Same enemy, same response: predator avoidance by an invasive and native snail

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Abstract

Novel or highly effective antipredator traits can facilitate successful invasions by prey species. Previous studies have documented that both the native New Zealand snail, *Potamopyrgus antipodarum*, and the highly successful, worldwide invader *Physella* (*Physa*) *acuta*, seek benthic cover to avoid fish predators. We asked whether an invasive, South Island population of *Physella* has maintained this avoidance response, and if so, how it compared to that of *Potamopyrgus* that has coevolved with native fish. We compared patterns of sediment surface and subsurface use between snail species and between sizes of conspecifics both in a 2nd –order reach with predatory fish and in a laboratory experiment where fish presence (common bullies [*Gobiomorphus cotidianus*]) was manipulated. Both snails sought protective sediment subsurfaces when with bullies. Proportionally, sediment subsurface use both in field collections and in fish treatments in the experiment were similar between species. Field-captured bullies ate more *Physella* than *Potamoprygus*, suggesting different consumptive risks, but overall, few snails were consumed. Instream densities and sizes (shell length) of *Physella* were greatest on cobbles, where most (>90%) egg masses were found. *Potamopyrgus* densities were evenly distributed across sand, gravel, and cobbles. Shell lengths were similar between snails on sediment subsurfaces and surfaces during daylight for both species, suggesting this avoidance response was not size-dependent. For *Physella*, retaining the ability to seek benthic refugia when exposed to novel predators likely greatly contributes to its invasion success. Given both snails are dominant primary consumers in many freshwater ecosystems, surface-density increases resulting from predation pressure decreases would predictably significantly affect system trophic dynamics.

Key words: bully predation – *Physella acuta* – *Potamopyrgus antipodarum* – sediment surface and subsurface use – shell length – sediment size

Introduction

Novel or highly effective antipredator traits can facilitate successful invasions by prey species. Traits that allow benthic macroinvertebrate invaders to effectively deter or avoid native predators, and hence to become successful, include armouring (spines) (Zaranko *et al.* 1997; Levri *et al.* 2007), inedibility (Strayer 2009), activity reductions (Pennuto & Keppler 2008), and movement to spatial refugia (Dalesman *et al.* 2007). Identifying and assessing the relative effectiveness of antipredator traits of native and non-native prey is important to predicting the potential rate and geographical extent of invader spread and impacts on native species numbers and assemblages (Levine *et al.* 2003; Temperton *et al.* 2004).

This study compares predator avoidance behaviours by a native and non-native snail. *Potamopyrgus antipodarum* (Gray 1843) is native to New Zealand streams and lakes, where it commonly co-exists with the highly successful, worldwide invader *Physella* (*Physa*) *acuta* (Draparanaud 1805) (McCarter 1986; Cope & Winterbourn 2004; Kristensen & Closs 2008), apparently introduced from the Mediterranean region of Europe or North America ca. 40 years ago (Winterbourn 1973). *Potamopyrgus* is now also found in southeastern Australia (Schreiber *et al.* 1998; 2003), Japan (Shimada & Urabe 2003), Europe (Statzner 1981), the Laurentian Great Lakes (Zaranko *et al.* 1997), and the western United States (Dybdahl & Kane 2005). So, both snails also widely co-occur as non-native species. When at high densities or biomass, grazing by both snails can significantly reduce algal biomass and richness, alter algal physiognomy and composition, and

hence displace other macroinvertebrates and fish (Lowe & Hunter 1988; Winterbourn & Fegley 1989; Biggs & Lowe 1994). In New Zealand, their populations seldom reach high densities, in part because of predation by native and non-native fishes (Levri 1998; Holomuzki & Biggs 2006; Holomuzki 2010).

Predation risk might be a key driver of microspatial patterns of both snails. *Potamopyrgus* generally resides on a broad range of sediment sizes (Jowett *et al.* 1991), but in streams, is most dense on cobbles in slow current speeds (≤ 15 cm/s) (Holomuzki & Biggs 2007). Regardless of sediment size, in streams with predatory fish, ~80% of all *Potamopyrgus* occur in sediment subsurfaces with limited predator access (Holomuzki *et al.* 2009). Moreover, *Potamopyrgus* will move to protective sediment subsurfaces when in the presence of molluscivorous bullies (*Gobiomorphus* spp.), a widespread native fish in New Zealand streams and lakes (Holomuzki & Biggs 2006). Similarly, *Physella acuta* will move under cover when in the physical or chemical presence of pumpkinseed sunfish (*Lepomis gibbosus*) (Turner 1996; Turner & Montgomery 2003) and creek chub (*Semotilus atromaculatus*) (Turner *et al.* 2000), important molluscivores in eastern North America (Brönmark *et al.* 1992). However, for invasive populations in New Zealand, it is unclear whether *Physella* has retained this response, and how this response, if retained, compares to predator-induced microspatial shifts by *Potamopyrgus* that has coevolved with native predators.

The magnitude of any avoidance response might also depend on predation risk and prey vulnerability. Bullies eat both *Physella* and *Potamopyrgus* (Sagar

& Glova 1995; Wilhelm *et al.* 2007), but it is unknown whether consumptive risk from bullies differs between these snails. Non-native, young brown trout (*Salmo trutta*) in New Zealand streams apparently eat similar numbers of *Potamopyrgus* and *Physella* (Holomuzki 2010), even though *Physella* is larger-bodied (~7 mm average length), softer-shelled, and energetically more profitable than *Potamopyrgus* (4–6 mm average length) (McCarter 1986). Moreover, in North America, *Physa integra* (= *P. acuta*, Dillon *et al.* 2002) are smaller at sites with fish than without fish (Bernot & Whittinghill 2003), but it is unclear if snails are smaller because of size-selective predation or because larger snails exhibit stronger avoidance behaviours that reduce predation risk than smaller ones. For *Potamopyrgus*, small, non-parasitized individuals (<3.8 mm length) are more active than large individuals on tops of rocks during daylight (Levri & Lively 1996), suggesting predation risk might vary with body size.

Here, we present results from field collections, gut-evacuation observations, and a laboratory experiment to examine 1) how densities of each snail vary with sediment size, 2) how patterns of sediment subsurface use differ between *Physella* and *Potamopyrgus* and between sizes of conspecifics when with predatory fish, and 3) whether these snails are equally important prey items for common bullies (*Gobiomorphus cotidianus* McDowall). Microdistributional patterns of *P. acuta* in streams are unknown, but clearly important to understanding trophic relationships. We also relate egg mass distributions to sediment sizes for *Physella*, but not for ovoviviparous *Potamopyrgus*, because egg-laying habitat preferences might affect sediment use patterns and snail size distributions.

Methods

Snail and sediment field sampling

Snails were sampled in the East Branch of the Kaiapoi River (a.k.a. Silverstream; lat 43.25°S, long 172.35°E) 26 km north of Christchurch on 1 and 2 February 2011. Snails were collected in a ~25-m-long, ~11-m-wide reach (current velocity: 5–16 cm/s; water depths: 12–31 cm) containing mainly coarse gravel to small cobbles armouring sand. Macrophytes, mostly watercress (*Nasturtium officinale*), were present only along shorelines. The predominant fishes in this 2nd-order reach were common bullies, short-finned eels (*Anguilla australis*), and brown trout (Holomuzki & Biggs, 2006). Indigenous *Paranephrops zealandicus* crayfish were absent (JRH, pers. obs.).

The reach was mapped to create a grid system for sampling snails and sediments. The grid contained 2 rows, each 1-m wide and 5 m-long near mid-channel, and spaced 1-m apart. Each row was divided into twenty 0.5 x 0.5 m plots. Plots were used to collect snails and sediments, and the 1-m wide space between the rows in the middle of the reach served as a walkway to minimize disturbance in sample plots. Twenty one of the 40 plots within the grid were randomly selected for sampling with a cylindrical stovepipe core sampler (40 cm height, 25.4 cm diameter). The sampler was pushed ~5 to 15 cm into sediments and all snails and sediments within the sampler were collected. However, collection procedure varied with water depth at plots. In depths <25 cm, all epibenthic snails in the sampler were removed by suctioning, then sedi-

ments were removed with a dip net (0.5 x 0.5-mm mesh) to a depth of ~5 to 15 cm. In depths from ~25 to 31 cm, epibenthic snails were collected by removing the sampler and suctioning snails within the border ring outlined in the sediments. A view box was sometimes used to detect epibenthic snails within the border. After suctioning, the sampler was repositioned on the border ring, and sediments were removed as described earlier. Sediments were gently placed in a white plastic tray (50-cm diameter), and endobenthic snails were hand-picked from sediments. Epi- and endobenthic snails from each sample were placed in separate 100-mL plastic jars and preserved in 80% ethanol. In addition, *Physella* egg masses attached to stones were counted in each sample. The predominant sediment type (sand, gravel [4–32 mm, a-axis], or pebble to small cobbles [32–128 mm]; Wentworth scale) in each sample was determined visually, and only one sample was taken per plot. Counts and identifications of snails were made with a dissecting microscope in the laboratory, and shell lengths (mm, outer lip of aperture to apex) were measured with an ocular micrometer.

Snail consumption by bullies

Twenty common bullies were electrofished on 2 February (1400–1500 h) from the East Branch of the Kaiapoi in a ~15-m long stretch ~25 m downstream of the snail collection site. Immediately after capture, fish were placed in white plastic tubs (17.0 x 17.0 x 8.5 cm high). Tubs were filled with 1.5 l of water from the East Branch, maintained at 18°C (± 1°C), and contained one fish. Water in tubs was not aerated but was changed after ~20 h to maintain oxygen levels (8.0 mg/l). Tubs were aligned in 2 rows of

10 in the laboratory between north- and west-facing windows to expose fish to a natural photoperiod (14–15 h daylight). Metal screens (2 x 2-mm mesh) atop tubs retained fish. Tubs were substrate-free to facilitate recovery of egested snails, and fish were not fed while in tubs. Snails egested by each fish were siphoned ~19 h and ~42 h after fish were placed in tubs. Snails retrieved from each time period were identified, counted, and measured (shell length). All fish were released at their site of collection after the last siphoning.

Laboratory experiment

Bullies were captured by electrofishing on 11 February 2011 from the same reach electrofished on 2 February. Immediately after capture, fish were individually placed in 17.0 x 17.0 x 8.5 cm high plastic tubs each filled with 1.5 l of high-quality aquifer water (19° ± 1°C; O_2: ~8.0 mg/l). Fish were kept indoors and starved for 27 h before moving them to experimental tubs.

On 12 February, 20 white plastic tubs (size as above) were each filled with a ~3–4-cm thick layer (~1500 g) of pebble and small cobbles (Wentworth scale; particle size, a-axis: 50.2 ± 0.2 mm [mean ± SE], 33–84 mm [range], n = 40) collected from riparian areas of the East Branch. Sediments were thoroughly washed to remove periphytic algae. High-quality aquifer water (1 l) was added to each tub, so fishless treatments also were devoid of fish chemical cues. Tubs with sediments were placed in a 2 x 10 array between north- and west-facing windows to expose organisms to a natural photoperiod. One bully (mean ± SE: 4.62 ± 0.6 cm total length) captured the day before was placed in each of 10 randomly selected

tubs 24 h before adding snails (n = 10 replicates both for fish and fishless treatments). Black plastic screens (7 x 7-mm mesh) placed atop tubs, even fishless ones, retained bullies.

On 13 February, ten similarly snails of each species (*Physella*: 2.9–7.0 mm shell length [range]; *Potamopyrgus*: 3.0–6.1 mm, all smooth-shelled [body whorls not ridged and devoid of spines; Haase 2003]) collected from the East Branch were added to each tub between 1000 and 1330 h. These densities (~350 snails m^{-2}) are representative of field densities for *Potamopyrgus*, but are high for *Physella* (Holomuzki & Biggs 2006; Holomuzki 2010). We chose to use equal densities and similar sizes of snails to equalize consumptive risk. Twenty four hours after additions, screens were removed, and all snails visible on surface sediments and tub walls, and floating, were suctioned from tubs. Although these snails were collectively considered as epibenthic, we separately noted the number and species of those floating to assess species-specific differences in this possible predator-induced dispersal mechanism (Crowl & Covich 1990). After these removals, sediments from each tub were thoroughly hand-sorted to retrieve all snails from subsurface sediments. Snails of each species recovered from surface and subsurface sediments were counted, preserved in 80% ethanol, and measured (shell length). We calculated proportions of snails in subsurface sediments by dividing numbers found in subsurface sediments by the total number retrieved to account for fish consumption. All fish were released in the East Branch at the end of the experiment.

Statistical analyses

For field collections, a one-way analysis of variance (ANOVA) was used to determine whether overall channel densities (log[x + 1]-transformed) differed between snails (SYSTAT v9.0). Two-way ANOVAs were used to test whether *Physella* and *Potamopyrgus* densities (log[x + 1]-transformed) and sizes (shell length; log(x)-transformed) differed among sediment types and between sediment surfaces and subsurfaces. Mean surface and subsurface sizes of snails in each sample were used in the ANOVA. Significant sediment-density or -size effects were followed by Bonferroni pairwise comparisons (*alpha* = 0.05).

In the laboratory experiment, a 2-way ANOVA was used to test whether bully presence differentially affected subsurface use (arcsine[x]-transformed proportions) by each snail species. Separate two-way ANOVAs were also used to determine whether bully presence affected mean snail size (log[x]-transformed shell lengths) on cobble surfaces and subsurfaces for each snail. A G-test of independence with Williams's correction tested whether the number of floating snails in different predator environments (fish, no fish) was independent of snail species (Sokal & Rohlf 1995).

Results

Instream sediment use

Potamopyrgus was significantly denser than *Physella* in stream-channel sediments (mean ± SE, *Potamopyrgus*: 395 ± 54 nos. m^{-2}; *Physella*: 29 ± 7 nos. m^{-2}) (1-way ANOVA: $F_{1,36}$ = 55.218, $P < 0.001$).

Densities varied across sediment types for *Physella* (2-way ANOVA: $F_{2,\,36}$ = 5.360, P = 0.009), but not for *Potamopyrgus* ($F_{2,36}$ = 0.763, P = 0.474) (Figure 1A, 1B). *Physella* was denser on cobbles than on sand (Bonferroni comparison: P = 0.010), but not between sand and gravel (P = 0.326) and cobbles and gravel (P = 0.296). Coincidently, 22 of 24 *Physella* egg masses were found on cobbles; the other two in gravel.

Densities of both snails were greater on sediment subsurfaces than on surfaces (2-way ANOVAs, *Physella*: $F_{1,36}$ = 3.795, P = 0.054; *Potamopyrgus*: $F_{1,36}$ = 4.261, P = 0.045) (Figure 1A, 1B). However, subsurface densities of both species were independent of sediment type, based on non-significant interaction terms (both P > 0.15). No *Physella* were found on sand surfaces (Figure 1A).

Physella shell length differed among sediment types ($F_{2,13}$= 4.868, P = 0.026), with snails being larger on cobbles than on gravel (Bonferroni comparison, P = 0.049; Figure 2A). In contrast, *Potamopyrgus* shell length did not differ among sediment types ($F_{2,33}$ = 0.715, P = 0.496) (Figure 2B). For both species, shell lengths were similar between individuals on sediment subsurfaces and surfaces (*Physella*: $F_{1,13}$ = 0.341, P = 0.569; *Potamopyrgus*: $F_{1,33}$ = 3.661, P = 0.064).

Snail consumption by bullies

A total of 7 snails, 6 *Physella* (mean ± SE; shell length: 2.1 ± 0.3 mm) and 1 *Potamopyrgus* (1.5 mm), were eaten by 5 of 20 bullies. Four fish egested a total of 5 snails after ~19 h in tubs, while one fish egested 2 *Physella* after ~42 h. All egested snails were dead. The most commonly

egested prey item was amphipods.

Laboratory experiment

Both *Physella* and *Potamopyrgus* responded to bully presence by increasing their use of cobble subsurfaces (2-way ANOVA, fish effect: $F_{1,36}$ = 12.357, P < 0.001) (Figure 3). However, this response did not differ between species (snail effect: $F_{1,36}$ = 2.000, P = 0.166). Although very few snails were found floating in tubs (*Physella*: 0, 3; *Potamopyrgus*: 6, 3; with and without fish, respectively), the behaviour was species-dependent (G = 5.182, df = 1, P < 0.025).

No difference in *Physella* shell length was detected between surface and subsurface sediments in tubs with (grand means ± 1SE; surface vs. subsurface: 4.92 ± 0.26 vs. 4.58 ± 0.11 mm) and without fish (4.55 ± 0.2 vs. 4.62 ± 0.2 mm) (surface effect: $F_{1,35}$ = 0.496, P = 0.486; fish effect: $F_{1,35}$ = 0.739, P = 0.396). Likewise, *Potamopyrgus* size did not differ between surface and subsurface sediments in fish (surface vs. subsurface: 4.03 ± 0.16 vs. 4.08 ± 0.11 mm) and fishless tubs (4.31 ± 0.1 vs. 4.20 ± 0.11 mm) (surface effect: $F_{1,36}$ = 0.082, P = 0.776; fish effect: $F_{1,36}$ = 2.556, P = 0.119).

All snails were recovered from fish and fishless tubs, except for one *Physella* in a fish treatment.

Discussion

Our results suggest that invasive *Physella* has retained the ability to seek benthic cover when exposed to a native New Zealand predator in a novel environment. Moreover, the strength of the response is similar to that of native *Potamopyrgus*, based on densities and proportions of sediment subsurface use by both snails
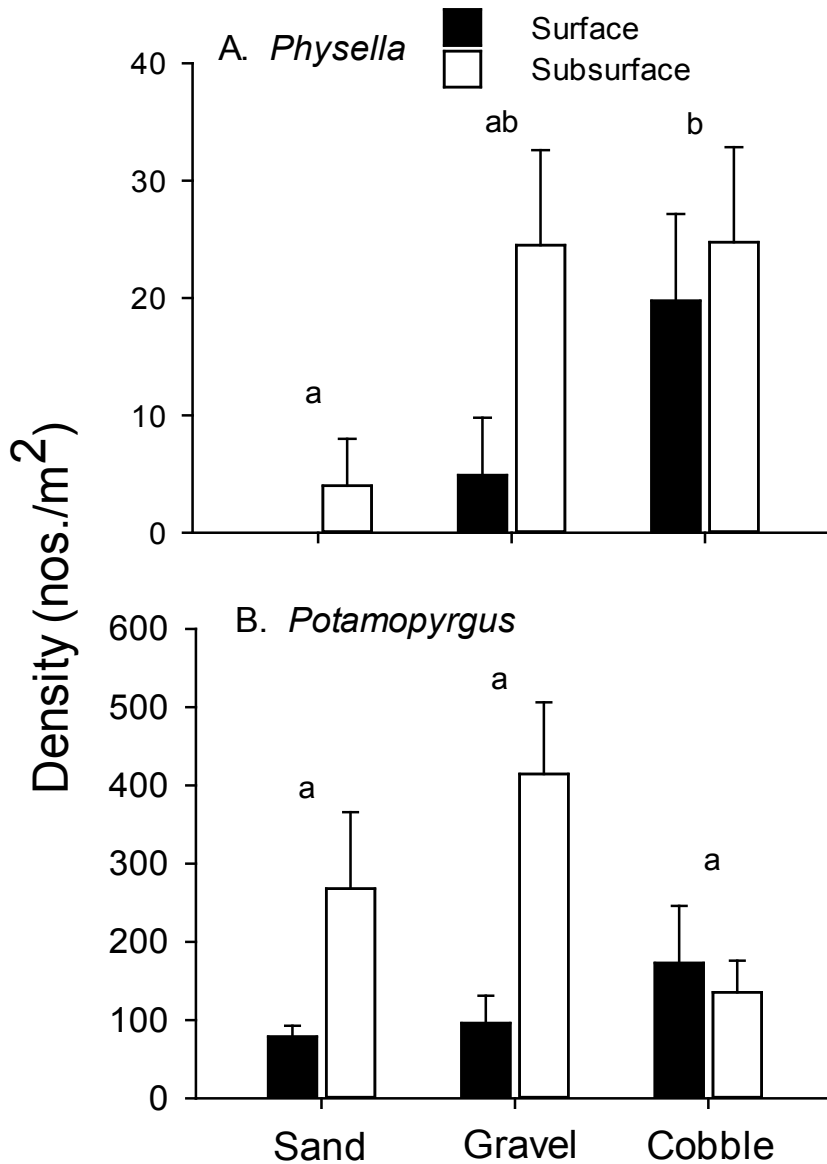
Figure 1. Mean (+1 SE) densities of *Physella acuta* (A) and *Potamopyrgus antipodarum* (B) on surfaces and subsurfaces in sediment types in the East Branch of the Kaiapoi River (n = 5, 8, and 8 samples from sand, gravel, and cobbles, respectively). Different lowercase letters represent significant differences in densities between sediment types (Bonferroni comparisons, *alpha* = 0.05). Densities of both snails were greater on sediment subsurfaces than on surfaces (both $P \leq 0.054$).
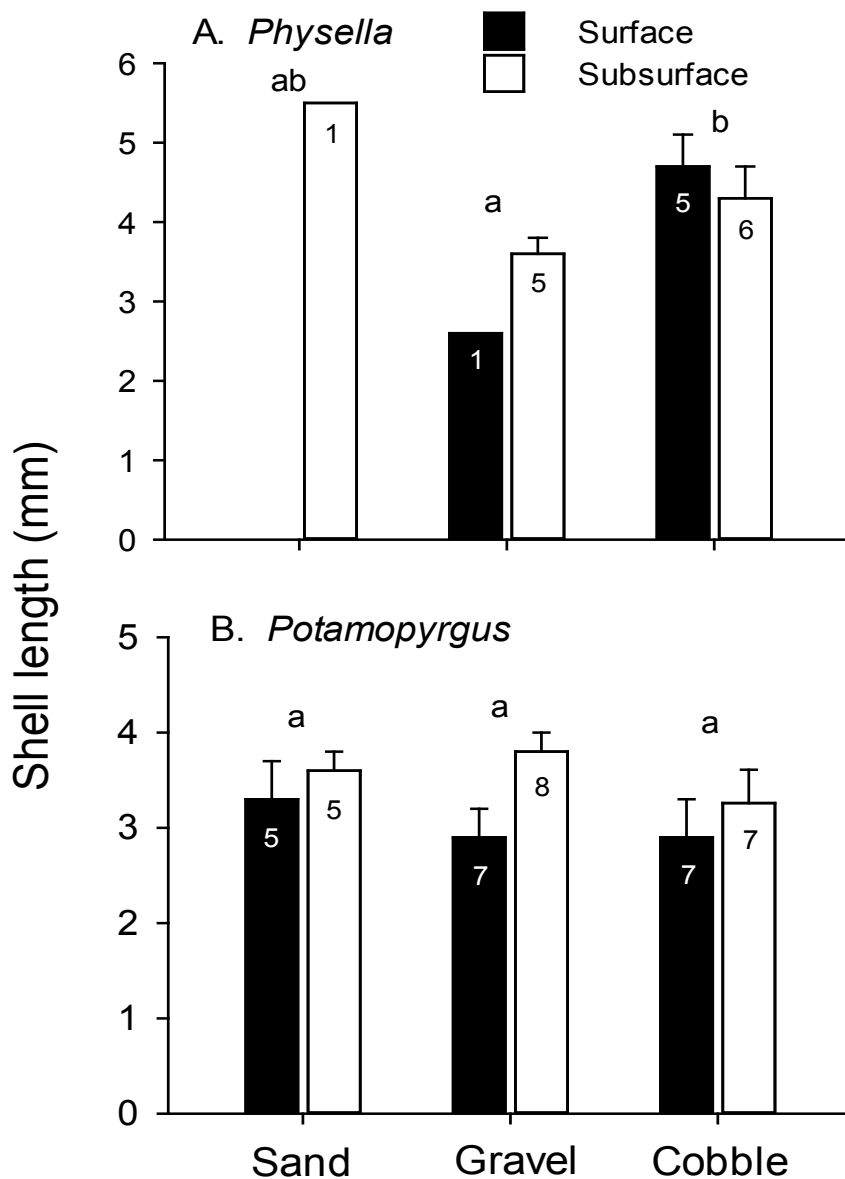
Figure 2. Mean (+1 SE) shell lengths of *Physella acuta* (A) and *Potamopyrgus antipodarum* (B) on surfaces and subsurfaces in sediment types in the East Branch. Numbers in bars indicate the number of surface and subsurface samples in which the species was collected (total number of snails measured: n = 32 and 420 for *Physella* and *Potamopyrgus*, respectively). Different lowercase letters represent significant differences in shell length between sediment types (Bonferroni comparisons, *alpha* = 0.05). Shell lengths of both snails were similar between sediment surfaces and subsurfaces (both $P \geq 0.064$).

in field collections and the laboratory experiment, respectively. This result is somewhat surprising, given our gut-egestion observations hint *Physella* might be preferred by *Gobiomorphus*, size selective feeders on benthic macroinvertebrates (Gregory *et al.* 2007). However, this result might be expected if the risk of predation is similarly perceived by both snails (Levri 1998) and if subsurface use is a generalised, non-discriminatory response to fish predators, regardless of the risk they pose. Yet, movement behaviours by *Physella* suggest they can identify some enemy types, perhaps by processing different chemical and physical cues (Turner *et al.* 1999). In contrast to their reactions to fish, *Physella* will crawl to or above the waterline to temporarily avoid crayfish (Alexander

& Covich 1991 [*Procambarus simulans*]; DeWitt *et al.* 1999 [*Orconectes rusticus*]; McCarthy & Fisher 2000 [*P. clarki*]; Bernot & Turner 2001 [*O. rusticus*]), and this response is stronger when crayfish are actively foraging or sifting through substratum interstices (McCarthy & Fisher 2000). We did not differentially score snails at the waterline on tub walls in our fish and fishless treatments, so we cannot say whether *Physella* is more likely than *Potamopyrgus* to exhibit this response in the presence of bullies. However, we did count floating snails, and albeit counts were low, *Potamopyrgus* appears more prone than *Physella* to float to escape risky habitats. This behaviour might also depend on the strength of injured-conspecific cues (McCarthy & Fisher 2000), which were negligible in
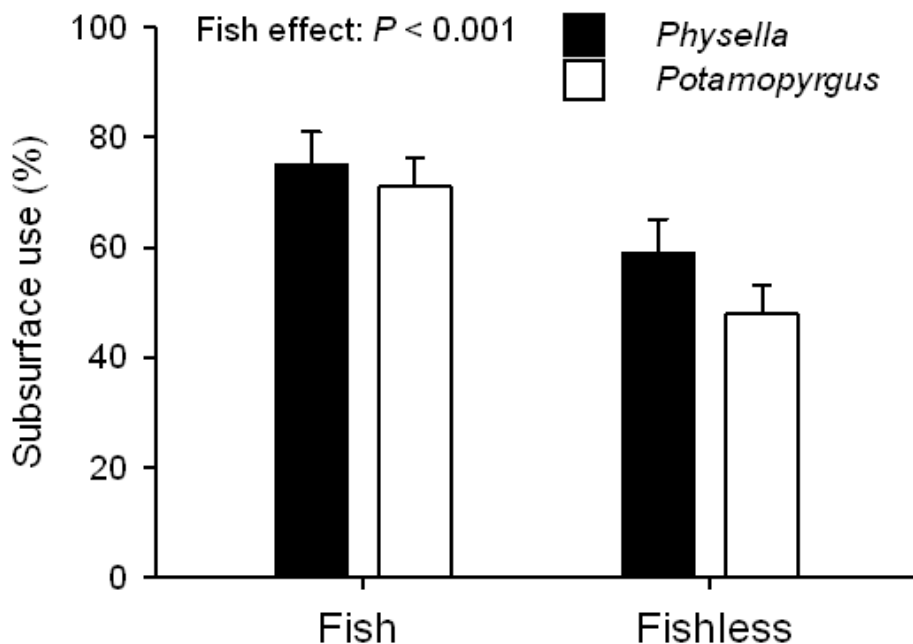

Figure 3. Mean (+1 SE) subsurface sediment use by *Physella* and *Potamopyrgus* in fish and fish treatments in the laboratory experiment (n = 10 replicates/treatment). *P*-value represents ANOVA results for a fish effect on subsurface use.

our experiment, and might, like other antipredator behaviours, be amplified in small-mesocosm experiments with standing water (Peckarsky *et al.* 2002). In addition, both *Physella* and *Potamopyrgus* are significantly more abundant on structurally-complex macrophytes than on diatom-coated stones on the bottoms of lakes and streams (Kelly & Hawes 2005; Holomuzki 2010), but it is unclear whether plant beds are actively sought to avoid predators. Thus, the use of less risky habitats regardless of predator identity appears to be a key general defence for both snails that likely contributes to their widespread invasion success.

Although spatial responses were similar, temporal relationships between movement and predator presence or kind could vary between snails. Our study design did not allow us to assess or compare the rapidity of the response by each species, nor the length of time individuals remain in subsurface sediments after exposure to fish, both of which could affect consumption risk. *Potamopyrgus* can remain on rock undersides for >20 h when exposed only to the chemical cues of bullies in laboratory tanks (Levri 1998), and for ~8 h (overnight) when coexisting with nocturnal predatory fish in natural streams (Holomuzki *et al.* 2009). Similarly, *Physella* can remain in spatial refugia (i.e., under ceramic tile, at or above the waterline) for at least 12 h to avoid fish (Bernot & Whittinghill 2003). However, unlike *Potamopyrgus*, use of benthic cover by *Physella* does not apparently differ between day and night, at least when exposed to diurnally-feeding creek chub (Bernot & Whittinghill 2003). Whether *Physella* responds to bullies faster than *Potamopyrgus*, or remains in protective sediment subsurfaces longer than *Potamopyrgus*, is unknown. However, it does

appear that movements to endobenthic surfaces by both species are independent of sediment size.

Field samples show that *Physella* shell lengths differed among sediment sizes. *Physella* were larger on cobbles, where most egg masses were detected, than on gravel. Larger, egg-bearing snails might prefer larger, more stable sediments to attach egg masses. In addition, cobbles provide a larger surface area for periphyton growth, and hence a larger surface for foraging, than gravel (Brown 1982). We did not detect a relationship between *Potamopyrgus* shell length and sediment size, nor a statistically significant size difference ($P = 0.064$) between individuals on sediment subsurfaces and sediment surfaces during sample times (~0900–1700 h). Moreover, we did not detect a body-size difference in space use in the laboratory experiment, where the size range of snails used for each species (none < 2.9 mm shell length) was narrower than that in Silverstream, which likely hindered the probability of detecting a difference. Levri & Lively (1996) reported that small, trematode (*Microphallus*)-free *Potamopyrgus* were more active than large individuals on tops of littoral rocks in Lake Alexandrina, South Island, during daylight (~1530 h). Although we did not assess parasitism, epibenthic snails in our study were probably also largely *Microphallus*-free, given frequency of trematode infection of the Silverstream population is very low (Holomuzki *et al.* 2009). Size differences between *Potamopyrgus* on sediment surfaces and subsurfaces in Silverstream might be more prominent at night when relatively few snails are active on rock surfaces, apparently to reduce encounters with nocturnally hunting bullies and shortfinned eels (*Anguilla australis*)

(Holomuzki *et al.* 2009). Even so, it is unclear whether trade-offs between foraging return and predator avoidance are associated with endobenthic activity. *Potamopyrgus* and *Physella* are herbivore-detritivores (Dillon 2000; Cope & Winterbourn 2004), capable of consuming diatom-dominated biofilms on stone surfaces (Talbot & Ward 1987; Suren 2005) or heterotrophic biofilms in sediment subsurfaces (Rounick & Winterbourn 1983). So, energetic costs associated with endobenthic activity are likely minimal. In addition, hydrodynamic forces (drag) are typically much stronger near tops of rocks than in sediment subsurface voids (Dole-Olivier *et al.* 1997; Holomuzki & Biggs 2000). Thus, snails residing in sediment subsurfaces apparently gain protection from predators, access to a viable food source, and relief from drag forces.

Comparative studies like the one described here are necessary to determine whether invasive species success depends on different mechanisms in different communities. It appears that both *Physella* and *Potamopyrgus* have the ability to move from areas of high predation risk to low predation risk in a variety of predator regimes, and that this ability is not amplified by invasive *Physella*. From an applied perspective, this means that surface-density increases of these dominant primary consumers, resulting from natural or anthropogenic perturbations that reduce predator abundance, could indirectly affect periphyton biomass and composition, the cycling of nutrients, and food availability for higher trophic level consumers (Lowe & Hunter 1988; Winterbourn & Fegley 1989; Biggs & Lowe 1994). This potential effect on trophic and benthic processes might be modified by bed-sediment composition, particularly for *Physella* which seems uncommon in sand-dominated habitats. These scenarios define perspectives for future multipopulational studies that investigate anti-predator phenotypic reactions by these snails across various predator regimes and habitat types.

Acknowledgements

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