

Phenotypically similar but ecologically distinct: differences in competitive ability and predation risk among amphipods

Rickey D. Cothran, Kate A. Henderson, David Schmidberg and Rick A. Relyea

R. D. Cothran (rdc28@pitt.edu), K. A. Henderson, D. Schmidberg and R. A. Relyea, Dept of Biological Sciences and Pymatuning Laboratory of Ecology, Univ. of Pittsburgh, 4249 Fifth Ave. Pittsburgh, PA 15260, USA.

Nature is often more diverse than expected with multiple species appearing to occupy the same niche. This observation is especially perplexing when the co-occurring species are cryptic (i.e. only distinguishable via molecular markers), because phenotypic similarity is expected to correspond with strong niche overlap. One way that phenotypically similar species can coexist is if fine-scale phenotypic differences affect how species interact with other members of the community that ultimately results in performance tradeoffs. An alternative explanation for co-occurrence is that phenotypic similarity leads to ecological equivalence allowing species to co-occur for long periods. We tested whether three phenotypically similar amphipod species that co-occur exhibit performance tradeoffs that may allow them to stably coexist in lakes. We found that despite their similarity the three species differed in how well they performed in competition with each other and their ability to avoid predation by fish and invertebrate predators. In some species comparisons, performance tradeoffs were apparent with species that perform well against heterospecifics performing poorly against predators and vice versa. We also found evidence for direct antagonistic interactions among amphipod species, in the form of wounding, which may play a role in structuring amphipod assemblages. Finally, the two species with the most similar phenotypes showed comparable responses to competitors and predators, which suggests that long-term co-occurrence via ecological equivalence may also be important in this system. Collectively, our results suggest that a mix of performance tradeoffs and ecological equivalence may allow for higher diversity than expected in amphipod assemblages.

A common observation in nature is the presence of several species in a community that appear to be occupying the same niche. This pattern should not happen because the best performing species (e.g. the best competitor or predator avoider) should eventually drive inferior species to local extinction (Gause 1932, Holt et al. 1994). Solutions to this problem have centered on two mechanisms that can operate simultaneously in communities (Chesson 2000, Leibold and McPeck 2006, Adler et al. 2007). One solution is that performance tradeoffs along important ecological axes allow species to stably coexist. Such tradeoffs are the result of selection on traits to improve performance of one ecological task having a negative effect on the performance of other ecological tasks (Kneitel and Chase 2004). For example, traits that make an individual a good resource competitor (e.g. large body size and high activity) may increase an individual's predation risk (Wellborn et al. 1996). Ultimately, such tradeoffs must lead to high relative fitness when rare but low relative fitness when common (i.e. density dependence) to provide stability to the community (referred to as stabilizing mechanisms, Chesson 2000).

A second solution is that species may co-occur for long periods in a community if they are phenotypically similar

and thus perform equally well in ecological interactions (also known as equalizing mechanisms, Chesson 2000, Hubbell 2006). While equalizing mechanisms can delay the loss of species for a long time, stable coexistence is not possible without stabilizing mechanisms (Chesson 2000). Moreover, as fitness differences between species become greater (i.e. equalizing mechanisms decrease in importance), stronger niche differentiation (i.e. stabilizing mechanisms) is necessary to maintain species diversity (Chesson 2000, Adler et al. 2007). Such niche differentiation may involve a variety of ecological interactions (e.g. resource use, predator avoidance, and habitat use) with performance tradeoffs between different ecological interactions facilitating coexistence (Chesson 2000, Leibold and McPeck 2006).

Given that morphologically similar species are expected to be ecologically similar with little niche differentiation, ecologists are left with the challenge of explaining the co-occurrence of cryptic species, which are so morphologically similar that molecular markers are needed to differentiate them (Fargione et al. 2003). Such species are common in nature and often co-occur at local scales (Gomez et al. 2002, Hebert et al. 2004, Witt et al. 2006). Whereas cryptic species might co-occur due to ecological equivalence but not stably coexist, there might also be fine-scale

phenotypic differences that lead to fine-scale niche differences allowing stable coexistence (Siepielski and McPeck 2010). Cryptic species may also coexist if they show density-dependent investment in diapause that allows rare species to rebound once environments change in their favor (i.e. the storage effect; Chesson and Warner 1981, Cáceres 1997) or through density-dependent sex ratio adjustment (i.e. rare species increase the relative number of females produced which has a positive effect on population growth; Zhang et al. 2004).

We explored the relative competitive ability and susceptibility to predation for three cryptic amphipod species in the genus *Hyaletta* that co-occur in natural lakes. It is not known whether these species stably coexist at local scales. We chose to focus on competitive ability and predator avoidance because these interactions play an important role in structuring aquatic communities, appear to be responsible for many of the trait differences observed among non-cryptic *Hyaletta* amphipods, and traits involved in these interactions may tradeoff in ways that allow species to coexist on local scales (Leibold 1997, Wellborn 1994a, Wellborn et al. 1996). Moreover, a lake survey showed that the three cryptic species used in the current study differ in their relative abundance in fish diets (Wellborn and Cothran 2007a). Theory predicts stable coexistence, where two species compete for a single resource and are prey for a single predator, at intermediate levels of resource availability and predation. Further, with the addition of environmental heterogeneity in productivity, more than two species can stably coexist (Leibold 1997). Because these amphipods do not have a dormant stage and sex ratios are typically female biased (80% to 60% female; Wellborn and Cothran 2007b), density-dependent dormancy and sex ratio adjustment are unlikely in this system.

We tested the ability of each species to compete against heterospecifics under high and low resource supply. To do this, we compared the abundance of each species with and without heterospecific competition. Further, we measured traits in individuals (female fecundity, a male sexual trait, and wounds) that may be sensitive to competition and resource availability. We also compared the susceptibility of the three species to predation by both bluegill sunfish and larval dragonflies. These two predators heavily prey on *Hyaletta* amphipods and have different foraging preferences for some prey traits (Wellborn 1994a, Stoks and McPeck 2006, Mikolajewski et al. 2010). Specifically, predatory fish often consume larger, more active prey whereas many predatory invertebrates are more likely to consume smaller, less active prey. Further, larger more active individuals are generally better resource competitors, which can result in tradeoffs between competitive ability and predator avoidance (Vanni 1986, Werner 1994). We predicted that fine-scale phenotypic (e.g. body size and activity) differences would affect how the three cryptic species interacted with competitors and predators. Moreover, we predicted tradeoffs in competitive ability and susceptibility to predators that may promote species coexistence (Leibold 1996, Adler et al. 2007).

Methods

Study system

Amphipods in the genus *Hyaletta* inhabit a wide range of permanent, freshwater habitats ranging from small springs to large lakes and reservoirs. Amphipods are often very abundant with densities ranging from hundreds to thousands of individuals m^{-2} (Wellborn 1994a). *Hyaletta* are typically considered grazers and detritivores and are an important prey of many invertebrate and vertebrate predators (Wellborn 1994a). In North America, the genus was thought to consist of a single species, *Hyaletta azteca*. Recently, however, molecular work and interbreeding studies have established that *Hyaletta azteca* is actually a species complex composed of more than 30 undescribed species (Witt and Hebert 2000, Witt et al. 2006, Wellborn and Broughton 2008). Within the group, two life history strategies are common and each strategy is represented by multiple species. In habitats with positive size-selective fish, amphipods are small, relatively inactive, and invest heavily in each reproductive event (hereafter 'small ecomorph'). In habitats without fish or where fish predation is weak and predatory invertebrates are major predators, amphipods are large, relatively active, and invest less in each reproductive event (hereafter 'large ecomorph'; Strong 1972, Wellborn 1994a).

Up to three small ecomorph species can co-occur in the littoral zone of lakes. Originally, these species were thought to be indistinguishable using morphology (i.e. cryptic species). However, we have discovered that they differ in subtle color patterns that are a perfect match to molecular markers that had been used to distinguish the three species (Wellborn and Cothran 2004, Cothran et al. unpubl.). A survey of two lakes in Michigan, USA found that the relative abundance of the three species changes along a distance from shore and depth gradient and that the species differ in their susceptibility to predation by positive, size-selective bluegill sunfish, *Lepomis macrochirus* (Wellborn and Cothran 2007a). Because these species have not been assigned scientific names, they are referred to as species A, B and C to be consistent with the previous literature on this group (Wellborn and Cothran 2004, 2007a). Species B is common near shore where invertebrate predators are abundant whereas species A and species C are more common in deeper water where predatory fish are more abundant. Within the deep-water habitat, species A is more abundant near the surface and species C is more abundant lower in the water column. These species also differ slightly in mean body size (although there is a large degree of overlap in size) that might affect their relative competitive ability and susceptibility to predation (Wellborn and Cothran 2004). Adults of species B are on average 16% and 12% larger than adults of species A and species C, respectively.

Collection of animals and husbandry

Amphipods were collected from Lake Le Boeuf (Erie County, PA, USA) and were housed outside in 90-l pools containing

well water and vegetation from the lake. Dragonflies *Erythemis simplicicollis* were collected from Geneva Pond (Crawford County, PA, USA), housed individually in 250-ml cups, and fed *Hyalella* daily. Bluegill sunfish *Lepomis macrochirus* were collected from Hartstown Marsh Pond (Crawford County, PA, USA), and housed in 1500-l cattle tanks in groups of ~10. Cattle tanks were stocked with vegetation and invertebrates (including amphipods) to provide structure and forage for fish. All experiments were conducted at the Pymatuning Laboratory of Ecology (Crawford County, PA, USA).

Competition experiment

We used a randomized factorial design with all combinations of the three species (three monocultures, three bicultures and one triculture) crossed with two resource levels (high and low). The 14 treatments were replicated 10 times for a total of 140 experimental units. Experimental units were 14-l plastic tubs containing 7.5 l of well water. A sand substrate (425 g) was added to each tub. A 3-m section of butcher's twine and four 2 cm² unglazed porcelain tiles served as refugia for amphipods and surfaces for periphyton growth. Pond water, collected from a local pond, was filtered through a 397- μ m net and a 150-ml aliquot was added to each tub as a source of algae. Resource levels were manipulated by spiking tubs with phosphorus (in the form of KH₂PO₄) to achieve molar concentrations of 20 μ g l⁻¹ P (low resource) or 100 μ g l⁻¹ P (high resource). Nitrogen was added in the form of NaNO₃ to achieve an N:P ratio of 16. The tubs were placed outdoors in 90-l wading pools filled with well water to buffer against rapid changes in temperature and covered with a 60% shadecloth lid to avoid colonization by amphibians and insects. Tubers were checked regularly and well water was removed or added to maintain a consistent water level.

Amphipods were added to tubs 15 d after the addition of algae and nutrients. The design was additive with monoculture tubs stocked with 40 adult amphipods of the assigned species and bi- and triculture tubs stocked with a total of 80 and 120 adult amphipods (40 individuals per species), respectively. These stocking densities (466 to 1398 individuals m⁻²) are lower than those typically found in nature (8300 to 18000 individuals m⁻²; Wellborn 1994a). This allowed populations to increase at the two resource levels under interspecific competition. The experiment lasted 67 d, which was enough time for stocked females to produce ~six clutches and for offspring produced early in the experiment to reach maturity (time to maturity is ~21 d; Wellborn and Bartholf 2005). Thus, populations were large by the end of the experiment, which should have imposed intense resource competition on individuals. By using an additive design where animals were allowed to increase in abundance within experimental units, we achieved one, two and three species treatments that did not differ in total amphipod abundance at the end of the experiment (GLM comparing total amphipod abundance for one, two and three species treatments; $F_{2,137} = 1.729$, $p = 0.181$; one species [mean \pm 1SD] = 83 ± 55 , two species = 98 ± 71 , three species = 111 ± 63). However, differences in initial stocking densities likely means that carrying capacities were

reached sooner in three species treatments causing differences in the duration of competitive interactions. Overall, our design avoids the pitfalls of substitutive designs (confounding intra and interspecific competition), while minimizing the problems of changes in total amphipod density that is common to most additive designs (Snaydon 1991).

Effects of heterospecifics and resource levels on amphipod abundance

At the end of the experiment, the tubs were sampled to determine relative abundances of adults for each amphipod species. Refugia and tiles were removed and placed in a sorting tray. The water in the tub was then poured through a 500- μ m sieve into a bucket. This sieve was small enough to collect all adult amphipods but large enough to allow juvenile amphipods to pass through into the bucket. The contents of the sieve were rinsed into a sorting tray filled with well water and adults of each species were counted. When population sizes were large, we subsampled the population by running a fine-mesh aquarium net widthwise through the tray, transferring the contents to a separate tray, and counting adults present in the subsample. This subsample represented approximately 1/3 of the adult population. After recording the abundance of each species, the amphipods were preserved in 70% ethanol.

For each species, we used a three-way ANOVA to assess whether the presence of each competing species, resource levels and their interactions affected the abundance of the focal species.

Effects of heterospecifics and resource levels on female fecundity, male gnathopod size and wounds

We quantified several individual-based measures of performance that should reflect the effects of competition on individuals (Wellborn 2002). These data were collected to inform us about potential mechanisms that might be driving patterns in abundance across heterospecific and resource treatments. For five randomly selected replicates, we measured the head length of males and females, the fecundity of females, a sexually selected male trait, and the number of wounds exhibited by males and females. For both sexes we measured head length, which is an indicator of body size to use as a covariate in analyses (Edwards and Cowell 1992). We did not test for a direct effect on body size because these animals have indeterminate growth and multiple generations were present in tanks. Therefore, body size variation could be due to differences in age (which is unknown), growth rate or a combination of the two. To quantify fecundity, we recorded the number of embryos in the marsupium (ventral brood pouch) of each female. To quantify a sexually selected trait of males, we measured posterior gnathopods, a sexually selected trait that is very sensitive to resource availability (Cothran and Jeyasingh 2010). In doing so, we hoped to gain insights into how the presence of heterospecifics and low resources affected male performance. We also recorded the number of wounds on each amphipod. Wounds were visible as melanized plugs through the body wall (Plastow et al. 2003) and may be sustained during antagonistic interactions for resources.

We used generalized estimating equations to test for the effects of heterospecifics and resource levels on measures of

individual performance. These generalized linear models can account for correlated data (e.g. clustered data) and are flexible to both unbalanced designs and the form of the response variable (Hanley et al. 2003). In all models, tub was included as a within-subject variable to account for correlations between subjects within tubs. Body size (i.e. head length) was included as a covariate in all analyses except for when analyzing wounds in species C, because preliminary analyses showed no relationship between these two variables in this species (Wald $\chi^2 = 1.234$, $p = 0.267$, $DF = 1$). Sex was included as a fixed effect in the model testing for effects on wounds. Gnathopod size was fitted using a normal distribution with an identity link function. Embryo number and the number of wounds were fitted using a Poisson distribution with a log link function.

Predation experiments

We tested the relative susceptibility of the three amphipod species to predation by larval dragonflies and bluegill. We chose these two predators because they are both important predators of *Hyalella* amphipods, they show complementary patterns of how they are distributed in the littoral zone of lakes (i.e. fish are found in deeper water whereas dragonflies are more abundant in shallow water), and they shape amphipod life histories in different ways (Wellborn 1994a). Specifically, fish select for amphipods that start reproducing earlier and at a smaller size but that have a higher size-specific investment in reproduction compared to amphipods living with predatory dragonflies.

Dragonfly predation experiment

The dragonfly predation experiment was done in 1-l plastic containers (14 × 14 × 6 cm) with a sand substrate and four pieces (each 5 cm long) of the macrophyte *Elodea* sp., which served as refugia for amphipods. Fifteen amphipods of each species and a caged larval dragonfly (head width [mean ± 1 SD] = 4.55 ± 0.536) were added to the containers. After a 5-h acclimation period, the dragonfly was released and allowed to forage for up to 96 h. Each day we assessed how much predation had occurred and ended a trial whenever at least 50% of the prey had been consumed (mean % consumed ± 1 SD = 60% ± 9). This assured that enough predation had occurred to detect any species differences in vulnerability to predation. Trial duration ranged from 48 h to 96 h. We conducted 25 replicates of the experiment and included three no-predator trials to assess recovery of amphipods in the absence of predators.

For each experimental unit, we calculated preference for each species using the following index (Manly 1974, Wellborn 1994a):

$$\alpha_{spX} = \frac{\ln\left[\frac{(N_{spX} - C_{spX})}{N_{spX}}\right]}{\ln\left[\frac{(N_{spA} - C_{spA})}{N_{spA}}\right] + \ln\left[\frac{(N_{spB} - C_{spB})}{N_{spB}}\right] + \ln\left[\frac{(N_{spC} - C_{spC})}{N_{spC}}\right]}$$

where N_{spX} and C_{spX} are the initial number and the number consumed of the focal amphipod species, respectively. Values of $\alpha_{spX} > 0.33$ indicate a preference for the focal species whereas values of $\alpha_{spX} < 0.33$ indicate an aversion for the focal species. We used a one-sample t-test to assess

whether dragonflies showed a preference or an aversion toward each amphipod species ($\alpha_{spX} = 0.33$ was used as a reference value to test the null hypothesis of no preference or aversion). Because we used same data table to assess preference or aversion for each species, we used the sequential Bonferroni to correct alpha for multiple tests (Holm 1979).

Bluegill predation experiment

The bluegill predation experiment was designed differently than the dragonfly experiment because bluegill consume many amphipods in each foraging bout (Wellborn and Cothran 2007a) and medium to larger sized bluegill often do not forage in laboratory settings. As a result, we designed the bluegill predation experiment using large mesocosms and provided large numbers of prey for the fish to forage on while providing adequate structure to ensure the survival of some prey. The experiment was conducted in 750-l cattle tanks filled with 60 l of soil and approximately 500 l of well water. To provide refugia for the amphipods, we collected macrophytes (*Ceratophyllum demersum*) from a local lake, washed the plants, and planted each tank with a 20-l bucket of macrophytes on 25–27 June. On 5–6 July, we stocked each tank with 500 amphipods of each species. We added the bluegill on 21 July. We randomly assigned the fish treatment to eight tanks and the no-fish treatment to seven tanks. Fish size ranged from 100 to 145 mm standard length (mean ± 1 SD = 125 mm ± 15).

On 1 September, we sampled the tanks to quantify the abundance of each amphipod species. This allowed time for the amphipods to produce ~five clutches and for F_2 amphipods (grandoffspring of stocked animals) to reach maturity. To sample the amphipods, we thrust a 0.3-m diameter stovepipe into the sediment of the tanks. A fine aquarium net was used to net contents within the pipe into a 14-l plastic tub. We washed contents of the tub through a 2 mm sieve to remove macrophytes. We then used a 500- μ m sieve to collect the adults and recorded the abundance of each species. We used a MANOVA to test whether the presence of bluegills affected the abundance of each amphipod species. All statistics were performed with SPSS 20 for Mac (SPSS Inc.).

Results

Competition experiment

Effects of heterospecifics and resource levels on amphipod abundance

Our first analysis examined the effects of the two heterospecifics and resource levels on the abundance of each amphipod

species. For species A's abundance, there were no two-way or three-way interactions. Species A's abundance was decreased by 59% in the presence of species B and 26% by species C (marginally non-significant, $p = 0.07$). Species A's abundance was not affected by resource levels (Table 1, Fig. 1A).

Table 1. ANOVA results for the effects of heterospecifics and resource level on abundance of adult amphipods. *F* statistics, degrees of freedom (DF) and *p*-values are presented. Sp. 1 and Sp. 2 refer to the two heterospecific species in alphabetical order. For example, Sp. 1 = Sp. B and Sp. 2 = Sp. C for focal Sp. A.

Source	Focal species		
	Species A	Species B	Species C
Sp. 1			
F	29.66	2.478	1.791
DF	1,71	1,71	1,69
<i>p</i>	<0.001	0.12	0.185
Sp. 2			
F	3.377	0.017	27.268
DF	1,71	1,71	1,69
<i>p</i>	0.07	0.896	<0.001
Resource			
F	2.005	7.387	5.109
DF	1,71	1,71	1,69
<i>p</i>	0.161	0.008	0.027
Sp. 1 × Sp. 2			
F	1.176	0.278	3.561
DF	1,71	1,71	1,69
<i>p</i>	0.282	0.6	0.063
Sp. 1 × Resource			
F	0	0.008	0.221
DF	1,71	1,71	1,69
<i>p</i>	0.987	0.931	0.64
Sp. 2 × Resource			
F	0.591	1.023	0.86
DF	1,71	1,71	1,69
<i>p</i>	0.444	0.315	0.357
Sp. 1 × Sp. 2 × Resource			
F	0.036	2.438	0.307
DF	1,71	1,71	1,69
<i>p</i>	0.85	0.123	0.581

For species B's abundance, we found no two-way or three-way interactions. Species B's abundance was not affected by heterospecifics, but was decreased by 41% under low resource availability (Table 1, Fig. 1B).

For species C's abundance, we found no three-way interaction and no two-way interactions involving resources. However, the two heterospecifics had interactive effects on species C's abundance. Species A had a stronger negative effect on species C when species B was present compared to when species B was absent. In contrast, species B had a similar negative effect on species C regardless of whether species A was present or not. Collectively, these results suggest that species B was responsible for the reductions in the abundance of species C. We also found a 29% decrease in species C abundance under low resource availability (Table 1, Fig. 1C).

Effects of heterospecifics and resource levels on female fecundity, male gnathopod size and wounds

Our next analysis examined the effects of heterospecifics and resources on individual-based measures of performance that might provide insights into the mechanisms driving the abundance patterns that we observed.

Female fecundity

For species A's fecundity, we found no three-way interaction, however, the two heterospecifics had interactive effects on fecundity (Table 2). Females were 23% less fecund in the

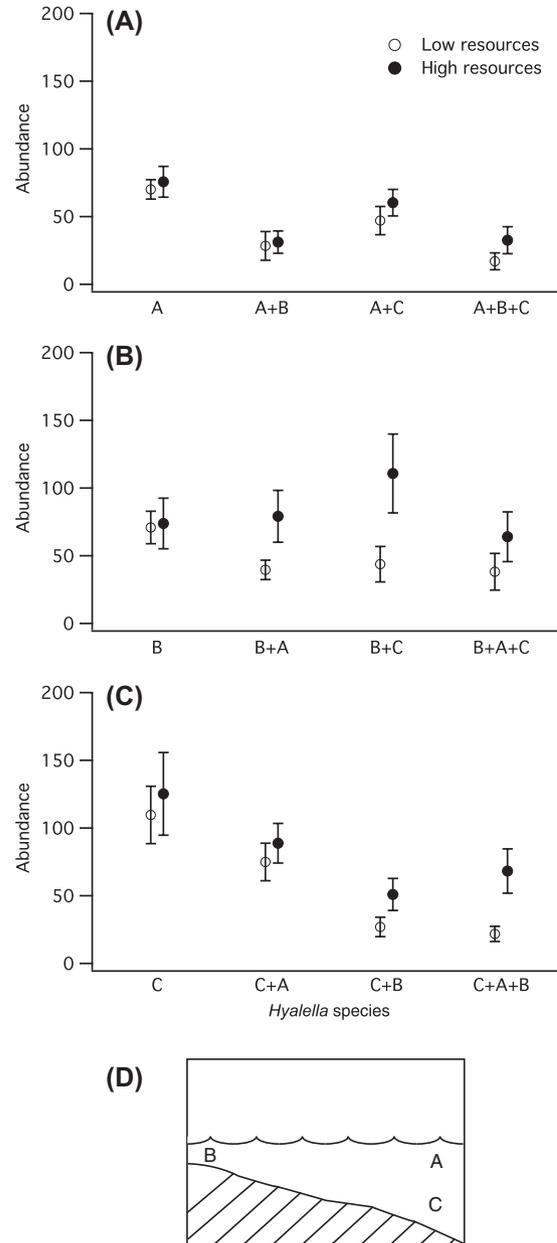


Figure 1. Abundance of adult amphipods across heterospecific and resource treatments at the end of the competition experiment. (A) species A abundance, (B) species B abundance, and (C) species C abundance. Data are means \pm 1 SE. Inset (D) shows where each species is most abundant in the littoral zone of lakes.

presences of species B, but only in the absence of species C (Fig. 2A). Species B's effect on the fecundity of species A was dependent on the resource environment. Species B caused a 21% reduction in species A's fecundity in high resource environments but only a 6% reduction when resources were low.

For species B, there was no three-way interaction effect on female fecundity. There was an interactive effect of the two heterospecifics (Table 2). The presence of species A and species C caused a 15% and 14% reduction in female fecundity, respectively. However, when both heterospecifics were present female fecundity did not differ from that observed in monoculture (Fig. 2B). There was also an interactive effect of species C and the resource environment

Table 2. Generalized estimating equation results for the effects of heterospecifics and resource level on fecundity. Wald χ^2 statistics and p-values (in parentheses) are presented. All tests have 1 degree of freedom.

Source	Species A	Species B	Species C
Sp. 1	17.251 (<0.001)	0.018 (0.893)	0.003 (0.955)
Sp. 2	5.269 (0.022)	0 (0.982)	6.279 (0.012)
Resource	0.187 (0.666)	0.02 (0.888)	0.001 (0.97)
Sp. 1 × Sp. 2	11.002 (0.001)	16.228 (<0.001)	26.157 (<0.001)
Sp. 1 × Resource	5.71 (0.017)	0.074 (0.785)	5.822 (0.016)
Sp. 2 × Resource	1.218 (0.27)	6.638 (0.01)	0.282 (0.596)
Sp. 1 × Sp. 2 × Resource	1.543 (0.214)	0.636 (0.425)	4.568 (0.033)
Head length	316.457 (<0.001)	108.316 (<0.001)	289.303 (<0.001)

driven by an increase in fecundity when species C was present in the low resource environment and a decrease in the high resource environment. These effects were weak, however, and none of the pairwise comparisons were significant.

Species C's fecundity was affected by a three-way interaction between the presence of heterospecifics and resources (Table 2). Under low resources, the presence of species B

caused a 20% reduction in fecundity, however, the presence of species A and the combination of species A and species B had no effect on fecundity (Fig. 2C). At high resources, all combinations of heterospecifics decreased fecundity, but the effect was stronger in bicultures than tricultures (Fig. 2C).

Male gnathopod size

For species A's gnathopods, our measure of male sensitivity to competitive stress, we found no three-way interaction or any two-way interactions involving resources. There was an interactive effect between the two heterospecifics that mirrored the result found for female fecundity (Table 3). Species B caused a 5% reduction in gnathopod size, but only when species C was absent (Fig. 3A).

For species B, we found a three-way interaction on male gnathopod size (Table 3). Relative to monocultures, there was 4% increase in gnathopod size when species C was present in the low resource environment and a 4% decrease when species A was present in the high resource environment (Fig. 3B). These effects, however, were weak and non-significant after correcting for multiple pairwise comparisons.

For species C, we found a three-way interaction involving heterospecific species and resources. At low resources, the presences of species A reduced gnathopod size by 5%, whereas species B and the combination of heterospecifics had no effect on gnathopod size (Table 3, Fig. 3C). At high resources, it was species B that had a negative effect on gnathopod size, reducing it by 9%. After correcting for multiple pairwise comparisons, species A and the combination of heterospecifics had no effect on gnathopod size.

Frequency of wounds

In species A, we found no four-way or three-way interaction effects on the prevalence of wounds. The presence of species B increased wounding, but the magnitude of this effect was dependent on the resource environment (Table 4, Fig. 4A, B). This effect was pronounced in the high-resource environment, where species B caused a 318% increase in wounding, but lower in the low-resource environment, where species B only caused a 23% increase in wounding. There was also an interactive effect between the presence of species C and the resource environment; there was an increase in wounding when species C was present in low-resource environments and the opposite pattern in high-resource environments. Pairwise comparisons, however, revealed no significant differences between treatments.

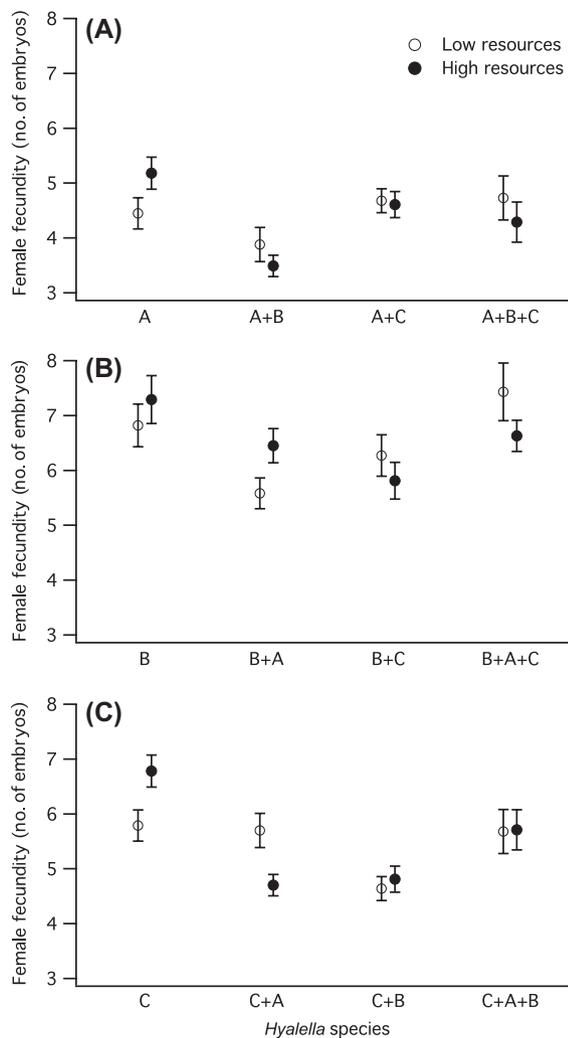


Figure 2. Effects of heterospecifics and resources on female fecundity. (A) species A fecundity, (B) species B fecundity, and (C) species C fecundity. Data are estimated marginal means \pm 1 SE at a head length of 0.5269, 0.5951 and 0.5199 mm for species A, B and C, respectively.

Table 3. Generalized estimating equation results for the effects of heterospecifics and resource level on male gnathopod size. Wald χ^2 -statistics, degrees of freedom (DF) and p-values are presented.

Source	Species A	Species B	Species C
Sp. 1	6.475 (0.011)	4.872 (0.027)	3.215 (0.073)
Sp. 2	1.237 (0.266)	2.027 (0.154)	0.037 (0.847)
Resource	1.454 (0.228)	0.238 (0.626)	22.281 (<0.001)
Sp. 1 \times Sp. 2	11.932 (0.001)	0.077 (0.781)	17.745 (<0.001)
Sp. 1 \times Resource	0.103 (0.748)	1.388 (0.239)	21.372 (<0.001)
Sp. 2 \times Resource	0.865 (0.352)	0.588 (0.443)	13.993 (<0.001)
Sp. 1 \times Sp. 2 \times Resource	1.28 (0.258)	3.874 (0.049)	13.721 (<0.001)
Head length	648.075 (<0.001)	179.449 (<0.001)	378.329 (<0.001)

For species B, there was no four-way interaction effect on the prevalence of wounding. We did find a sex-by-species C-by-resource interaction; females had fewer wounds in the presence of species C in low-resource environments and more wounds in the presence of species C in high-resource environments combined with no corresponding effects

on males (Table 4, Fig. 4C, D). There was also a species A-by-resource interaction. In the absence of species A, wounds were 41% more prevalent in high resource environments than low resource environments, however, in the presence of species A there was no effect of resources on wounding.

For species C, there was no evidence for a four-way interaction on the prevalence of wounding (Table 4, Fig. 4E, F). We did find a sex-by-species B-by-resource interaction. At low resources, the presence of species B resulted in increased wounding in both sexes, however, this effect was much more pronounced at high resources. In the high-resource environment, species B caused a 144% and 763% increase in wounding in females and males, respectively. Species A's effect on wounding in species C was contingent upon the presence of species B (species A-by-species B interaction). In the absence of species B, the presence of species A decreased wounding. However, when species B was present wounding was much higher than in monocultures and was not affected by the presence of species A. Finally, species A's effect on wounding differed between the sexes. The presence of species A reduced wounding in females by 28% but had no effect on wounding in males.

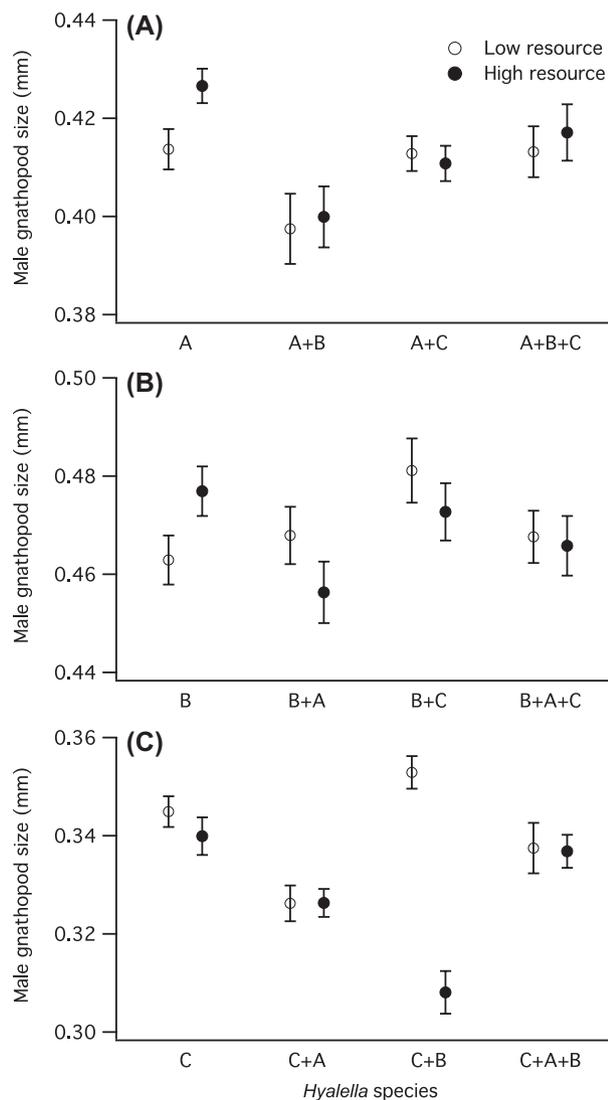


Figure 3. Effects of heterospecifics and resources on male posterior gnathopod size. (A) species A gnathopod size, (B) species B gnathopod size, and (C) species C gnathopod size. Data are estimated marginal means \pm 1 SE at a head length of 0.5027, 0.5746 and 0.4442 mm for species A, B and C, respectively.

Predation experiments

Dragonfly predation experiment

The three *Hyalella* species differed in their susceptibility to dragonfly predation (Fig. 5A). In the dragonfly diets, species B was overrepresented ($t_{24} = 4.456$, $p < 0.001$, $\alpha_{\text{adjusted}} = 0.017$), species A underrepresented ($t_{24} = -5.491$, $p < 0.001$, $\alpha_{\text{adjusted}} = 0.025$), and species C did not differ from that expected by random ($t_{24} = 1.757$, $p = 0.092$, $\alpha = 0.05$). Therefore, species B is the most susceptible to dragonfly predation whereas species A is the least susceptible.

Bluegill predation experiment

Bluegill predation had a multivariate effect on amphipod abundance (MANOVA Pillai's trace = 0.677, $F_{3,11} = 7.699$, $p < 0.001$). This effect was driven by bluegills reducing the abundance of species B ($F_{1,13} = 10.873$, $p = 0.006$) but not affecting the abundance of species A and species C (species A: $F_{1,13} = 0.342$, $p = 0.569$; species C: $F_{1,13} = 1.938$, $p = 0.187$; Fig. 5B).

Discussion

The three cryptic species of small ecomorphs that coexist in the littoral zone of lakes differed in their performance in the

Table 4. Generalized estimating equation results for the effects of heterospecifics and resource level on wounds. Wald χ^2 -statistics and p-values (in parentheses) are presented. All tests have 1 degree of freedom.

Source	Species A	Species B	Species C
Sp. 1	71.791 (<0.001)	1.709 (0.191)	1.103 (0.294)
Sp. 2	0.028 (0.867)	0.004 (0.949)	99.485 (<0.001)
Resource	1.22 (0.269)	6.13 (0.013)	3.356 (0.067)
Sex	10.1 (0.001)	16.341 (<0.001)	31.467 (<0.001)
Sp. 1 × Sp. 2	1.001 (0.317)	0.311 (0.577)	5.849 (0.016)
Sp. 1 × Resource	39.924 (<0.001)	6.113 (0.013)	1.415 (0.234)
Sp. 2 × Resource	5.951 (0.015)	2 (0.157)	25.647 (<0.001)
Sp. 1 × Sex	0.006 (0.936)	0.086 (0.769)	4.68 (0.031)
Sp. 2 × Sex	1.452 (0.228)	0.184 (0.668)	13.802 (<0.001)
Resource × Sex	0.016 (0.9)	0.252 (0.616)	0.094 (0.76)
Sp. 1 × Sp. 2 × Resource	0.773 (0.379)	0.723 (0.395)	0.563 (0.453)
Sp. 1 × Sp. 2 × Sex	0.267 (0.605)	0.467 (0.495)	0.778 (0.378)
Sp. 1 × Resource × Sex	2.983 (0.084)	0.028 (0.867)	1.864 (0.172)
Sp. 2 × Resource × Sex	0.078 (0.78)	6.718 (0.01)	6.884 (0.009)
Sp. 1 × Sp. 2 × Resource × Sex	1.406 (0.236)	0.885 (0.347)	0.024 (0.876)
Head length	22.141 (<0.001)	50.412 (<0.001)	

competition experiment and susceptibility to predation by bluegill sunfish and larval dragonflies. Species B significantly depressed the abundance of both species A and species C. Individual-based measures of performance suggest that this

effect was not only driven by competition for limited resources but also antagonistic, physical interactions between species B and the two smaller amphipod species. In the predation trials, species B was consumed more by both

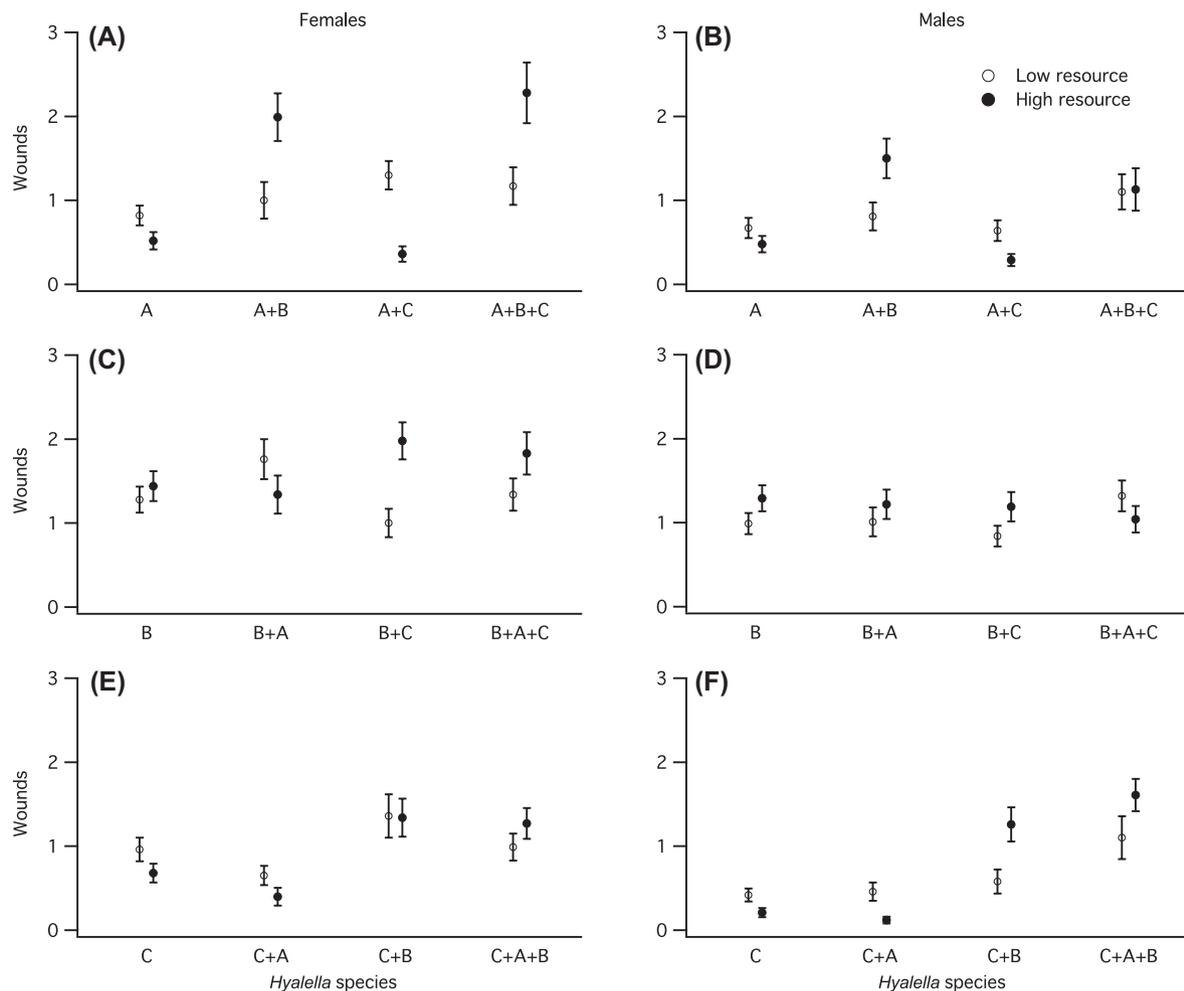


Figure 4. Effects of heterospecifics and resources on the frequency of wounds in male and female amphipods. Wounds were apparent as melanized patches on the exoskeleton of the animal. (A and B) species A wounds, (C and D) species B wounds, and (E and F) species C wounds. Data are estimated marginal means \pm 1 SE at a head length of 0.5094 and 0.5758 mm for species A and B, respectively. Covariate data is missing for species C because wounding was not dependent on body size (i.e. head length).

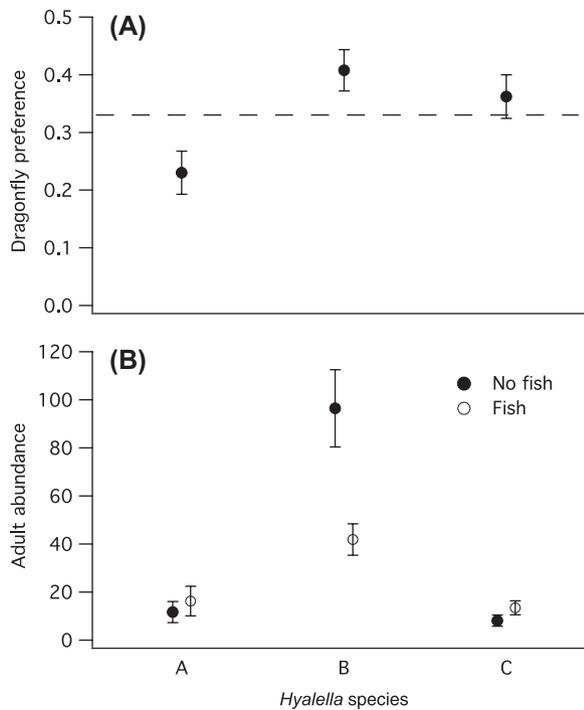


Figure 5. Predation on the cryptic amphipod species. (A) Species differences in susceptibility to dragonfly predation. The dotted line represents the expectation if dragonflies show no preference for a particular species. Data are means \pm 95% CI of the difference between the mean and test value, 0.33. (B) The effect of bluegill on the abundance of the three *Hyalella* species. Data are means \pm 1 SE.

bluegill sunfish and larval dragonflies. Species A survived well against both predators and species C survived well against bluegill sunfish and was not preferred by larval dragonflies.

Our results demonstrate ecological-based performance tradeoffs among cryptic species that may promote their coexistence. Despite their morphological similarity, the three cryptic amphipod species displayed strong differences in their response to the presence of heterospecific amphipods. Species differences in body size may be partially responsible for performance asymmetries among the species, because it is often a good predictor of competitive ability (Parker 1974). In studies of *Hyalella* species that have compared large versus small ecomorphs – in which the large ecomorph is 43% larger than the small ecomorph (measured as head length, Edwards and Cowell 1992) – the link between competitive ability and body size has been demonstrated. The large ecomorph causes a large decrease in body size (presumably via reduced growth rates) and fecundity of the small ecomorph that translates to a seven-fold reduction in the abundance of the small ecomorph (Wellborn 2002). The large ecomorph can also depress resources to a greater extent than the small ecomorph (Wellborn 1994b). These studies suggest that the large ecomorph has a competitive advantage that stems from its ability to exploit resources to a greater degree than the small ecomorph (Tilman 1990).

In the current study, however, all three species are small ecomorphs. As a result, the size differences among the three

cryptic species are small; species B is only 16% and 12% larger than species A and species C, respectively (Wellborn and Cothran 2004). Unlike the earlier studies comparing large and small ecomorphs, we did not find strong effects of competition for food resources on the abundance of the three cryptic species. If interspecific food competition was solely responsible for reductions in abundance, we expected reductions in the abundance and individual performance of inferior competitors to be greatest under low-resource availability. While species B caused reductions in the fecundity of both smaller heterospecifics, the magnitude of this effect was greatest under high-resource availability. This pattern was also true for the male performance trait, the size of the male posterior gnathopod. In fact, the presence of species B only caused reductions in the gnathopod size of species C under high resource availability. These results suggest that an alternative mechanism may be responsible for the decreased abundance of the smaller two amphipod species especially in high resource environments.

One mechanism is aggressive interactions among the amphipod species. The presence of species B caused an increase in the number of wounds sustained by species A and species C individuals. If wounds were inflicted by species B during interference competition for food resources and this contributed to reduced abundance of the smaller species, we would have expected the lowest fecundity and smallest gnathopod size of the two smaller species at low-resource availability. However, we found that the smaller species were wounded more often under high-resource availability. Wounds may also indicate intraguild predation attempts by species B, which may have contributed to the decreased abundance of the smaller amphipod species (Polis et al. 1989). The diets of amphipods in general are poorly understood and tend to be overgeneralized (MacNeil et al. 1997). *Hyalella* amphipods are typically considered grazers of epiphytic microorganisms (Hargrave 1970). However, several freshwater amphipod species are known to be omnivorous and intraguild predation is common in *Gammarus* spp. (a genus that is in the same sub-order [Gammaridea] as *Hyalella* and has a similar body plan; Dick et al. 1990, Bollache et al. 2007). Species B individuals may have been in better condition in high resource environments putting them in a better position to attack and wound the smaller amphipod species.

An alternative explanation for the increased wounding, especially in high resource environments, is that they were sustained during fights over the initiation of precopulatory mate guarding, a prerequisite for mating in these amphipods. Reproductive interference has been considered as an explanation for species replacements in *Gammarus* species, although it appears to be less important than intraguild predation (Dick and Elwood 1992). In *Hyalella*, males are indiscriminate in their mating effort; they attempt to mate with individuals regardless of age, sex or even whether they are alive (Wellborn and Cothran 2007b). Males initiate pairing by grabbing individuals with their posterior gnathopods. This muscular appendage – that resembles a claw – is 15 times larger in males than females and may cause injuries during mating attempts (Wellborn and Bartholf 2005). Moreover, males grow larger posterior gnathopods under high resource availability

(Cothran and Jeyasingh 2010). Therefore, at high resource availability, species B males in good condition may have been particularly effective at wounding heterospecifics during misguided mating attempts. However, males did not have larger gnathopods in high resource treatments under interspecific competition. Therefore, intraguild predation attempts are a more likely source of wounding patterns found in the current study.

The cryptic amphipod species also differed in susceptibility to predation in ways that contrasted with relative performance in the competition experiment. Species B, the species that performed the best in the interspecific competition study, was the poorest species at avoiding predation by larval dragonflies and bluegill sunfish. The latter result was expected given that species B is slightly larger than the other two species and bluegills are positive size-selective predators (Wellborn 1994a). Although species B experienced a large drop in abundance during the 42-d predation experiment, it was still more abundant than species A and species C in tanks with bluegill. The bluegill predation experiment lasted 42 d and with more time species B's abundance may have been further depleted by the bluegills. This seems a more likely explanation for the observed pattern than species B being able to maintain higher abundance than species A and species C in habitats with bluegill given that field surveys have documented low relative abundance of species B in habitats with bluegill and that it is overrepresented in bluegill stomach contents (Wellborn and Cothran 2007a). On the other hand, we expected species B to perform better against larval dragonflies, which typically are not size selective or prefer smaller prey (Wellborn 1994a). Although body size has received a good deal of attention for explaining differential predation on *Hyaella* species, other traits probably also contribute to species differences in predator avoidance among amphipod species (Holomuzki and Hoyle 1990, Bollache et al. 2006). A mechanistic understanding of species differences in predator avoidance will require an integrative approach that examines how suites of traits (e.g. activity levels, refuge use, morphological traits [e.g. dorsal spines], and color-based crypsis) affect predation (DeWitt and Langerhans 2003, Bollache et al. 2006).

Performance tradeoffs and species coexistence

Regardless of mechanisms responsible for differential predator avoidance among cryptic *Hyaella* species, our results suggest that tradeoffs between predator avoidance and the ability to compete with heterospecifics may be important in explaining their distribution and local diversity. Species B performs well in the presence of heterospecific amphipods but is poor at avoiding predators whereas species A and C show a complementary pattern for these two ecological interactions. Whether such tradeoffs allow for coexistence is still an open question (Siepielski and McPeck 2010). For stable coexistence to occur, species differences in performance would have to translate to each species having higher relative fitness when rare in the community (Chesson 2000, Adler et al. 2007). Experiments that address whether species are able to increase when rare in a community across ecological gradients would be particularly informative

for addressing whether cryptic *Hyaella* species stably coexist (Chesson 2000, Siepielski and McPeck 2010). Our results suggest that manipulations of the predator and species composition of the resident community in such experiments may shed light on coexistence in this system.

Our discovery of increased wounding in smaller amphipod species when species B is present suggests that antagonistic, physical interactions – specifically intraguild predation and reproductive interference – may contribute to the distribution patterns of the cryptic species. Intraguild predation may promote or inhibit coexistence of intraguild predators and prey. Specifically coexistence is expected at intermediate resource levels when the intraguild prey is the superior competitor (Holt and Polis 1997), but may also occur over a broader range of conditions (Křivan 2000, Mylius et al. 2001, Borer 2002, Holt and Huxel 2007, Amarasekare 2008). This mechanism may maintain coexistence in cryptic amphipod communities if the smaller species are more efficient at exploiting attached algae while also falling victim to predation by species B. Experiments designed to test the ability of each species to depress algal resources and limit the recruitment of heterospecifics will shed light on the importance of intraguild predation in this system.

Alternatively, antagonistic physical interactions may be responsible for exclusion of species from preferred microhabitats. Both intraguild predation and reproductive interference may limit habitat use by negatively affected species (Polis et al. 1989, Gröning and Hochkirch 2008). Studies that address performance (e.g. growth and fecundity) on resources available in different microhabitats (e.g. near shore areas vs offshore areas) and whether distribution patterns match those expected by performance studies will be particularly informative.

So far, we have focused on how minor phenotypic differences among species lead to differences in relative competitive ability and predation risk, however, the two most phenotypically similar species, species A and species C, showed very similar responses to competitors and predators. Other than color patterns, these two species are very similar in ecologically important traits including body size and life history traits (Wellborn and Cothran 2004). These two species are primarily found in deeper areas within the vegetated zone of lakes and are more likely to interact with each other than either interacts with species B (Wellborn and Cothran 2007a). Competitive asymmetries between these two species were not apparent. Both species caused similar reductions in the other's density (species A caused a 31% reduction in species C and species C caused a 26% reduction in species A) and both were more negatively affected by species B. Similarly, both species were unaffected by the addition of fish, whereas the abundance of species B declined sharply. Species A was better at avoiding dragonfly predation, but these predators are not typically found in deeper areas of lakes accessible to predatory fish where species A and species C are most abundant (Thorpe and Bergey 1981, Morin 1984, Wellborn et al. 1996). Collectively, our results suggest that ecological similarity, perhaps driven by strong selection by fish for a similar suite of traits that help reduce susceptibility to predation, may allow species A and species C to co-occur in deeper areas of

lakes (Bell 2000, Hubbell 2006). While ecological similarity may allow for these species to co-occur for long periods, given enough time one would expect one of the species to be dropped from the community via neutral processes (Chesson 2000). However, such species loss may be buffered by reciprocal differences in production in surface waters vs mid-depth microhabitats in lakes (Wellborn and Cothran 2007a). Therefore, it appears that a combination of equalizing (similarities in body size and life history) and stabilizing (differences in habitat use) mechanisms may allow for the coexistence of these two phenotypically similar species (Leibold and McPeck 2006).

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