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Occurrence and Distribution of the Freshwater Amphipods *Gammarus pseudolimnaeus* and *Gammarus fasciatus* in Southeastern Virginia

Lindsey L. Postaski[1,3], Gregory M. Capelli[1], and Randolph M. Chambers[2,*]

Abstract - The freshwater amphipod, *Gammarus fasciatus,* and a population that keys to *Gammarus pseudolimnaeus* are broadly sympatric in southeastern Virginia. By documenting the successful formation of pre-copulatory mate-guarding pairs between individuals collected from Virginia and New York, we confirmed the occurrence of a *G. pseudolimnaeus* population strongly disjunct from the previously described range in the Mississippi and St. Lawrence River drainage basins. *Gammarus pseudolimnaeus* appears restricted to high-quality, spring-fed streams that occur at low density across an increasingly fragmented natural landscape in Virginia. *Gammarus fasciatus*, however, occurs in lakes and streams of developed landscapes that typically are more degraded, and this species does not co-occur with *G. pseudolimnaeus* in high-quality habitat. *Gammarus pseudolimnaeus* reproduces year-round, with adults and juveniles of all size classes continuously present. *Gammarus fasciatus* reproduces primarily from February through June, at which point the adults die, and by late summer the population consists solely of immature individuals. If the two species overlapped in distribution, the smaller *Gammarus fasciatus* amphipods would have to compete with adult *G. pseudolimnaeus* for resources. We hypothesize that this competitively disadvantageous life cycle could account, in part, for the absence of *G. fasciatus* in high-quality streams occupied by *G. pseudolimnaeus*.

Introduction

The family Gammaridae, found in both marine and freshwater habitats, is the largest and most diverse of the eighty families that make up the order Amphipoda (Bousfield 1977). Gammarids are the only group of amphipods that occupy a broad range of continental freshwaters (Holsinger 1976), with the majority of species occurring in streams, rivers, and lakes of relatively high water quality (Holsinger 1972, MacNeil et al. 2001, Rinderhagen et al. 2000). As mostly shredders or collector-gatherers (Cummins 1973) with population densities of up to 10,000 m^{-2} (Smith 2001), gammarid amphipods are important in aquatic ecosystems for nutrient cycling (Hanson and Waters 1974) and energy flow (Marchant and Hynes 1981, Newman and Waters 1984). In addition, their sensitivity to a wide variety of pollutants makes them valuable bioindicators (Rinderhagen et al. 2000).

Gammarus pseudolimnaeus Bousfield and *G. fasciatus* Say are two of the four most commonly collected amphipods in the eastern United States (Smith 2001). *Gammarus pseudolimnaeus* is widely distributed in the Mississippi and St. Lawrence River drainage basins, from Texas and Arkansas north to Wisconsin,

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Ontario, and western Quebec (Bousfield 1958, Holsinger 1976). Throughout its range, *G. pseudolimnaeus* occupies large rivers, lakes, and ponds (Bousfield 1958). G*ammarus fasciatus* occurs in sympatry with *G. pseudolimnaeus* in the Great Lakes region of the United States (Holsinger 1972), and also occupies the St. Lawrence, Hudson, Delaware, and Susquehanna river drainage-basins (Bousfield 1958). Throughout its range, *G. fasciatus* primarily inhabits lakes and slow-moving, often turbid rivers (Bousfield 1958), but the species may also occur in springs and small streams, especially in the southern part of its range (Holsinger 1976).

We identified amphipods recently collected from numerous isolated populations in southeastern Virginia (VA) as *G. pseudolimnaeus* (Holsinger 1972, Zehmer et al. 2002). No previously published information is available on *G. pseudolimnaeus* and *G. fasciatus* distribution in the region. Preliminary observations suggest that these disjunct, southeastern populations of *G. pseudolimnaeus* occur in sympatry with *G. fasciatus*, but with a non-overlapping local distribution. Abiotic factors such as temperature (Smith 1973, Sprague 1963), particle size, current velocity, dissolved oxygen (Rees 1972), biotic factors including food availability (Dobson and Hildrew 1992), and predation (González and Burkart 2004)) can influence local gammarid distributions.

Details reported on the reproductive cycles of *G. pseudolimnaeus* and *G. fasciatus* tend to vary by study and geographic location. For example, according to Hynes and Harper (1972), *G. pseudolimnaeus* reproduces from February through July in Ontario, but Miller (1982) described a longer reproductive period lasting from mid-January through September in Wisconsin. Waters (1981) observed an annual life cycle of *G. pseudolimnaeus* in Minnesota similar to the period reported by Hynes and Harper (1972), suggesting that reproductive activity virtually ceased in winter months. For *G. fasciatus*, ovigerous females have been observed from May to September (Bousfield 1958), but from February to April in more southern parts of its range (Holsinger 1976). In fact, most life history studies of *G. pseudolimnaeus* and *G. fasciatus* were conducted decades ago in the northern portion of their distributional ranges; to date no studies have documented the reproductive cycle of *G. fasciatus* in southeastern VA, nor of *G. pseudolimnaeus* recently discovered there.

To fill these information gaps, we sought to document the occurrence of *G. pseudolimnaeus* in southeastern VA by confirming our species identifications using observations of reproductive behavior with conspecifics from the St. Lawrence River drainage basin. We also documented the distribution of *G. pseudolimnaeus* and *G. fasciatus* in a small VA watershed, and described the physicochemical conditions in which these species occur. Finally, we documented the timing of reproduction by *G. pseudolimnaeus* and *G. fasciatus*, and examined factors influencing the distribution of sympatric gammarid species in local aquatic environments.

Field Site Description

All studies were completed in a freshwater lake and streams in southeastern VA (Fig. 1). Lake Matoaka is a 16-ha, hyper-eutrophic lake located on the College of William and Mary campus in Williamsburg, VA. The lake is fed by five small

streams; of these, three are perennial, first-order streams (Strawberry Creek, Pogonia Creek, Berkeley Creek) that enter from the western portion of the watershed which is dominated by forest (72–96%; Wach and Chambers 2007) . These streams arise as springs in which dissolved oxygen is typically near saturation (Zehmer et al. 2002) and temperature does not exceed 25 °C (L. Postaski, unpubl. data). The primary source of organic matter in these streams is allochthonous material from the surrounding deciduous forest preserve (Mahon 1997). We identified the most abundant invertebrate within these streams as the amphipod *G. pseudolimnaeus* (Zehmer et al. 2002).

Three other streams were included for study, all of which are dominated by *G. fasciatus* (Fig. 1). Crim Dell Creek and College Creek discharge into Lake Matoaka, and both streams are significantly degraded, as evidenced by lower forest cover in their watersheds (25 and 69% forest, respectively; T.M. Russell, Kekc Lab,

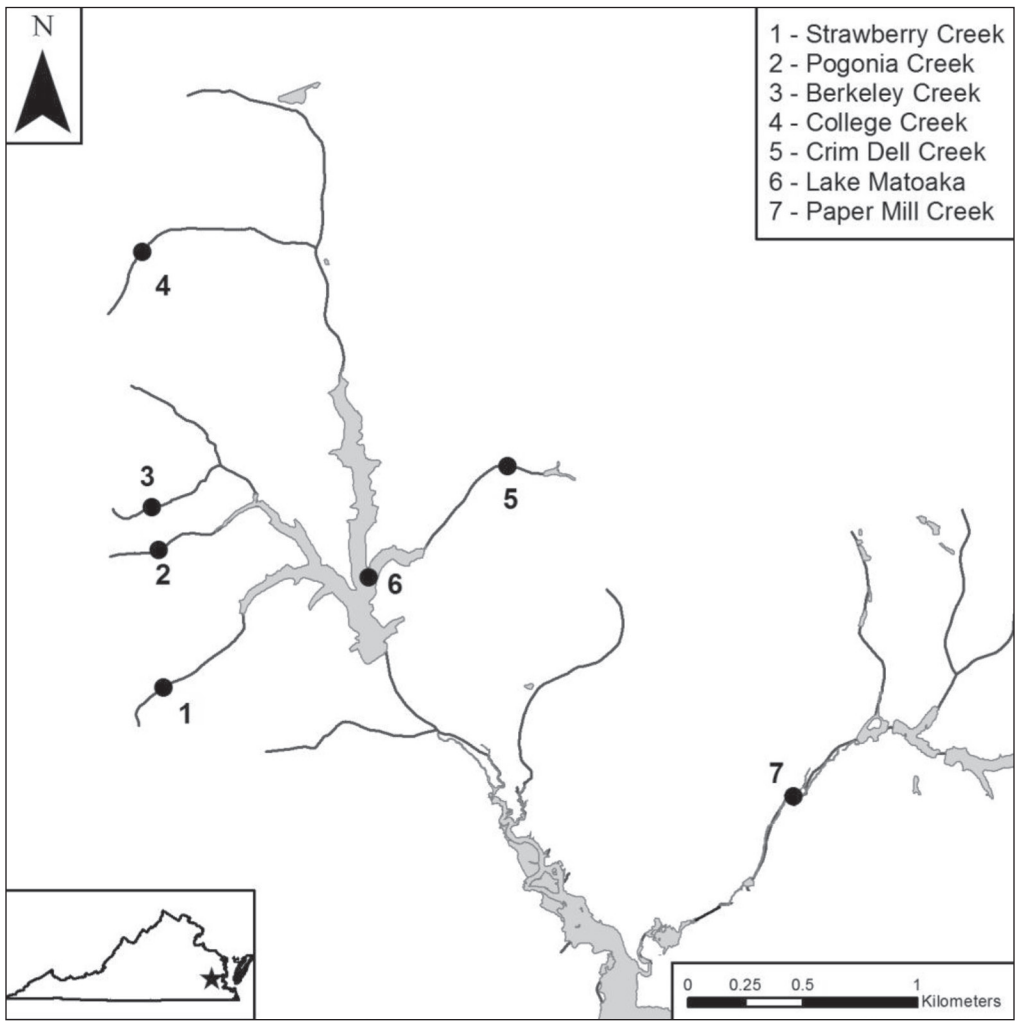

Figure 1. Site map of study location in southeastern Virginia, showing Lake Matoaka and the six streams sampled for amphipods.

College of William and Mary, Williamsburg, VA, pers. comm.), and by reduced dissolved oxygen levels, high turbidity from channel erosion, and low species diversity (L. Postaski, unpubl. data). Downstream from Lake Matoaka, Paper Mill Creek is a tributary of College Creek, and it receives runoff from two golf courses and from local roads, with only 40% forest cover in the watershed (T.M. Russell, pers. comm.). The annual water temperature fluctuation in Paper Mill Creek, Crim Dell Creek, and College Creek is greater than the temperature fluctuation observed in the streams from the western portion of the Lake Matoaka watershed (L. Postaski, unpubl. data).

Methods

Documentation of *G. pseudolimnaeus*

As with many other crustaceans, male gammarids guard females as the females approach molting. In *G. pseudolimnaeus*, males use their gnathopods to attach themselves to the dorsal side of a female approximately four days before the female molts. The pair remains intact until the female begins to molt; after molting the male fertilizes eggs released into the marsupium. Because this behavior is considered species-specific, formation of pre-copulatory mate guarding (PCMG) pairs between suspected and known *G. pseudolimnaeus* individuals was used to verify the species' occurrence in southeastern VA. In October 2008, PCMG pairs of amphipods from southeastern VA were collected from Strawberry Creek using a hand-held aquarium net. PCMG pairs of *G. pseudolimnaeus* from the St. Lawrence River drainage basin were collected similarly from Spring Creek, a perennial, first-order stream in the town of Caledonia, NY (see Sutton 1995). From each collection, we separated males from local PCMG pairs and transported them in continuously oxygenated containers (water temperature ≤25 °C) to the other state, where we collected females from local PCMG pairs. Then, we placed 5 transported males and 1 local female in a 12-cm x 12-cm plastic container with equal amounts of water from the respective original streams to a depth of 5 cm. We observed amphipods until mate guarding occurred, and then the PCMG pair was transferred to another container of the same type and observed for 1 h. We conducted 25 trials with VA males in NY. Due to higher mortality of NY males in transport, only 10 trials of NY males in VA were conducted. We also conducted 25 trials using suspected VA *G. pseudolimnaeus* paired with VA *G. fasciatus* (males with females, watched for one hour for evidence of PCMG pair formation).

Gammarid amphipod distribution

We compared the environments in five streams and in Lake Matoaka where gammarid amphipods occurred (College Creek was not included). We sampled each stream at upper, middle, and lower reaches; in Lake Matoaka, we sampled along the shoreline. Along each reach, we used a random numbers table (1–10) to determine the distance (meters) traveled downstream or along shore to a sampling location. We took samples from the area with the largest amount of leaf litter within one meter of

the randomly chosen sampling location. In June and November 2008, and February 2009, we collected amphipods at each site using a 20-cm-diameter metal cylinder. We drove the cylinder into the sediment, then visually gridded it, and estimated the percentage of leaf litter cover within the cylinder to the nearest 10%. Amphipods were then collected by disturbing the substrate within the confined area using a hand-held aquarium net and sweeping the area to collect the dislodged individuals. Sweep sampling in the cylinder continued until three consecutive sweeps yielded no amphipods. We preserved amphipods in 70% ethanol for subsequent identification.

We also recorded dissolved oxygen, temperature, conductivity, and calcium from the middle of each stream site and from the lake surface during the three sampling periods. Amphipod abundance by species was plotted as a function of percentage of leaf-litter cover (arcsine square-root transformed), and analyzed using Pearson correlation.

Timing of reproduction

Conclusions regarding timing of reproduction and other life-history information were determined based on the results of year-long sampling for gammarid amphipods in local streams. We collected samples weekly from 18 March 2008 to 16 March 2009 from the same sampling reach along the Lake Matoaka shoreline and from Strawberry Creek. Organisms were collected by scooping leaf-litter patches with a D-frame net (0.3m-wide at base, 750-µm mesh). We finished sampling when a maximum of three net samples was taken, or when collections yielded at least 100 individuals. We used existing taxonomic keys to confirm identification of amphipod species (Holsinger 1972, Smith 2001). Body length, from the tip of the telson to the base of the antennae, was measured using a micrometer. We recorded the number of amphipods engaged in pre-copulatory mate guarding for each species in each sample.

Based on preliminary data on relative size, amphipods were categorized as adults (body length ≥8.0 mm) or juveniles (body length <8.0 mm). Prior studies from more northern locations grouped *G. pseudolimnaeus* and *G. fasciatus* into adult and juvenile categories ≥6 mm and <6 mm, respectively (Hynes 1955, Hynes and Harper 1972, Miller 1982). In our VA samples, however, mean body length of *G. fasciatus* PCMG individuals (i.e., sexually mature) was 9.9 mm (n = 100); while the mean body length of *G. pseudolimnaeus* PCMG individuals was 9.3 mm (n = 100), suggesting that a body length ≥8 mm was an appropriate designation for adult *G. pseudolimnaeus* and *G. fasciatus*. Monthly variation in the percentage of adults and juveniles for each species was determined with a chi-square goodness-of-fit test.

In June 2009, when sampling in Lake Matoaka yielded very few adult *G. fasciatus*, sediment samples were collected from the lake bottom to locate smaller juvenile amphipods (≈2 mm body length). Using a plastic scoop, a 500-cm^3 sediment sample was collected from the top 1–4 cm of lake sediment. Samples were sorted, and amphipods were preserved in 70% ethanol for measurement separate from the weekly tallies of adult and juvenile amphipods.

Results and Discussion

Documentation of *G. pseudolimnaeus*

In all VA/NY trials, a PCMG pair developed within 3 minutes and was sustained for the 1-h observation period. This rapid occurrence of sustained PCMG behavior between NY and VA populations is strong evidence that the disjunct populations are conspecific. In contrast, no PCMG pairs formed in the 25 trials between VA *G. pseudolimnaeus* and VA *G. fasciatus*. The occurrence of interspecific PCMG in amphipods has never been documented. The European species *Gammarus pulex* L. and *Gammarus duebeni* Lilljeborg will not form PCMG pairs (Dick and Elwood 1992), and in previous field trials from our study site, *G. pseudolimnaeus* and *G. fasciatus* did not form PCMG pairs (G.M. Capelli, pers. observ.). As with mating systems in general, interspecific pairing should be strongly selected against to prevent inappropriate wasted reproductive effort. Species-specific pheromones are probably involved in amphipod signaling (Dunham 1978), and interspecific morphological differences also may be sufficient to prevent PCMG (J. Holsinger, Old Dominion University, Norfolk, VA, pers. comm.). Although documentation of viable offspring from interstate pairs would be more fully conclusive, mate guarding provides strong evidence that amphipods from VA and NY are conspecific.

That these disjunct populations are conspecific raises questions about the spatial separation of habitat. *Gammarus pseudolimnaeus* is not known to occur within any other area of the Susquehanna River drainage except for a small tributary of the Patuxent River in Maryland, that might support a population (G. Capelli, pers. observ.). Perhaps *G. pseudolimnaeus* was at one time much more widely distributed both locally and probably regionally as well. In southeastern VA, most headwater streams in which *G. pseudolimnaeus* now occurs flow into either impoundments or other streams with somewhat degraded environmental conditions, e.g., with silty substrates, higher summer temperatures, reduced oxygen, and generally poorer water quality. In addition, stream habitats where *G. pseudolimnaeus* may have occurred historically would have been more broadly connected (Larsen 1998), because the entire Susquehanna River drainage area from NY to VA was freshwater until the end of the last ice age about 15,000 years ago. Since then, with warming global temperatures, sea level rise, and formation of the Chesapeake Bay estuary, freshwater tributaries to the Susquehanna River have been effectively segregated from one another. Thus, the current distribution of *G. pseudolimnaeus* in VA may reflect, at least in part, the fragmentation of habitat driven by warming temperatures, estuary formation, and most recently, general alteration of aquatic habitats by humans.

As an alternate to invoking habitat fragmentation to account for the disjunct populations in VA, the occurrence of *G. pseudolimnaeus* in the Chesapeake Bay basin could be the result of recent introduction. Little is known about the passive transport of amphipods from one drainage basin to another, and amphipods are not generally adapted to withstand drought and other adverse environmental conditions (Smith 2001). Some proposed dispersal methods include transport on the feet of waterfowl (Figuerola and Green 2002), transport on the fur of aquatic mammals (Peck

1975), and arrival on aquatic plants and stocked fish (Mills et al. 1993). Evidence for each mechanism, however, is anecdotal, with little quantitative information available. Although other species have been introduced via human activities including fishing, we have no evidence linking the occurrence of *G. pseudolimnaeus* to any of them.

Gammarid amphipod distribution

The abundance of *G. pseudolimnaeus* and *G. fasciatus* fluctuated over the three sampling dates and was greatest for both species in November (Table 1). Our results suggest that variable seasonal abundance may be connected to availability of deciduous leaves in the streams either as a food source or as cover from predators; the number of amphipods present and leaf-litter coverage were positively correlated (Fig. 2; $r = 0.76$, $P < 0.001$). Although we did not measure it, the number of amphipods could vary seasonally or spatially not only with relative leaf abundance, but also with leaf quality. For example, Carrick et al. (2011) found the amount of algae growing on leaves covaried with the abundance of gammarid amphipods. Finally, amphipod numbers are lower and individual size is greater in sections of Lake Matoaka streams occupied by fish (Wach and Chambers 2007), suggesting possible top-down regulation of amphipod abundance.

Table 1. Number of amphipods and associated water quality parameters (mean ± s.d.) at six sites sampled in June and November 2008, and February 2009. *G.p.* = total number of *G. pseudolimnaeus* in three samples comprising 942 cm^2; *G.f.*= total number of *G. fasciatus* in three samples comprising 942 cm^2; temperature in ºC; dissolved oxygen in mg L^{-1}; conductivity in µS cm^{-1}; calcium in mg L^{-1}.

Month/Site	*G.p.*	*G.f.*	Temp.	Oxygen	Conductivity	Calcium
JUN 2008						
Strawberry Creek	331	0	19.4 ± 1.5	8.9 ± 0.5	221 ± 31	126 ± 10
Berkeley Creek	207	0	19.3 ± 1.6	8.9 ± 0.7	70 ± 32	26 ± 17
Pogonia Creek	209	0	19.1 ± 0.8	8.9 ± 0.6	62 ± 34	38 ± 13
Lake Matoaka	0	108	26.5 ± 0.3	3.0 ± 4.5	277 ± 21	111 ± 12
Crim Dell Creek	0	219	25.3 ± 0.5	5.2 ± 0.9	757 ± 136	255 ± 17
Paper Mill Creek	0	588	25.8 ± 0.2	8.1 ± 0.6	1050 ± 40	137 ± 49
NOV 2008						
Strawberry Creek	576	0	11.3 ± 2.3	9.6 ± 1.5	250 ±32	193 ± 32
Berkeley Creek	532	0	12.1 ± 1.0	8.8 ± 0.8	146 ± 58	40 ± 18
Pogonia Creek	338	0	9.1 ± 0.5	9.5 ± 0.7	136 ± 29	44 ± 14
Lake Matoaka	0	257	19.3 ± 2.9	7.9 ± 0.7	274 ± 19	117 ± 16
Crim Dell Creek	0	367	12.2 ± 0.5	5.4 ± 1.0	759 ± 99	207 ± 60
Paper Mill Creek	0	232	9.6 ± 2.9	9.1 ± 0.7	1181 ± 189	152 ± 27
FEB 2009						
Strawberry Creek	212	0	10.1 ± 1.8	8.9 ± 0.3	240 ± 29	142 ± 18
Berkeley Creek	192	0	8.1 ± 1.2	9.0 ± 1.1	130 ± 27	34 ± 15
Pogonia Creek	232	0	7.9 ± 1.2	8.8 ± 0.4	60 ± 26	48 ± 14
Lake Matoaka	0	159	6.9 ± 1.2	11.6 ± 4.4	263 ± 42	105 ± 12
Crim Dell Creek	0	207	8.9 ± 1.5	5.6 ± 1.1	598 ± 90	192 ± 57
Paper Mill Creek	0	415	6.9 ± 1.9	7.0 ± 1.8	959 ± 281	154 ± 35

In comparing the distribution of the two gammarid amphipods in southeastern VA, we found the species were completely isolated with no syntopic occurrences at the local level (Table 1). *Gammarus pseudolimnaeus* was exclusive to Berkeley Creek, Pogonia Creek, and Strawberry Creek; *G. fasciatus* was exclusive to Lake Matoaka, Crim Dell Creek, and Paper Mill Creek. Temperature and dissolved oxygen content tended to be more variable at sites containing *G. fasciatus*, and we considered these to be lower quality sites (Table 1), although we have no data comparing, for example, nutrient or trophic status of the sites (e.g., Dodds et al. 1998). Measurements of conductivity and calcium appeared to be within tolerable ranges of both species (Zehmer et al. 2002). *Gammarus fasciatus* often is associated with habitats with lower water quality relative to those occupied by *G. pseudolimnaeus*, but we suspect *G. fasciatus* should be able to colonize areas of higher water quality. Smith (1973) describes *G. fasciatus* as surviving at temperatures that range from 10–30 °C, whereas the much narrower range at which *G. pseudolimnaeus* survives is 15–18 °C. In contrast, the literature suggests that *G. pseudolimnaeus* would not be able to tolerate the low summer dissolved oxygen levels present in areas where *G. fasciatus* predominates (Lake Matoaka: 3.02 ± 4.5 mg/L; Crim Dell Creek: 5.2 ± 0.9 mg/L). For example, Hoback and Barnhart (1996) tested the effects of low dissolved oxygen on *G. pseudolimnaeus* by examining survival under hypoxic conditions. Negative physiological and behavioral

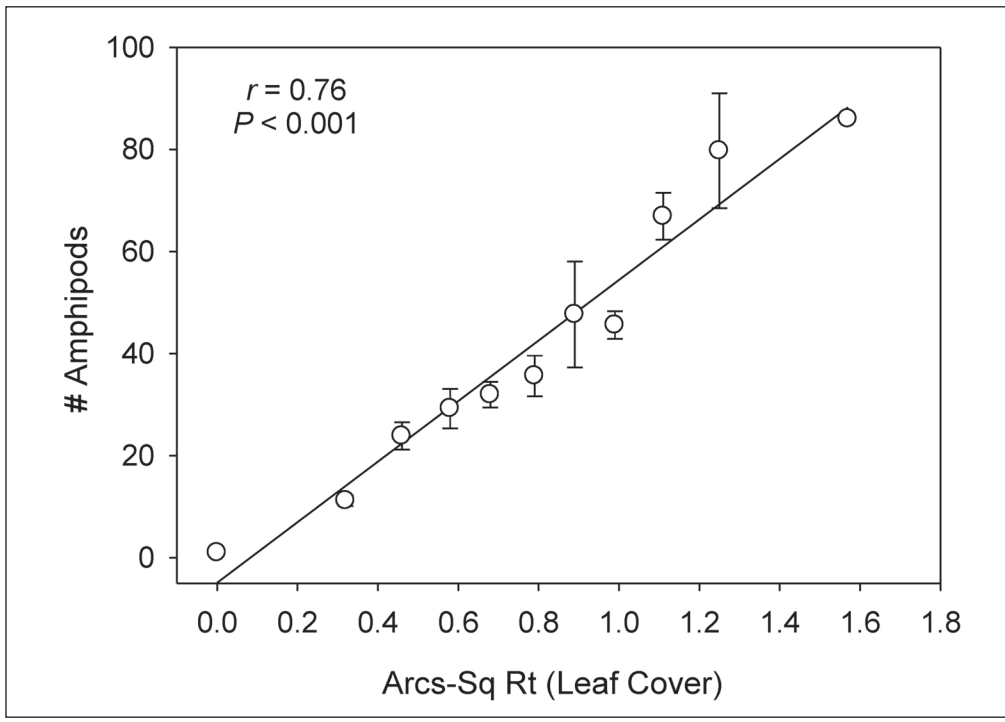

Figure 2. Relationship between leaf-litter coverage and amphipod abundance, from monthly sample collections of *Gammarus fasciatus* and *G. pseudolimnaeus* (sample *n* = 162). Percent cover data were arcsine square-root transformed prior to analysis.

effects, some of which directly affected reproduction, were observed to occur below 6 mg/L (Hoback and Barnhart 1996).

The literature also suggests that *G. pseudolimnaeus* would not be able to tolerate the high summer water temperatures in habitats occupied by *G. fasciatus* (Lake Matoaka: 26.5 ± 0.3 °C, Crim Dell Creek: 25.3 ± 0.5 °C; Paper Mill Creek: 25.8 ± 0.2 °C). For example, Smith (1973) found that *G. pseudolimnaeus* could only tolerate temperatures in the range of 21–26 °C for brief periods. Peak reproduction of *G. pseudolimnaeus* occurs at 18 °C, with higher temperatures resulting in the production of fewer eggs (Smith 1973). Lake Matoaka, Crim Dell Creek, and Paper Mill Creek would not be able to sustain ecologically significant populations of *G. pseudolimnaeus* because of this physiological constraint. Hynes and Harper (1972) reported a similar temperature restriction on the distribution of *Gammarus lacustris limnaeus* Smith along the entire length of a spring-fed stream in Ontario. The species was absent from the connected lake and its outflow, where summer temperatures rose into a range generally avoided by *G. lacustris limnaeus* (Hynes and Harper 1972).

Although the absence of *G. pseudolimnaeus* from some of the habitats we studied may be ascribed to reduced water quality, the restriction of *G. fasciatus* to the same lower-quality waters may be ascribed to biotic interaction. MacNeil et al. (2000) observed similar, mutually exclusive distributions of *Gammarus* spp. and *Crangonyx pseudogracilis* Bousfield within two river systems in Ireland, and concluded *Gammarus* spp. precluded *Crangonyx pseudogracilis* from higher quality habitats. We observed strong seasonal variation in stream leaf litter that serves as both food and shelter for amphipods, but we saw no evidence suggesting that differences in the quantity or quality of this food resource (Gee 1988) could account for the differential distribution of the species. However, amphipods may compete for resources (Van Dolah 1978), and many gammarids are predatory or cannibalistic, with larger individuals typically consuming small individuals (McGrath et al. 2007, Polis 1981). Dick et al. (1990) and Dick and Elwood (1992) used mutual, but differential predation to describe the elimination of *G. duebeni celticus* (Stock & Pinkster) from certain habitats by *Gammarus pulex*. Although interspecific predation between *G. pseudolimnaeus* and *G. fasciatus* has not been documented in the field, size-asymmetric, intraspecific predation has been observed in laboratory settings (L. Postaski, pers. observ.). We hypothesize that habitat partitioning between species is achieved by interspecific interactions that displace *G. fasciatus* from high-quality habitats occupied by *G. pseudolimnaeus* and restrict *G. fasciatus* distribution to habitats with lower water quality.

Timing of reproduction

The relative percentage of adult and juvenile *G. pseudolimnaeus* in stream samples did not vary significantly throughout the year (chi-square goodness of fit: $P > 0.05$), with PCMG pairs found in each sample every month (Fig. 3). In contrast, only juvenile *G. fasciatus* occurred in all samples throughout the year (Fig. 4); adult *G. fasciatus* were found every month except September and October. The percentage

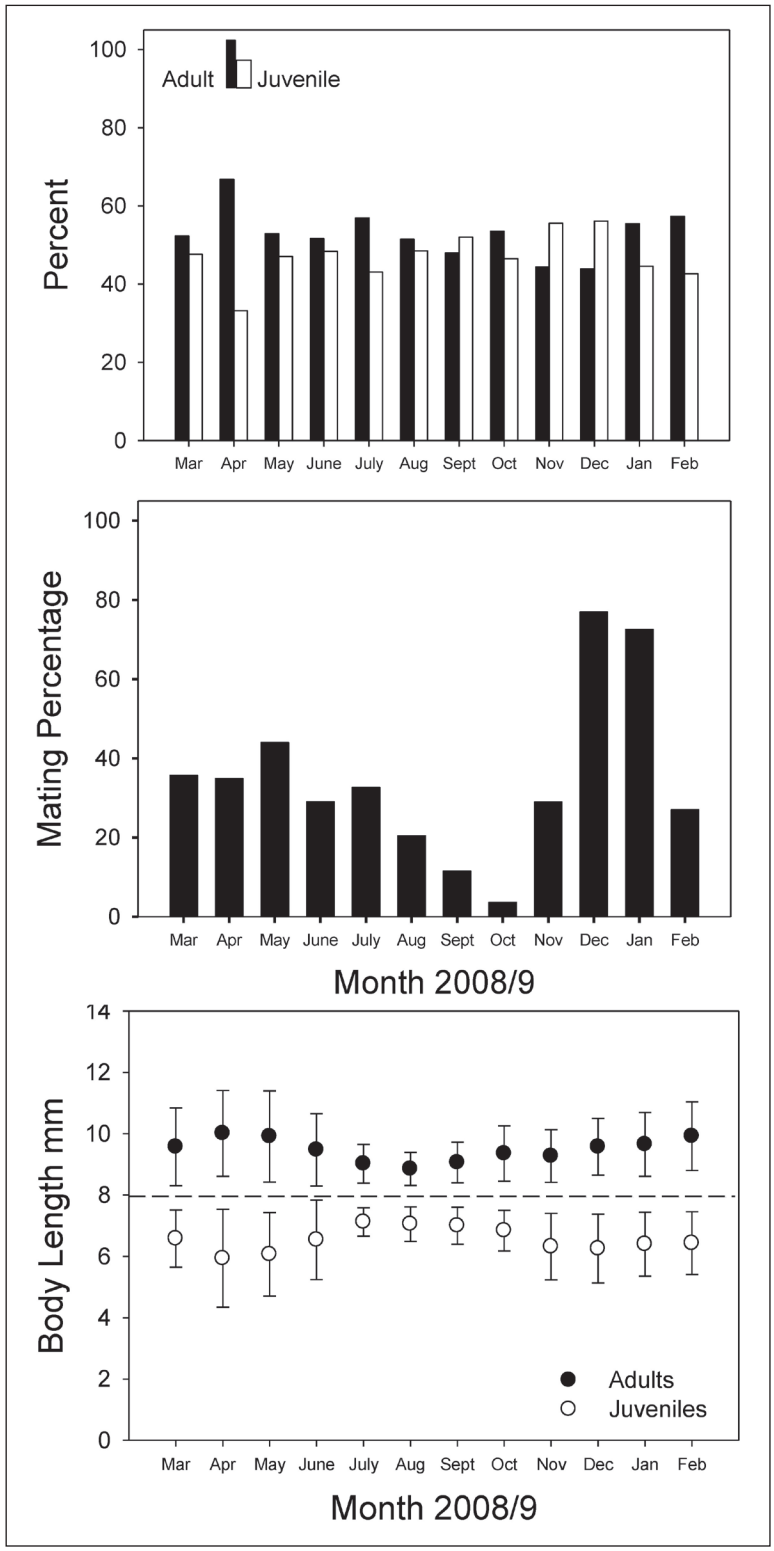

Figure 3. Structure of *Gammarus pseudolimnaeus* populations in southeastern Virginia streams. Top panel: Monthly relative percentage of adults and juveniles. Middle panel: Monthly percentage of adults forming pre-copulatory mate-guarding pairs. Bottom panel: Monthly size distribution of adults and juveniles.

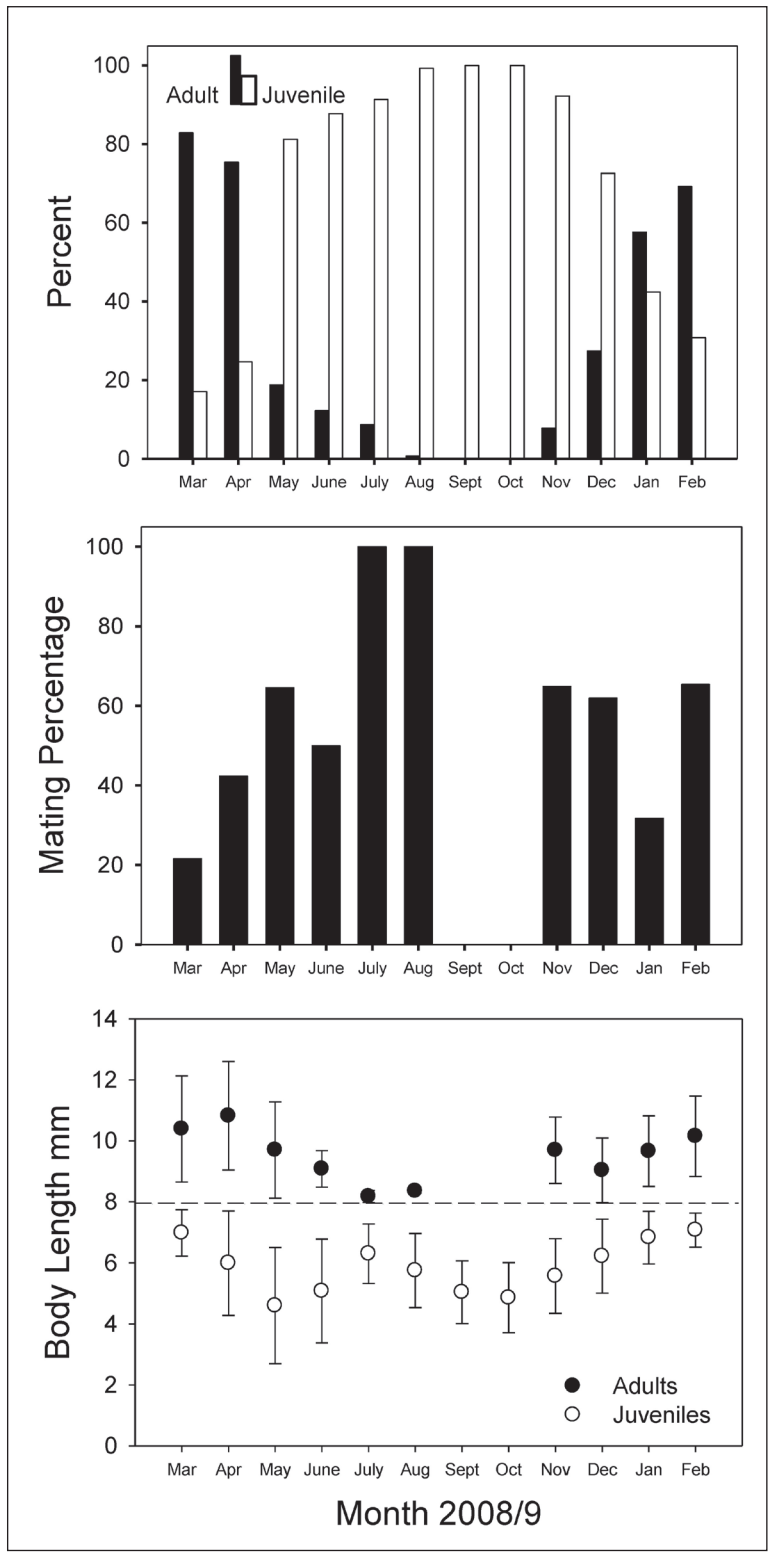

Figure 4. Structure of *Gammarus fasciatus* populations in southeastern Virginia streams. Top panel: Monthly relative percentage of adults and juveniles. Middle panel: Monthly percentage of adults forming pre-copulatory mate-guarding pairs. Bottom panel: Monthly size distribution of adults and juveniles.

of mating adult *G. fasciatus* increased from March through August (Fig. 4). In July and August, all adults collected were found in mating pairs. In September and October, however, no adults were found in mating pairs. The relative percentage of adult and juvenile *G. fasciatus* present in the population varied significantly throughout the year (Fig. 4; chi-square goodness of fit: $P < 0.05$). Populations of *G. fasciatus* were dominated by very small individuals (mean body length = 2.2 mm) that were burying into the sediment collected in June from Lake Matoaka.

A high percentage of PCMG pairs suggested a peak in reproductive activity of *G. pseudolimnaeus* during the coldest months of the year (December and January; Fig. 3). Kostalos (1979) similarly reported an increased occurrence of PCMG pairs of *Gammarus minus* Say during the coldest months (December, January, and February) in a small Pennsylvania stream. In addition to the occurrence of PCMG pairs all year, we also observed fairly equal numbers of adults and juveniles throughout the year (Fig. 3), suggesting that the population of *G. pseudolimnaeus* is continuously replenished. The continuous reproduction we observed is evidence that life history of *G. pseudolimnaeus* in southeastern VA differs from what has been observed farther north, where reproductive periods occur between mid-January and early fall (Hynes and Harper 1972, Miller 1982).

Previous studies have documented *G. fasciatus* reproducing from March and April through September and November (Bousfield 1973, Hynes 1955). Based on the presence of PCMG pairs, we found reproductive activity of *G. fasciatus* occurring from November to August with an abrupt cessation in reproductive activity from September through October, concomitant with the decline and subsequent disappearance of adults from the population during these months (Fig. 4). Interestingly, as the percentage of adult *G. fasciatus* decreased, the percentage of PCMG pairing increased, suggesting male *G. fasciatus* were spending more time mate-guarding to ensure reproductive success—a strategy used by Crustacea as the rate at which females are encountered decreases (Jormalainen 1998).

Conclusions

We confirmed the disjunct occurrence of *G. pseudolimnaeus* in southeastern VA. *Gammarus fasciatus* and *G. pseudolimnaeus* exhibit non-overlapping distributions in six streams from this region. *Gammarus pseudolimnaeus* occupies cool, spring-fed streams with high water quality, whereas *G. fasciatus* occupies relatively warm, less-oxygenated waters. Although typically given a higher tolerance value for stream conditions (e.g., Bode et al. 1996, Maxted et al. 2000), *Gammarus fasciatus* should be able to survive the physicochemical conditions where *G. pseudolimnaeus*—with a lower tolerance value (Hilsenhoff 1987)—occurs, but differences in life history may convey a competitive advantage to *G. pseudolimnaeus*. *Gammarus fasciatus* populations are dominated by juveniles with few to no adults in September and October, whereas adult *G. pseudolimnaeus* are present and reproduce year-round. Whether via more efficient resource exploitation, interference competition, or interspecific predation (Dick et al. 1993), the outcome of biotic interaction is that the species partition habitats, with *G. pseudolimnaeus* occupying higher-quality streams.

Acknowledgments

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