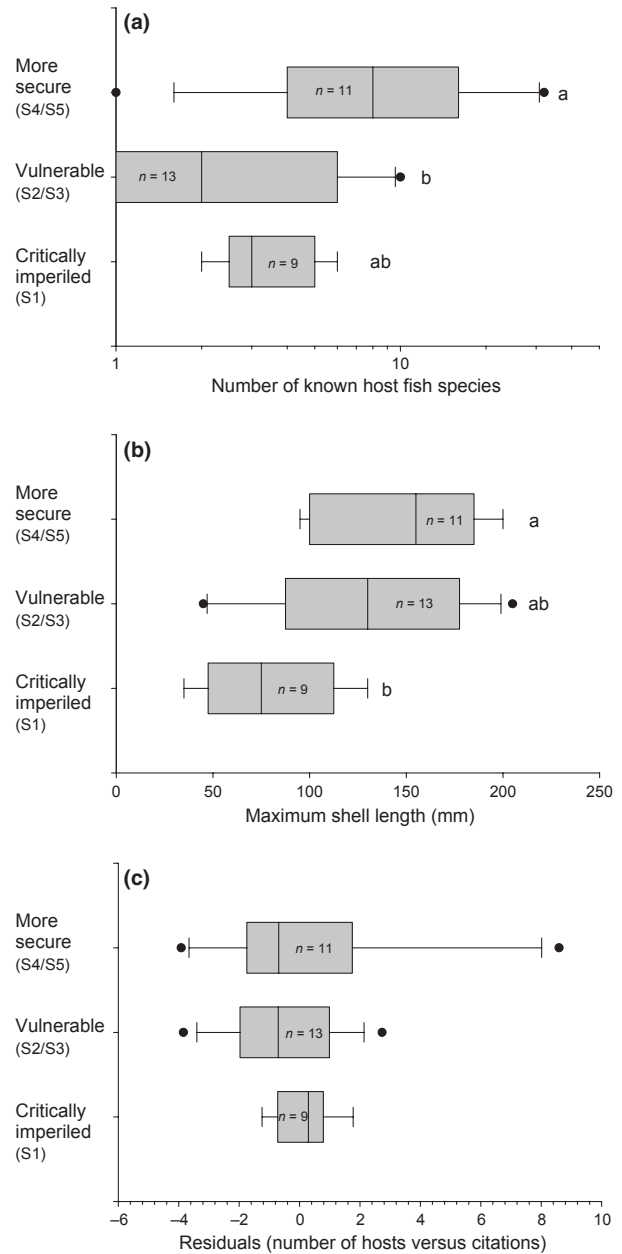


Fig. 2 (a) Number of known host fish species in relation to the conservation status of unionid mussels in south-western Ontario. (b) Body size (maximum shell length) in relation to conservation status of mussels. (c) Residuals of the linear regression (host fish vs. citations) in relation to conservation status of mussels. The boundaries of the box plot indicate the 25th and 75th percentiles, the whiskers the 10th and 90th percentiles, points indicate outliers, and the line in the box marks the median. The line in the box indicates the median. Different letters indicate a significant difference (Tukey test, $P < 0.05$).

tionship between the residuals of the linear regression (host fish vs. number of studies) and conservation rank ($R^2 < 0.01$, $P = 0.65$; Fig. 2c).

Abundance and distribution – catchment scale

Twenty-seven of the 33 mussel species used in the regional analysis were found in the semi-quantitative survey in the Sydenham River in 1997-98, including 6 critically imperilled species (Metcalf-Smith *et al.*, 2007), and 48 of the 57 host fish species (Poos *et al.*, 2007, 2008). The average local abundance of mussel species varied between 0.2 and 7.4 ind p-h⁻¹ ($n = 17$ sites). Mussels in the Sydenham River had 6 ± 1 host fish species. Only four species, all of which were more secure mussels, had more than 7 hosts (triangles in Fig. 3a). Three of these four species also had lower abundances (<1.5 ind p-h⁻¹) and a more restricted distribution ($<40\%$ of occupied sites). However, no relationship was found between the number of host fish and local mussel abundance or mussel distribution (ANCOVA $F_{5,21} = 1.4$, $P = 0.32$ and ANCOVA $F_{5,21} = 1.3$, $P = 0.28$, respectively) using conservation status as the covariate.

All critically imperilled species ($n = 6$) and the vulnerable species *Ligumia recta* (Lamarck) had low average abundances (<1.5 ind p-h⁻¹) and low estimated dispersal abilities (<30 m; Fig 3b). In general, species with estimated dispersal abilities of less than 10^2 m had lower abundances (<1.5 ind p-h⁻¹), whereas species with estimated dispersal abilities $>10^2$ m ranged from low to high abundances (0.2–7.4 ind p-h⁻¹). There were no species with estimated dispersal abilities of $<10^2$ m that had an abundance >1.5 ind p-h⁻¹. Similarly, 5 of the 6 critically imperilled species had a more restricted distribution (found in $<40\%$ of 17 sites) and low average estimated dispersal abilities (<30 m, data not provided), except for *Ptychobranchus fasciolaris* (Rafinesque), which was found in 53% of the sites. However, no relationship was found between estimated dispersal abilities and local mussel abundance or mussel distribution (ANCOVA $F_{5,21} = 0.9$, $P = 0.50$ and $F_{5,21} = 1.1$, $P = 0.40$, respectively) using conservation status as the covariate.

Discussion

Differences in conservation status among mussel species have been attributed to differences among taxonomic groups and functional traits such as mussel body size and the number of host fish (Strayer, 2008). This is reasonable given that these factors are somewhat related (Fig. 2). For example, species losses and

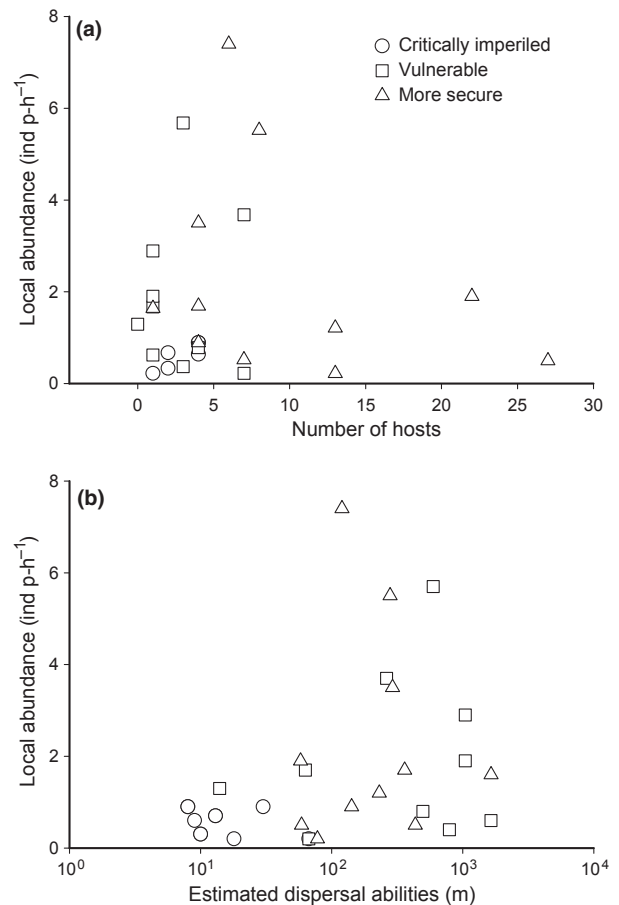


Fig. 3 (a) Number of host fish and (b) estimated dispersal abilities in relation to the average local abundance of each unionid mussel species in the Sydenham River, Ontario (over 17 sampling sites). The index of local abundance is individuals counted per person-hour (ind p-h⁻¹). Seasonal migration data not included.

declines in Ontario's lower Great Lakes Drainage Basin have most likely been caused by human impacts and have resulted in a historical shift from dominance by Lampsilini to Anodontini species (Metcalf-Smith *et al.*, 1998a). However, the mechanisms behind the different responses of these taxa to human impact are not understood (Strayer, 2008). It is possible that restricted dispersal abilities, as indicated by our results in which critically imperilled mussel species rely on host fish with shorter movement distances, could also be responsible. Moreover, differences in dispersal abilities may also serve to explain differences in conservation status among mussels and why some mussels show a fragmented distribution (Strayer, 2008). Species with low dispersal abilities

would be less able to recover from adverse effects than species with greater dispersal abilities. Specifically, mussels relying exclusively on dispersal via fish with low movement distances will recover more slowly after local fish kills caused, for example, by a chemical spill (Albanese, Angermeier & Peterson, 2009).

The relationship between the number of host fish and the conservation status of mussels is less clear because there is an observation bias (i.e. the number of host fish identified depends on the number of host fish studies). Whereas the specialisation of a mussel species on one or a few host fish may be advantageous in terms of successful metamorphosis (Barnhart, Haag & Roston, 2008), it can lead to vulnerability when host fish decline or are extirpated (Zanatta *et al.*, 2010; McNichols *et al.*, 2011). Similar arguments could be applied to the lack of a clear relationship between dispersal abilities and abundance and distribution of mussels on a catchment scale. For example, the disappearance of the primary host fish of *Epioblasma torulosa rangiana* (Lea) in the Sydenham River has probably led to low abundance in this species (McNichols *et al.*, 2011). Moreover, high abundances of species such as *Actinonaias ligamentina* (Lamarck) and *Cyclonaias tuberculata* (Rafinesque) may be related to their high dispersal abilities. On the other hand, physical factors such as the lack of fine mud and sand substrate in the Sydenham River may be the reason for the low abundance of *Lampsilis siliquoidea* (Barnes) (McRae, Allan & Burch, 2004). It is difficult to resolve the factors that affect unionid mussel abundance at small spatial scales (Strayer, 2008).

Whether the seasonal migration of fish over winter affects the dispersal of mussels depends on the reproductive timing of the mussels, as fish can migrate tens to hundred of kilometres during seasonal migrations (e.g. Pegg, Bettoli & Layzer, 1997; Lucas & Baras, 2001). Many mussel species reproduce in summer, when fish tend to have smaller home ranges (Lucas & Baras, 2001). However, some mussel species may have multiple broods or use multiple reproductive strategies, including host overwintering (glochidia being attached to fish over winter; Watters & O'Dee, 2000), which could lead to large-scale dispersal.

Several recent studies have found that dispersal limitation can impede or slow the recovery of aquatic organisms including fish (Albanese *et al.*, 2009) and

aquatic insects (Blakely *et al.*, 2006). In the case of unionid mussels, it is evident that more information is necessary to better understand the nature and role of fish-mediated dispersal. First, the host fish need to be identified using quantitative data and analysis, because the percentage of successfully transformed glochidia provides information on host quality (McNichols *et al.*, 2011). This is most urgent for the critically imperilled species. Secondly, data on host use in the field are needed, ideally in conjunction with the study of transformation success. For example, glochidia of *Anodonta kennerlyi* (Lea) were found on motile non-benthic fish (salmonids) in low numbers as well as on small more sedentary benthic fishes (sculpins and sticklebacks) where they were found at high densities (Martel & Lauzon-Guay, 2005). Thirdly, data on the movement behaviour of host fish and especially small benthic fish are needed because fish movement can vary with season, discharge conditions and ecosystem (Woolnough, Downing & Newton, 2009). For example, large fish may move very little while nesting (e.g. many Centrarchidae), whereas small benthic fish may be washed downstream during high discharge caused by storms (Hill & Grossman, 1987).

The difference in dispersal abilities between critically imperilled and more secure species has important implications for the conservation of mussel species (Lydeard *et al.*, 2004; Strayer, 2008). For example, barriers such as dams that block fish movement and/or disrupt the connectivity and colonisation of mussel populations should be avoided (Watters, 1996; Bogan, 2008; Newton *et al.*, 2008). Moreover, mussel conservation efforts including augmentation, reintroduction and relocation efforts (Hoftyzer *et al.*, 2008) should ensure the maintenance of a functioning metapopulation (i.e. connectivity and facilitation of (re)colonisation). Suitable habitat must be available in the area where species are augmented, reintroduced or relocated, as well as in neighbouring areas within their range of dispersal.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Conservation status, number of hosts, estimated dispersal distance of host fish, and

maximum shell length of 33 unionid mussel species used in the analysis.

Appendix S2. Mussel species and their host fish occurring in the Sydenham River, Thames River, Ausable River and Grand Rivers. Average size (total length) and movement distances (without seasonal movement) of host fish used in the analysis.

Appendix S3. Movement distance of host fish, (a) Fig. S1 average movement distances of host fish vs. average size of host fish. (b) References used for determining movement data for (i) host fish and (ii) non-host fish in the same genus.

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