Distribution of Freshwater Amphipoda in the Lake Matoaka/College Woods Area, Williamsburg, Virginia

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College of William & Mary - Arts & Sciences

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DISTRIBUTION OF FRESHWATER AMPHIPODA IN THE LAKE MATOAKA/COLLEGE WOODS AREA, WILLIAMSBURG, VIRGINIA.

A Thesis
Presented to
The Faculty of the Department of Biology
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

by
Sue Mahon
1997
APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Arts

[Signature]
Author

Approved, June 1997

____________________________
G. M. Capelli

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N. J. Fashing

____________________________
S. L. Sanderson
for my husband Chuck,
who was integral in all aspects of this project,
and without whom none of this would have happened.
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ABSTRACT

The small lake/stream ecosystem on the College of William and Mary campus encompasses habitat with wide natural and anthropogenic variation, including a shallow, hardwater eutrophic lake, three significantly disturbed tributary streams flowing through developed areas, and three pristine tributary streams confined to the College Woods. The latter also exhibit extreme chemical variation, beginning as very dilute softwater springs (conductivity 15 umhos, calcium <3.1 mg/l CaCO₃) but ending 0.7 km downstream at Lake Matoaka with much higher levels of solutes (conductivity 250 umhos, calcium 120 mg/l CaCO₃).

Four species of amphipod were found in the study area: Hyalella azteca, Gammarus fasciatus, G. pseudolimnaeus, and Synurella chamberlaini. H. azteca was found in the disturbed standing water of Lake Matoaka along with G. fasciatus, which was also found at two stream sites. G. pseudolimnaeus, which was not expected in this area, was found only in the pristine flowing water of the Woods streams and seeps. S. chamberlaini was found at one location in Berkeley in water with low amounts of dissolved materials at the approximate limit of G. pseudolimnaeus distribution. Closer examination of G. pseudolimnaeus habitats showed that it was significantly more abundant in leaf litter than it was in sand. No general relationships were found relating abundance to conductivity, calcium, magnesium, or pH. However, in two of the Woods streams, Berkeley and Pogonia, G. pseudolimnaeus distribution limit was located downstream of the stream source, possibly because of chemical limitations involving calcium. When populations of G. pseudolimnaeus were moved from a mid-stream site to sites near and above the distribution limit, the population just below the distribution limit showed no differences in survivorship from the collection site population. The above-distribution-limit population showed 100% mortality after 32 days, which is consistent with calcium stress associated with molting. Overall, distribution patterns appear to involve a combination of competitive interactions and variation in environmental tolerances among species.
DISTRIBUTION OF FRESHWATER AMPHIPODA IN THE LAKE MATOAKA/COLLEGE
WOODS AREA, WILLIAMSBURG, VIRGINIA.
Introduction

Literature Review

Amphipoda, benthic crustaceans comprising an order, are common worldwide in freshwater and marine habitats; there are also a few terrestrial species. In North America there are about 150 described species, with probably at least 100 more awaiting description (Pennak, 1989). Under favorable conditions densities may reach 10,000/m²; they are often important in food chains, especially when fish are present (Pennak, 1989). Because of their widespread distribution, they are commonly included in biomonitoring work, with most common species assumed to be indicative of clean water.

Amphipods are laterally flattened and range in length as adults from 4-22 mm. Their bodies consist of a cephalothorax, a seven-segmented thorax, a six-segmented abdomen, and a telson (Fig. 1). Mouthparts and two pairs of antennae are located on the cephalothorax. In almost all species the first antennae include a small accessory antenna ("flagellum") arising at the base of the third peduncle segment. Each of the seven thoracic segments has a pair of legs, known as periopods (variously "peraeopods," "pareopods", pereiopods"). The first two pairs, called gnathopods, are modified for grasping. The second gnathopod is often somewhat larger in males, in which a primary function involves grasping females in connection with mating. The five remaining periopods are used for locomotion. Periopods 2-7 have gills on the first segment, which is called the coxa. In mature females, coxa 2-5 give rise to marsupial plates which collectively form the brood pouch where eggs and developing young are held. The additional six periopod segments vary morphologically among species. For unknown reasons, there is especially large variation in the second segment, known as the basis or "base", of the seventh periopod. Each of the first three abdominal segments has a pair of pleopods, which aerate the coxal gills and also aid in movement. The last three paired abdominal appendages are called uropods and are used in
Figure 1. General amphipod anatomy showing major taxonomic features.
locomotion. The telson, a flap-like structure, is attached to the last abdominal segment; it has no reported function.

Species are distinguished on a wide variety of morphological characteristics. However, a few fairly-easily observed traits can often be used to distinguish small groups of taxa at various levels, including species. These include: the relative length of the first and second antennae, the presence/absence or degree of development of the accessory flagellum, the shape of the posterior margin of the basis of the seventh periopod, and the structure of the third uropod.

Typical life-span is about a year, but life-cycles vary substantially among species. In many, mating and production of young seem to occur over an extended portion of the year (even where cold temperatures occur), generally somewhere from January through October. In some species, adults die shortly after a relatively brief reproductive period in which females produce only one brood; at certain times, therefore, these populations may contain only small, early instar individuals. In other species, adults may live up to 16 months; this, in combination with an extended reproductive period in which females produce several broods, results in populations containing a mix of adults and immatures of different instars at most times of the year.

Basic mating behavior involves males grasping other amphipods from behind, by hooking their gnathopods between the dorsal edges of the other amphipod's thoracic plates. If the other amphipod is a male it will struggle until released; females ready to mate remain docile. In many, but not all, species mating does not proceed immediately. Instead, a pre-copulatory mate-guarding phase ensues, lasting up to 7 days. During this time, the pair remains attached but continues to move and forage freely. Eventually, the male releases the female briefly to allow molting, and then quickly re-establishes the pair for mating. Fertilization is external, with the male curling around the female and releasing sperm which are transferred to the brood pouch by sweeping movements of the female's pleopods. The female then releases eggs into the pouch where they are fertilized. The young develop in the pouch until the female molts. In some species the female may form another "mating-pair" with a male while carrying eggs, so that young from a previous mating are released immediately prior to the next fertilization (Dunham et al., 1986; Pennak, 1989).
Growth rate and molting frequency depend on water temperature, food availability, age, and species; reported molt intervals range from 3-40 days (Pennak, 1989).

Amphipods are “voracious feeders” that consume “all kinds of animal and plant matter” (Pennak, 1989). However, they are not generally described as active predators on other benthic invertebrates, but may sometimes cannibalize members of their own species, or consume other amphipod species (Sexton, 1924; Dick et al., 1990).

All North American freshwater amphipods are in the suborder Gammaroidea, which contains five families: Corophiidae, Haustomiidae, Pontogeneiidae, Talitridae, and Gammaridae. The most common and abundant species are in the Gammaridae. Within this family there are eight genera forming three taxonomic groupings: Gammarus group—Gammarus, Crangonyx group—Crangonyx, Synurella, Apocrangonyx, Stygonectes, Stygobromus, and Bactrurus; Allocrangonyx group—Allocrangonyx (Holsinger, 1976). The family Talitridae contains a single species, Hyalella azteca (Saussure), which is also common.

Based on published distributions and habitat descriptions (Bousfield, 1958; Holsinger, 1976; Holsinger, pers. com.; Pennak, 1989), the following species were considered as likely or possibly occurring in the Williamsburg vicinity:

*Gammarus fasciatus* Say, described as occurring in lakes, rivers, and small streams from the upper Mississippi River drainage, across the Great Lakes, and down the Atlantic coast to North Carolina.

*Synurella chamberlaini* (Ellis), described as occurring in ponds and ditches in Virginia, South Carolina, and northern Florida.

*Crangonyx serratus* (Embody), described as occurring in sloughs, ponds, and ditches of the eastern areas of Virginia, extending south to northern Florida.

*Crangonyx shoemakeri* (Hubricht and Mackin), described as occurring in temporary pools and ponds, springs, small streams, and bogs of Maryland, DC, and Virginia.

*Crangonyx obliquus-richmondensis*, a species complex, described as occurring in temporary and permanent small streams, sloughs, swamps, bogs, ditches, ponds, drains, and in shallow water along the shore of lakes in the eastern half of the United States, including Southeastern Virginia.
Hyalella azteca (Saussure) is described as common in a wide variety of habitats across most of North America.

Despite their commonness, relatively little is known about the ecology of amphipods, particularly regarding factors affecting specific distribution patterns within general ranges. The most common species are described generally as occurring in "unpolluted clear waters" with "an abundance of dissolved oxygen" (Pennak, 1989). Presumably, as with any species, they are limited by some combination of physical/chemical factors and biological interactions such as competition or predation. However, most information is fragmentary, contradictory, or simply descriptive of where a given species is found. Following is a summary of existing literature, most of which involves chemical factors that have been discussed in relation to amphipod distribution.

Early work by Schuman (1928), as reported in Hynes (1954), suggested that distributions were determined at least in part by minimum levels of dissolved materials, especially calcium (or possibly the calcium/magnesium ratio). Hynes (1954), however, in work on the ecology of the European species G. duebeni Lilljeborg and G. pulex Linnaeus was not able to relate the distribution of either species to any of the following factors, or any combination of these: calcium, magnesium, pH, potassium, sodium, alkalinity, total dissolved materials, geological formation, or associated macrofauna. He concluded that "It is clear therefore that the distribution of G. pulex and G. duebeni is difficult to explain." Sutcliffe and Carrick (1973) found in a descriptive study of G. pulex in England that this species was not found below a pH of 5.7, and concluded that calcium per se is less important than levels of bicarbonate (with which calcium is usually associated, and which affects pH by its buffering ability). Schrimpff and Foeckler (1985) developed a model that was successful in predicting the presence/absence (not abundance) of G. fossarum Koch and G. roeseli Gervais in Germany on the basis of calcium and magnesium levels in combination with pH. Broadly, amphipods occurred in the ranges of calcium 82.5-850 mg/l CaCO_3 1, magnesium 41.2-164.8 mg/l CaCO_3, and pH 7.5-8.8; of these variables, magnesium seemed to be the most important. In a macroinvertebrate study of Pennsylvania springs, G. minus Say was found at total

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1 Calcium and magnesium are typically reported in various ways, including as the uncombined forms (i.e. mg/l Ca^{2+} or Mg^{2+}) or as the equivalent form of CaCO_3 hardness (i.e. mg/l CaCO_3). All results reported here have been converted to the latter.
hardness (calcium plus magnesium) levels of 20-272 mg/l CaCO₃ on substrates with particle sizes ranging from silt to gravel (Glazier and Gooch, 1987). In some Canadian lakes, *H. azteca* was found at calcium levels ranging from 1.4-4.75 mg/l CaCO₃ and magnesium levels ranging from 1.4-3.34 mg/l CaCO₃ (Schell and Kerekes, 1989).

In part because of concerns about the broad problem of acid rain and the more localized problem of acid mine drainage, a number of studies have looked specifically at amphipod distribution or survival in relation to pH. In lakes in Ontario and Nova Scotia, the minimum pH level required by *H. azteca* appeared to be in the range 3.6-5.7, with the exact limiting value apparently depending on the concentrations of sodium, potassium, calcium, and magnesium (Franze and LaZerte, 1987; Stephenson and Mackie, 1986; Schell and Kerekes, 1989; Grapentine and Rosenberg, 1992). In laboratory flow-tank experiments the northern-US/Canadian species *G. pseudolimnaeus* Bousfield showed increased "stress" (manifested by increased downstream movement) at pH 5, and 100% mortality at pH 2.5 (Williams and Moore, 1982). In a stream-transfer experiment in Sweden, *G. pulex* showed 99% mortality at a pH less than 5 (Hargeby, 1990).

In summary, amphipods appear to occur over rather wide ranges of these variables, with apparent minimum levels also varying substantially. It is very important to keep in mind, however, that many of these studies are simply field observations that do not involve the experimental manipulation of variables, and which do not rule out other factors that may be restricting amphipods at their distribution limits.

Complicating the assessment of potential limiting chemical factors is the absence of information within the physiological literature on any simple mechanism that might hinder survival. Calcium has multiple roles physiologically, affecting such functions as membrane permeability and the oxygen affinity of hemocyanin; it is also a major component of the exoskeleton (Hilton et al, 1984; Hargeby, 1990; Taylor and Spicer, 1986; Morritt, 1989). Physiological studies have not established any minimal environmental requirement, nor is there any information on the possible importance of dietary calcium in amphipods. Under acid stress, the calcium carbonate in the exoskeleton may be eroded to help buffer internal fluids (Hargeby and Peterson, 1988; Schell and Kerekes, 1989). More broadly, lower pH may not be immediately fatal, but may cause physiological stress of some kind that increases the costs of
homeostasis, in turn decreasing fitness (Hargeby, 1990). For at least some of the possible mechanisms, amphipods are probably most susceptible immediately after molting, when the exoskeleton is highly permeable (Hargeby and Peterson, 1988). Although magnesium has been suggested as important by some field studies, and is thought by physiologists to behave similarly to calcium in some functions, no clear physiological role has been established in amphipods.

Very little work has addressed, or even suggested, the possible importance of biological interactions such as competition and predation in explaining distribution patterns of amphipods. Brief accounts of typical habitats that accompany taxonomic keys indicate significant niche differences among many species, although conversely there are also many species that appear to overlap broadly. In one study that did address apparent competitive exclusion, Dick et al (1990) suggested that male *G. pulex* eliminated *G. duebeni* through predation on females of the latter.

**Focus of Thesis**

Preliminary observations indicated that amphipods are common in many, but not all, freshwater habitats on the William and Mary Campus. However, no information is available on species composition or distribution of species.

In this work I document the species present on the campus, and begin an assessment of potential factors determining distributions with particular emphasis given *G. pseudolimnaeus* which, as described later, was unexpected in the area, but which occurred in abundance in some locations. The work involves four aspects: 1) a general survey of all habitats to determine general species composition and distribution, 2) a closer focus on *G. pseudolimnaeus* within its favored habitat (Woods streams) in relation to selected variables, 3) determination of the small-scale distribution of *G. pseudolimnaeus* in the immediate vicinity of its upstream distribution limit, in relation to selected variables, 4) experimental displacement of *G. pseudolimnaeus* into upstream areas where it does not naturally occur.
Materials/Methods

Study Area

Lake Matoaka, a shallow (5.7 m maximum depth) highly eutrophic body of water encompassing approximately 16 ha, forms the major division between the developed areas of the William and Mary campus to the east and the undeveloped areas of the campus to the west (Fig. 2). Although the lake is protected to some degree by some undeveloped areas in its watershed, the overall impact of the developed areas has been sufficient to seriously degrade the habitat. Specific problems potentially relevant to amphipod occurrence include periodic reductions in oxygen concentration, and large areas of silt substrate presumably not favorable to most species. The lake contains an abundant fish population, including several species that are likely to feed on amphipods. Potential invertebrate predators, such as Odonata nymphs, are also abundant.

The six main tributaries of the Lake reflect the dichotomy of the Lake's location. Three originate and are contained completely within the College Woods to the west of the Lake (Fig. 2). These streams, known as Strawberry, Pogonia, and Berkeley, are approximately 700-900 m long, generally with widths of only 2 m or less and depths of 10 cm or less. By virtue of their protected location in the Woods, water quality is high with no evidence of any pollution. Oxygen levels are usually near saturation in most areas. Substrates are generally firm, consisting of sand and other materials, with little silt. Overall diversity of benthic invertebrate species is very high, but population levels for most species, including potential amphipod predators, are low. The only fish present is the Least Brook Lamprey, which occurs sporadically in very small numbers, and does not feed during its active adult stage.

Although these streams appear generally favorable for amphipods, they exhibit an extreme chemical gradient in regard to dissolved materials. Conductivity (an index to the total amount of dissolved materials in water) ranges from a low of 12-20 micromhos at their sources to about 250
Figure 2. Map of the study area showing Lake Matoaka, streams, tributaries, roads, and the different areas of campus. Seeps are indicated by s.
micromhos at their mouths in the Lake. This is due in part to a change in the underlying geologic formations; the Windsor formation is upstream, but gives way to the Yorktown formation closer to the Lake. Aside from various general chemical differences that relate to these geological differences, perhaps the most noteworthy distinction between the two formations is the near-absence of soluble calcareous material in the Windsor, contrasting with an abundance of such material in the Yorktown. The streams reflect this, with extremely low levels of calcium near their sources, but high levels near the lake.

Two streams, Crim Dell and Rec Run (Fig. 2), flow through the developed Campus area. Crim Dell Stream is approximately the same size as the Woods streams; Rec Run is about half the length of the others. However, like Lake Matoaka, these streams are significantly degraded as evidenced by reduced oxygen levels, frequent turbidity from run-off and the associated accumulation of silty substrates, and very low species diversity.

College Creek, entering at the Lake's north end, is about 1.5 km long, and somewhat larger than the other streams, particularly near the Lake during times of high flow. The area between Monticello Avenue and the Lake is highly disturbed, but the portion above Monticello is mostly surrounded by woods and appears to be less impacted.

In addition to these main tributaries, numerous smaller "seeps" occur throughout the area, primarily in the more protected areas. These are generally less than 100 m in length, with water depths sometimes less than 1 cm and typically no greater than 3 cm. I included 15 of these in this study: four that flow into Berkeley, four flowing into Strawberry, 2 flowing into College Creek, and five flowing directly into the Lake (Fig. 2).

1. **General Survey**

Between April 20 and August 6, 1995, I conducted a general non-quantitative survey of the lake and streams. The primary purpose of this survey was to determine the presence/absence of amphipod species, and their relative proportions, at the various sites.

With the exception of College Creek, each stream had four survey sites located as follows: one approximately 50 meters above the mouth, two mid stream sites approximately one third and two thirds upstream respectively, and a fourth site near the upper limits of the stream. College Creek was surveyed
only in the region above Monticello Avenue where conditions are similar to the woods streams; four sites encompassing most of this area and located approximately equidistant from each other were sampled. Ten seeps that feed into the streams and five that feed into Lake Matoaka were also surveyed, with the number of sites per seep ranging from one to three, depending on seep length. Eighteen sites in Lake Matoaka were surveyed, located around the periphery of the lake along the immediate shoreline and in shallow open areas within 50 meters of the shore.

In streams and all seeps, collections were obtained by scooping leaf litter and other substrates into a bucket, adding water, stirring to loosen the amphipods, and pouring the water and contents over a 3 mm wire screen (small enough to capture adults of any described North American species). Amphipods were removed and stored in 70% ethanol. Collecting continued until at least 40 individuals were obtained or until 30 minutes had elapsed.

Collections in the lake were made from a boat with a long handled, 3 mm mesh net in order to gather leaves, algae, and other substrates, with the associated macrobenthos. These materials were transferred to a bucket, to which lake water was added. The contents of the bucket were poured over a 3 mm wire mesh screen. Amphipods were removed and stored in 70% ethanol. Collecting continued until 40 individuals were obtained or four net samples were taken.

2. *G. pseudolimnaeus*² distribution in the Woods streams

Results of the general survey, as described below, indicated that an unexpected species, *G. pseudolimnaeus*, was present in the area, and especially abundant in the Woods streams (Berkeley, Pogonia, and Strawberry). This species, described previously only from parts of the Great Lakes and upper Mississippi River drainages, appeared to be by far the dominant benthic organism in these streams. Therefore I conducted an additional survey on the Woods streams, which were known to have a substantial gradient in the concentration of dissolved materials, to provide more information on the distribution of *G. pseudolimnaeus* and to assess possible relationships between abundance and selected environmental variables.

² The taxonomic status of the specimens discussed here has not been determined definitively. Specimens appear to be *G. pseudolimnaeus*, and for convenience will be referred to as such for the remainder of this thesis. See further discussion in the General Results section.
The survey was carried out from June 26 to June 28, 1996. Berkeley, Pogonia, and Strawberry were sampled at four sites, with one stream sampled per day. Sample sites were the same as used in the general survey, with the first site approximately 50 meters from the lake, and sites two and three approximately 1/3 and 2/3 upstream. Site four was near the uppermost area of the stream, but still within the general region of amphipod occurrence.

At each site conductivity and pH were measured prior to sampling. One liter of water was also collected from each site for laboratory determination of calcium and magnesium levels, based on a mean of two subsamples using Hach Company digital titration protocols.

Two amphipod samples were taken at each site using a 24 cm diameter bottomless bucket pushed into the substrate to a depth of 7.5 cm (G. pseudolimnaeus does not inhabit substrate below a depth of 4-5 cm (Miller, 1982)). For one sample, the bucket was placed over an area completely covered with leaf litter, and for the other over a sandy area lacking leaf litter. The 7.5 cm of substrate was removed to another bucket with a garden trowel. A 1 mm mesh net was then swirled through the water to capture amphipods which had not been removed with the substrate. Stream water was added to the bucket of substrate and the contents were poured over a 3mm wire mesh screen to trap the amphipods, which were stored in 70% ethanol. In the lab, the amphipods were identified and counted.

3. Distribution limit studies

Preliminary sampling in the uppermost areas of Berkeley and Pogonia indicated that amphipods were not present despite their abundance a short distance downstream. It also appeared that the reduction in numbers was quite sharp in Berkeley, and somewhat less so in Pogonia. This survey involved closely spaced sampling in both streams, on both sides of the approximate limit of distribution, in order to determine the sharpness with which numbers declined and the chemical conditions in the area of decline.

This work was carried out June 3 and 4, 1996 and repeated January 7 and 8, 1997. A reference site was established in both streams at what appeared to be the approximate limit of amphipod distribution; this site was approximately 850 meters upstream in Berkeley and 650 meters upstream in Pogonia. Samples were collected on either side of this location. In Berkeley, samples were taken 20.
and 2 meters below the initial site, and 2, 4, 8, 12, 16, and 20 meters above that site. In Pogonia samples were taken 100, 50, and 5 meters below the initial site, and 5, 10, 15, 20, 25, and 29 meters above this site. Samples were taken following the procedures in the G. pseudolimnaeus survey described above in Part 2 except that the maximum number of amphipods collected at any site was 50, a number large enough to confirm that amphipods were abundant.

Conductivity and pH were measured at each site in the June survey; in January only conductivity was measured due to a malfunction of the pH meter. Additionally, chemical information was obtained for two sites: one where the number of amphipods collected had declined substantially relative to numbers collected a short distance downstream, but had not reached zero, and another, above this site, where amphipods were absent. For each of these sites, one liter of water was collected and brought back to the lab to measure calcium and magnesium, following the procedures described in the Part 2.

4. Displacement.

As noted above, G. pseudolimnaeus is not present in the upper regions of Berkeley and Pogonia. The purpose of this work was to begin assessing possible reasons for the absence of G. pseudolimnaeus through a controlled displacement of individuals into those areas. More specifically, the work provides preliminary information on chemical conditions vs. possible interspecific interactions as likely factors in limiting G. pseudolimnaeus. This work was carried out from May 24 to June 25, 1996 and repeated from August 9 to September 10, 1996 in Pogonia.

Covered plastic food storage boxes, 22.5x15x5 cm, with an 8x2 cm opening cut into both ends were used to hold the amphipods. Openings were covered with fiberglass insect screen which was held in place with silicone caulk. Unsexed adult G. pseudolimnaeus, larger than 10 mm, were collected from Berkeley approximately 550 meters above the lake, where they are common. Twenty amphipods were placed in each of two boxes, which were set into a shallow depression in the substrate at the collection site. Boxes were held in place with a brick placed on top. These boxes served as a control to determine if either handling or containment in the boxes had a negative effect on the amphipods. Two other boxes, each containing twenty amphipods collected from this same site, were set up approximately four meters below the approximate distribution limit (as determined in Part 3), where amphipods were still present.
This site controlled for possible effects of handling, transfer, and acclimation to chemical differences in the water. A third site was established approximately 40 meters above the distribution limit, where amphipods do not occur; two boxes were placed in this area, using procedures identical to those for the other sites.

The same experiment was carried out in Pogonia, with the collection area located approximately 250 meters above the lake. Two boxes were set up there as the first control treatment and two more were set up as the second control treatment approximately ten meters below the distribution limit. The third pair of boxes was placed approximately 40 meters above the distribution limit, where *G. pseudolimnaeus* was not present.

No substrate or other material was added initially to any boxes, but they accumulated sediment and detritus that was removed at each observation.

The boxes were checked twice during the first week to count the number of amphipods remaining alive, but after it became apparent that very rapid changes were not taking place, they were checked every 6-8 days. Amphipods were counted by removing the box from the water, pouring accumulated sediment inside the box onto a 3 mm wire mesh screen, and rinsing until only the amphipods remained. They were then counted and returned to the box, which was restored to its original position. Boxes were monitored for 32 days, at which time, as described below, 100% mortality had occurred at the uppermost site in both streams.
Results/Discussion

1. General Survey

Four species of amphipod were found in the study area: *Hyalella azteca, Gammarus fasciatus, apparent* *G. pseudolimnaeus* (see below), and *Synurella chamberlaini* (Fig. 3). *H. azteca* and *G. fasciatus* were found in Lake Matoaka in both open water and shore sites (Fig. 4). *G. fasciatus* was found at 12 of the 18 sites, ranging in number from 1-37 and *H. azteca* was found at 14 of the 18 sites ranging in number from 1-33; at most sites *G. fasciatus* was the numerically dominant species. *G. fasciatus* was also found at site one (closest to the lake) in both Berkeley and Crim Dell Stream (25 individuals at each location). *C. serratus, C. shoemakeri, and C. obliquus richmondensis* were not found in the study area.

*G. pseudolimnaeus* was found at all sites in Berkeley, Pogonia, Strawberry, and College Creek in numbers ranging from 19 to 91 per site (Fig. 4). It was also found in three seeps that flow into Berkeley, two seeps that flow into Strawberry, two College Creek seeps, and two Lake Matoaka seeps in numbers ranging from 10-115 per site. Four *S. chamberlaini* were found at one location at Berkeley Site 4. No amphipods were found in Rec Run and Sites 2-4 of Crim Dell Stream.

Based on published distributions, *G. pseudolimnaeus* was not expected to be found in this area. Its range is described as the drainages of the upper Mississippi River and Great Lakes (Pennak, 1989); any population in the William and Mary area would be highly disjunct. Description of my specimens as *G. pseudolimnaeus* is based on 1) examination of organisms in conjunction with three available keys, in which they match, exclusively, the description given for *G. pseudolimnaeus*, 2) personal communication with J. Holsinger (Old Dom. Univ.) who confirms a close match with *G. pseudolimnaeus* but not with any other described species. Further work, both taxonomic and ecological, will be necessary to determine definitively whether this amphipod should be called *G. pseudolimnaeus* or designated a new species. For
Figure 3. The four species of amphipod found in the study area. (Left to right) *Gammarus fasciatus*, *G. pseudolimnaeus*, *Synurella chamberlaini*, (bottom center) *Hyalella azteca*. 
Figure 3. Results of the General Survey, showing the study area and the species of amphipod collected at the various sites. Seeps are designated by s. Circles with combined colors indicate the presence of two species.
simplicity, I will refer to this species as *G. pseudolimnaeus*.

Previous literature on *G. pseudolimnaeus* and *G. fasciatus* does not suggest the kind of habitat differences I found here, involving both general habitat type and degree of disturbance within the habitat. *G. pseudolimnaeus* is described as occurring in the clear water of springs, streams, pools, ponds, and lakes often in association with *H. azteca* (Bousfield, 1958; Holsinger, 1976; Pennak, 1989). Bousfield (1958) suggests that it migrates from large rivers and lakes to breed in smaller streams and springs which remain cool in the summer, but this latter observation is unconfirmed by other authors.

*G. fasciatus* is described similarly as inhabiting a wide range of habitats, including both lentic and lotic habitats of all sizes (Bousfield, 1958; Holsinger, 1976; Pennak, 1989). Bousfield (1958) also reports that it is frequently associated with *G. pseudolimnaeus* in rivers and lakes.

Although the habitats suggested by the literature for the two species are similarly broad, and they are documented as occurring together in some cases *G. pseudolimnaeus* was found in pristine streams and seeps while *G. fasciatus* was found essentially in disturbed standing water. The two species were found together only at Berkeley site 1 (nearest to Lake Matoaka).

My findings for *H. azteca* also are not completely consistent with its published ecology. It is reported in all types of freshwater habitats, both standing and flowing, with extensions into highly alkaline and brackish waters (Pennak, 1989). Bousfield (1958) reports it as often associated with *G. pseudolimnaeus* in streams, and occurring in “all permanent shallow freshwater that reaches a monthly mean summer temperature of more than 10°C”; Grapentine and Rosenberg (1992) likewise suggest it is tolerant of a wide range of environmental conditions. Here it was found only in Lake Matoaka, associated with *G. fasciatus*. The absence of *H. azteca* species from all of the streams was unexpected since the Woods streams appeared to be ideal habitat and Crim Dell Stream and Rec Run, though significantly impacted, were considered potential habitat in light of the reported wide tolerances of this species.

Ecological information on *S. chamberlaini*, which is limited to brief comments in various keys, places this species in the Atlantic coastal plain from Maryland to South Carolina. It is reported in small streams, ponds, bogs, and ditches (Holsinger, 1976; Pennak, 1989). Based on this information it was anticipated to be potentially present in all streams in the study area. In contrast, it was found in one
isolated location near the source in Berkeley, where the water is very low in dissolved materials.

My findings, in combination with the existing literature, suggest some broad hypotheses regarding distribution patterns of amphipods in my study area, as follows. *G. pseudolimnaeus* is competitively superior to the other three species, but also requires the highest water quality of the four. Thus it competitively excludes the other species from the undisturbed woods streams, which provide the most favorable habitat for it. However, it cannot tolerate more degraded conditions, and therefore does not occur in Lake Matoaka; this allows the more tolerant *G. fasciatus* and *H. azteca* to occur in the lake. Presumably, however, conditions in both Crim Dell Stream and Rec Run are too adverse for even these species.

The occurrence of *S. chamberlaini* in Berkeley provides the basis for further hypotheses. Results from other collecting not described here and personal communication from G. Capelli indicate that a small population of *S. chamberlaini* extends approximately ten meters upstream from the distribution limit of *G. pseudolimnaeus* in Berkeley. Presumably *G. pseudolimnaeus* is the superior competitor, but is limited at some point in its upstream distribution by the increasingly dilute water. *S. chamberlaini* is a little more tolerant of low dissolved materials, and therefore occurs in a small area above the limit of *G. pseudolimnaeus*, but is itself limited by water quality a short distance above this. In Pogonia, which provides a broadly parallel situation regarding habitat, *G. pseudolimnaeus* similarly does not occur above a certain point, but no *S. chamberlaini* are present above this limit.

The situation in Berkeley, involving a very small isolated population of *S. chamberlaini* occurring over a very short distance of stream raises questions about the history of possible population changes in the stream. Specifically, is this a long-term, sustained situation, or is it the result of relatively recent changes? Two further considerations may be relevant. First, *S. chamberlaini* appears to be broadly tolerant to a wide range of environmental conditions. Although not collected in my sampling, a few individuals have been found in Rec Run, Crim Dell Stream, and in the lower, highly disturbed area of College Creek (Capelli, pers. com.). Second, Berkeley may have been significantly disturbed in the recent past as a result of sustained farming activity that occurred until about 1982 on the non-College property bordering much of the stream to the north. In light of this, a possible scenario is as follows. *G.*
pseudolimnaeus was historically dominant in the stream. However, runoff from the field, possibly involving silt, pesticides, etc., significantly disrupted the stream (there is a large delta at the stream’s mouth, suggesting high silt load at some time in the past). Under these conditions I hypothesize that G. pseudolimnaeus was unable to thrive. S. chamberlaini, more tolerant, occupied a larger part of the stream. G. pseudolimnaeus did not become extinct in the stream however, possibly because it was able to occupy several small seeps connecting to the stream which were not affected by the runoff. Since 1982 farming has not occurred, and the land has remained undisturbed as it moves through the early stages of old-field succession. During this time water quality has returned to its more natural undisturbed state; concomitant with that, G. pseudolimnaeus has been able to re-establish itself throughout the stream, thereby eliminating S. chamberlaini except in the small stretch upstream where dissolved materials are too low for G. pseudolimnaeus. Thus, S. chamberlaini has become “trapped” in a small isolated area.

Although these scenarios are consistent with our observations, no definitive information exists on potential limiting factors or mechanisms of competitive exclusion. Also, it is perhaps relevant that the Woods streams contain no apparent significant predators on G. pseudolimnaeus. If predators (most likely fish) were present, the dynamics of any competitive interaction favoring G. pseudolimnaeus might change. Various further studies of potential competitive or limiting mechanisms through laboratory or field experimentation should provide valuable insight.

2. G. pseudolimnaeus distribution in the Woods streams

G. pseudolimnaeus was found at all sample sites in Berkeley, Pogonia, and Strawberry. In all three streams conductivity and calcium levels were relatively high at site 1 (Fig. 5). In Berkeley, both conductivity and calcium remained consistently high through site 3, after which both dropped to much lower levels by site 4. In Pogonia, both conductivity and calcium declined steadily until site 3, and then declined more rapidly until site 4, the approximate limit of G. pseudolimnaeus distribution. In Strawberry, calcium remained constant and high throughout the stream, while conductivity remained high until site 3, after which it declined slightly before the stream ended just above site 4.

G. pseudolimnaeus was found at all sample sites in all three streams. Total number (the combination of leaf litter and sand samples at each site) was examined to see if it appeared to be related in
Figure 5. Conductivity and calcium results from the G. pseudolimnaeus survey.
a general way to conductivity, calcium, magnesium, or pH (Figs. 6 and 7). The small sample size precludes statistical analysis, but visual inspection of the data strongly suggests no apparent relationships. Although in all streams there was a general increase in dissolved material downstream, *G. pseudolimnaeus* abundance did not show consistent patterns within individual streams, or from one stream to another. Similarly, for all streams combined, there are no apparent relationships between increasing variable values and *G. pseudolimnaeus* abundance.

*G. pseudolimnaeus* was generally more abundant in leaf litter than in sand (Tab. 1). However, numbers in individual samples varied substantially within both types of substrate. The large variation is probably a result of variations in the substrate sampled because there was no way to control precisely amounts or proportions of leaf litter, other detritus, silt, sand, etc. in each sample.

It appears that *G. pseudolimnaeus* is able to survive over a broad range of chemical conditions and, within that range, differences in chemistry are not the major determinant of abundance. Other factors, such as substrate, are a more important influence on small scale distribution and abundance.

Presumably both hiding in leaf litter and burrowing in sand are advantageous in reducing predation (Williams and Moore, 1982). Other possible advantages, such as a reduction in downstream drift, or a reduction in the amount of energy needed to maintain position, could also apply to both (Rees, 1972; Gee, 1982). However, the leaves not only provide shelter but are also an important food source. They would also have the obvious advantage of allowing easier movement (for foraging, mating, etc.). To the extent that visual predators, such as fish, might be important (in other habitats) amphipods in leaf litter might be able to be continuously active; those in sand might be restricted to darkness for large-scale movements. Although my results indicate a clear preference for leaf litter, the fact that some amphipods do occur on sand requires some explanation. Perhaps the most likely reason involves simple competitive exclusion. Pennak (1989) reports that amphipods may occur at densities as high as 10,000/m². The highest density in my study was equivalent to about 4500/m². This may be high enough that some individuals are physically excluded from the most favorable areas.

Other scenarios may be hypothesized. For example, amphipods in sand appear to be generally smaller than those in leaf litter. This would still be consistent with general competitive exclusion, but
Figure 6. The number of *G. pseudolimnaeus* collected at each site in the three Woods streams, in the *G. pseudolimnaeus* stream distribution survey, in relation to conductivity and pH.
Figure 7. The number of *G. pseudolimnaeus* collected at each site in the three Woods streams, in the *G. pseudolimnaeus* stream distribution survey, in relation to calcium and magnesium.
Table 1. Results from the *G. pseudolimnaeus* stream distribution survey. Table shows the number of *G. pseudolimnaeus* collected at each site, separated by substrate.

<table>
<thead>
<tr>
<th>Stream</th>
<th>Substrate</th>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
<th>Site 4</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Berkeley</td>
<td>sand</td>
<td>7</td>
<td>2</td>
<td>35</td>
<td>9</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>leaves</td>
<td>4</td>
<td>16</td>
<td>144</td>
<td>43</td>
<td>207</td>
</tr>
<tr>
<td>Pogonia</td>
<td>sand</td>
<td>39</td>
<td>4</td>
<td>8</td>
<td>5</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>leaves</td>
<td>12</td>
<td>20</td>
<td>28</td>
<td>87</td>
<td>147</td>
</tr>
<tr>
<td>Strawberry</td>
<td>sand</td>
<td>11</td>
<td>59</td>
<td>6</td>
<td>18</td>
<td>84</td>
</tr>
<tr>
<td></td>
<td>leaves</td>
<td>23</td>
<td>201</td>
<td>47</td>
<td>161</td>
<td>432</td>
</tr>
<tr>
<td>Total</td>
<td>sand</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>193</td>
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<tr>
<td>Total</td>
<td>leaves</td>
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<td></td>
<td></td>
<td></td>
<td>786</td>
</tr>
</tbody>
</table>
could also relate to various other hypothetical possibilities, such as predation of larger individuals on smaller ones.

3. Distribution limit studies

In Berkeley in the 1996 study *G. pseudolimnaeus* declined from abundant levels to absent over a very short length of stream. *G. pseudolimnaeus* was abundant four meters below the reference site, had reduced in number by the reference site, and absent four meters above it (Fig. 8). One *S. chamberlaini* was found twelve meters above the reference site. At the reference site, the approximate limit of *G. pseudolimnaeus* distribution, calcium was 3.1 mg/l CaCO₃, magnesium was 4.2 mg/l CaCO₃, pH was 6.8, and conductivity was 40 umhos (Fig. 8). In Pogonia, *G. pseudolimnaeus* abundance also declined rapidly, but somewhat less so than in Berkeley. *G. pseudolimnaeus* was abundant five meters below the reference site, reduced in number between the reference site and ten meters above it, and absent fifteen meters above the reference site (Fig. 9). Five meters above the reference site, the approximate limit of *G. pseudolimnaeus* distribution, calcium was 7.6 mg/l CaCO₃, magnesium 2.7 mg/l CaCO₃, pH 6.9, and conductivity 24 umhos (Fig. 9).

When the study was repeated in January 1997 results were largely consistent in both streams. In Berkeley, the approximate distribution limit appeared to have shifted slightly downstream from the reference site in 1996 to four meters below it, where calcium was 7.5 mg/l CaCO₃, magnesium 5.0 mg/l CaCO₃, and conductivity 43 umhos (Fig. 8). *S. chamberlaini* was present from four meters below the reference site to the reference site. In Pogonia the approximate distribution limit appeared to remain in the same location, at five meters above the reference site, where calcium was 7.2 mg/l CaCO₃, magnesium 2.0 mg/l CaCO₃, and conductivity 21 umhos (Fig. 9).

While the conditions at the approximate *G. pseudolimnaeus* distribution limit in both streams were similar, they were not identical. In Berkeley, the conductivity at the approximate distribution limit ranged from 40-43 umhos, while at this level in Pogonia *G. pseudolimnaeus* was abundant. Also, in three of four studies, the calcium level at the distribution limit ranged from 7.2-7.6 mg/l while in the fourth study it was 3.1 mg/l. The lack of exact consistency between the chemical conditions measured
**June 1996**

Ca = 3.1 mg/l CaCO₃  
Mg = 4.2 mg/l CaCO₃  
PpH = 6.8

<table>
<thead>
<tr>
<th>Amphipod Number</th>
<th>50+</th>
<th>50+</th>
<th>1</th>
<th>3</th>
<th>1</th>
<th>0</th>
<th>0</th>
<th>0</th>
<th>0</th>
<th>0</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site (m from Ref.)</td>
<td>-20</td>
<td>-4</td>
<td>-2</td>
<td>R</td>
<td>+2</td>
<td>+4</td>
<td>+8</td>
<td>+12</td>
<td>+16</td>
<td>+20</td>
</tr>
<tr>
<td>Conductivity (umhos)</td>
<td>80</td>
<td>45</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>40</td>
</tr>
</tbody>
</table>

**January 1997**

Ca = 7.5 mg/l CaCO₃  
Mg = 5.0 mg/l CaCO₃

<table>
<thead>
<tr>
<th>Amphipod Number</th>
<th>50+</th>
<th>1</th>
<th>0</th>
<th>0</th>
<th>0</th>
<th>0</th>
<th>0</th>
<th>0</th>
<th>0</th>
<th>0</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site (m from Ref.)</td>
<td>-20</td>
<td>-4</td>
<td>-2</td>
<td>R</td>
<td>+2</td>
<td>+4</td>
<td>+8</td>
<td>+12</td>
<td>+16</td>
<td>+20</td>
</tr>
<tr>
<td>Conductivity (umhos)</td>
<td>72</td>
<td>43</td>
<td>34</td>
<td>33</td>
<td>33</td>
<td>33</td>
<td>33</td>
<td>33</td>
<td>33</td>
<td>32</td>
</tr>
</tbody>
</table>

**Figure 8.** Berkeley Distribution Limit Graphs showing the number of *G. pseudolimnaeus* collected at each site in Berkeley with the conductivity (umhos) shown at each site. Additional chemical information was collected at the indicated site (arrow). Sites are numbered in meters away from the reference site, which is designated by R.
June 1996

Amphipod Number

<table>
<thead>
<tr>
<th>Site (m from Ref.)</th>
<th>Amphipod Number</th>
<th>Conductivity (umhos)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>50+</td>
<td>85</td>
</tr>
<tr>
<td>-100</td>
<td>50+</td>
<td>73</td>
</tr>
</tbody>
</table>

January 1997

Amphipod Number

<table>
<thead>
<tr>
<th>Site (m from ref.)</th>
<th>Amphipod Number</th>
<th>Conductivity (umhos)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>50+</td>
<td>75</td>
</tr>
<tr>
<td>-100</td>
<td>14</td>
<td>63</td>
</tr>
</tbody>
</table>

Figure 9. Pogonia Distribution Limit Graphs showing the number of *G. pseudolimnaeus* collected at each site in Pogonia with the conductivity (umhos) shown at each site. Additional chemical information was collected for the indicated site (arrow). Sites are numbered in meters away from the reference site, which is designated by R.
here at the approximate distribution limits suggests that the interaction of other factors may play a role in survivorship of amphipods. More work needs to be done in this regard, including repeated sampling to determine the extent to which the distribution limit may shift, and expanded chemical analysis over smaller distances to determine more precisely the extent to which chemical conditions vary, and the extent to which any changes in chemistry correlate with changes in distribution limits.

At the approximate distribution limit pH ranged from 6.8-6.9, which is higher than any apparent minimums reported in the literature for other North American species. Descriptions of distributions and experimental work indicate that the following species can occur at a pH at least as low as indicated: *G. pseudolimnaeus*, pH 5 (Williams and Moore, 1982). *G. pulex*, pH 5.7 (Sutcliffe and Carrick, 1973). *H. azteca*, pH 3.6-5.8 (Stephenson and Mackie, 1986; Franze and LaZerte, 1987; Schell and Kerekes, 1989; Grapentine and Rosenberg, 1992). As my minimum pH results are significantly higher than results found for *G. pseudolimnaeus* and other North American species, they suggest pH is not a primary limiting factor for *G. pseudolimnaeus* in Berkeley and Pogonia.

Calcium levels at the distribution limit ranged from 3.1-7.6 mg/l CaCO$_3$, which is in the range of minimum levels reported in some descriptive and experimental work. Minimum levels for the following species are as indicated: *G. pulex*, 6 mg/l CaCO$_3$ (Minshall and Minshall, 1978). *H. azteca*, 3.1 mg/l CaCO$_3$ (Grapentine and Rosenberg, 1992).

Magnesium levels at the distribution limit ranged from 2.0-5.0 mg/l CaCO$_3$; little information exists on either the possible physiological importance or ecologically limiting levels of this variable. *H. azteca* can occur at magnesium levels at least as low as 1.4 mg/l CaCO$_3$ (Grapentine and Rosenberg, 1992).

Hynes and Harper (1972), working on the life histories of *G. pseudolimnaeus* and another gammarid, were puzzled by the distribution of *G. pseudolimnaeus*. They reported it to be “strangely restricted” and noted that, in one river it was abundant for several hundred meters before it “quite abruptly, and for no apparent reason, ceased to occur” (Hynes and Harper, 1972). This situation seems similar to the one in Berkeley and Pogonia. While pH seems unlikely as a primary limiting factor, calcium and magnesium remain possible limiting agents that could be responsible for the abrupt decline.
in amphipod abundance. However, other factors, such as competition, predation, and food availability cannot be ruled out.

4. Displacement

The other three experiments all showed the same trend in that the amphipods survived in the boxes placed within their natural range but had 100% mortality after a steady, gradual decline in survivorship when moved to a location above their range (Figs. 10 and 11). In each trial by day 32, 100% mortality was reached in the most upstream treatment, during which time a maximum of 22.5% mortality was reached in any of the control treatments. In all trials the amphipods were able to withstand the introduction to a new habitat at the second site with no significant differences in mortality from the collection site control treatment (Chi-square, p>0.05). While there was no statistical difference between the results of the two sites located below the approximate distribution limit in any of the trials, the above-distribution treatment was always significantly different from the other two treatments (Chi-square analysis, p<0.01).

These results are consistent with the hypothesis that the upper limit of distribution is determined by unsuitable chemical conditions. The possibility of predation or direct competitive interactions appears to be ruled out because the amphipods were protected within the boxes.

In light of the relatively slow, steady mortality seen in the above-distribution treatment, the chemical conditions there appear to be unfavorable but not immediately fatal. This finding is consistent with several possibilities involving physiological stress. Calcium levels may not have been low enough to cause immediate mortality, but they may have been low enough to prevent adequate uptake of the essential ion after molting when it is needed in order to generate a new exoskeleton (Greenaway, 1972; Hilton et al, 1984). Individuals would probably have molted at least once during the 32 day period (Pennak, 1989) but would not have been synchronized with other individuals in this. Thus mortality associated with molting would have resulted in a steady decline like the one observed. There may also be other factors causing the area to be unfavorable, such as food—the microscopic community associated with the food particles may be critical for amphipods and they may be different in this area because of the chemical conditions.
Figure 10. Graph of Berkeley Displacement Results, June 1996, showing the number of amphipods remaining alive in the three treatments for the duration of the experiment.
Figure 11. Graph of Pogonia Displacement Results, May 1996 and August 1996, showing the number of amphipods remaining alive for the duration of the experiments.
Summary and Future Work

Four species of amphipod were found in the study area: Hyalella azteca, Gammarus fasciatus, G. pseudolimnaeus, and Synurella chamberlaini. H. azteca was found in the disturbed standing water of Lake Matoaka along with G. fasciatus, which was also found at two stream sites. G. pseudolimnaeus, which was not expected in this area, was found only in the pristine flowing water of the Woods streams and seeps. S. chamberlaini was found at one location in Berkeley in water with low amounts of dissolved materials at the approximate limit of G. pseudolimnaeus distribution.

Closer examination of G. pseudolimnaeus habitats showed that it was significantly more abundant in leaf litter than it was in sand. No general relationships were found relating abundance to conductivity, calcium, magnesium, or pH. However, in two of the Woods streams, Berkeley and Pogonia, the limit of G. pseudolimnaeus distribution was located downstream of the stream source, possibly because of chemical limitations involving calcium. When populations of G. pseudolimnaeus were moved from a mid-stream site to sites near and above the distribution limit, the population just below the distribution limit showed no differences in survivorship from the collection site population. The above-distribution-limit population showed 100% mortality after 32 days, which is consistent with calcium stress associated with molting. Predation and more direct competitive interactions appeared to be ruled out because the amphipods were protected.

On the basis of my work, there are a number of directions for possible future studies, beginning with the definitive determination of the taxonomic status of G. pseudolimnaeus. Distributions will need to be rechecked and monitored to see if there are any changes that might be able to be linked to short-term changes in physical/chemical characteristics of the habitat. Displacement studies moving caged G. pseudolimnaeus into the lake and G. fasciatus and H. azteca into the streams would be a good first step in assessing possible mechanisms limiting distribution. Lab manipulations, both physiological and
behavioral, would be useful in examining the limiting requirements for any of the species.
References


Hilton, J., Sutcliffe, D. W., Carrick, T. R., and Rigg, E. (1984). Major inorganic components in some freshwater crustaceans (Malacostraca), their exuviae and food items, and thermogravimetric-


VITA

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