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Active dispersal of an aquatic invader determined by resource and flow conditions

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Abstract New Zealand mudsnails (NZMS) have spread rapidly across the globe, but little is known about mechanisms that drive their secondary spread within invaded streams. We used a field experiment to test if upstream movement is a potential mechanism of spread and how this movement is modified by flow velocity and resource availability. We found that movement direction and rates were related to flow velocity, while resource availability influenced movement frequency. In slow-flow treatments, individuals moved upstream at rates approaching 3 m/h. In fast-flow treatments, many individuals were dislodged downstream and upstream movement rates were less than 2 m/h. In low-resource treatments, individuals were more likely to move away from their initial starting locations. We suggest that upstream movement may be important in establishing new populations within local invasions and that increases in flow velocity may be an effective means to slow upstream spread. The surprisingly fast movements that we recorded predict greater distribution of NZMS within invaded streams than has actually occurred, which suggests that factors in addition to movement rate limit population spread.

Keywords Experiment · Flow · Invasive · Movement · New Zealand mudsnail · *Potamopyrgus antipodarum* · Resource

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Introduction

The expanding invasion of aquatic habitats by *Potamopyrgus antipodarum*, the New Zealand mudsnail (NZMS), is causing increasing levels of concern (e.g., Davidson et al. 2008). The NZMS can outcompete native fauna (e.g., Riley et al. 2008), provides little energy to consumers, and is capable of passing through the gut of fishes unharmed (Vinson and Baker 2008). With a high rate of clonal reproduction and the ability to dominate invertebrate stream secondary production (Hall et al. 2003, 2006), NZMS are poised to have effects on ecosystem function analogous to those of the zebra mussel (Hall et al. 2003).

The first recorded occurrence of NZMS in North America is from the Snake River in Idaho in 1987 (Lysne and Koetsier 2006). It is now common in the Western United States, especially the Greater Yellowstone Ecosystem (GYE). NZMS have expanded the geographic extent of their invaded range in part through passive transport by humans, birds, and fish (Alonso and Castro-Díez 2008; Kappes and Haase

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2011). In contrast, very little is known about mechanisms of local dispersal within a stream once a population has established. Research on NZMS local dispersal is needed because identification of site vulnerability requires an understanding of all transport vectors (Vander Zander and Olden 2008; Kappes and Haase 2011).

Active, upstream movement is likely to be important in establishing new populations at the local scale but previous estimates of NZMS movement capabilities are largely anecdotal. Rates of freshwater snail movement are highly variable and depend in part on the time-frame and substrate of the measurements. For example, Ribi (1986) observed movement of NZMS in fine sand of 0.44 m/15 min, Richards et al. (2001) observed upstream movement of NZMS on flat substrate of >1 m/h, and Adam (1942) observed that NZMS on rocky substrate moved upstream just 60 m over 3 months. Hoffman et al. (2006) reported that *Physa* sp. moved up to 4.8 m/h, but Burris et al. (1990) reported less than 5 m/day for *Elimia clavaeformis*. A better understanding of the dynamics and drivers of NZMS movement is needed to help managers anticipate stream reaches that are vulnerable to invasion.

Hypotheses explaining upstream movements often invoke the search for food (Holomuzki and Biggs 2006), but variation in food resources may interact with other habitat parameters, like water velocity, known to influence both dispersal rate and direction (reviewed by Kappes and Haase 2011). For example, NZMS had consistent upstream movement rates in water velocities of 0.17 m/s (Adam 1942; Haynes et al. 1985). In contrast, Holomuzki and Biggs (1999) observed that NZMS burrowed in sediments as flows increased to 0.5 m/s and Holomuzki and Biggs (1999) and Richards et al. (2001) found that NZMS were likely to detach from substrate and drift downstream at flows >0.9 and 0.34 m/s, respectively. These data suggest that faster flowing water may limit upstream colonization, while slower flows may facilitate upstream colonization. Results from these studies indicate the need for detailed studies to understand the active upstream dispersal capabilities of NZMS under conditions of varying resource availability and flow.

In this study, we used a manipulative field experiment to determine for NZMS (1) upstream movement rates, (2) the dominant movement direction, (3) how movement rates and direction are modified by flow velocity and resource availability, (4) and the rate at which NZMS are likely to spread by active movements. If flow velocity limits upstream dispersal, then we predict that upstream movements will be rare in faster flows. If resource availability drives upstream movement, then we predict that movement will increase as resources become scarce.

Materials and methods

Study organism and site

The NZMS is a herbivorous and detritivorous scraper. In the GYE, they reach a maximum size of 6 mm shell length and reach sexual maturity at 3–3.5 mm shell length (Richards 2002). Populations in the GYE can build rapidly to large sizes because individuals typically are female from a single clonal lineage and reproduce through parthenogenesis (Kerans et al. 2005).

We conducted our field experiments in Polecat Creek, a geothermal spring stream near the South Boundary area of Yellowstone Park (see Hall et al. 2003 and 2006 for detailed site descriptions). Our site (UTM 12 524770E, 4884227N) was 400 m upstream of the Huckleberry Hot Springs outlet (2 km from Flagg Ranch) in the John D. Rockefeller National Parkway. Experiments were performed at base flow conditions ($\approx$1.9 m^3/s) during July 13–20th, 2010; stream temperature ranged from 17 to 21°C during this period.

Experimental design

Movement experiments were conducted in three artificial arenas placed directly within the stream. Each arena consisted of a 600 × 20 cm galvanized steel frame upon which 152 unglazed porcelain tiles (5.08 × 15.24 cm) were arranged into 38 rows and 4 columns (Fig. 1). The arenas received water directly from Polecat Creek.

We used conditioned and unconditioned tiles to create three resource treatments: low, medium, and high. Conditioned tiles had been cultured in the stream adjacent to our arenas for 5 weeks prior to our experiments and had uniform, low-profile algal mats (high resource treatment). Unconditioned tiles were not cultured in the stream and had no algal mats (low resource treatment). Medium resource treatments

Fig. 1 Photograph of the mid-point of an artificial arena used to conduct NZMS movement experiments. Tiles were arranged in 4 columns and 38 rows and each tile was 5.08 × 15.24 cm. A bottomless canister, placed at the mid-point of the arena, was used to acclimate NZMS to the arena (shown in the foreground). A measuring tape that spanned the length of the arena (shown on the right of the arena) was used to record NZMS movement distances

consisted of an equal number of conditioned and unconditioned tiles in a checkered arrangement.

We placed sandbags in front of each arena to create two flow velocity treatments: slow and fast. Sandbags were placed in front of the arena entrance to block flows (slow treatments) or to funnel flows (fast treatments). Slow treatments had flow velocities <0.05 m/s and fast treatments had flow velocities of 0.48–0.53 m/s. We measured flow immediately above the tiles at the upstream and downstream ends of each arena with a current velocity meter. These velocities were within the range of velocities recorded near base flow conditions immediately upstream and downstream of our experiment (A.J. Sepulveda, *unpublished data*). In these reaches, flow velocities that exceeded 0.55 m/s constituted fewer than 2% of observed values; such rates were not used in our experiments because they moved the tiles.

We assessed the response of NZMS movement to all possible combinations of resource level and flow velocity treatments. Each combination was assigned randomly to an artificial arena each day and replicated eight times over 8 days. Fresh, treated tiles were used for each high and medium resource replicate, but we reused unconditioned tiles for the low and medium resource replicates. Experimental animals were collected by hand in Polecat Creek and starved 12 h prior to a movement trial. To ensure that all individuals were large enough to be observed during movement trials, we used individuals that were >3.5 mm in shell length so our experimental results only provide inferences about mature adults.

Fifty NZMS per trial were placed in a bottomless canister at the center of the experimental arena (Fig. 1) and allowed to acclimate for 10 min. We initiated an experiment by removing the canister slowly and allowing individuals to move. During each trial, we recorded (1) the maximum upstream and downstream movement distance of the farthest moving individuals, (2) the number of individuals on each tile row, (3) the number of individuals on conditioned versus unconditioned tiles for the medium resource treatment, and (4) the size (mm) of the individuals that moved the longest and shortest distances at the completion of the experiment. These data were recorded at 20-min intervals for a 120-min period. Movement of experimental individuals was measured as distance from the arena center (cm).

Analysis of movement

Movement rate

To test if NZMS movement rate varied by resource level and flow velocity, we used the movement distances of the farthest moving individuals recorded at 20-min intervals for each 120-min trial. We used the fastest downstream rate and the fastest upstream rate observed in each trial as response variables because it only takes one individual to establish a new population. For downstream movement rates, we used the position of the farthest moving individual. Downstream movements were truncated because individuals moved beyond the downstream boundary of our experimental arenas, but this was of little concern because our focus was on upstream movement. We used a mixed model to test for the response of movement rate to flow speed and resource level. Arena location, which served as our block, was modeled as a random effect. Tukey honestly-significant-difference (HSD) post hoc tests were used to assess significant differences among treatment levels. To ensure that maximum movement rates did not only occur at the beginning of each trial as a response to being in a foreign environment, we tested for correlation

between movement rate of the fastest individuals and time. To test if upstream movement rate was influenced by NZMS size, we used *t* tests to compare the size of the fastest moving individual to the slowest moving individual in each replicate.

Movement direction

To test if NZMS movement direction varied by resource level and flow velocity, we generated histograms of the frequency of distances moved at the completion of each experiment (i.e., after 120 min), assigning negative values to downstream moves and positive values to upstream moves. We assessed directional bias by testing for skewness of the distribution (Zar 1984). We used mixed models and Tukey HSD post hoc tests to test if the difference between numbers of NZMS moving upstream and downstream and the median distance of displacement at the completion of the experiment varied by flow speed and resource level. We used *t* tests to test if the median distance of displacement was >0 cm for each treatment combination.

Movement behavior

To test how resource level influenced movement, we used a mixed model and Tukey HSD post hoc tests to compare the number of individuals on conditioned versus unconditioned tiles in medium resource treatments. The hypothesis that resource quantity influences NZMS movement would be supported if individuals avoid unconditioned tiles.

Diffusion

The ability to predict the rate at which invasive species, like NZMS, spread after they have been established provides a basis for classifying sites according to vulnerability (Vander Zander and Olden 2008). We tested if NZMS secondary spread could be characterized by simple diffusion, which predicts that the variance of distance moved increases linearly with time (Skellam 1951). For this analysis, we regressed the estimated variance of distance moved on time (0–120 min at 20-min intervals) using the polynomial equation, $Y = C_0 + C_1 t + C_2 t^2$ where y is the variance and t is time. The hypothesis predicts $C_0 = 0$, $C_1 > 0$, and $C_2 = 0$. This analysis describes the spread of animals from a single release point. We also calculated the diffusion coefficient (D) based only on upstream movement rates. If movement occurs by simple diffusion and there is a point release of individuals, as in our experiments, then D can be estimated as MSD/4t, where MSD is the mean square displacement of released individuals at time t (Kareiva 1983). We used a mixed model to test for the response of D to flow speed and resource level. All analyses were completed using JMP 8.0.2 (SAS Institute Inc., Cary, NC).

Results

We found that NZMS can move upstream rapidly across all treatment combinations. Multiple individuals (<5%) moved upstream and outside of the experimental arenas (i.e., >300 cm). These individuals reached the upstream boundary of the arenas only during the last 20-min observation period so the upstream tails of the movement distributions were minimally truncated and estimates of movement rate were minimally biased to the first 100-min of each trial. The fastest upstream movement rate observed was 288 cm/h. Individuals also moved downstream and beyond the experimental arena (>300 cm), especially in fast flows. However, more individuals moved upstream than downstream across all treatment combinations ($\chi^2 = 6.92$, $df = 1$, $P < 0.01$).

Movement characteristics

Movement rate

Maximum upstream movement rates varied by flow velocity and resource level, but there was no interaction of flow × resource (Fig. 2, Table 1). Individuals moved faster in slow flows than in fast flows and in low resource treatments than in high resource treatments. We found no difference in movement rates between low and medium resource treatments and medium and high resource treatments. Maximum movement rates were not correlated with time for any resource combination ($r < 0.30$ for all tests). We also found no difference in size (mm) between individuals that moved upstream at a fast rate and individuals that did not move far from the arena center (*t* test: $t_{57} = -1.15$, $P = 0.26$).

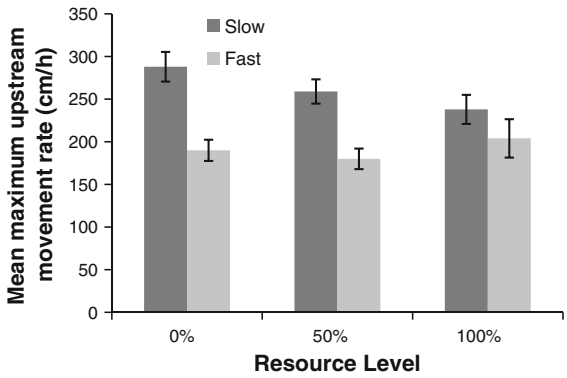

Fig. 2 The mean maximum upstream movement rate (cm/h, ±1 SE) observed for NZMS in each flow velocity and resource level combination. The maximum movement rate was estimated from 6, 20-min observations per replicate

Table 1 Random designs mixed model table for (a) the maximum upstream movement rate and (b) the frequency of upstream movements of NZMS

Source	*df*	*F*	*P*
a. Max. upstream movement			
Flow	1	154.49	<0.01
Resource	2	3.94	0.03
Arena	4	0.14	0.97
Flow × Resource	2	0.74	0.48
Error	38		
b. Frequency of upstream movement			
Flow	1	80.91	<0.01
Resource	2	8.95	<0.01
Arena	4	0.83	0.52
Flow × Resource	2	3.28	0.05
Error	38		

Movement rates and direction were compared among flow velocity and resource level treatments. Arena was treated as a random factor nested within flow velocity

Maximum downstream movement rates also varied by flow velocity and resource level, but we found no interaction of flow × resource ($F_{2,38} = 0.56, P = 0.58$). Individuals in fast flows moved downstream faster than individuals in slow flows ($F_{1,38} = 13.36$, $P < 0.01$) and individuals in low resources moved downstream faster than individuals in medium and high resources ($F_{2,38} = 6.16, P < 0.01$).

Movement direction

The frequency distributions of distances moved were not upstream biased (i.e., skewness was not >0) and skewness did not vary by flow or resource levels ($F = 0.76$–1.63, $P > 0.15$). However, more individuals moved upstream compared to downstream in slow flows, at medium and high resource levels (Fig. 3, Table 1). We also found a significant interaction of flow and resource. Populations in slow flows at medium and high resource levels had more individuals that moved upstream than populations in slow flows/low resource levels and populations at fast flows at all resource levels.

The median movement distances of each population were influenced by flow, but not by resource level (Fig. 4). Populations in slow flows moved further

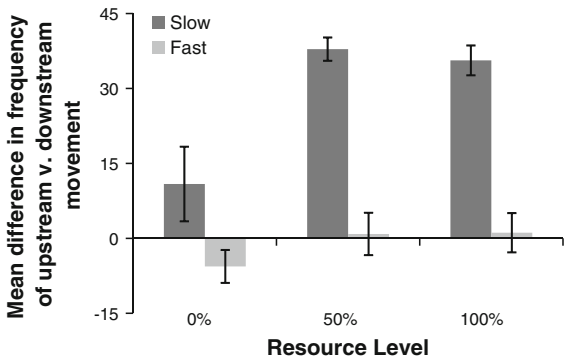

Fig. 3 The mean difference (±1 SE) in the number of individuals that moved upstream versus downstream. *Positive numbers* indicate that more individuals moved upstream, while *negative numbers* indicate that more individuals moved downstream

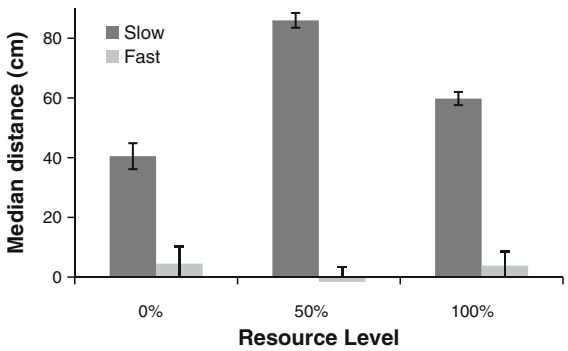

Fig. 4 The median distance moved (cm, ±1 SE) by populations of NZMS in each flow velocity and resource level combination

upstream than populations in fast flows ($F_1 = 11.58$, $P < 0.01$). The median distance moved by populations in slow flows was 76.8 cm ± 7 cm (1 SE) and significantly greater than 0 (t test: $t_{23} = 5.09$, $P < 0.0001$). The median distance in fast flows did not differ from 0 cm (t test: $t_{23} = 0.79$, $P = 0.44$) because many individuals moved downstream and because those going upstream did not go far.

Movement behavior

In medium resource treatments for slow and fast flow velocities, the median proportion of individuals on conditioned tiles was greater than the proportion of individuals on unconditioned tiles ($F_1 = 1447.87$, $P < 0.01$). More than 86% of observed NZMS were on conditioned tiles. NZMS in slow and fast flow velocities had a similar preference for conditioned tiles ($F_1 = 0.03$, $P = 0.87$).

Diffusion

NZMS movement in slow flows, across all resource levels, was consistent with a model of simple diffusion. Variance in distance moved increased linearly with time (linear regression for slow flow treatments across all resource levels: $F_{1,5} > 100$, $P < 0.005$, $r^2 > 0.96$). The estimated intercepts of the variance in distance by time polynomial regressions did not differ from zero ($t = -0.93$ to -0.45, $P > 0.07$), the slopes were significantly positive ($t > 9.73$, $P < 0.0001$), and the quadratic terms did not differ from zero ($t = -0.98$ to 0.57, $P > 0.40$). However, NZMS movement in fast flows, across all resource levels, did not fit a model of simple diffusion. Variance in distance moved did not increase linearly with time ($F_{1,5} < 2.75$, $P > 0.17$, $r^2 < 0.41$). The estimated intercepts of the variance in distance by time polynomial regressions were not different from zero, the slopes did not all differ from zero, and the quadratic terms did not differ from zero.

The diffusion coefficient (D) was greater in slow flows ($F_1 = 37.68$, $P < 0.01$), but did not differ significantly across resource levels ($F_2 = 3.28$, $P = 0.05$). Populations in slow flows had a $D = 18.66$ m^2/day (15.36–21.96, 95% CI), while individuals in fast flows had a $D = 5.43$ (2.13–8.72, 95% CI).

Discussion

Identifying the drivers of movement is essential for predicting NZMS secondary spread. We tested two variables that influence movement in other aquatic invertebrates: resource availability and flow velocity. Our results suggest that spatial variation in resources is linked to movement propensity and flow rate influences the direction and magnitude of movement. In our experimental channels, NZMS moved more rapidly away from the point of release in low resource treatments, whereas individuals in slow flow treatments moved upstream at rates three times faster than previously recorded (Adam 1942; Haynes et al. 1985; Richards et al. 2001). However, these rates may be inflated because they occurred on smooth substrate (Hoffman et al. 2006). We suggest that upstream movement may be important in establishing new populations within local invasions and that increases in flow velocity may be an effective means to constrain the upstream spread of NZMS.

In theoretical models, spatial variation in habitat quality is a driver of dispersal rate (e.g., McPeek and Holt 1992). Specifically, dispersal distance is predicted to increase when spatial variation in habitat quality is low because individuals must move farther to encounter higher-quality habitats (Lowe 2009). Our results support the predicted relationship between spatial variation in habitat quality (i.e., tile resource level) and distance moved because movement rate was greatest in low resource treatments. As spatial variability in food resources increased, movement rate decreased. Alternative models of dispersal that emphasize inbreeding and kin competition as drivers (e.g., Perrin and Goudet 2001) do not explain our results because NZMS are clonal.

In addition to displaying heterogeneity in upstream movement rates, downstream movement rates of NZMS also varied among treatments. In slow flow/low resource treatments and in fast flows across all resource levels, individuals moved downstream. Drifting, rather than active movement, was the dominant means of moving downstream. Because these downstream movements occurred more frequently in slow flow/low resource treatments than in slow flow/medium resource and slow flow/high resource treatments, it is likely that individuals in slow flows actively detached from tiles and drifted downstream to search for patches

of higher resource quality. In contrast, many individuals in fast flows dislodged actively or passively from the experimental tiles and were transported downstream during the first 10 min of each observation. Consequently, populations in fast flows did not meet a key assumption of simple diffusion: the variance of distance moved increases linearly with time.

The frequency distributions of movement distances were not skewed in an up- or downstream direction because the distances moved by downstream drift offset upstream movements across all treatments. However, we did find that movement direction was biased upstream in slow flow treatments and medium and high resource levels. At fast flows and low resource levels there was no bias because individuals detached from tiles and drifted downstream. These results suggest that flow speed and food resources can limit the upstream spread of NZMS and increase the likelihood of disjunct downstream populations as observed by Richards et al. (2001). Potential management strategies that may slow the upstream spread of NZMS include releases of high flows into invaded reaches downstream of dams. However, caution should be advised before using our results to inform management—Schreiber et al. (2003) found that fast flows can facilitate NZMS invasion because NZMS recolonized denuded areas, which resulted from high flow events, faster than native stream invertebrates.

Hypotheses that may explain the upstream movement bias we observed include the search for food or space, avoidance of predation, hydrodynamic effects, and upstream compensation. We can reject the food hypothesis because we found that individuals were more likely to move downstream when food was limited in low resource conditions. There is also little evidence to support the predation hypothesis because native fish are ineffective consumers of NZMS (Vinson and Baker 2008 but see Hellmair et al. 2011) and fish occur throughout Polecat Creek. We cannot evaluate the influence of hydrodynamics because we did not measure shell variation along multiple axes. However, we measured shell lengths of >2,400 snails and did not observe variation in morphology and found that movement direction and rate were not correlated with NZMS shell length. There is also little evidence to support the hydrodynamic torque force hypothesis presented by Huryn and Denny (1997), which predicts that snails face and move upstream in order to reduce torque and stabilize orientation. In our experiments, we observed downstream orientation and movement in all treatments and we observed upstream movement even in low flow treatments that were below the threshold velocities for torque forces. Finally, we found no support for the upstream compensation hypothesis, which predicts that upstream movements compensate for downstream drift (Muller 1954), because the proportion of individuals that moved upstream was much less than the proportion of individuals that moved downstream in fast flow treatments. However, compensation in clonal species like NZMS may only take one successful individual.

Though movement was not upstream biased, we did find that NZMS have the potential to rapidly extend their range by moving upstream throughout invaded stream networks. Based on our movement rate estimates, NZMS should have the capacity to move through most watersheds within a few summers. This rapid rate of movement suggests a high probability of coming into contact with new vectors (e.g., humans, birds) that could extend the range of NZMS within an invaded watershed and transport them to an uninvaded watershed. However, we anticipate that the realized movement rate may fall between our slow and fast flow velocity estimates because our artificial arenas had minimal roughness (Hoffman et al. 2006). Rougher substrate might aid movement in fast flows by providing refugia, but the topographic relief would decrease movement in both slow and fast flows. The difference in substrate smoothness may explain why our observed movement rates were greater than those observed by Adam (1942), Richards et al. (2001) and Haynes et al. (1985). Interstitial space may also slow the potential movement rate of large snails (>3.8 mm), which have been found in the native range to be less active and spend more time below rocks during daylight hours than smaller individuals (Levri and Lively 1996). In our study, in which most experimental individuals were >3.8 mm, NZMS size was not related to movement distance.

It is not known if short-term movement rates can be extrapolated to the long-term spread of NZMS. We found that movement rates were not correlated with time in our 120-min observation periods. In contrast, Haynes et al. (1985) found that movement rate estimates depended on the time frame of observation; NZMS in current speeds <0.17 m/h moved up to 15 cm in 30 min (30 cm/h), 51 cm in 5 h (10 cm/h) and 120 cm in 24 h (5 cm/h). Nevertheless, Ribi (1986) demonstrated that short-term movement rates can be used as an initial step

to test hypotheses of NZMS spread. Using simple extrapolations of 15-min movement rates, he found that active dispersal alone could not explain the current distribution of NZMS in Lake Zurich, Switzerland. Other mechanisms, such as passive dispersal by birds, fish, or on floating algae must also occur.

Like Ribi (1986), we compared our experimental movement rates to the observed, temporal patterns of NZMS occurrence in the field in order to determine whether active dispersal ability limits population spread. If the observed movement is much less than expected, then dispersal does not limit population spread and other factors (e.g., conductivity levels; Herbst et al. 2008) restrict population movements to less than their maximum potential. If the observed and expected movement rates are similar, increasing flow velocity may be an effective means of slowing upstream NZMS spread. If the observed rate is greater than the expected rate, then passive dispersal mechanisms such as birds, fish, and humans may drive NZMS spread. In our study stream, NZMS were first observed in 1994 and currently occupy <7 km of stream channel (R.O. Hall, University of Wyoming, personal communication). Even accounting for lower movement rates on natural substrate, simple extrapolation from our results predicts that NZMS had the potential to occupy the entire watershed by 2010. In this stream, factors other than dispersal ability may be combining to limit population spread. We suggest that our estimates of NZMS movement rate and the coefficient of diffusion (D) can be used as tools to determine whether dispersal is limiting (and thus flow controls might be useful) or whether other physical and biotic factors are more effective in controlling NZMS spread in any given invaded watershed.

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