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Life history and ecology of the freshwater amphipods *Gammarus pseudolimnaeus*
and *Gammarus fasciatus* in southeastern Virginia

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A Thesis presented to the Graduate Faculty
of the College of William and Mary in Candidacy for the Degree of
Master of Science

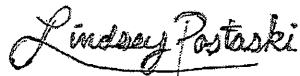
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Lindsey L. Postaski

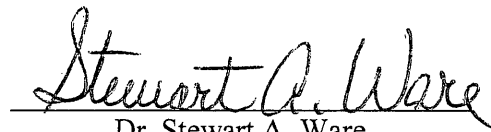
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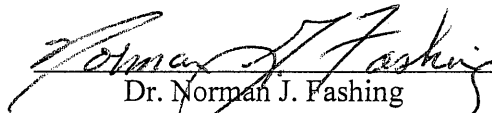
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ABSTRACT PAGE

The freshwater amphipod *Gammarus fasciatus* and a population that keys to *Gammarus pseudolimnaeus* are broadly sympatric in southeastern Virginia. By documenting the successful establishment of mate-guarding between inter-population individuals collected from Virginia and New York, I showed that this Virginia population is *G. pseudolimnaeus*, strongly disjunct from the previously described range in the Great Lakes drainage basin. From the results of my sampling in SE Virginia, *G. pseudolimnaeus* appears restricted to lotic habitats, usually high-quality (non-eutrophic) first order streams. *Gammarus fasciatus*, however, occurs in lakes and streams that are typically degraded (eutrophic) and does not co-occur with *G. pseudolimnaeus* in high quality habitat. I hypothesize that *G. pseudolimnaeus* outcompetes *G. fasciatus* in high quality areas, but cannot tolerate the higher temperatures where *G. fasciatus* occurs. *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 very small (~ 2 mm in length) individuals buried in the substrate. These smaller individuals must then compete with adult *G. pseudolimnaeus*. I hypothesize that this life cycle is competitively disadvantageous in the presence of *G. pseudolimnaeus*, perhaps accounting in part for the absence of *G. fasciatus* when *G. pseudolimnaeus* is present.

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INTRODUCTION

The family Gammaridae is the largest and most diverse of the eighty families that make up the order Amphipoda (Bousfield 1977). Although gammarids are found in both marine and freshwater habitats, it is the only group of amphipods that has occupied continental freshwaters on a broad basis (Holsinger 1976). The genus *Gammarus* is composed of numerous species widely distributed throughout the northern hemisphere (Holsinger 1976; Appendices B, D). In general, the majority of gammarids are found in smaller bodies of water, including streams, rivers, and lakes and generally occur in relatively high quality waters (Holsinger 1972, MacNeil *et al.* 2001, Rinderhagen *et al.* 2000).

Gammarids are an ecologically important group of benthic crustaceans. With densities that may exceed 10,000/m² (Smith 2001), they are important in 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). Within the eastern United States, *G. pseudolimnaeus* and *G. fasciatus* are two of the four most commonly collected amphipods (Smith 2001).

Gammarus pseudolimnaeus is widely distributed in the Mississippi drainage basin, as well as the southwestern St. Lawrence system, from Texas and Arkansas north to Wisconsin, Ontario and western Quebec (Bousfield 1958, Holsinger 1976; Appendices B, C). Occurrences also include three localities in southwestern Massachusetts¹

¹ These localities represent the southeastern range limit along the Atlantic seaboard and are possibly glacial relict populations (Massachusetts Division of Fisheries and Wildlife 2008).

(Massachusetts Division of Fisheries and Wildlife 2008). Throughout its range, *G. pseudolimnaeus* occupies large rivers, lakes, and ponds (Bousfield 1958). For example, *G. pseudolimnaeus* has been documented in spring-fed ponds² (20-40 cm deep) in Genesee, Wisconsin (Tarutis et al. 2005), the Credit River near Belfountain, Ontario (12-15 m wide) (Marchant and Hynes 1981, Bärlocher and Kendrick 1975), and in Lake Taneycomo³, a man-made reservoir on the White River in Taney County, Missouri (Missouri Department of Natural Resources Water Protection Program 2010).

Gammarus fasciatus occur sympatrically with *G. pseudolimnaeus* in the Great Lakes region of the United States (Holsinger 1972; Appendices B, D). *Gammarus fasciatus* occupies the St. Lawrence, Hudson, Delaware, and Chesapeake drainage systems (Bousfield 1958). Throughout its range, *G. fasciatus* primarily inhabits lakes and slow moving, often turbid rivers (Bousfield 1958); however, it also occurs in springs and small streams, especially in the southern part of its range (Holsinger 1976).

Gammarus pseudolimnaeus has not previously been documented to occur in southeastern Virginia; however, individuals collected from numerous isolated populations have been determined to be *G. pseudolimnaeus* based on existing keys (Holsinger 1972). Little is known about the passive transport of amphipods from one drainage system to another. Amphipods are not generally adapted to withstand drought and other adverse environmental conditions (Smith 2001). Some proposed dispersal

² *Gammarus pseudolimnaeus* was collected from two spring fed ponds in Genesee, Wisconsin where temperatures of the ponds ranged from 10.6-12.6°C and between September and November 2002 dissolved oxygen ranged from 7.7-8.6ppm (Tarutis et al. 2005).

³ Lake Taneycomo is approximately 2000 surface acres in size. Lake Taneycomo has the characteristics of both a river and a lake. It is reported to sustain lake temperatures between 45-55°F from May through December though periodic high water temperature and low dissolved oxygen (<6mg/L) conditions have documented. *Gammarus pseudolimnaeus* was introduced into Lake Taneycomo in 1961 (Missouri Department of Natural Resources Water Protection Program 2010).

methods include transport on the “feet of ducks” (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) however, evidence for each mechanism is anecdotal with little quantitative information available.

Regardless of dispersal mechanism, preliminary observations suggest that *G. pseudolimnaeus* does occur in southeastern Virginia, occurring sympatrically with *G. fasciatus*, but exhibiting a non-overlapping local distribution with it. Abiotic factors such as temperature (Smith 1973, Sprague 1963) and dissolved oxygen (Rees 1972) influence local gammarid distributions. For example, Rees (1972) examined the influence of substratum, oxygen concentration, and current velocity on the distribution of *G. pseudolimnaeus*. He concluded that *G. pseudolimnaeus* may have evolved a behavioral response to particle size (substratum) and the associated conditions (interstitial oxygen concentration and current velocity), possibly affecting its abundance and distribution.

Biotic factors such as, food availability (Dobson and Hildrew 1992) and predation (Dick *et al.* 1993, 1999, Holomuzki and Hoyle 1990, Van Dolah 1978, González and Burkart 2004) also influence local gammarid distribution. For example, Dick *et al.* (1993) demonstrated the influence of cannibalism and mutual predation on the distribution of *Gammarus pulex* and *Gammarus duebeni celticus*, concluding that the superior ability of *G. pulex* to prey on molted *G. d. celticus* may explain the replacement of the latter species by the former.

Smith (2001), Bousfield (1958) and Holsinger (1969, 1972), have compiled general descriptions of the ecology of *G. pseudolimnaeus* and *G. fasciatus*; specific descriptions of habitat distributions between *G. pseudolimnaeus* and *G. fasciatus* are

scattered throughout the aquatic literature. For example, *G. pseudolimnaeus* is a lotic amphipod (Williams and More 1985, Olyslager and Williams 1993) but is also found in some lentic waters (Kulesza and Holomuzki 2006, Grigorovich *et al.* 2005). *Gammarus pseudolimnaeus* has been collected from eutrophic, shallow wetlands (Kulesza and Holomuzki 2006) and other marshes and open water shorelines in the Great Lakes region (Grigorovich *et al.* 2005). No previously published information is available on *G. pseudolimnaeus* and *G. fasciatus* distribution in southeastern Virginia.

Similar the variable information on habitat distribution, aspects of the life histories of *G. pseudolimnaeus* and *G. fasciatus*, vary by source and geographic location (Hynes 1955, Hynes and Harper 1972, Waters 1981, Clemens 1950, Miller 1982). For example, according to Hynes and Harper (1972) *G. pseudolimnaeus* reproduces from February through July⁴ while Miller (1982) describes a longer reproductive period lasting from mid-January through September⁵. Waters (1981) describes an annual life cycle of *G. pseudolimnaeus* that is similar to Hynes and Harper (1972) in that reproductive activity virtually ceases in winter months⁶. 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* have been conducted in the northern portion of their distributional ranges; no studies have documented the life history of *G. fasciatus*, nor the more recently discovered *G. pseudolimnaeus* there.

⁴ Collections by Hynes and Harper (1972) were from the Credit River at Credit Forks in southern Ontario.

⁵ Collections by Miller (1982) were from a small, shallow, high gradient, spring-fed stream, named Parfrey's Glen Creek in Sauk County Wisconsin.

⁶ Collections by Waters (1981) were from Valley Creek, a small tributary of the St. Croix River in east-central Minnesota.

My study has three main objectives. The first objective is to document the occurrence of *G. pseudolimnaeus* in southeastern Virginia. To meet this objective, species confirmation will be based on reproductive behavior. The second objective is to document the distribution of *G. pseudolimnaeus* and *G. fasciatus* in a small Virginia watershed and describe the physicochemical conditions in which these species occur. The third objective is to document the life history of *G. pseudolimnaeus* and *G. fasciatus* and to examine possible correlations between life history features and physicochemical conditions influencing the distribution of *G. pseudolimnaeus* and *G. fasciatus*.

METHODS

This study includes three components of the life history and ecology of the freshwater gammarid amphipods in southeastern Virginia. First, I document the apparent disjunct occurrence of *G. pseudolimnaeus* based on mate-guarding pair formation between individuals from Virginia and New York. I then compare the environments occupied by *G. pseudolimnaeus* and its congener, *G. fasciatus*. Finally, I compare the timing of reproduction by the two species as a possible factor influencing the outcome of interspecific competition for higher-quality stream habitat.

Site Description

All studies were completed in freshwater ponds and streams in southeastern Virginia. Lake Matoaka is a 16 hectare, hyper-eutrophic lake located on the College of William and Mary campus in Williamsburg, Virginia (Appendix A). The lake is fed by five small streams: Berkeley Creek, Pogonia Creek, Strawberry Creek, College Creek and Crim Dell Creek. The first three creeks are perennial, first-order streams that enter from the

forested, western portion of the watershed (Appendix A). These arise as springs in which dissolved oxygen typically is near saturation (Zehmer et al. 2002) and temperature does not exceed 25°C (L. Postaski, College of William and Mary, unpubl. data). The primary source of organic matter in these streams is allochthonous material from the surrounding forest preserve (Mahon 1997). The most abundant invertebrate within these streams is the amphipod *G. pseudolimnaeus* (Zehmer et al. 2002).

Crim Dell Creek and College Creek run through the college campus and the city of Williamsburg, respectively. Both are significantly degraded, as evidenced by reduced dissolved oxygen levels, high turbidity from runoff of silty substrates, and low species diversity (L. Postaski, pers. obs.). Paper Mill Creek runs along part of the Colonial Parkway, a scenic parkway linking Jamestown, Williamsburg, and Yorktown, Virginia. Although the area is shielded from commercial development, the creek receives runoff from two golf courses upstream and is exposed to runoff from the impervious surface of the parkway. Over the year, water temperature in Paper Mill Creek, Crim Dell Creek and College Creek fluctuates more dramatically than in the streams from the western portion of the watershed. *Gammarus fasciatus* is the most abundant amphipod in these three streams.

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 strongly suggests that species are conspecific, formation of PCMG pairs between known and suspected *G. pseudolimnaeus* individuals was used to verify species occurrence in SE Virginia. Virginia amphipods were collected from Strawberry Creek using a hand-held aquarium net. New York amphipods were collected from Spring Creek, also a perennial first order stream, in the town of Caledonia (*see* Sutton 1995 for description). In each case, males were separated from local pre-copulatory mate-guarding (PCMG) pairs and transported to the other state. There, females were collected from PCMG pairs. Then, 5 foreign males and 1 local female were placed in a 12 cm x 12 cm plastic container with equal amounts of water from the respective original streams at a depth of 5 cm. Amphipods were observed until mate guarding occurred, and then the PCMG pair was transferred to another container of the same type and observed for 1 hr. With Virginia males in New York, 25 trials were conducted. Due to higher mortality of New York males in transport, 10 trials of New York males in Virginia were conducted. Twenty-five trials were also conducted using Virginia *G. pseudolimnaeus* and a closely related amphipod, *G. fasciatus*.

Gammarid amphipod distribution

I compared the environments of occurrence of gammarid amphipods in Berkeley Creek, Pogonia Creek, Strawberry Creek, Crim Dell Creek, and Paper Mill Creek. Each stream was sampled at upper, middle, and lower reaches. Along each reach, a random numbers table (1-10) was used to determine the distance (meters) traveled downstream to a sampling location. Samples were taken from the area with the largest amount of leaf litter within one meter of the randomly chosen sampling location. At Lake Matoaka, this same method was used along the shoreline. Amphipods were collected at each site using a metal cylinder (diameter = 20 cm). The cylinder was driven into the sediment and the percentage of leaf litter cover within the cylinder was estimated to the nearest 10% and recorded for each sample. 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. Sampling was continued until three consecutive sweeps contained no amphipods. Amphipods were preserved in 70% ethanol for identification.

Dissolved oxygen, temperature, conductivity, and calcium were also recorded mid-stream at each site. Both biological and environmental sampling was carried out at each site during June 2008, November 2008, and February 2009. Pearson correlation procedures were used to evaluate relationships between amphipod abundance and percent leaf litter coverage. Amphipod abundance was plotted to show trends between abundance and percentage of leaf litter cover.

Timing of reproduction

Life history information was determined based on the results of year-long sampling for gammarid amphipods in local streams. Amphipods were collected from within the Lake Matoaka watershed on the College of William and Mary campus in Williamsburg, Virginia (Appendix A). Samples were collected weekly from March 18, 2008 to March 16, 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 μ m mesh). Sampling ceased when a maximum of three net samples were taken, or collections yielded 100 individuals. All amphipods from the sweeps were collected even if sweeps yielded > 100 individuals. Amphipods were identified to confirm species using existing taxonomic keys (Holsinger 1972, Smith 2001). Body length, from the tip of the telson to the base of the antennae, was measured using a micrometer (Appendix E, F). For each species in each sample, the number of amphipods engaged in PCMG was recorded.

Based on literature (Hynes and Harper 1972) and preliminary data, amphipods were categorized as adults (body length > 8.0 mm) or juveniles (body length < 8.0 mm) depending on body length. Hynes and Harper (1972) and Miller (1982) used a similar approach, size-grouping *G. pseudolimnaeus* adult (> 6 mm) and juvenile (< 6 mm) individuals. Hynes (1955) also size-grouped *G. fasciatus* adult (> 6 mm) and juvenile (< 6 mm) individuals. Although these studies used 6 mm as the dividing line, preliminary data suggested that 8 mm would be more appropriate to differentiate adults and juveniles for this study. In preliminary collections, mean body length of *G. fasciatus* PCMG individuals (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 would be an appropriate designation for adult *G. pseudolimnaeus* and *G. fasciatus*

Sampling in June 2009 resulted in very few *G. fasciatus*; sediment samples were collected from Lake Matoaka to locate smaller juvenile amphipods (~ 2 mm body length). Using a plastic scoop, a 500 cm³ sediment sample was collected from the top 1-4 cm of sediment. Samples were sorted and amphipods were preserved in 70% ethanol for measurement (note: the results of the sediment sampling were not combined with weekly amphipod data collected March 2008- March 2009).

RESULTS AND DISCUSSION

Documentation of *G. pseudolimnaeus*

In all Virginia/New York trials, a PCMG pair developed within 3 minutes and was sustained for the 1 hr observation period. This rapid occurrence of sustained PCMG behavior between New York and Virginia populations is strong evidence that the disjunct populations are conspecific. Zero PCMG pairs formed between *G. pseudolimnaeus* and *G. fasciatus*. The occurrence of possible interspecific PCMG in amphipods has not been well described, but it is known that the European species *Gammarus pulex* Linnaeus and *Gammarus duebeni* Lilljeborg will not form PCMG pairs (Dick and Elwood 1992), nor did *G. pseudolimnaeus* and *G. fasciatus* in previous field trials (G. Capelli, College of William and Mary, unpubl. data). As with mating systems in general, there has probably been strong selection to prevent inappropriate wasted effort. Pheromones are probably involved in amphipod signaling (Dunham 1978), which are species specific, and

interspecific morphological differences are probably sufficient to prevent PCMG as well (J. Holsinger, Old Dominion University, pers. comm.). Therefore, although documentation of viable offspring from interstate pairs would be fully conclusive, mate guarding provides strong evidence that they are conspecific.

That these disjunct populations are conspecific raises questions about the mechanism(s) by which *G. pseudolimnaeus* has colonized southeastern Virginia. Perhaps *G. pseudolimnaeus* was, at one time, much more widely distributed, both locally and probably regionally as well. Locally, most streams where *G. pseudolimnaeus* now occurs flow into either reservoirs or other streams with environmental conditions that are significantly different, e.g., silty substrates, higher summer temperatures, reduced oxygen, and other anthropogenic disturbances. Historically, however, present habitats would have connected to streams of similar high quality where *G. pseudolimnaeus* probably occurred.

On a regional scale, *G. pseudolimnaeus* is not known to occur within any other area of the Chesapeake Bay drainage except at the far northern end in New York as described, and possibly a population in a very small tributary of the Patuxent River in Maryland (G. Capelli, pers. obs.). It may be relevant however, that the entire drainage area from New York to Virginia was fresh water until the end of the last ice age about 15,000 years ago. Before then, the current Chesapeake Bay estuary system did not exist, and *G. pseudolimnaeus* may have occurred over a much larger geographic area, including down the East coast. (Larsen 1998). Stream habitats would have been both cooler and undisturbed compared to the present situation. If so, the current regional and local distribution in Virginia may reflect at least in part the forced retreat of *G. pseudolimnaeus*

in the face of increased salinity due to sea level rise and estuary formation, warming temperatures, and, most recently, general habitat degradation by humans.

Gammarid amphipod distribution

In comparing the distribution of the two gammarid amphipods in SE Virginia, I 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. Differences in temperature and dissolved oxygen measurements between sites containing *G. pseudolimnaeus* and *G. fasciatus* were noted and measurements of conductivity and calcium appear to be within tolerable ranges of both species (Table 1).

The abundance of *G. pseudolimnaeus* and *G. fasciatus* fluctuated over the sampling year. Abundance for both species was greatest in November (Table 1). This higher abundance may be connected to resource availability (i.e. detritus) in the streams, as the Pearson correlation revealed a positive correlation ($r = 0.729395$) between the number of amphipods ($n = 162$) and percent leaf litter coverage (Figure 1).

Month	Site	N GP	N GF	Mean Temp. (°C)	Mean D.O. (mg/L)	Mean Cond. (µS/cm)	Mean Ca. (mg/L)
June	Strawberry Creek	331	0	19.4 ± 1.5	8.9 ± 0.5	221.3 ± 30.8	125.7 ± 9.7
	Berkeley Creek	207	0	19.3 ± 1.6	8.9 ± 0.7	69.9 ± 32.4	25.7 ± 16.9
	Pogonia Creek	209	0	19.1 ± 0.8	8.9 ± 0.6	62 ± 33.9	38.3 ± 13.4
	Lake Matoaka	0	108	26.5 ± 0.3	3.02 ± 4.5	277 ± 20.6	111 ± 11.9
	Crim Dell Creek	0	219	25.3 ± 0.5	5.2 ± 0.9	757 ± 136.3	254.7 ± 17.0
	Paper Mill Creek	0	588	25.8 ± 0.2	8.1 ± 0.6	1050 ± 40.1	137 ± 48.5
November	Strawberry Creek	576	0	11.3 ± 2.3	9.6 ± 1.5	249.7 ± 32.0	193.2 ± 32.2
	Berkeley Creek	532	0	12.1 ± 1.0	8.8 ± 0.8	146.2 ± 57.5	39.5 ± 17.9
	Pogonia Creek	338	0	9.1 ± 0.5	9.5 ± 0.7	135.6 ± 28.8	43.8 ± 13.8
	Lake Matoaka	0	257	19.3 ± 2.9	7.9 ± 0.7	274.2 ± 18.6	117.3 ± 16.4
	Crim Dell Creek	0	367	12.2 ± 0.5	5.4 ± 1.0	758 ± 98.6	207 ± 59.8
	Paper Mill Creek	0	232	9.6 ± 2.9	9.1 ± 0.7	1180.6 ± 189.3	152.3 ± 27.0
February	Strawberry Creek	212	0	10.1 ± 1.8	8.9 ± 0.3	240 ± 28.7	141.8 ± 17.6
	Berkeley Creek	192	0	8.1 ± 1.2	9.0 ± 1.1	130.1 ± 26.9	34.4 ± 14.7
	Pogonia Creek	232	0	7.9 ± 1.2	8.8 ± 0.4	59.6 ± 26.4	48 ± 13.9
	Lake Matoaka	0	159	6.9 ± 1.2	11.6 ± 4.4	263 ± 42.3	105 ± 12.0
	Crim Dell Creek	0	207	8.9 ± 1.5	5.6 ± 1.1	597.8 ± 89.8	191.7 ± 56.6
	Paper Mill Creek	0	415	6.9 ± 1.9	7 ± 0.8	959.1 ± 281.0	153.6 ± 35.3

Table 1. Physiochemical summary of sample sites. Listed are number of *G. pseudolimnaeus* (N GP), number of *G. fasciatus* (N GF), mean temperature (Mean Temp.; °C), mean dissolved oxygen (Mean D.O.; mg/L), mean conductivity (Mean Cond.; µS/cm), and mean calcium (Mean Ca.; mg/L).

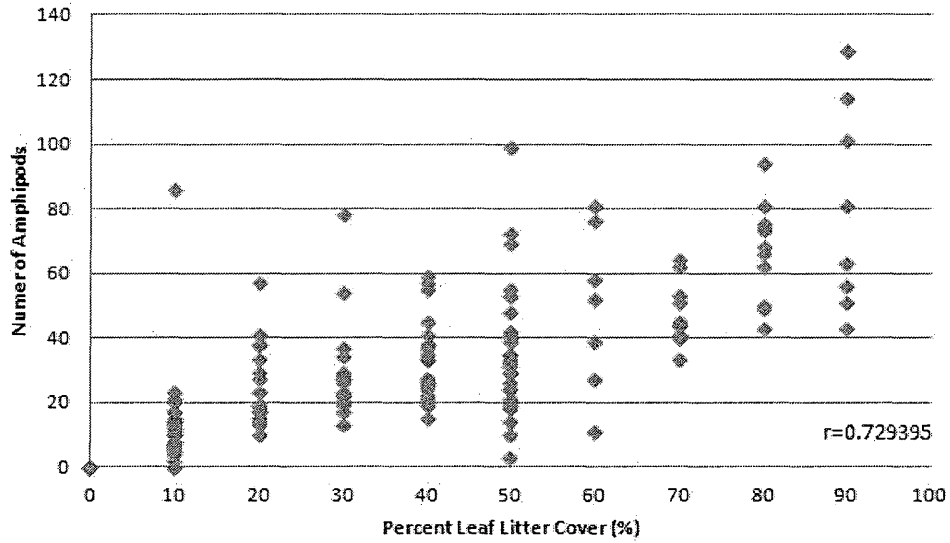


Figure 1. Correlation of amphipod abundance and leaf litter coverage. Pearson correlation displaying number of amphipods (n=162) collected in correlation with percentage leaf litter coverage ($r=0.729395$).

Although sources may commonly associate *G. fasciatus* with low water quality, it does not follow that this species is unable to colonize areas of higher water quality. In general, *G. fasciatus* is found to have broader and overlapping dissolved oxygen and temperature requirements than *G. pseudolimnaeus*; thus, it should be able to occupy similar habitats. Smith (1973) describes *G. fasciatus* as surviving well at temperatures between 10-30°C whereas *G. pseudolimnaeus* survives well at temperatures between 15-18°C. According to Smith's (1973) description, the broader tolerance range of *G. fasciatus* should be adequate for survival in the localities dominated by *G. pseudolimnaeus*.

Based off the literature, it seems possible that *G. fasciatus* could survive as well as *G. pseudolimnaeus* in areas where *G. pseudolimnaeus* predominates. In contrast, literature suggests that *G. pseudolimnaeus* would not be able to tolerate the low dissolved oxygen (Lake Matoaka: 3.02 ±4.5 mg/L; Crim Dell Creek: 5.2 ±0.9 mg/L) in summer months in areas where *G. fasciatus* predominates. For example, Hoback and Barnhart (1996) tested the effects of low dissolved oxygen on *G. pseudolimnaeus* by examining survival in anoxia and lethally low dissolved oxygen concentrations. Physiological and behavioral effects, some of which directly affected reproduction, were observed to occur below 6 mg/L (Hoback and Barnhart 1996).

Literature also suggests that *G. pseudolimnaeus* would not be able to tolerate the high water temperatures (Lake Matoaka: 26.5 ±0.3 °C, Crim Dell Creek: 25.3 ±0.5°C; Paper Mill Creek: 25.8±0.2 °C) in the summer months in *G. fasciatus* areas. For example, Smith (1973) notes that *G. pseudolimnaeus* can 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). Overall, the high summer temperatures of Lake Matoaka, Crim Dell Creek, and Paper Mill Creek would not be able to sustain ecologically significant populations of *G. pseudolimnaeus*. Hynes and Harper (1972) reported a situation, similar to the distribution of *G. pseudolimnaeus* in the Lake Matoaka watershed, where *Gammarus lacustris limnaeus* occurred the entire length of a spring-fed stream (Alton Stream, Credit River system, Ontario) yet was absent from the connected lake and its outflow. Hynes and Harper (1972) attributed the restricted distribution to summer temperatures which rose above 13°C, a temperature range generally avoided by *G. lacustris limnaeus*.

Though the absence of *G. pseudolimnaeus* in Crim Dell creek may be ascribed to water quality, the restriction of *G. fasciatus* to lower quality waters cannot be explained by physicochemical conditions; thus, it seems reasonable to believe that the distribution of *G. fasciatus* may be ascribed to a biotic factor. Biotic factors, including resource availability and interspecific competition, have been documented to influence amphipod populations (Gee 1988). In this study, both *G. pseudolimnaeus* and *G. fasciatus* increased in abundance in November (Table 1; Figure 1) when the amount of detritus, a food source, in the streams was highest. Although the amount of detritus peaked in the autumn months, detritus was present in each location throughout the entire year; this suggests that resource availability was not a large factor in limiting the distribution of *G. fasciatus*.

Competition is another biotic factor used to explain amphipod distributions (Van Dolah 1978). Although amphipods are generally assumed to be shredders or collectors-gatherers (Cummins 1973), many gammarids are predaceous or cannibalistic (McGrath *et*

al. 2007). In predaceous species, larger individuals typically consume small individuals (McGrath *et al.* 2007; Polis 1981). For example, Dick *et al.* (1990) and Dick and Elwood (1992) uses mutual, but differential, predation to describe the elimination of *G. duebeni celticus* by *Gammarus pulex*. Although interspecific competition between *G. pseudolimnaeus* and *G. fasciatus* has not been documented, laboratory studies suggest that size-asymmetric intraspecific predation occurs among these species (L. Postaski, unpublished data); thus, it seems likely that interspecific predation may occur.

Overall, it appears that the distribution of *G. pseudolimnaeus* is limited by physicochemical conditions while some form of biotic factor, presumably competition, between *G. pseudolimnaeus* and *G. fasciatus* is limiting the realized niche of *G. fasciatus*. MacNeil *et al.* (2000) observed similar mutually exclusive distributions of *Gammarus* spp. and *Crangonyx pseudogracilis* within two river systems in Ireland. It was observed that *Gammarus* spp. dominated stretches of well oxygenated, high quality water, whereas *C. pseudogracilis* dominated stretches of poorly oxygenated, lower quality water. MacNeil *et al.* (2000) observed that physicochemical requirements limited the movement of *Gammarus* spp. into *C. pseudogracilis* area, whereas *C. pseudogracilis* was limited by some form of biotic interaction with *Gammarus* spp.

Timing of reproduction

Adult and juvenile *G. pseudolimnaeus* occurred in all stream samples throughout the year (Figure 2-A) with precopulatory pairs found in each sample (Figure 2-B). In contrast, only juvenile *G. fasciatus* occurred in all samples throughout the year (Figure 3-A); adult *G. fasciatus* were found every month except September and October. The percentage of

mating adult *G. fasciatus* increased from March through August (Figure 3-B). In July and August all adults collected were found in mating pairs. In September and October no adults were found in mating pairs. The percentage of adult *G. fasciatus* present in the population decreased from March through August and increased from November through March (Figure 3-A).

Though the percentage of juvenile *G. fasciatus* was high in June 2009 (Figure 3-A), the actual number of individuals collected was low. June sediment sampling of *G. fasciatus* from Lake Matoaka confirmed that during that time, populations were being dominated by very small individuals (mean body length = 2.2 mm) which were burying into the sediment.

The life history of *G. pseudolimnaeus* in southeastern Virginia differs from life history studies in northern parts of its range. Previous studies farther north have shown reproductive periods between mid-January and early fall (Miller 1982, Hynes and Harper 1972) while this study shows a longer continuous reproductive season, evidenced by the occurrence of PCMG pairs in all months (Figure 2-B). This continuous reproductive season is also exhibited in the population structure; throughout the year there are fairly equal numbers of adults and juveniles, suggesting that the population of *G. pseudolimnaeus* is constantly being replenished (Figure 2-A).

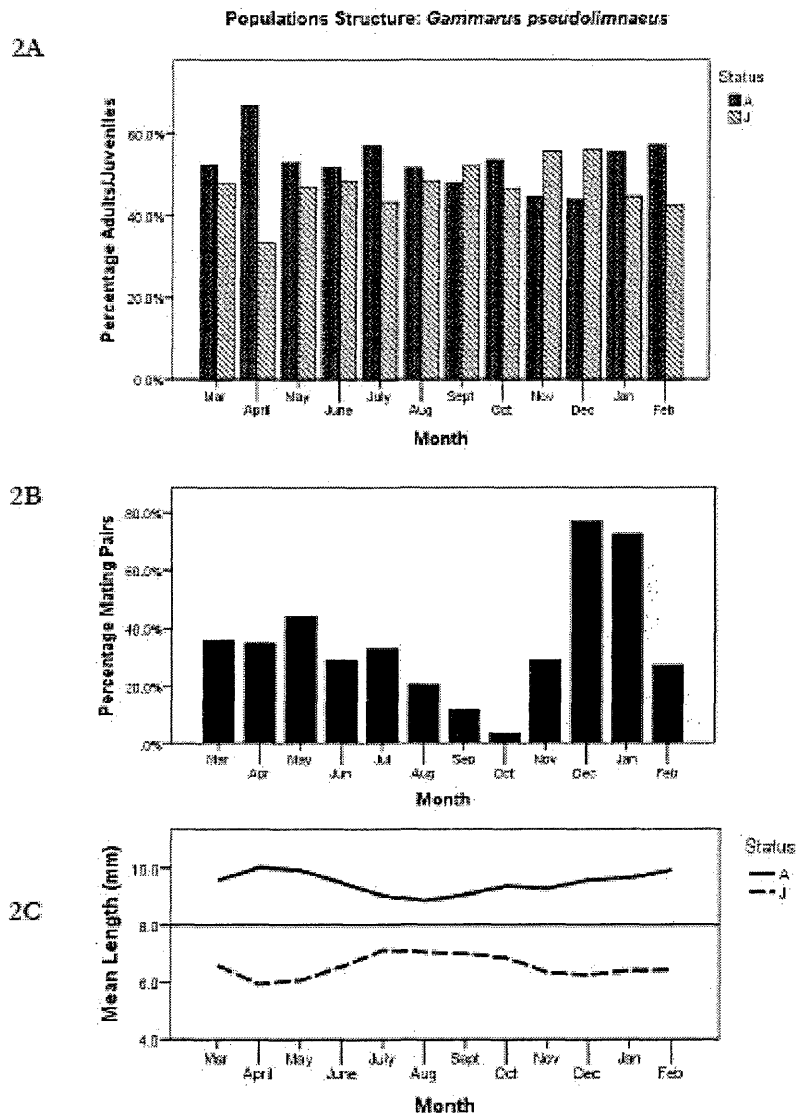


Figure 2. *Figure 2A:* Monthly population structure of *G. pseudolimnaeus* displaying percentage of adult amphipods (double hash) and percentage of juvenile amphipods (single hash). *Figure 2B:* Monthly percentage of collected adult *G. pseudolimnaeus* in mating pairs. *Figure 2C:* Monthly mean body length (mm) of adult (>3.0mm; solid line) and juvenile (<3.0mm; dashed line) *G. pseudolimnaeus*.

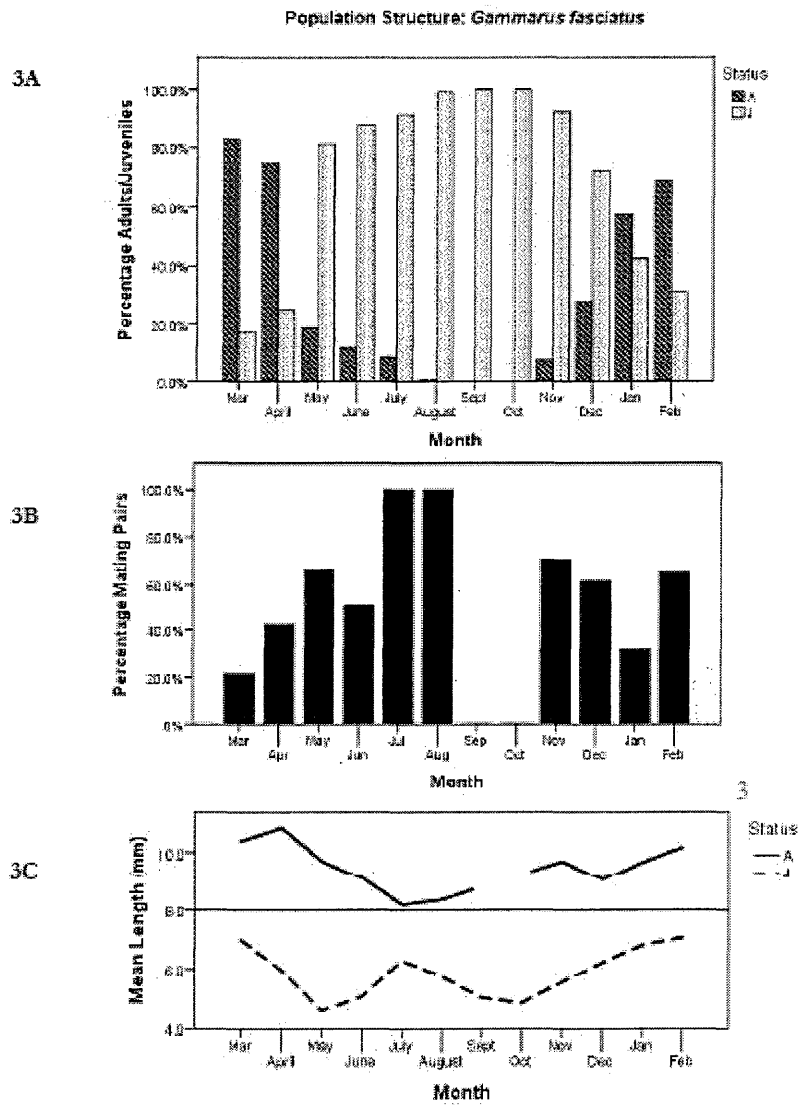


Figure 3. *Figure 3A:* Monthly population structure of *G. fasciatus* displaying percentage of adult amphipods (single hashed) and percentage of juvenile amphipods (double hash). *Figure 3B:* Monthly percentage of collected adult *G. fasciatus* in mating pairs. *Figure 3C:* Monthly mean body length (mm) of adult (>8.0mm; solid line) and juvenile (<8.0mm; dashed line) *G. fasciatus*.

Although the breeding period in Virginia occurs throughout the entire year, there is a distinct peak in reproductive activity during the coldest months (December and January), evidenced by the large numbers of *G. pseudolimnaeus* in PCMG in the stream at this time. This observance is similar to Kostalos (1979) who reported an increased occurrence of PCMG in *Gammarus minus* during the coldest months (December, January, and February) in a small Pennsylvania stream (Falls Ravine Creek, Pittsburgh, Pennsylvania).

The lengthened reproductive season and peak in reproductive activity may be correlated with resource availability. Frequently, organisms may adjust their life histories according to seasonally available resources. For example, both *Gammarus oceanicus* and *Gammarus salinus* time the release of broods in correlation with blooms of ephemeral algae, allowing newly hatched juveniles to have access to those abundant resources (Skadsheim 1984). It is possible however, that cold stream temperature in December and January is extending the duration of PCMG (G. Capelli, unpublished data) and that the apparent increase in PCMG (Figure 2-B) may be the result of the extended duration of PCMG as influenced by low temperature, rather than an actual increase in rate of reproduction.

Previous studies have documented *G. fasciatus* reproducing from March-April through September-November (Bousfield 1973, Hynes 1955). In contrast, this study shows reproductive activity (PCMG) of *G. fasciatus* occurring from November to August with an abrupt cessation in reproduction activity from September through October (Figure 2-B). The abrupt cessation in reproductive activity is linked to the decline and

subsequent disappearance of adults from the population during these months (Figure 3-A; Table 2).

As the percentage of adult *G. fasciatus* decreased, the percentage of PCMG increased (Figure 3-A, 3-B). It seems likely that as mates are becoming scarce, male *G. fasciatus* may be spending more time in PCMG to ensure reproductive success. This type of strategy is common among Crustacea; in general, males invest more time in PCMG as the encounter rate of females decreases (Jormalainen 1998).

Though the percentage of juvenile *G. fasciatus* was high in June 2009 (Figure 3-A), the actual number of individuals collected was low. June sediment sampling of *G. fasciatus* from Lake Matoaka confirmed that during that time, populations were being dominated by very small (~ 2 mm) individuals which were burying into the sediment. These juveniles are likely the offspring of the adults in July and August when the percentage of PCMG was highest. According to this timeline, female *G. fasciatus* would brood eggs for 3-4 weeks and individuals would reach maturity after six weeks (Hynes 1955). This cohort sustains the population during September and October when adults are absent from the population.

It is important to note that the life history of *G. fasciatus* may be competitively disadvantageous in the presence of *G. pseudolimnaeus*. Adult *G. pseudolimnaeus* occur year-round; in contrast, adult *G. fasciatus* diminish September through October, leaving only immature individuals present. During months when *G. fasciatus* populations are predominated by small, immature individuals, they may be outcompeted by larger, adult *G. pseudolimnaeus*. As with most Crustacea, the larger individuals of a species are often more aggressive and therefore dominate smaller individuals (Wellborn 1994).

Month	<i>G. pseudolimnaeus</i>		<i>G. fasciatus</i>	
	Adult	Juvenile	Adult	Juvenile
Mar	9.6	6.6	10.4	7
April	10	5.9	10.8	6
May	9.9	6.1	9.7	4.6
Jun	9.5	6.5	9.1	5.1
Jul	9	7.1	8.2	6.3
Aug	8.8	7.1	8.4	5.8
Sep	9.1	7	-	5
Oct	9.3	6.8	-	4.9
Nov	9.3	6.3	9.7	5.6
Dec	9.6	6.3	9	6.2
Jan	9.6	6.4	9.7	6.8
Feb	9.9	6.4	10.2	7.1

Table 2. List of sample months, monthly mean body lengths of adult and juvenile *G. pseudolimnaeus*, and monthly mean body lengths (mm) of adult and juvenile *G. fasciatus*.

For both *G. pseudolimnaeus* and *G. fasciatus*, the adult mean body lengths decreased during the summer (Figure 2-C). This is consistent with findings reported by Hynes (1955). Typically, warmer temperatures speed maturation rates, resulting in smaller, sexually mature individuals. Growth may also be restricted by resource availability; for example, Gee (1988) showed that the growth of *G. pulex* was restricted in late summer by low food availability.

Conclusions

Although closely related, *G. pseudolimnaeus* and *G. fasciatus* have very different life histories. As previously mentioned, these differences may be regulated by environmental condition (i.e., resource availability, temperature). *Gammarus pseudolimnaeus* occupies cool, spring-fed, high quality streams while *G. fasciatus* occupies relatively warm, eutrophic waters. In southeastern Virginia, *G. pseudolimnaeus* and *G. fasciatus* occur sympatrically (L. Postaski, unpublished data) and appear to be locally restricted in regard to habitat in which they occur. *Gammarus pseudolimnaeus* occupies Strawberry Creek, Berkeley Creek, and Pogonia Creek, three pristine streams that feed into Lake Matoaka, while *G. fasciatus* occupies Lake Matoaka, Crim Dell Creek, a much disturbed tributary of the Lake, and Paper Mill Creek, a non-pristine stream in an adjacent watershed. It appears that *G. pseudolimnaeus* is restricted to its three streams due to high summer temperatures in Lake Matoaka. *Gammarus fasciatus* should be able to survive the physicochemical conditions of Strawberry Creek, Berkeley Creek, and Pogonia Creek but does not occupy these streams presumably because it is excluded by *G. pseudolimnaeus*. It seems likely that *G. pseudolimnaeus* may have a competitive advantage over *G. fasciatus* as a result of life history differences. During the summer, the population of *G. fasciatus* is dominated by juveniles with few to no adults from August to October. In contrast, adult *G. pseudolimnaeus* are present year-round. Adult *G. pseudolimnaeus* may be capable of outcompeting juvenile *G. fasciatus* when the *G. fasciatus* population is lacking adults. Whether the exact mechanism is more efficient resource exploitation, interference competition or interspecific predation (Dick *et al.* 1993) is yet to be determined.

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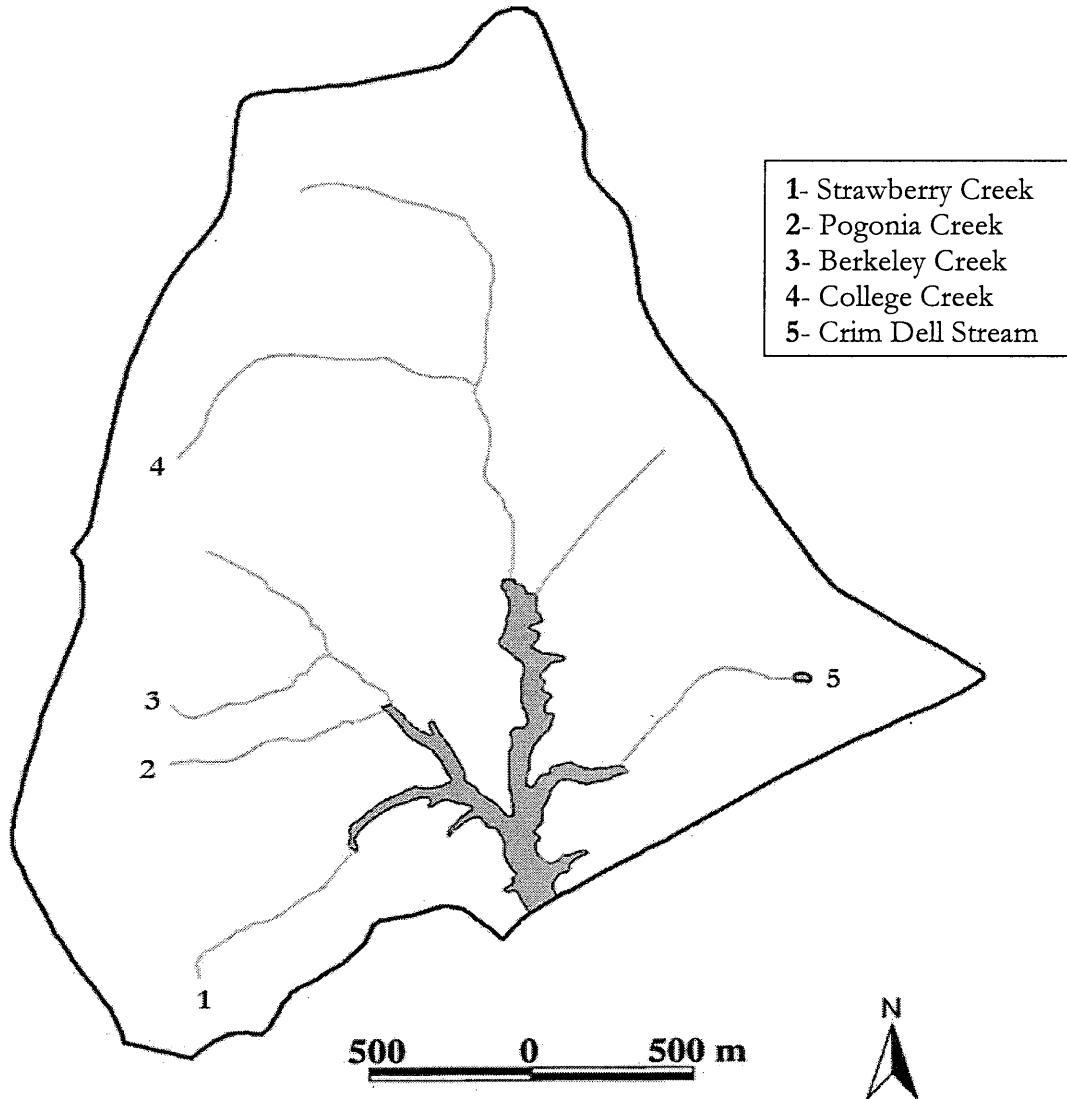
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APPENDICES

Appendix A: Map of Lake Matoaka watershed⁷ on the Virginia coastal plain showing the locations of study sites. *Note: Paper Mill is outside of the Lake Matoaka watershed in Williamsburg, VA.



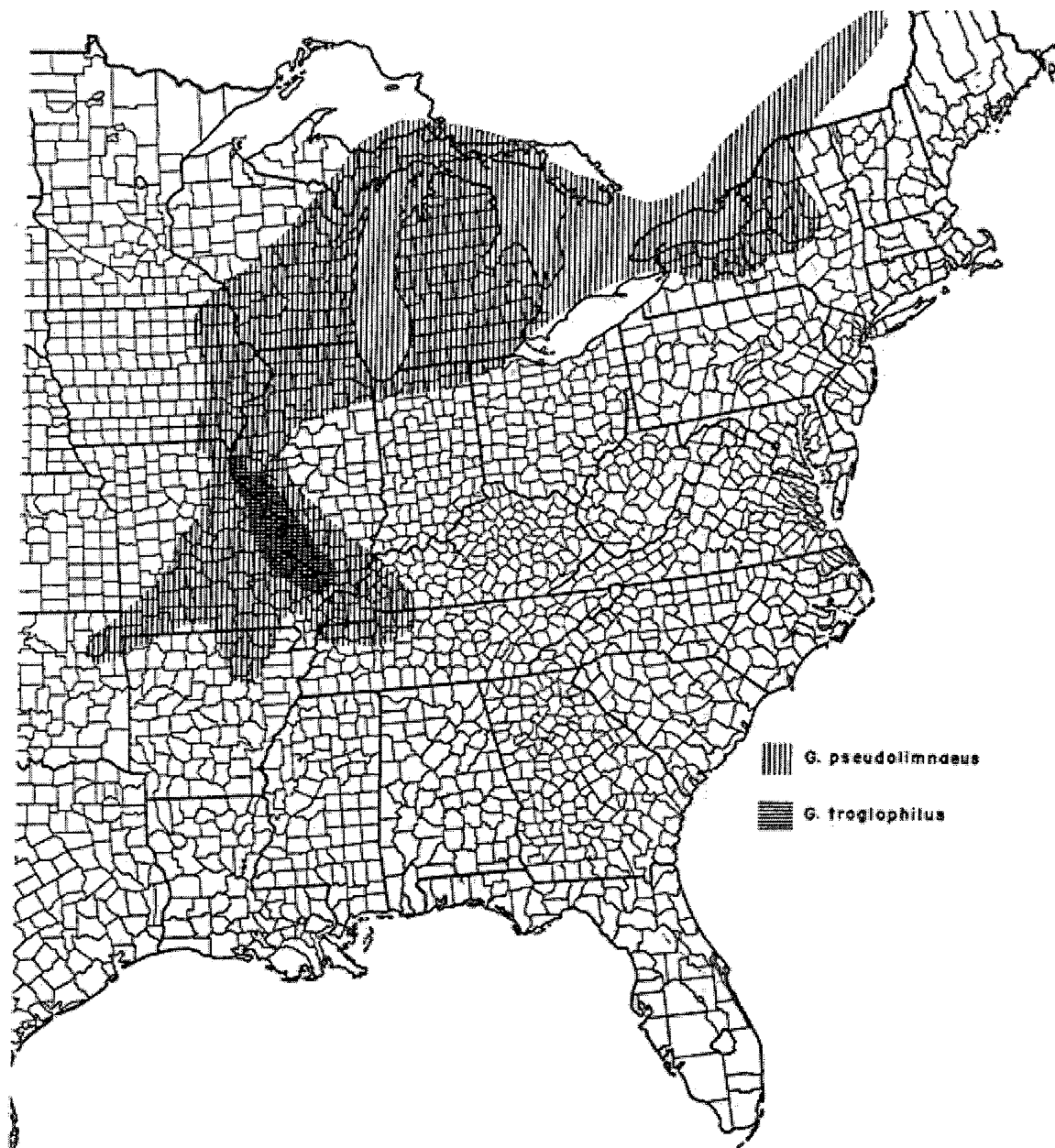
⁷ Figure adapted from Wach, E.A. and R.M. Chambers. 2007. Top-down effect of fish predation in Virginia headwater streams. *Northeastern Naturalist* 14:461-470.

Appendix B: Geographic distributions of *Gammarus fasciatus* and *Gammarus pseudolimnaeus*.

Amphipod, *Gammarus pseudolimnaeus*, occupies a wide range, extending from western Quebec across Ontario into central New York (Holsinger 1976). This species is common throughout the Great Lakes region of Michigan, Wisconsin, and Illinois; furthermore, it has been observed in eastern Iowa, central Missouri, northwestern Oklahoma, northern Arkansas, western Kentucky, and northwestern Tennessee (Holsinger 1976). Far disjunct from the normal range, *G. pseudolimnaeus* has been found in southeastern Virginia (G. Capelli, pers. comm.). Other disjunct areas include the Patuxent River drainage in Maryland (G. Capelli, personal comm. 2009) and three localities in southwestern Massachusetts (Massachusetts Division of Fisheries and Wildlife 2008). Throughout its range, it is often found in streams, rivers, and springs.

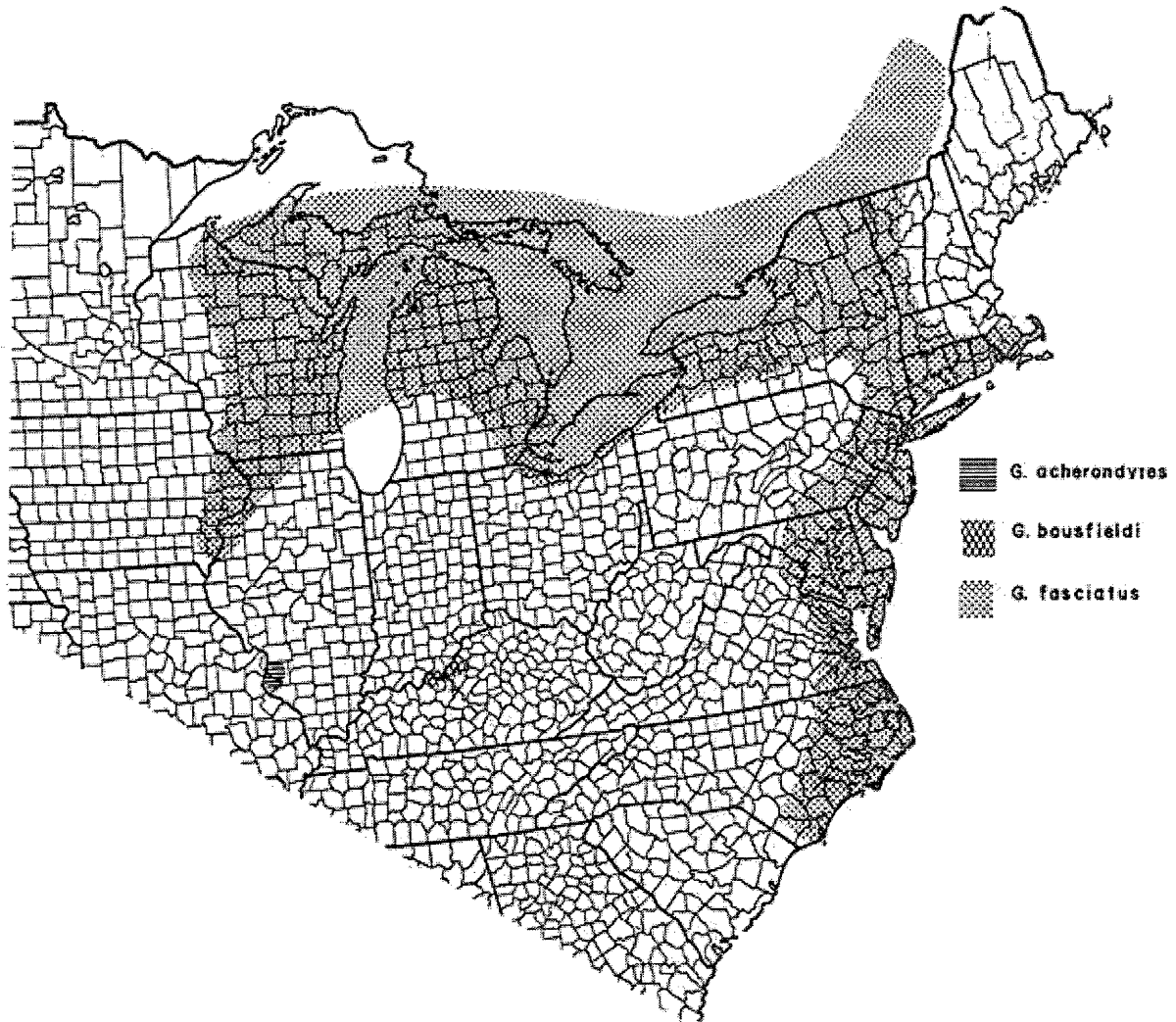
G. fasciatus is also widely distributed. Its range extends from the upper Mississippi River drainage eastward throughout the Great Lakes region; *G. fasciatus* can also be found along the Atlantic Coastal plain to southern North Carolina (Holsinger 1976). Throughout its range, *G. fasciatus* primarily inhabits lakes and slow moving rivers and streams however; it also occurs in springs and small streams (Bousfield 1958).

Appendix C: Geographic range map of *Gammarus pseudolimnaeus*.⁸



⁸ Range map adapted from Holsinger, John R. 1972. Biota of Freshwater Ecosystems Identification Manual No. 5. The Freshwater Amphipod Crustaceans (Gammaridae) of North America. Environmental Protection Agency.

Appendix D: Geographic range map of *Gammarus fasciatus*⁹



⁹ Range map adapted from Holsinger, John R. 1972. Biota of Freshwater Ecosystems Identification Manual No. 5. The Freshwater Amphipod Crustaceans (Gammaridae) of North America. Environmental Protection Agency.

Appendix E: Description of the general external anatomy of Gammarid amphipods.

Amphipods are many-segmented crustaceans (Smith 2001). The body is laterally flattened and divided into three parts; the cephalothorax, the pereon, and the pleon (Appendix F). The cephalothorax is the anterior tagma (segment) consisting of antennae, eyes, mandibles, and maxillae in addition to the first thoracic segment. Crustaceans possess two pair of antennae. The antennae are composed of a peduncle (base) and a long flagellum. Some species possess a short accessory flagellum on the first pair of antennae (Smith 2001).

The middle tagma, the pereon, is composed of the thorax minus its first segment which is fused with the cephalothorax. The pereon consists of seven segments, each of which bears a pair of appendages. The first two pair, called gnathopods, include pincer-like structures are used to gather food and are also used by male amphipods to hold onto the female during copulation. The other thoracic legs (pereopods) are used for crawling, swimming, and burrowing. They also create water current which aerates the gills on the thorax. Large epimeral plates and coxae enclose the brachial chamber. In females, the coxal plates form a marsupium in which they brood their young until they are ready to be released into the environment (Smith 2001).

The posterior tagma is the abdomen. The abdomen is divided into two regions of three segments each. The first three segments form the pleon and bear appendages called pleopods. Pleopods are brush-like appendages used for swimming and circulating

oxygen over the gills. The posterior three abdominal segments form the urosome. Each segment of the urosome bears a uropod; the uropods act as rudders. At the end of the abdomen is a small, tail-like segment called the telson (Smith 2001).

Appendix F: Diagram of external amphipod anatomy.

