CHAPTER 2. POPULATION STRUCTURE, LIFE HISTORY, AND SECONDARY PRODUCTION OF TWO POPULATIONS OF THE AMPHIPOD, *GAMMARUS MINUS*

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Abstract. I compared annual production, life history, and potential food sources of two stream populations of the amphipod *Gammarus minus* in Montgomery County, Virginia. In one stream, Richards Creek, *G. minus* were found in watercress (*Nasturtium officiniale*) beds and gravel. In the other stream, Bradley Run, *G. minus* occupied leaf, bark, and wood detritus. Annual production of *G. minus* in Richards Creek was 3.9 g/m^2 (95% C.I. 3.2-4.5), while that in Bradley Run was 1.8 g/m^2 (95% C.I.: 1.6-2.1 g/m^2). Population density was higher at Richards Creek. At Richards Creek, breeding occurred throughout the year. At Bradley Run, breeding occurred in a yearly cycle. Ovigerous females were found only during late fall and winter at Bradley Run, and the smallest size class was absent from October through December. Density of the smallest size class at Bradley Run was greatest when the quantity of ash-free dry mass (AFDM) of wood and bark was greater than AFDM of leaves. Wood and bark or, possibly, biofilm on wood and bark, may have been an important food source for young gammarids in Bradley Run. At Richards Creek, food sources available to young amphipods may include detritus in the interstices of gravels, biofilm on gravels, or particulate matter from the water column.

Key Words: *Gammarus minus*, Amphipoda, habitat, secondary production, life history, stream

Introduction

Even among different local populations of the same species, life history features and production can differ. Studying a species that occupies different habitats provides insight into the causes of those differences (Griffith et al. 1994, Short et al. 1987) and contributes to the development of tools for predicting energetic characteristics on a regional or global scale (Benke et al. 1988).

Amphipods of the genus *Gammarus* successfully occupy a wide variety of freshwater habitats throughout the northern hemisphere (Barnard and Barnard 1983). One reason for the success of this genus is its adaptability to various habitats. Demes of the same species may occupy habitats that differ considerably in characteristics such as light availability, temperature fluctuations, and food sources (e.g., cave streams with no aquatic vegetation and spring runs with abundant aquatic vegetation). Thus, *Gammarus* species are excellent subjects for studies of intraspecific variation.

Gammarus minus is a common amphipod found in cave springs, springs, and streams throughout limestone regions of Pennsylvania, Maryland, West Virginia, Virginia, Tennessee, Kentucky, Alabama, Ohio, Indiana, Illinois, Missouri, and Arkansas (Holsinger 1969, 1972, Culver et al. 1995) (Fig. 1). It is a dominant macroinvertebrate in certain habitats, particularly hard-water limestone springs (Kostalos 1979, Glazier 1991), and thus could play a dominant role in the functioning of the spring and stream communities it inhabits.

A body of work examining intraspecific variability in the species already exists. Much of this work has focused on morphological and behavioral differences among cave populations or between cave populations and surface populations (Culver and Fong 1986, Culver et al. 1995, Fong 1989, Gooch and Wiseman 1980, Holsinger and Culver 1970, Vawter et al. 1987) and demonstrates that considerable differences can exist among populations.

Comparative ecological studies of surface stream populations of *G. minus* were conducted by Minckley (1963) and Minckley and Cole (1963), who studied several populations of the amphipod in Kentucky. Minckley and Cole discovered *G. minus* populations occupying beds of the moss *Fissidens*, beds of the water milfoil *Myriophyllum heterophyllum*, packets of leaves in debris dams and gravels in riffles, beds of debris in pools, and deposits of wet leaves on banks (Minckley and Cole 1963). The greatest numbers of animals were observed in *Fissidens* beds and in leaf packets. Observations of gut contents demonstrated that the amphipods ate the plant and fecal detritus (but not animal material) available in the habitats they occupied.

Glazier et al. (1992) determined the relationship of population density, body composition, and reproductive output of *G. minus* to pH and ionic content in spring habitats. Population density, brooding female dry mass, and brooding female body fat content were positively correlated with Ca^{2+} and Mg^{2+} hardness.

Several gaps in the study of intraspecific variability of *G. minus* remain. Although Minckley and Cole (1963) observed reproductive features, they did not relate them to habitat differences. Secondary production estimates are necessary in any attempt to quantify energy flow pathways in food webs (Benke 1984). Despite the abundance of amphipods in many streams, only a few secondary production estimates (and even fewer comparative studies) are available for freshwater amphipod species. Annual production of two other freshwater *Gammarus* species, the North American *G. pseudolimnaeus* (Waters and Hokenstrom 1980, Waters 1981, 1984) and the European *G. pulex* (Iversen and Jessen 1977, Welton 1979 and Mortensen 1982) has been estimated. Waters (1984) and Iverson and Jessen (1977) compared annual production estimates of populations occupying different habitats. Annual production of *G. minus* was determined in a comparative study of macroinvertebrate shredders in four headwater streams differing in pH (Griffith et al. 1994), but the amphipod was rare in three of the four streams studied, probably because of the relatively low pH in the three streams.

The purpose of this study was to : 1) compare annual secondary production of two populations of *G. minus* occupying different habitats; 2) compare features of population structure and life history of the two populations; and 3) correlate habitat characteristics, particularly potential food sources, with the differences observed in 1) and 2).

Methods

Study Sites

I studied populations in two streams in Montgomery County, Virginia. Both streams are characterized by hard water and alkaline pH and are tributaries of the North Fork of the Roanoke River.

One of the streams is a spring-fed, first-order stream (lat 37º11'N, long 80º20'W) in the Falls Ridge Preserve of the Nature Conservancy at an elevation of approximately 515 meters above mean sea level. In honor of the late Bill Bradley, who fostered the conservation of this unique area, this stream will be called Bradley Run. Physical variables measured from October 1986 through November 1987 are shown in Table 1. The stream was characterized by steep riffles alternating with pools and was bounded on both sides by steep banks. The banks are lined with a variety of shrubs and deciduous trees, including American Sycamore. Canopy cover in spring and summer was nearly 100%. At the edges of pools, where all samples were collected, there was no aquatic vegetation. However, the main bodies of the pools contained the speedwell *Veronica americana* during spring and summer. The study reach was approximately 87 meters long and 3 to 5 meters wide. Only leaf detritus, wood, and bark habitats at the edges of pools, where water depth was approximately 5-10 cm, were sampled. Preliminary observations had indicated that animals were most often found here and only rarely in or on other other substrates, such as aquatic vegetation in the pools. A striking feature of Bradley Run is the heavy encrustation of marl that covers the rims of pools and any material, including leaves that fall into the stream.

The previously unnamed second stream is a shallow spring run that arises from a small cave and enters Falling Branch Creek (lat 37º07'N, long 80º20'W). It is referred to as Richards Creek in honor of the Richards family who owned the property when this study was conducted. The elevation of this stream is approximately 543 meters above mean sea level. Physical variables are provided in Table 2. The study reach was approximately 29 m long and 0.5 meters to 2 meters wide. This stream contained no pools and is bounded by a flat, open meadow on one side and a sharply rising hill covered with deciduous trees on the other. The meadow is grassy in the winter and full of a variety of wildflowers and tall (approximately 1 1/2 m high) herbaceous plants in the summer. *Gammarus minus* was found in bare gravel habitat and in watercress (*Nasturtium officiniale*) beds. Leaf detritus did not accumulate in this stream, as leaves were carried away by the current or remained on top of the watercress. During summer, the major *Gammarus* habitat was emergent watercress, which filled nearly the entire stream and grew above its surface. In winter months the major habitat was gravel with small patches of watercress cover. *Gammarus minus* was collected from watercress roots and from bare gravels.

Although water in Richards Creek was nearly as hard as Bradley Run, marl was not present. One explanation for this difference is that the average annual pH in Richards Creek is approximately 8.0, while that at Bradley Run is considerably higher, 9.7 (Tables 1 and 2). $CaCO_3$ is less likely to be precipitated at pH’s below approximately 8.3 (Cole 1983).

Sample collection and preparation

At Bradley Run, samples for the production and life history studies were taken at one month intervals between October 1986 and September 1987 and at Richards Creek, from November 1986 through October 1987. At Bradley Run, samples of whole leaves and leaf detritus found at the edges of 5 pools were collected each month. The same transects were used throughout the year, but each month a different location along a given transect was sampled. Sampling at both sites was also conducted at less frequent intervals from January 1986 through September 1986.

I collected samples by shoving an open metal cylinder, 16 cm in diameter (area of opening 0.02 m^2), into the detritus (mostly leaves) until solid rock was felt, quickly removing all the detritus within the sampler by hand, and transferring the detritus to a plastic freezer container. The sampler was immediately moved to an area next to the first and all of the detritus there was removed and placed in the plastic container. No animals were observed escaping during sampling; rather, they seemed to move into the detritus when disturbed. Four percent formaldehyde, buffered with sodium acetate, was added to the samples in the freezer container.

Five samples were also taken each month at Richards Creek. Because of the nature of the habitat in this stream, two sampling techniques were used. Gravel areas were sampled by pushing the metal cylinder firmly into the gravel and then pushing a shovel under it. The shovel, held closely against the cylinder, together with the cylinder, were quickly moved to a rubber dishpan and the contents were dumped into the pan. These contents were then transferred to a smaller container.

Because water cress plants grew very large in the summer, the above technique did not work with them. Instead, the cylinder was put down over the water cress and all plants within the cylinder were rapidly and firmly pulled up along with most of their roots. The plants were immediately transferred to the rubber dishpan, pieces of roots that remained in the stream were quickly collected by hand and added to the rest of the sample and then all was transferred to plastic freezer containers. This technique was not entirely satisfactory because it is likely that some animals escaped, causing an underestimation of their numbers. As at the Bradley Run Preserve site, all samples were preserved in 4% formaldehyde, buffered with sodium acetate.

At the time of sampling, air temperature, dissolved oxygen, pH, and water temperature were measured. Dissolved oxygen and water and air temperatures were determined with a YSI oxygen meter. A Hach kit was used to determine pH. Water samples were returned to the laboratory to be tested for hardness, alkalinity, and conductivity.

In the laboratory, individual amphipod samples were placed in a seive, rinsed with tap-water, and hand-picked. An estimate of the degree of breakdown of leaves from of the Bradley Run samples was determined (see discussion of technique below). Body lengths of the amphipods were measured their curved state. Using a drawing tube attached to a dissecting microscope, I traced the length of each animal (from the base of the first antenna to the base of the telson) with a mouse on a Jandel Scientific Digitizing Pad. Animal length was recorded by means of a Sigmascan program. Lengths were rounded to the nearest whole mm and these 1-mm size classes were used for further analysis.

Amphipods from Bradley Run were sexed under a dissecting microscope. The Bradley Run population did not exhibit the intersexuality noted in the Richards Creek population by Buikema, et al. (1980). Animals with brood plates of any size were called female, animals with penial projections were called males, and animals with neither brood plates nor penial projections were called immatures. Miller (1977) determined the sex ratios at Richards Creek; therefore, it was decided that this would not be repeated in the current study.

The amphipods were then dried at 60 ^{o}C to a constant weight. Dry weight of each animal was determined to the nearest 0.001 milligram with an electrobalance. Secondary production was calculated by the size-frequency method, with 95% confidence intervals determined by the method of Kreuger and Martin (1980).

Quantification of detritus

After animals were removed from the detritus, I estimated the percentage of material that was in each of three categories of breakdown: whole leaves, leaves missing only one or two lobes, or leaf pieces smaller than a leaf missing only two lobes.

Ash-free dry mass (AFDM) of leaf and other detritus was determined for each sample collected at the Bradley Run site. After animals were removed from the detritus, the detritus was placed in a paper bag and dried overnight in an oven at 60 ^{o}C. Detritus was cooled, air-dried in the bags, and ground in a Waring blender and weighed. Aliquots of 0.5 mg were transferred to aluminum pans and ashed in a muffle furnace at 500 ^{o}C. Distilled water was added to each ashed aliquot and these were then dried overnight at 60 ^{o}C. The pans were kept in a desiccator until they were weighed on an electrobalance.

Statistics

Regression analysis was used to examine the relationship between total density and density of animals that were ≤3 mm and water chemistry and temperature for the two populations. Regression analysis was also used to examine the relationship between total density, density of animals ²3 mm, the percentage of ovigerous females and water temperature, total ash-free dry mass (AFDM), leaf AFDM, and wood/bark AFDM. Regressions were performed using the Data Analysis Tools in Microsoft Excel Version 6.0 for Macintosh and StatView SE + Graphics for the Macintosh.

Results

Water chemistry and temperature

Values for alkalinity, conductivity, hardness, pH, water temperature, percent oxygen saturation, and air temperature were similar at the two sites, with the exception of water temperature and pH (Tables 1 and 2). At Bradley Run, water temperature fluctuated from 8.0 to 16.6 ^{o}C during the year, while at Richards Creek it remained fairly constant between 12 and 13 ^{o}C. Water temperatures taken at Bradley Run at the times of sampling were correlated with maximum air temperatures for the days of the sampling ($r^2=0.80$, $p < 0.01$). The Bradley Run pH averaged 9.5, while that at Richards Creek averaged 8.0.

Production and life history

Annual production of *Gammarus minus* at Bradley Run was estimated to be 1.8 g/m^2 (95% C.I.: 1.6-2.1 g/m^2) from October 1986 through September 1987 (Table 3). At Richards Creek, annual production was 3.9 g/m^2 (95% C.I. 3.2-4.5) from November 1986 through October 1987 (Table 4).

At Bradley Run, the sex ratio (female/male) changed during the year (Table 5). Most of the population consisted of sexually immature animals in the spring and summer and of adults in the fall and winter. Animals released from brood pouches earlier in the year were nearly all sexually mature by October. Breeding apparently began during fall, as evidenced by the sharp increase (4 to 71% in 1985, 2% to 52% in 1986) in the percentage of females that became ovigerous between October and November (Table 5).

From October through March the percentage of females becoming ovigerous increased. Nearly all the females were ovigerous by March. Young animals ($\leq$ 3 mm) were probably released from brood pouches beginning in January (data from January 1986), but the greatest numbers of young were apparently released in May and June (Fig. 2). From July through October ovigerous females were essentially absent from the population. Most of the generation released in the previous spring probably died during summer, judging by the declining numbers of animals greater than 8 mm long (Fig. 2 and 3). Very few young animals were released from brood pouches in October through December.

At Richards Creek, on the other hand, members of the smallest size classes were present all year (Figs. 4 and 5) and, except for April, made up at least 10% of the population during the year. For most of the year, the majority of this population consisted of animals in the smallest size classes. As in the Bradley Run population, there was a peak of newly released animals, but it occured in February and March rather than May and June (Fig. 4).

Potential food sources

Standing stock of all coarse particulate organic matter (CPOM) int he samples at Bradley Run ranged from approximately 100 g AFDM/m^2 in July and September of 1987 to nearly 500 g/m^2 in May of 1987 (Fig. 6). Leaf detritus was the predominant type of CPOM throughout the year except for May and June, 1987, when wood and bark were predominant (Fig. 6). Small leaf pieces, particularly pieces smaller than 1 cm, made up the majority of the leaf detritus in December 1986 and February, May and June 1987, while whole leaves predominated during November 1986 and July, August and September 1987 (Fig. 7). In March and April 1987, the percentages of leaf detritus in each category were relatively similar. Information on leaf condition is not available for October 1986 or January 1987. Field notes from other work conducted at the site in January 1988 indicate that whole leaves were present in the stream. These leaves probably had washed into the stream from the banks.

Leaves began falling in July, and all had fallen by November. Many leaves did not fall into the water, but remained on the bank. Whole leaves were also found in the water at other times of the year, perhaps carried there by high stream flows after storms or by snow melting from the banks.

Discussion and Conclusions

Life history

The Bradley Run population exhibited a yearly breeding cycle, while the Richards Creek population appeared to breed all year. The Bradley Run animals reached a larger size and lower density (Fig. 8) than the Richards Creek population. The higher density of animals at Richards Creek was probably due to the constant influx of young throughout the year. Data from 1985-86 and 1986-1988 (Table 5) indicate that the reproductive cycle at Bradley Run stayed consistent from year to year. The Richards Creek population was not as consistent over the same time. One reason for this lack of consistency may be the influence of anthropogenic effects on the stream, a more unlikely occurence at the Bradley Run site because it runs through a protected reserve. On one occasion, in May 1986, the owner of Richards Creek removed watercress from the site. Watercress roots remained in the stream, and *G. minus* were in them. Dale Miller also reported that someone had removed watercress from the site. He noted that after the removal, there was a reduction in the proportion of larger animals in the bare gravel habitat adjacent to the disrupted watercress beds.

Possible role of temperature and food sources on the life history of *G. minus* at Bradley Run

The variable water temperature in Bradley Run (Table 1) may have been a factor in stimulating breeding. Linear regression analysis demonstrated no significant correlation between water temperature values measured at the times of sampling and total density or density of newly released animals ($\leq$3 mm) at the Bradley Run site. However, there was a significant negative correlation between the water temperature one month before the sampling and the percentage of females that were ovigerous in the sample ($r^2 = 0.72$, $p = 0.002$). Kostalos (1979), in her study of a Pennsylvania population of *G. minus* that inhabited fallen leaves, found the same relationship. A possible explanation of the correlation between the ovigerous females and water temperature is that the onset of cooler temperatures stimulates breeding. In other amphipods, such as *Hyalella azteca*, temperature is known to affect reproduction (de March 1981).

There was also a positive corrrelation ($r^2 = 0.61$, $p = 0.004$) between the percentage of ovigerous females and the quantity of leaf detritus AFDM (not the percentage of whole leaves) present at the time of sampling (Fig. 9). Newly fallen leaves are generally colonized by aquatic microbes, including fungi, within a few days after reaching the water (Webster and Benfield 1986). Kostalos and Seymour (1976) reported that survivorship of adult *G. minus* was enhanced by feeding them fungus-enriched leaves. If the fungi remained in the leaf detritus for some time after initital colonization, leaf detritus, even in small pieces, may provide high quality nutrition for the ovigerous females. High quality nutrition would be necessary for growth and maturation of the eggs and the continued survival of females who carry the eggs and developing young until the young are sufficiently developed to survive on their own.

Declining temperatures were accompanied by leaf fall and decreasing daylight, so it is difficult to determine which of the three factors, if any, was more important. Photoperiod is known to affect the reproductive cycle of amphipods (de March 1981, Borowsky 1991) and cannot be ruled out as a factor in this case.

There was a strong positive correlation (r^2=0.95, p<0.001) between the density of the smallest size class (²3 mm) and the AFDM of bark (mostly sycamore) and wood in Bradley Run (Fig. 10). Most of the leaf material that was left at the time the young were released had not only been reduced to small pieces, but may also have been limited nutritionally value, especially in June, when the organic content of the leaf detritus was reduced to its lowest value. Wood, on the other hand, and possibly bark, may harbor nutritious biofilms (Tank, et. al. 1993, Golladay and Sinsabaugh 1991). Golladay and Sinsabaugh (1991) found that microbial biomass was consistently greater on wood than leaves. In a comparison of microbial respiration on sticks and leaves at the Coweeta Hydrologic Laboratory in North Carolina, Tank et al. (1993) found that mean respiration rate per unit surface area of substrate was highest for sticks.

Young animals may have taken advantage of microorganisms available on the wood and bark detritus. In May and June, wood and sycamore bark made up a greater percentage of the organic matter available at the site than leaf material (Fig. 6). Wood and bark may be better substrates for microbial colonization than leaves, because wood and bark are not mechanically broken down as rapidly and so provide more time for colonization. Wood also provides more surface area for colonization than leaves.

Having wood available as a food source may provide other advantages to young amphipods. There is evidence that fungi that colonize wood are capable of producing lignocellulose-degrading enzymes. And, because relative to leaves, the chemical composition of wood varies very little over time, a broad spectrum of lignocellulases may develop. The many lignocellulases may make up for limited "chewing" ability of young amphipods and provide nutrients for them. Thus, the wood and bark may actually be more nutritious than the well-decayed (and, presumably, lacking in an appreciable fungal community — Webster and Benfield 1986) and leaf pieces available in the spring. The wood may also provide refuge for the smaller animals.

The *G. minus* population at Richards Creek did not exhibit the degree of seasonal variation shown by that at Bradley Run, in spite of a seasonal increase and decline in mass of the water cress vegetation that appeared to be a source of food for the organisms. The watercress was available in the stream for most of the year. Because young animals in this stream are more often found in gravels than in watercress, it is possible that they can use other sources of food, for example, aquatic plant detritus that collects among the gravels, particles suspended in the water column, or biofilms on the gravels.

Constant water temperature at Richards Creek is probably conducive to year-long reproduction. Under constant laboratory conditions, females of most of ten amphipod species studied reproduced continually (Borowsky 1991). The abundance of food throughout the year also supports the continual influx of new animals. The watercress life cycle may, however, be a factor in the surge of recruitment in February and March. At this time of the year the cress is young and is probably less tough than it is later in the year. It may be easier for young amphipods to eat. Another possibility is that chemical deterrent effect of watercress that has been observed in populations of the plant (Newman, et al. 1992) is less when the water cress is young.

The large reduction in the number of young animals at Richards Creek between March and April 1987 may have been the result of high streamflows in March (USGS data). Drift may be an important factor in controlling the amphipod population in this stream when watercress is not plentiful. Waters and Hokenstrom (1980) suggested that when production is high, greater drift may occur among organisms such as amphipods that have a high propensity to drift. If the substrate carrying capacity of Richards Creek had been exceeded at the time of high water, amphipods carried away may not have returned upstream. Watercress offers at least some protection from disturbances. In May 1986, when the landowner was digging watercress out of the stream, some watercress roots remained in the sediment and amphipods were in the roots.

Animals in the Bradley Run population reached greater total body lengths than those in the Richards Creek population. Monthly density at Bradley Run was always lower than that at Richards Creek (Fig. 8), and average dry weights of individual organisms were generally higher at Bradley Run. These trends reflect the greater numbers of animals in the smallest size classes at Richards Creek. Differences in sizes between different populations of *G. minus* have been reported by other authors (Miller and Buikema 1977, Minckley and Cole 1963, and Holsinger and Culver 1970). Miller (1977) also noted that the Richards Creek population was at the small end of the size range for *G. minus*. The size differences between populations of *G. minus* may be related to spatial considerations (Miller and Buikema 1977, Minckley and Cole 1963), predation (Glazier, et al. 1992, Man 1991), and competition with other amphipod species (Minckley and Cole 1963). Temperature has been shown to affect the size of individuals in populations of gammarids and isopods (Steele and Steele 1975, Sinervo and Doyle 1990, and Aston and Milner 1980) and may also be important in *G. minus*. Glazier et al. (1992), in a comparative study of *G. minus* populations, discovered that the smallest adult body size was found in the warmest spring. In laboratory cultures, the size of *Hyallela azteca* adults was inversely proportional to temperatures at early development (de March 1981). In the Bradley Run population, temperatures were colder at the time of early development than were those at Richards Creek (Tables 1 and 2).

Comparisons with other life history studies of *G. minus*

1. Comparison of Bradley Run and Falls Ravine Creek, Pennsylvania populations.

The life history of *G. minus* in Bradley Run is similar to one in Falls Ravine Creek (hereinafter referred to as the Pennsylvania site) in Allegheny County, Pennsylvania (Kostalos 1979). Both streams were well- oxygenated and had very hard. Available food consisted primarily of detritus from riparian vegetation in both streams, and yearly litter falls were the same.

Annual cycle of breeding and variations in sex ratio, total density, and size class proportion were similar were similar in the two populations (Figs. 11 and 12). The details of timing varied somewhat from year to year, but the overall pattern of one major breeding period remained the same (Kostalos 1977, Mary Kostalos, unpublished data transmitted to me, 1992).

As in the Bradley Run population, but a month later, the percentage of ovigerous females in the Pennsylvania population increased sharply from 5% in November to over 40% in December (Fig. 12). The proportion of immatures began to rise in January, and the increase continued until the numbers of newly released immatures peaked in May. By July, the percentage of females that were ovigerous declined sharply and the percentage remained low throughout the summer and early autumn. The ovigerous female percentage peak occurred in May in Pennsylvania, while at Bradley Run it occurred in March, consistent with the earlier start in breeding at Bradley Run.

As in the Bradley Run population, newly released amphipods made up the lowest percentage of the population in December and January (Kostalos 1979). At Bradley Run, immatures were at their lowest point in November and December. In both populations, females made up the greatest proportion of the population in January (Table 5 and Kostalos 1979).

2. Comparison of Richards Creek population in 1986-1987 and in 1974-75

Miller (1977) studied the Richards Creek population (Site 2 in his thesis). For the purposes of this comparison, I combined his density data for the watercress and gravel habitats because I sampled both habitats in my study. As in the 1986-87 study, 1) young were produced throughout the year, 2) there was a reduction in density of the smallest size classes between November and December and between September and October, and 3) the density of the smallest size class varied throughout the year. It appears that this population is consistent in certain features of its life history.

Secondary production

There are at least two explanations for the differences in production between the two Virginia populations. One is that there is a source of error in the study. Morin et al. (1987) explored some of the sources of error in production studies, including incorrect assumptions about populations. For example, different life spans would affect production values. If the Bradley Run population had a life span of only one year, and the Richards Creek population, with its low, constant temperature, had a longer lifespan (Iversen and Jessen 1977) of two years, then production in the Richards Creek population would have to be halved (Waters 1979) and would be 1.95 g/m^2, nearly the same as the production at Bradley Run. It is difficult to determine whether the life span of the Richards Creek animals is greater than a year.

The other explanation of the difference in production values is that some aspect of the habitat, such as food sources, spatial parameters, temperature, or water chemistry is responsible for the difference in production. For example, it is possible that food sources in the Richards Creek site (living macrophytes, detrital matter, and particles suspended in the water column) are easier to eat or more nutritious than conditioned terrestrial leaves. Water cress grows thickly in this stream and puts out a dense mass of fine roots. When growing, it captures sediment. Even though very little watercress was present from October through January during the study, the sediment it left behind was no doubt rich in organic matter. Sediments occupied by watercress can be several cm deep.

Other studies of production in amphipods (Table 6) provide some insight into factors that may affect annual production. At Richards Creek, sediments, watercress roots, and gravels provide many more surfaces and spaces for food to grow on or get trapped in and spaces for concealment. At Bradley Run, the leaves rest on rock and no sediment builds up under them. The only source of food and refugia are the fallen leaves, bark, wood, and, possibly, particles in the water column.

Waters (1984) observed that annual production of *G. pseudolimnaeus* was generally higher in fine sand, sand-gravel, and gravel substrates than in cobble substrates. His explanation of this trend was that more interstitial space may be available to the amphipods, perhaps because smaller substrates are easier to move around to provide suitable space.

Iversen and Jessen (1977) compared production values of *Gammarus pulex* at three different stations along a spring in Denmark. They estimated that at the second and third stations, which were similar in habitat (stones with pebbles and gravel and aquatic vegetation) to the Richards Creek site, had production values of 5-7 g dry weight m^{-2} yr^{-1}, while the computed production at the first station, where the main habitat was fallen leaves (similar to the Bradley Run habitat) was 3.8 g dry weight m^{-2} yr^{-1}. I saw a similar trend in the Richards Creek and Bradley Run populations. These results add support to the idea that food sources or spatial considerations in the two types of habitats vary sufficiently to cause differences in production. The greater amount of sediment, rocks, and gravel in the Richards Creek habitat may provide an additional source of nutrition in the form of biofilm in the sediment (Barlocher and Murdoch 1989), particularly for smaller animals that may be able to get into the sediment.

Griffith et al. (1994), in a study of shredder production in headwater streams in West Virginia, calculated annual production of *G. minus* to be 2.43 ± 0.42 g/ m^2/yr (mean ± 95% confidence limits) in one second order stream in West Virginia. In that stream, *G. minus* represented 64% of total shredder production. Although not clear from the description of the study site in the paper, it appears that terrestrial leaves were the major source of food at the site.

Alkalinity, pH, and temperature can affect stream macroinvertebrate secondary production (Griffith et al. 1994). Alkalinity was similar in Richards Creek and Bradley Run. At Bradley Run, pH was higher. While gammarid amphipods generally prefer streams with alkaline pH, it is possible that the pH at Bradley Run exceeds an optimum level.

I attempted to determine the secondary production of the animals collected in Miller's study (1977). After correcting his size classes for the difference in our measuring methods, I used his size class densities. I assumed that the average weights of the size classes were the same for both studies. The estimated value was 11.0 g/m^2. However, given the differences in sampling technique (Miller sampled from a much smaller part of the stream, a 6 m reach; I sampled a 29 m reach), it is difficult to draw any conclusion concerning possible differences in secondary production.

Production values are similar to that estimated by Griffith, et al. for a West Virginia population of *G. minus* and fall within the range reported for *G. minus pulex* (Iversen and Jessen 1977). For example, Mortensen (1982) estimated production of G. *pulex* at 3.9 g/m^2 dry weight with a P/B ratio of 2.6. The stream he studied was similar to the Richards Creek stream — a bed composed of sand, gravel, and small stones with patches of a vascular macrophyte (*Berula erecta*) and trees growing along the banks. See also Iversen and Jessen's study above. Annual production values for *Gammarus pseudolimnaeus* (Waters 1981,1984) ranged from 5.2 to 27.1 g/m^2 (Table 6), most considerably higher than those of either of the Bradley Run or Richards Creek *G. minus* populations or those of Iversen's *Gammarus pulex*.

P/B ratios fall within the range of herbivorus and carnivorous benthic invertebrates (Wetzel, 1983) and for univoltine amphipods (Waters 1977).

Just as some cave-dwelling *G. minus* populations differ morphologically from spring- and stream dwelling-populations, populations living among aquatic macrophytes appear to differ in life history and productivity from those inhabiting fallen leaf, bark, and wood detritus. This study adds further support to the idea that populations occupying similar habitats exhibit similar population and trophic dynamics.

Conclusions

Surface populations of *Gammarus minus* are capable of at least two types of life histories, depending on their habitat. Constant temperature and year-long availability of suitable food sources may contribute to year-long breeding, while fluctuating temperatures and varying food sources may contribute to seasonal breeding.

Annual production appears to be related to habitat. It is possible that smaller substrates and algae and aquatic macrophytes contribute to greater production.

Wood and bark appear to play an important role in the survival of newly released *G. minus* in some populations. These materials may provide substrates for biofilm, a potentially nutritious food source.

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Table 1. Values for water-chemistry variables and temperature at Bradley Run.

Year	Month	pH	Hardness (mg/L as $CaCO_2$)	Alkalinity (mg/L as $CaCO_2$)	Conductivity (micromhos/ cm)	Water Temp. (^oC)	% Saturation of Dissolved Oxygen
1986	O	9.5	248.0	208.5	394.6	14.0	89.2
	N	9.8	339.0	333.3	644.6	10.7	92.9
	D	9.7	355.0	338.6	402.0	8.0	97.4
1987	F	9.8	249.0	234.0	405.6	9.0	105.7
	M	9.9	281.0	292.8	535.3	8.4	101.0
	A	10.0	344.0	318.3	576.0	9.2	94.6
	M	9.6	330.0	297.9	557.8	10.8	93.9
	J	9.5	331.0	316.0	570.0	15.0	93.7
	J	9.0	350.0	325.5	715.0	16.0	91.2
	A	9.5	353.0	327.0	587.0	16.0	92.3
	S	10.0	342.0	330.3	554.5	16.6	90.2
Mean(SD)		9.7(0.3)	320.2(38.8)	302.0(40.7)	540.2(97.6)	12.2(3.2)	94.7(4.7)

Table 2. Values for water-chemistry variables and temperature at Richards Creek.

Year	Month	pH	Hardness (mg/L as $CaCO_2$)	Alkalinity (mg/L as $CaCO_2$)	Conductivity (micromhos/ cm)	Water Temp. (^oC)	% Saturation of Dissolved Oxygen
1986	N	8.0	321.0	301.3	558.4	13.0	84.7
	D	7.7	308.0	280.8	482.6	12.2	87.3
1987	F	7.9	316.7	316.6	503.3	12.2	101.6
	M	8.0	309.0	297.3	572.8	12.0	105.5
	A	8.2	343.3	311.5	630.7	12.1	92.6
	M	8.0	342.0	321.5	587.0	12.5	81.1
	J	7.8	348.0	322.5	597.0	13.1	66.7
	J	8.0	340.0	315.7	578.0	13.3	79.7
	A	7.9	318.0	304.0	571.0	13.3	79.7
	S	7.9	323.3	303.8	563.4	13.0	83.7
	O	8.1	328.0	303.5	563.4	12.7	70.7
Mean(SD)		8.0(0.1)	327.0(13.6)	307.1(11.6)	564.3(39)	12.7(0.5)	84.8(11.2)

Table 3. Secondary production table for Bradley Run population of <u>Gammarus minus</u> from October 1986 through September 1987. Negative values dropped.

Size class (mm)	**Mean density (No./m^2)**	**Mean Indiv. Wt. (mg)**	**Standing stock (mg/m^2)**	**No. lost/m^2**	**Wt. at Loss (mg)**	**Total Wt. Lost (mg/m^2)**	**No. Size Classes**	**Production (g/m^2)**
3	46.000	0.047	2.162					
				-4.212	0.0865	-0.364	13	-0.005
4	50.212	0.126	6.327					
				-19.418	0.177	-3.437	13	-0.045
5	69.630	0.228	15.876					
				10.514	0.319	3.353	13	0.044
6	59.116	0.410	24.238					
				3.322	0.529	1.757	13	0.023
7	55.795	0.649	36.211					
				10.384	0.849	8.816	13	0.115
8	45.411	1.049	47.636					
				-7.993	1.309	-10.463	13	-0.136
9	53.404	1.570	83.844					
				16.027	1.834	29.394	13	0.382
10	37.377	2.097	78.379					
				4.979	2.224	11.073	13	0.144
11	32.397	2.351	76.165					
				13.130	2.497	32.786	13	0.426
12	19.267	2.644	50.942					
				14.295	2.687	38.411	13	0.499
13	4.973	2.730	13.567					
				3.390	3.060	10.373	13	0.135
14	1.582	3.391	5.365					
				1.055	3.486	3.678	13	0.048
15	0.527	3.582	1.888					
				0.527	3.582	1.889	13	0.025
	Mean standing stock		0.442 g/m^2			Secondary production		1.841
	P/B Ratio		4.2					

Table 4. Secondary production table for Richards Creek population of Gammarus minus from November 1986 through October 1987. Negative values dropped.

Size class (mm)	**Mean density (No./m^2)**	**Mean Indiv. Wt. (mg)**	**Standing stock (mg/m^2)**	**No. lost/m^2**	**Wt. at loss (mg)**	**Total Wt. Lost (mg/m^2)**	**No. Size Classes**	**Production (g/m^2)**
3	695.329	0.042	29.204					
				- 147.014	0.065	-9.556	10	-0.096
4	842.342	0.088	74.126					
				277.712	0.133	36.936	10	0.369
5	564.630	0.178	100.504					
				250.753	0.261	65.447	10	0.654
6	313.877	0.343	107.659					
				103.904	0.488	50.705	10	0.507
7	209.973	0.633	132.913					
				54.192	0.784	42.487	10	0.425
8	155.781	0.934	145.499					
				66.260	1.076	71.296	10	0.713
9	89.521	1.217	108.947					
				39.945	1.328	53.047	10	0.530
10	49.575	1.442	71.487					
				32.849	1.571	51.606	10	0.516
11	16.726	1.701	28.451					
				14.671	1.849	27.127	10	0.271
12	2.055	1.997	4.104					
				2.055	1.997	4.104	10	0.041
	Mean standing stock		0.803 g/m^2		Secondary production			4.0
	P/B ratio		4.9					

Table 5. Percentages of Bradley Run population that were immatures, females, and males and the percentages of females that were ovigerous from August 1985-January 1988. All data collected by author.

Date	% Immatures	% Females	% of females that were ovigerous	% Males
Aug. 85	32	41	0	28
Oct. 85	5	54	4	41
Nov. 85	6	53	71	40
Jan. 86	11	57	90	32
Apr. 86	84	9	78	6
June 86	71	12	13	16
July 86	53	19	0	27
Sep. 86	40	32	0	29
Oct. 86	11	38	2	51
Nov. 86	2	50	52	48
Dec. 86	3	55	82	41
Feb. 87	24	37	83	39
Mar. 87	56	22	100	22
Apr. 87	42	39	93	19
May. 87	73	17	63	10
June 87	66	14	8	20
July 87	58	20	0	22
Aug. 87	30	33	2	37
Sep. 87	24	35	0	41
Jan. 88	18	47	96	35

Table 6. Comparison of secondary production values of different species of amphipods. All values were estimated using the size-frequency method, with the exception of the first two items. For the population in the first row, the values were estimated from P/B ratio of animals from another site and biomass at this site and in the second row, from Allen production curves.

Species	Type of habitat	Production Value (g dry wt $m^{-2}yr^{-1}$)	Citation
Gammarus pulex	spring with stones, pebbles, gravel, aquatic vegetation	5-7	Iversen and Jessen 1977
G. pulex	spring with fallen leaves	3.8	Iversen and Jessen 1977
G. pulex	stream with sand, gravel, small stones, small patches of aquatic vegetation	3.9	Mortensen 1982
G. minus	headwater stream with (assumed) fallen leaves	2.4	Griffith, et al. 1994
G. minus	spring-fed stream with fallen leaves	1.8	this study
G. minus	spring run with gravel, small stones, aquatic vegetation	3.9	this study
G. pseudolimnaeus	creek, sand substrate	21.4[1] (range: 9.4-41.4)	Waters 1984
G. pseudolimnaeus	creek, sand-gravel substrate	21.8[1] (range: 9.0-44.9)	Waters 1984
G. pseudolimnaeus	creek, gravel substrate	15.0[1] (range: 7.5-22.1)	Waters 1984
G. pseudolimnaeus	creek, cobble	11.0[1] (range: 5.2-14.7)	Waters 1984
Hyalella montezuma	thermal collapsed spring mound, in pelagic zone with phytoplankton	29.0[2]	Dehdashti and Blinn 1991
Hyalella montezuma	thermal collapsed spring mound, in littoral zone with dense stand of aquatic vegetation	6.7[2]	Dehdashti and Blinn 1991

[1] These are mean values of production estimates for five years. The range of values is shown in parentheses. At the middle of the five year study, a “serious siltation” occurred. In all cases, the highest values occurred before the siltation.

[2] The authors converted production estimates in cubic meters to square meters.