FACTORS REGULATING THE DISTRIBUTION AND POPULATION DYNAMICS OF THE AMPHIPOD *GAMMARUS PALUSTRIS* IN AN INTERTIDAL SALT MARSH COMMUNITY[1,2]

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Abstract. Seasonal changes in the intertidal distribution, abundance and population dynamics of the epifaunal amphipod *Gammarus palustris* were studied in salt marshes bordering 2 estuarine rivers flowing into the Chesapeake Bay. The amphipod populations inhabiting the Patuxent River study site showed abundance peaks during the spring and autumn, and major declines in density during the summer and winter. Populations at 2 study sites in the Rhode River showed only 1 peak of abundance during the late spring and early summer which was followed by a decline in density throughout the remainder of the year. In both rivers, the low amphipod densities observed during the winter corresponded with a subtidal migration. Migrations did not account for the low numbers observed at other times and an examination of the life cycle of this species as well as an egg-ratio analysis of the populations indicated that low densities during the summer (Patuxent) or late summer and fall (Rhode) were not due solely to life-cycle events.

The tolerance of *G. palustris* to 3 environmental parameters was tested in the laboratory. These included low-salinity, heat/desiccation and freezing-stress experiments. Comparisons of the results with observed fluctuations of these variables at the study sites demonstrated that only freezing stress would probably cause significant mortality in intertidal populations of this species. Insufficient tolerance to this stress was postulated as the reason for the observed distributional shift to subtidal areas during the winter. Amphipod distribution within the intertidal zone at other times of the year was highly correlated with *Spartina* density. Substratum preference experiments indicated that this was due to a strong behavioral preference by this species for *Spartina* culms.

Intraspecific and interspecific competition for food were tested by an analysis of 3 reproductive indices: the estimated birth rate as calculated by the egg-ratio method, the average brood size and the average brood size/ovigerous ♀. The former 2 indices declined during the early summer as a result of natural adult female mortality and a decreased proportion of ovigerous to nonovigerous ♀ ♀. The average brood size/ovigerous ♀ did not decline significantly throughout the reproductive period indicating that food limitation did not induce the observed summer decline in amphipod abundance.

Intraspecific competition for space was tested in the laboratory by crowding and competitive-displacement experiments. The results indicated that competition for space was not directly responsible for the summer decrease in amphipod density but did influence amphipod distribution when *Spartina* culms were a limited resource. In this situation, *G. palustris* was capable of intraspecific displacement and evidence is presented which indicates that adults are able to displace juveniles from the preferred substratum. Interspecific competition was not examined experimentally because most of the associated fauna inhabiting the marsh beds were infaunal species.

Laboratory predation experiments showed that 3 species, *Fundulus heteroclitus*, *Rhithropanopeus harrisii* and *Paleomonetes pugio* could potentially regulate *G. palustris* densities. Furthermore, *F. heteroclitus* predation decreased significantly with increased *Spartina* density and was strongly size selective for large amphipods. *Rhithropanopeus harrisii* and *P. pugio* predation was not significantly affected by *Spartina* density when amphipod abundance was low and predation by both species was significant with high amphipod and culm density, similar to that observed at the Rhode River sites. Although adult *R. harrisii* showed some indication of size selective predation, neither species was strongly size selective for large *G. palustris* when *Spartina* culms were dense. Field caging experiments combined with estimates of predator density indicated that *Fundulus* predation was the primary source of mortality in the Patuxent River population during the summer. The results of caging experiments in the Rhode River were inconclusive but large increases in predator density correlated with major declines in amphipod abundance. Therefore, predation is postulated as the major source of mortality during the summer and fall at the Rhode River sites.

Thus, both environmental and biological factors regulate these amphipod populations with the former important during the winter only and the latter important at other times of the year.

Key words: Amphipods; competition; Fundulus heteroclitus; *Gammarus; Maryland; Osteichthyes;* Palaemonetes; *Physical factors; population regulation; predation;* Rhithropanopeus harrisii; *salt marsh;* Spartina *spp.*

INTRODUCTION

Estuarine salt marshes comprise a substantial and valuable portion of coastal areas of eastern North America, yet relatively little is known about the manner in which their intertidal populations are regulated
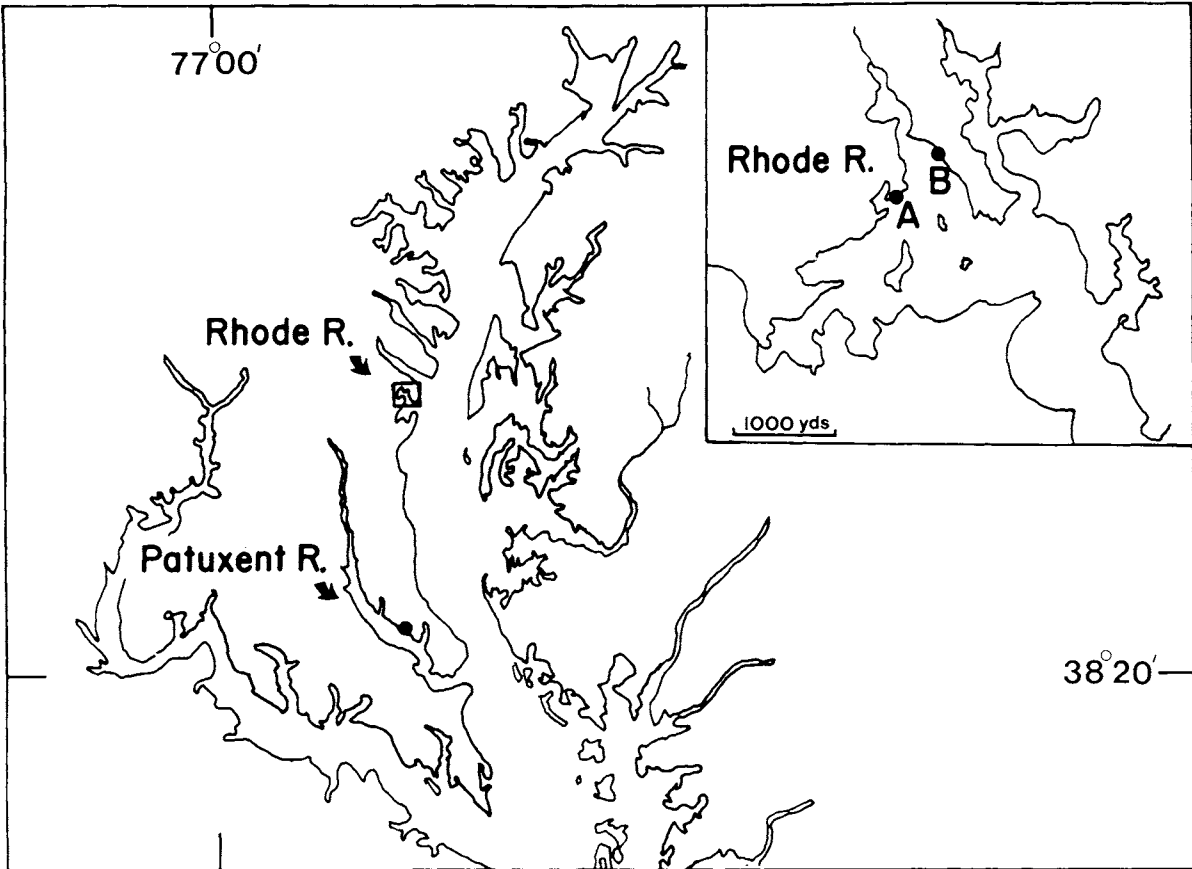
Fig. 1.   Map showing the upper Chesapeake Bay and study areas. 1000 yrd = 914 m.

in distribution and abundance. Most past work in salt marshes has emphasized energy flow (Odum and Smalley 1959, Kuenzler 1961, Teal 1962, Nixon and Oviatt 1973), whereas most studies of species regulatory mechanisms have utilized epifaunal communities of the rocky intertidal (see Connell 1972 for review) or infaunal communities of mud flats (Cassie and Michael 1968, Bloom et al. 1972, Woodin 1974, 1976) and sand beaches (Croker 1967, Dexter 1967, Sameoto 1969a, b). Furthermore, the majority of populations studied have been sessile or relatively slow-moving invertebrates.

Mobile epifaunal amphipods are 1 of the principle macrofaunal populations present in many salt marshes and therefore represent an important link between the plant detritus and larger predators. One species in particular, *Gammarus palustris* Bousfield, is the predominant amphipod present in much of the Chesapeake Bay marsh system. This species lives in close association with *Spartina alterniflora* and is distributed along the Atlantic seaboard from New Hampshire to northern Florida (Bousfield 1973). A few recent studies have examined the life cycle and population dynamics of *G. palustris* (Gable 1972, Rees 1975, Van Dolah et al. 1975). However, as is the case for most

epifaunal amphipods, very little is known about the regulatory factors operating on populations of this species.

These factors can be divided into 2 major categories: environmental and biological. Thermal stress, desiccation, wave action, and substratum composition are environmental parameters known to influence the abundance and distribution of other intertidal invertebrates (Frank 1965, Croker 1967, Kensler 1967, Sameoto 1969a, Dayton 1971, Menge 1974, Branch 1975) and may affect epifaunal amphipods as well. An additional potential stress on intertidal estuarine populations may occur from daily and seasonal salinity fluctuations. Biological factors, which include competition and predation, have also been shown to be important in regulating a variety of epifaunal and infaunal intertidal communities (Croker 1967, Sameoto 1969b, Connell 1972, Paine 1974, Woodin 1974). With respect to epifaunal amphipods, Connell (1963), Nagle (1968) and Culver (1970) have shown that intra- and/or interspecific competition influences the distribution and, to some extent, the abundance of fresh water and subtidal marine populations. Recently, Van Dolah et al. (1975) and Vince et al. (1976) have also presented evidence supporting the hypothesis that predation is

TABLE 1. Description of levels in sampling areas of Chesapeake Bay, Maryland, USA

	Patuxent River	Rhode River (Site A)	Rhode River (Site B)
Level 1	In lower portion of *Spartina alterniflora* zone (0.2 m from lower edge of intertidal shelf)	In lower portion of *S. alterniflora* zone (0.2 m from lower edge of intertidal shelf)	In lower portion of *S. alterniflora* zone (0.2 m from lower edge of intertidal shelf)
Level 2	In middle of *S. alterniflora* zone (1.0 m from lower edge)	In upper portion of *S. alterniflora* zone (1.2 m from lower edge, 0.4 m from upper edge)	In middle of *S. alterniflora* zone (1.0 m from lower edge)
Level 3	At upper edge of *S. alterniflora* zone (1.8 m from lower edge)		In middle of *S. alterniflora* zone (1.7 m from lower edge)
Level 4	In *S. patens* zone (2.4 m from lower edge)		In upper portion of *S. alterniflora* zone (2.4 m from lower edge)

an important regulatory mechanism operating on these organisms in salt marshes. However, no comprehensive studies utilizing both field and laboratory experimentation have examined the relative impact of all of these factors on the epifaunal amphipods of marsh systems.

This study describes a quantitative analysis of the environmental and biological mechanisms influencing the population dynamics and distribution of *G. palustris* at 3 locations in the Chesapeake Bay. The important regulatory mechanisms operating in different seasons are elucidated, and the contribution of environmental stress, competition and predation to the regulation of *G. palustris* is compared with other intertidal studies.

STUDY AREAS

The 3 study sites were located in estuarine rivers on the western coast of the Chesapeake Bay and represent typical intertidal marsh zones found throughout much of the Bay. One site was in the lower Patuxent River at Broomes Island in Calvert County, Maryland and the other 2 sites were located in the Rhode River in Anne Arundel County, Maryland (Fig. 1).

The Patuxent River site is characterized by an intertidal peat shelf ≈2.4 metres wide and 1 metre above a subtidal sand substratum. The flora of the peat shelf is predominantly *Spartina alterniflora* with *Spartina patens* growing only in the upper portion of the intertidal zone. The Rhode River study sites (A and B) were located at the mouth of Sellman Creek (Fig. 1). Site A is characterized by an intertidal sand–peat shelf which is narrow (1.2 m) and only 0.1 m above a subtidal sand substratum. This site is more protected from wave action than the Patuxent River and has denser stands of *S. alterniflora* with little *Spartina patens* present. Site B is similar to site A but has a wider intertidal zone (2.4 m) and peat substratum with no sand.

AMPHIPOD POPULATIONS

Field collections

Intertidal populations.—Quantitative estimates of the intertidal amphipod populations were obtained in both rivers using a modified suction pump. This device consisted of a swimming pool vacuum pump (Marlow® model #1½ H19) with a strainer (Marlow® model #B-2) attached to the pump intake. The strainer was lined with 1.0-mm wire mesh to prevent most amphipods and associated fauna from passing through the pump. Those amphipods which did pass through the pump were collected in an outflow bag made of 0.5-mm mesh screening. A flexible hose was attached to the strainer intake and a plastic sampler inserted on the intake end of the hose. The sampler consisted of a short plastic pipe (3.5 cm long, 4.0 cm in diameter) which was open on the end and had holes in the side covered with 0.5-mm mesh screen. When the sampler was placed tightly on the substratum, only water entered the sides while the faunal constituents and detritus within the sampling area were sucked into the pump. All samples were collected in daylight during high tide and each was obtained by placing the sampler onto the peat substratum 10 times at ≈0.3-m intervals. After the 10th suction, the pump was stopped and the contents of the strainer and outflow bag emptied and preserved in a 10% solution of buffered Formalin. Thus, 10 suctions comprised a sample which covered an area of 125.6 cm². This technique is superior to others as quantitative samples may be taken with minimal disturbance to the peat substratum.

In the Patuxent River, 3 replicate areas were selected at Broomes Island. Each area was ≈3 metres long and spanned the entire width of the intertidal zone. Whenever possible, 4 levels from low to high intertidal were sampled in each replicate area and 1 sample consisting of 10 suctions (125.6 cm²) was collected at each level (see Table 1 for description of levels). Occasionally, insufficient tidal height prohibited sampling the fourth level.

In the Rhode River, 5 replicate areas (each 3 m long) were sampled at Area A. Only 2 levels were monitored at this site due to the narrow width of the intertidal zone (Table 1). As *S. alterniflora* density at Area A was substantially altered during the winter of 1974, Area B was sampled in 1975. At this site, 4 levels were sampled in each of 3 replicate areas (3 m long; Table 1).
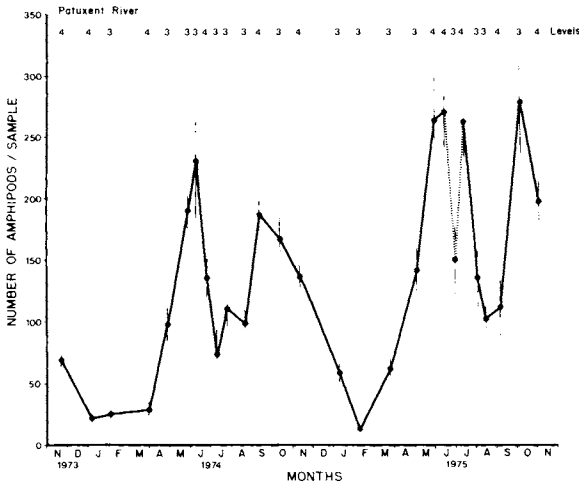
FIG. 2. Total number of *Gammarus palustris* sampled at Patuxent River site from 1973 to 1975. The dots represent the mean number from all sampling levels combined and the bar lines represent the standard error. The total number of levels sampled on each date are indicated at the top of the figure. See text for explanation of dotted line.
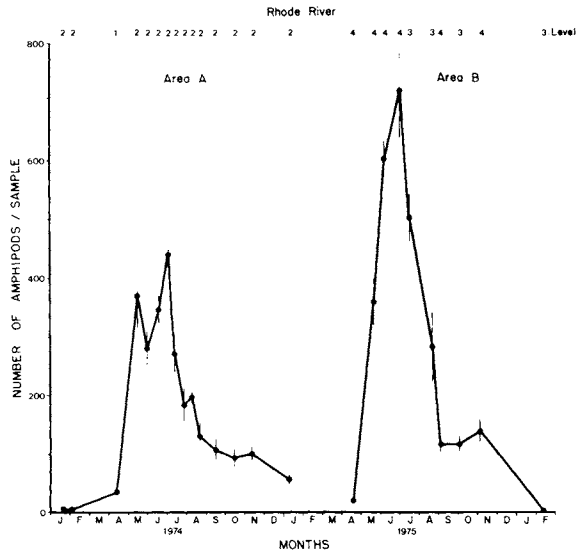

FIG. 3. Total number of *Gammarus palustris* sampled at Rhode River sites from 1974 to 1976. The dots represent the mean number from all sampling levels combined and the bar lines represent the standard error. The total number of levels sampled on each date are indicated at the top of the figure.

In both rivers, samples were collected twice monthly during the summer and monthly during the remainder of the year over a 2-yr period. After collection, the samples were brought to the laboratory and stained in a solution of Phloxine B (0.1 g/litre) and Formalin (150 ml/litre). The amphipods and associated fauna were then sorted from the detritus and preserved in a solution of 70% alcohol and 2% glycerol. Samples with a very high amphipod abundance were subsampled using the following procedure. The sample was placed in a pan marked into 8 equal areas. After mixing well, all of the amphipods and associated fauna were picked from either 2 or 4 of the areas which were chosen using a random-numbers table. The number of areas selected was dependent on amphipod density but at least 50 amphipods were sorted from each sample. Every specimen of *G. palustris* was then measured by body length (from the base of antennae to the end of

telson) to the nearest 0.5 mm as an indication of age and separated into 4 categories: males, females, ovigerous females, and juveniles (see Table 2 for criteria). The number of eggs in all ovigerous females was also recorded.

Subtidal populations.—To determine whether *G. palustris* migrates offshore at any time of the year, subtidal nets were sampled monthly throughout the study period in both rivers. The nets were a modified version of the net collection technique used by Clemens (1950) and consisted of a standard concrete block which had each end hole filled with a folded piece (1.2 × 0.6 m) of minnow seine netting (6.3-mm mesh). The holes were covered with a removable wire screen (6.3-mm mesh) which allowed amphipods access to the folded netting but excluded large vertebrates. A surface buoy allowed the block to be relo-

TABLE 2. Criteria employed to distinguish juveniles, ♂♂, ♀♀ and ovigerous ♀♀

Category	Size (mm)	Morphological correlations
Juvenile	2.0–4.0[a]	Immature individuals having no secondary sexual characteristics
♂♂	4.0–12.0	Second antennae displaying whorls of simple setae extending onto the flagellae; relatively large first and second gnathopods, presence of the penis papillae projecting medio-ventrally from the sternum near the bases of the coxae of peraeopod 7.
♀♀	4.0–9.0	Typically with relatively shorter, weaker and less setose second antennae and weakly developed gnathopod propods; brood plates present on pereonite segments 2 to 5.
Ovigerous ♀♀	4.0–10.0	Eggs present in the marsupium.

[a] Specimens <2.0 mm were excluded because of differential effects of the preservative in releasing young held by ovigerous ♀♀ as well as potential loss of this size class through screens during collection.
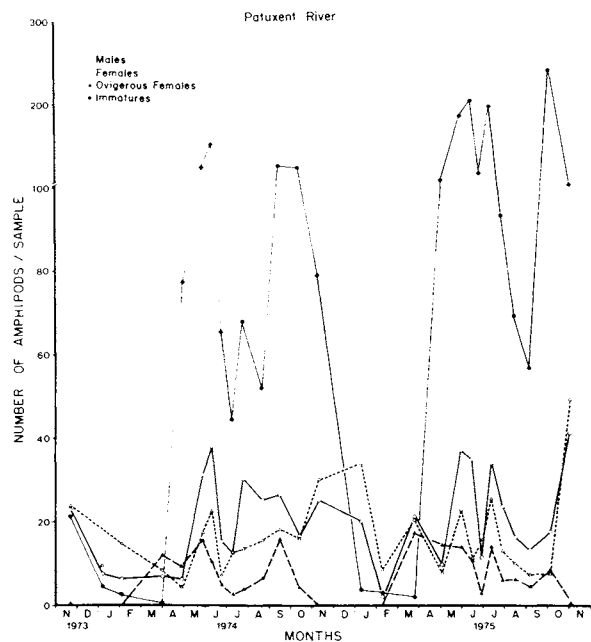
FIG. 4. Total number of ♂♂, ♀♀ (ovigerous and nono-vigerous) and juveniles of *Gammarus palustris* sampled at the Patuxent River site from 1973 to 1975. Dots represent mean numbers.

FIG. 5. Total number of ♂♂, ♀♀ (ovigerous and nono-vigerous) and juveniles of *Gammarus palustris* sampled at Rhode River sites from 1974 to 1976. Dots represent mean numbers.

cated. Samples were collected by pulling the block to the surface and vigorously shaking the nets in a bucket of water to remove the amphipods and associated fauna. Blocks were then returned to their original positions. Excess water was removed from the sample using a 0.5-mm mesh sieve, then amphipods were preserved in a 10% buffered Formalin solution. Several subtidal blocks with netting were sampled in each river but only data from nets located at the base of the intertidal shelf will be presented in this paper.

Seasonal population abundance

Based on the quantitative collections of this study, the intertidal populations of *Gammarus palustris* show definite trends of seasonal abundance in both the Patuxent and Rhode rivers (Figs. 2 and 3). The intertidal density of *G. palustris* is quite low during the winter months in the Patuxent River (Fig. 2). This is followed by a sharp increase in abundance during the spring to a peak density by June. Throughout the rest of the summer, the population density declines and remains low through September. A second rapid increase in amphipod abundance occurs in the fall which is again followed by a decline in numbers to the low intertidal density observed during the winter. This trend is exhibited in both years of the sampling period with the exception of the apparent sharp decline of numbers in June of 1975. However, I believe this to be a sampling artifact because only 3 intertidal levels could be sampled in late June whereas 4 levels were sampled in
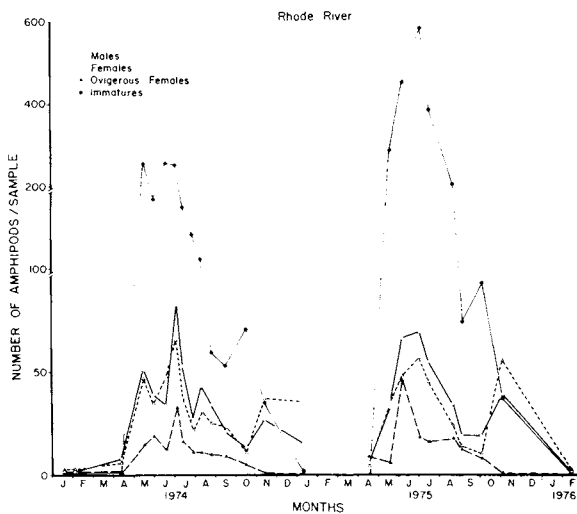
early June and late July. As will be shown later, a large proportion of the population was in the fourth level at this time. The later decline in July to a low amphipod density through September is not a sampling artifact, as the September sample also included all 4 levels.

A somewhat different trend in seasonal abundance of *G. palustris* populations is observed in the Rhode River areas (Fig. 3). In this river there is also a low intertidal density of this species during the winter months followed by a rapid increase in abundance during the spring to a maximum intertidal amphipod density by July. However, amphipod abundance then declines throughout the remainder of the year to the low winter density in both sampling areas with no substantial increase in abundance during the autumn months.

Life cycle

The life cycle of *G. palustris* in the Chesapeake Bay is elucidated by an examination of the sexual components of the total population (Figs. 4 and 5) and a size-frequency analysis (Figs. 6 and 7). The results are similar in both rivers and correspond with Gable's (1972) data for this species at the northern limit of its range, as well as confirming on a more quantitative basis the findings of Rees (1975) and Van Dolah et al. (1975).

Gammarus palustris populations appear to be composed of 2 generations. The overwintering generation is predominantly adults with only a few juveniles, which mature by April. By late March, the majority of females are ovigerous, and juveniles from these females are released in April and May, which accounts for most of the spring increase in intertidal abundance.
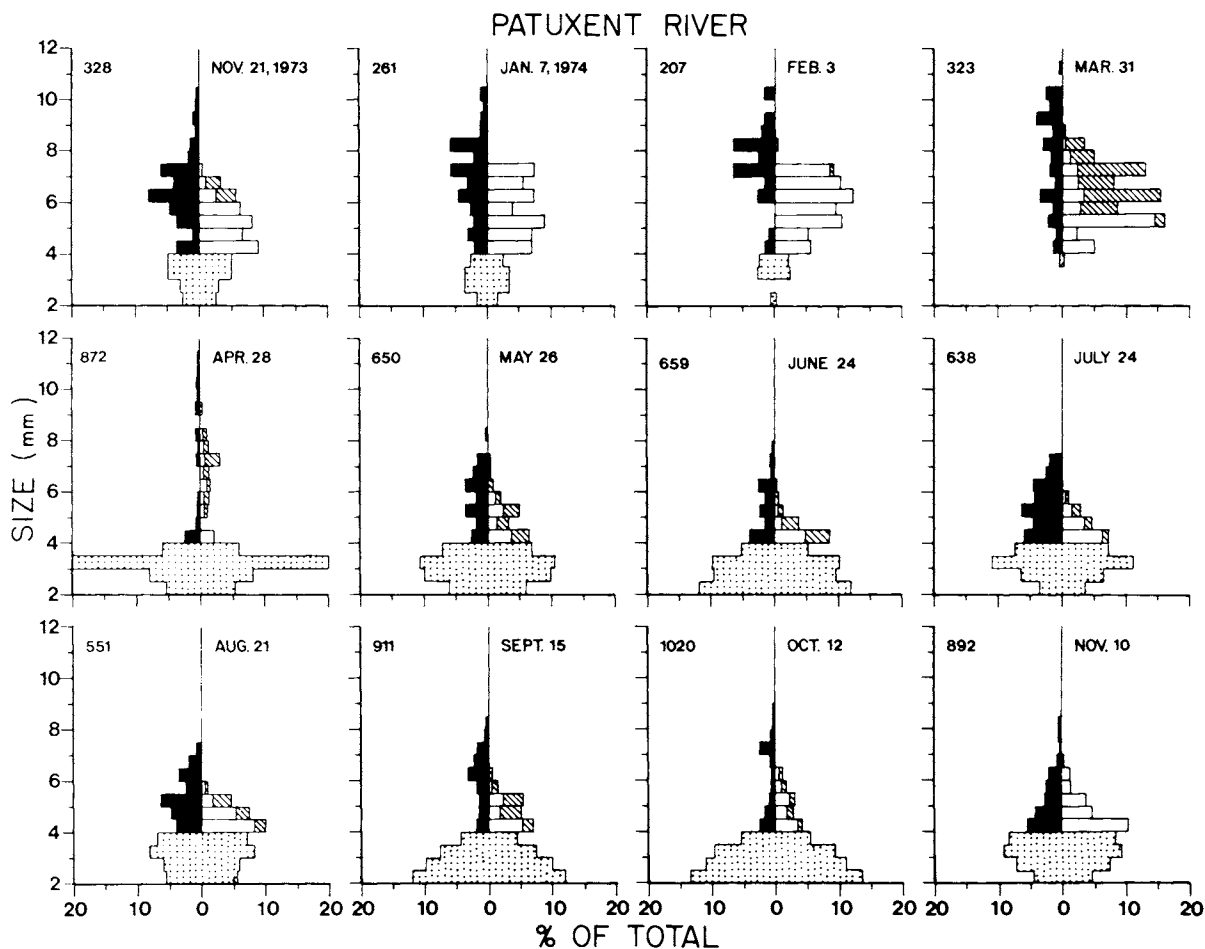
PATUXENT RIVER

FIG. 6.   Size distribution of ♂♂, ♀♀ (ovigerous and nonovigerous) and juveniles of *Gammarus palustris* collected at Patuxent River site from 1973 to 1974. Below 4.0 mm, juveniles are represented by dots. Above 4.0 mm, ♂♂ are shown at left and ♀♀ on right. Hatched portions represent ovigerous ♀♀. Numerals indicate the number of amphipods counted on each sampling date. A similar distribution was observed in 1975 (Van Dolah 1977).

The overwintering generation then declines in proportion to the total population by late June or early July. Juveniles released in the spring form the summer generation and mature throughout the spring and summer. Reproduction by this generation begins early in the summer as evidenced by the small ovigerous females at this time, and continues through October.

Bousfield (1973) and Gable (1972) indicate that females of this species produce 3–5 broods per lifetime. There is evidence of a pulse of reproductive activity during the spring and fall in the Patuxent River, whereas in the Rhode River, the number of ovigerous females increased during June and July but not during the autumn months. This difference between the 2 study areas occurred in both years. However, with the exception of August and September, juveniles comprised the majority of the population throughout the breeding season with the smallest size classes well represented at all times. As ovigerous females were always present during this time, the population ap-

pears to be breeding continuously with individual female reproductive output temporally staggered. This constant addition of juveniles to the population throughout much of the year prohibits following a particular cohort of individuals through their life cycle. Thus, an analysis of the population using life-table information is not feasible. However, it is possible to obtain estimates of birth rates ($\hat{b}$), death rates ($\hat{d}$) and per capita rates of change (r) through an analysis of the populations by a modified version of the egg-ratio method (Van Dolah 1977). The results of this analysis are presented in Figs. 8 and 9.

The Patuxent River estimates (Fig. 8) show the birth rate rising above 0 from February to October in both years. During this time, there are 3 observable increases in $\hat{b}$: a large increase during the spring and fall and a smaller rise during the summer. The decline from the spring peak in activity is largely due to the release of juveniles from the overwintering generation. The second increase in $\hat{b}$ may be attributed to a combina-
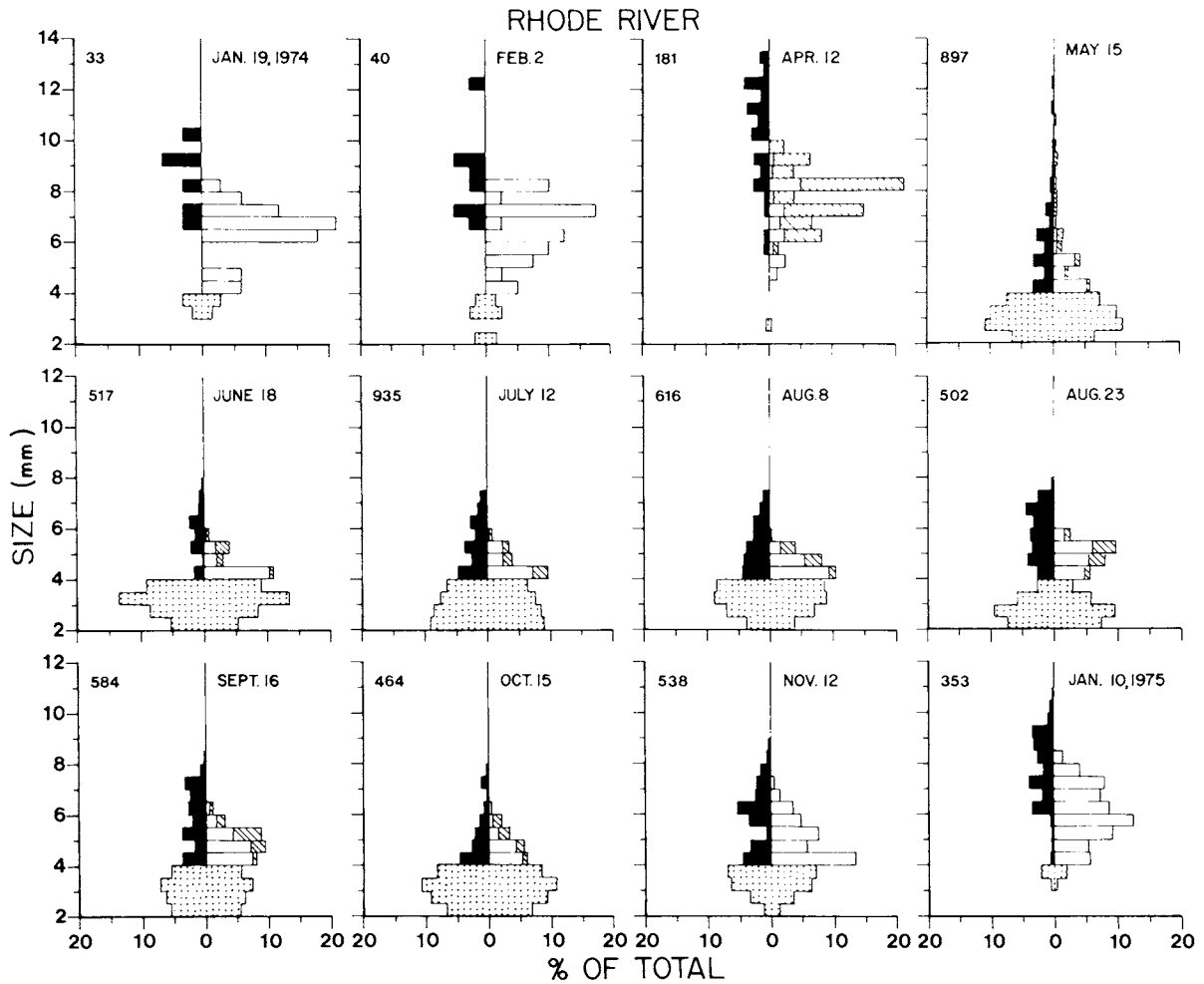
FIG. 7. Size distribution of ♂♂, ♀♀ (ovigerous and nonovigerous) and juveniles of *Gammarus palustris* collected at Rhode River sites from 1974 to 1975. Below 4.0 mm, juveniles are represented by dots. Above 4.0 mm, ♂♂ are shown on left and ♀♀ on right. Hatched portions represent number of amphipods counted on each sampling date. A similar distribution was observed from 1975 to 1976 (Van Dolah 1977).

tion of reproduction from the summer generation females and the remaining females of the overwintering generation. The autumn increase in $\hat{b}$ represents the final reproductive output of the summer generation females before the onset of winter.

The estimated death rate rose in the spring with increased mortality most probably resulting from the natural die-off of overwintering adults (Gable 1972, Rees 1975). During the summer months, $\hat{d}$ was greater than $\hat{b}$ despite a continued reproductive output. The death rate also rose above $\hat{b}$ during the winter months because no reproduction occurred at this time and intertidal amphipod densities were decreasing.

In the Rhode River, a similar trend was observed in the birth rate of amphipod populations (Fig. 9), although the values w re greater as a result of the larger average female size (Fig. 7) which will in turn result in larger brood sizes (Van Dolah et al. 1975). Note that this analysis also shows 3 increases in reproductive

activity which were not detectable in Figs. 5 and 7. The death rate exhibited a different trend than observed in the Patuxent River as it rose above $\hat{b}$ in June and remained higher throughout the remainder of the year.

During the spring months, $\hat{d}$ was negative in both rivers. Such values are either the result of an increase in the intertidal population abundance not attributable to birth (i.e., are due to immigration), or an error in the estimates caused by inaccurate sampling. As will be shown later, *G. palustris* migrates subtidally during the winter. Therefore, the negative death rates in the spring are probably the result of immigration into the intertidal zone rather than sampling error.

Sex ratio

The sex ratio for *G. palustris* over the entire study period in both rivers is presented in Table 3. For males and females ⩾4.0 mm there was a general 1:1 ratio
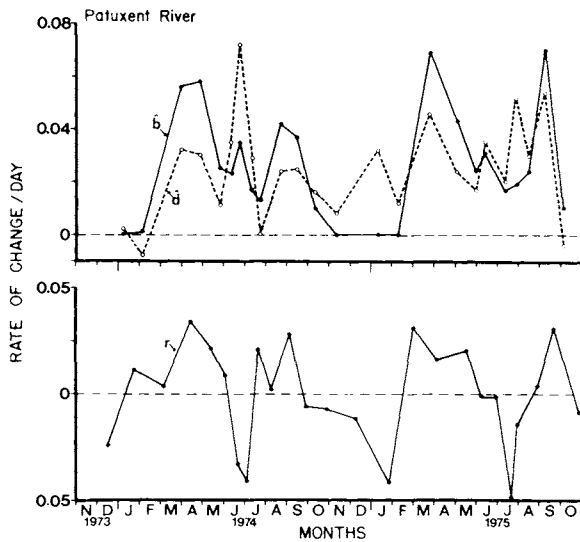
FIG. 8. Seasonal variation in the estimated birth rate (b), death rate (d) and per capita rate of change (r) for *Gammarus palustris* collected at Patuxent River site from 1973 to 1975.

over most of the year except for the early spring months, where the ♂:♀ ratio decreased (Table 3, Column A). Gable (1972) also found a general 1:1 ratio for

TABLE 3. Seasonal variation of *Gammarus palustris* sex ratio. Column A represents the number of ♂♂ (≥4.0 mm) to ♀♀ (≥4.0 mm) and Column B represents the number of ♂♂ (≥6.5 mm) to ♀♀ (≥4.0 mm). Ratios were calculated from the total number of amphipods collected on each sampling date

| Patuxent River			Rhode River		
Date	A	B	Date	A	B
21 Nov 1973	0.98	0.41	19 Jan 1974	0.25	0.25
7 Jan 1974	0.74	0.62	2 Feb	0.29	0.29
3 Feb	0.42	0.34	2 Apr	0.32	0.30
31 Mar	0.39	0.26	15 May	0.88	0.17
28 Apr	0.45	0.22	30 May	0.75	0.08
26 May	1.01	0.25	18 Jun	0.49	0.09
10 Jun	1.21	0.26	2 Jul	0.85	0.11
24 Jun	0.95	0.10	12 Jul	1.06	0.16
9 Jul	0.76	0.17	26 Jul	0.80	0.06
24 Jul	1.91	0.25	8 Aug	0.93	0.14
21 Aug	1.08	0.12	23 Aug	0.97	0.28
15 Sep	0.78	0.25	16 Sep	0.71	0.23
12 Oct	0.78	0.31	5 Oct	0.84	0.11
10 Nov	0.84	0.08	2 Nov	0.75	0.21
9 Jan 1975	0.64	0.44	10 Jan 1975	0.42	0.31
8 Feb	0.22	0.16	18 Apr	0.39	0.38
24 Mar	0.56	0.37	19 May	0.82	0.11
3 May	0.41	0.36	6 Jun	0.65	0.16
30 May	1.12	0.18	1 Jul	0.93	0.13
15 Jun	1.37	0.17	15 Jul	0.91	0.11
29 Jun	0.96	0.10	20 Aug	0.82	0.04
12 Jul	0.94	0.06	5 Sep	0.86	0.12
27 Jul	1.42	0.08	3 Oct	1.22	0.19
14 Aug	1.03	0.07	5 Nov	0.67	0.18
6 Sep	0.71	0.20	13 Feb 1976	0.25	0.25
5 Oct	1.15	0.33			
2 Nov	0.77	0.20			
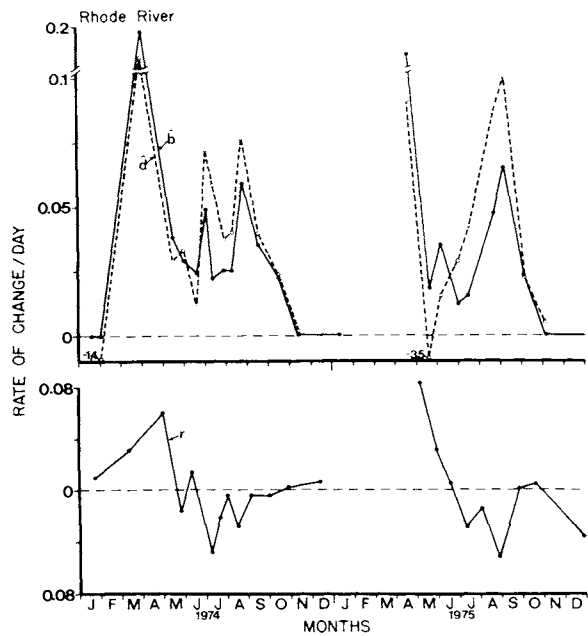
FIG. 9. Seasonal variation in the estimated birth rate (b), death rate (d) and per capita rate of change (r) for *Gammarus palustris* collected at the Rhode River sites from 1974 to 1976.

this species with the only major deviation occurring in September and October when males significantly outnumbered females. Further, he found males to always be slightly more abundant whereas my results indicate that females are slightly more abundant than males. Sex-ratio data by Rees (1975) also support my observations of a 1:1 sex ratio over most of the year for this species with the exception of the spring.

The effect of female predominance is further enhanced if one examines the ratio of sexually mature individuals only. Gable (1972) defined adult males of this species as one length class longer than mature females (≈4.0–5.5 mm for summer generation). Rees (1975) considered males ≥5.0 mm to be adults. A more accurate estimate of the minimum adult male size at maturity was obtained in this study by collection of *G. palustris* in precopula throughout the year at both study areas. A regression analysis (Fig. 10) shows a strong correlation between male and female length (r = .92). I only rarely collected ovigerous females as small as 3.0 mm and the smallest females in precopula I obtained were 4.0 mm. Therefore, I consider 4.0 mm to be the minimum average adult female size. Using this criterion, the regression analysis indicates that 6.5 mm is the minimum average adult male size. Minimum size at sexual maturity may increase slightly in other seasons (Gable 1972) but I observed several ovigerous females which were 4.0 mm in length in the overwintering generation. Thus, I will delimit maturity as 4.0 mm for females and 6.5 mm for males throughout the year. Examination of the sex ratio of mature amphi-
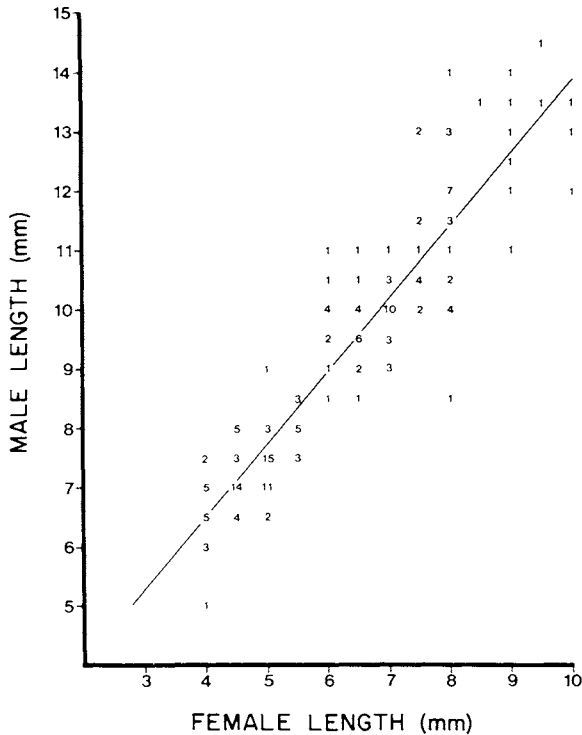
FIG. 10. Relationship of ♂ to ♀ body length of *Gammarus palustris* in precopula. $Y = 1.55 + 1.23X$, $r = .92$, $N = 175$ pairs.

TABLE 4. Seasonal variation of *Gammarus palustris* collected from subtidal nets located at the base of the intertidal peat shelf in the Patuxent and Rhode rivers

Patuxent River		Rhode River	
28 Jul 1973	−	19 Jan 1974	+ +
26 Aug	−	2 Feb	+ +
29 Sep	−	13 Mar	+ +
3 Nov	−	12 Apr	+
21 Nov	+ +	15 May	+
7 Jan 1974	+ +	30 May	−
3 Feb	+ +	2 Jul	−
6 Mar	+ +	26 Jul	−
31 Mar	+ +	23 Aug	−
28 Apr	+	16 Sep	−
26 May	−	15 Oct	−
24 Jun	−	10 Jan 1975	+ +
24 Jul	−	24 Feb	+ +
21 Aug	−	19 May	−
15 Sep	−	17 Jun	−
12 Oct	−	10 Jul	−
10 Nov	+	29 Aug	−
14 Dec	+ +	3 Sep	−
9 Jan 1975	+ +	5 Nov	−
8 Feb	+ +	13 Feb 1976	+ +
24 Mar	+ +		
3 May	−		
15 Jun	−		
12 Jul	+		
14 Aug	−		
5 Oct	−		
2 Nov	−		

− = Absent, + = Present (<100 amphipods), + + = Present (>100 amphipods).

pods only (Table 3, Column B) shows a consistant predominance of females in both rivers.

Seasonal distribution and behavior

The results of the subtidal net collections (Table 4) generally agree with earlier reports by Bousfield (1973) and Gable (1972) in that *G. palustris* appears to be restricted to the intertidal zone throughout the spring, summer and fall. However, whereas Gable (1972) never found *G. palustris* in offshore plankton tows or dredge samples, in this study, net collections demonstrated a subtidal migration by *G. palustris* during the winter months in both rivers. The population began the migration in November and remained subtidally through March with hundreds of *G. palustris* observed clinging to the nets on each collection date (Table 4). This was a short-range migration because most of the amphipods were found close to the base of the intertidal shelf and few, if any, *G. palustris* were collected in other offshore nets (Van Dolah 1977). By April, only a few individuals remained subtidally, indicating a shift back to the intertidal zone. This immigration resulted in the negative death rates and, combined with the release of juveniles by the overwintering generation, accounts for the sharp increase in intertidal amphipod abundance during the spring (Figs. 4 and 5).

Following the spring immigration, some interesting seasonal changes in the distribution of *G. palustris*

occurred within the intertidal zone. Throughout the spring, the majority of the Patuxent River population was located in the lower 3 levels with the highest numbers observed in level 1 (Fig. 11). By late June, there was a distinct shift in intertidal amphipod abundance shoreward with maximum densities observed in levels 3 and 4. The distribution remained concentrated in the upper intertidal zone throughout the summer and fall whereupon the amphipod abundance in all levels declined to the winter low. In contrast, in the Rhode River, there was no distinct seasonal shift in the intertidal distribution at either study area (Fig. 12). Furthermore, whereas level 4 in the Patuxent River had high amphipod abundance during the summer, level 4 in the Rhode River had the lowest amphipod density at this time with maximum densities present in levels 2 and 3 (1975).

One possible explanation is that distributional differences between rivers may be due to differences in *Spartina* density. In the Patuxent River, I observed increased *Spartina* density at the higher intertidal levels with the highest level (4) having extremely dense and uniform stands of grass with no patches of peat substratum observable. In the Rhode River, *Spartina* was very dense throughout the intertidal zone with the exception of level 4 (Area B), which had fewer culms present.

As there appeared to be a correlation between grass
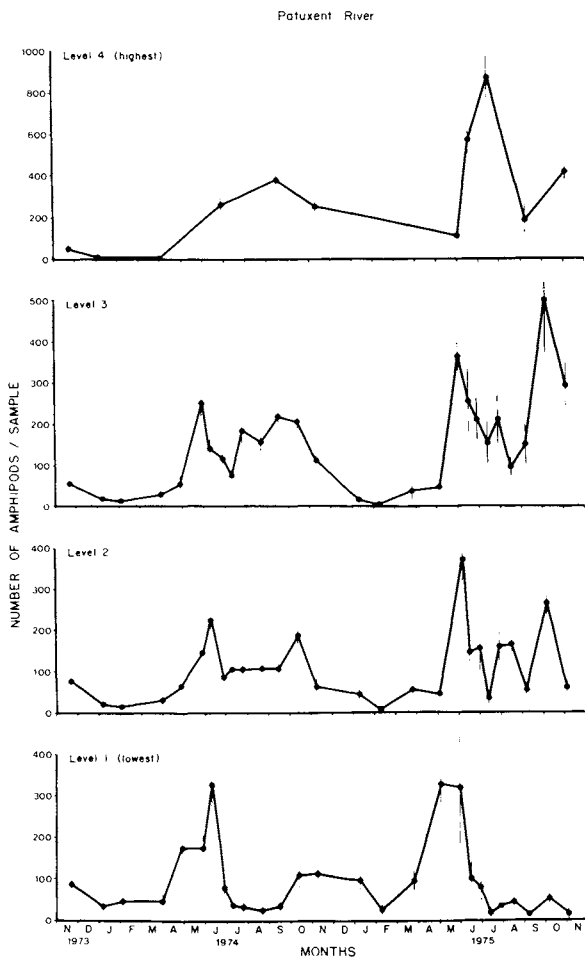
Patuxent River

FIG. 11. Seasonal variation in *Gammarus palustris* abundance at the various intertidal levels. Patuxent River, 1973 to 1975. Dots represent means, bar lines represent standard error. Note the change in scale between levels as well as the shift in amphipod abundance from low levels during the spring to high levels during the summer and fall.
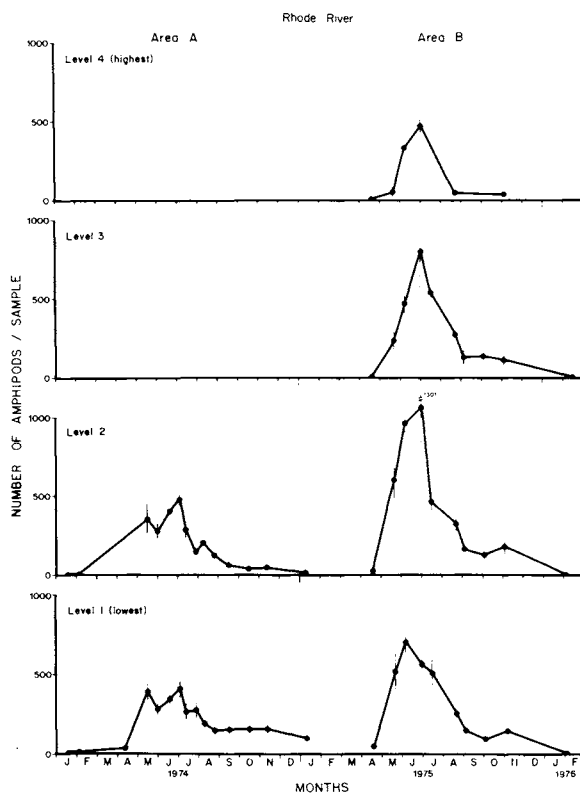
Rhode River

FIG. 12. Seasonal variation in *Gammarus palustris* abundance at the various intertidal levels. Rhode River, 1974 to 1976. Dots represent means, bar lines represent standard error.

density and amphipod density, a portion of the intertidal zone in the Patuxent River was selected which had a gradient of grass density. Three replicate pump samples (5 suctions/sample) were collected in areas having different culm densities (high, medium, low). All samples were collected from the same intertidal level and there were no observable differences in grass density between replicate samples. The results (Fig. 13A) demonstrate that *G. palustris* density decreases significantly with decreasing *Spartina* density ($P <$ .05, Kruskal–Wallis test). Gable (1972) observed that *G. palustris* prefers the substratum immediately around the bases of *Spartina* culms. To determine whether *G. palustris* exhibits similar distributional patterns in my study areas, 5 replicate samples (5 suctions/sample) were collected by placing the sampler directly on small *Spartina* culms. Comparison samples were collected from the peat substratum between

culms in the same manner. The results concur with Gable's (1972) observations that this species aggregates immediately around the bases of *Spartina* culms (Fig. 13B).

Substratum preference tests

Laboratory experiments were conducted to determine whether the above observations on the intertidal distribution of *G. palustris* are the result of active substratum preference.

Methods.—Prior to all laboratory experiments, amphipods were collected from the Patuxent River and brought to the laboratory where they were maintained at ambient river temperature and salinity in a controlled-temperature room with natural substratum and detritus present as a food source. Experiments conducted at temperatures $>20°C$ also had 0.5 mg/litre of penicillin and 0.5 mg/litre of streptomycin sulfate (Sigma Chemical Company) added to the water to eliminate bacterial growth.

The substratum preference tests presented amphipods with 3 substratum choices: peat with *S. alterniflora* culms, peat without culms, and subtidal sand. Two finger bowls filled with each substratum type were alternately positioned in a large, circular, Plexiglas® trough (see Rees 1972 for description of dimen-
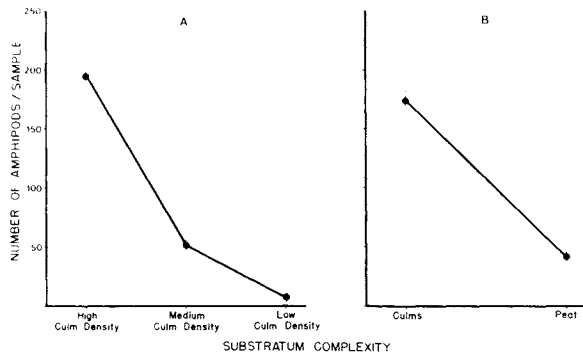
FIG. 13. A. Relationship of *Gammarus palustris* abundance to *Spartina alterniflora* density. B. Comparison of number of amphipods in close proximity to grass culms relative to number found on the peat between culms. Dots represent means. Bar lines represent standard error.
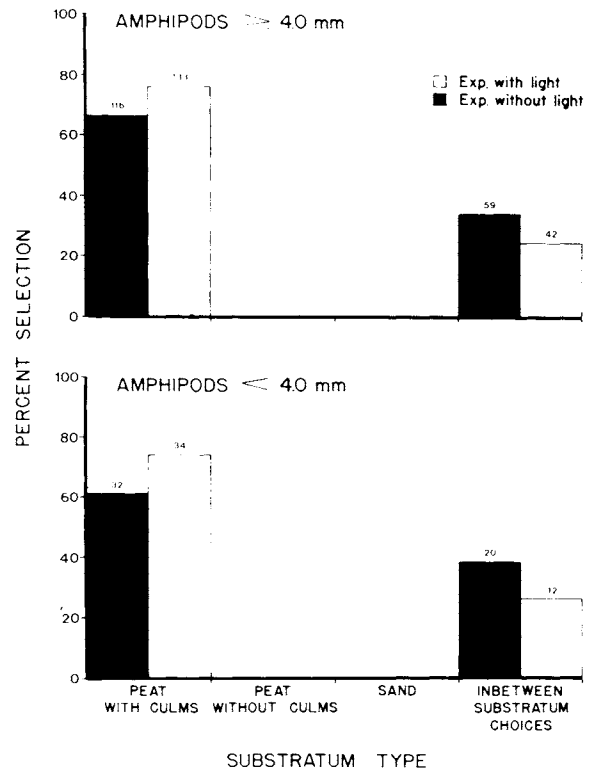

FIG. 14. Substratum preference among different substrata by *Gammarus palustris*. Experiments without light were run with a cover shielding the test chamber from all external light. Numbers at top of histograms represent total number of amphipods in all replicates found on substratum type.

sions) which was filled with 10 litres of aerated estuarine water (26°C, 9.5‰). Adult preference was tested by placing 10 amphipods in each finger bowl and allowing 24 h for selection of a preferred substratum. Following this, the finger bowls were isolated with plastic cylinders and the substratum carefully searched for amphipods. Those amphipods found between finger bowls were also noted. Three replicate tests were conducted under both light and dark conditions.

Juveniles were tested using a similar experimental design. However, only 5 amphipods were initially placed in each finger bowl and 2 replicate tests were completed under light and dark conditions.

Results.—Both adult and juvenile *G. palustris* had a very strong preference for peat substratum with culms under light and dark conditions (Fig. 14, $P <$ .005 in all tests by chi-square). In fact, the only amphipods not found in the bowls with *Spartina* culms at the end of each test were located between the finger bowls (not included in chi-square test). Thus, the shift in the distribution of *G. palustris* from low to high intertidal during the spring at the Patuxent River site is due to the strong behavioral preference of this species for the more complex substratum found in the high intertidal.

ENVIRONMENTAL FACTORS

Environmental factors potentially important in causing the changes in intertidal amphipod density presented in the previous section include (1) salinity stress, (2) freezing stress during the winter, and (3) heat or desiccation stress during the summer. Though wave action may be important in some intertidal areas (Dayton 1971), waves were never very large in my study areas but were sufficient to provide a well-aerated water column (C. P. Rees, *personal communication*).

Field measurements.—Salinity was measured on each sampling date in both rivers using a Beckman model RB-3 Solubridge™ salinometer. Water temperature was measured just above the intertidal substra-

tum during high tide. Minimum and maximum (air or water) temperature measurements were initiated in the spring of 1974 using a min–max thermometer placed at the highest sampling level of each study site.

Seasonal salinity fluctuations

The monthly salinity fluctuations at both study areas are presented in Fig. 15. With the exception of August and September, 1974, the Rhode River had consistently lower salinities than the Patuxent River at Broomes Island. The general trend observed was high salinities during the late summer and fall followed by a decline to lower salinities during the spring and early summer. There are a few deviations from the trend in 1975, but the data generally agree with previous studies in the Patuxent River (Nash 1947, Cory and Nauman 1970) and Rhode River (R. L. Cory, *personal communication*).

The maximum salinities observed were 13‰ at Broomes Island and 12‰ in Sellman Creek while the minimum salinities were 7 and 4‰ respectively. However, Rees (1975) observed salinities as low as 3.6‰ in an area just south of my Patuxent River site and R. L. Cory (*personal communication*) observed temporary salinity decreases as low as 1‰ in the Rhode River with the normal low salinity ranging between 3 and 5‰.
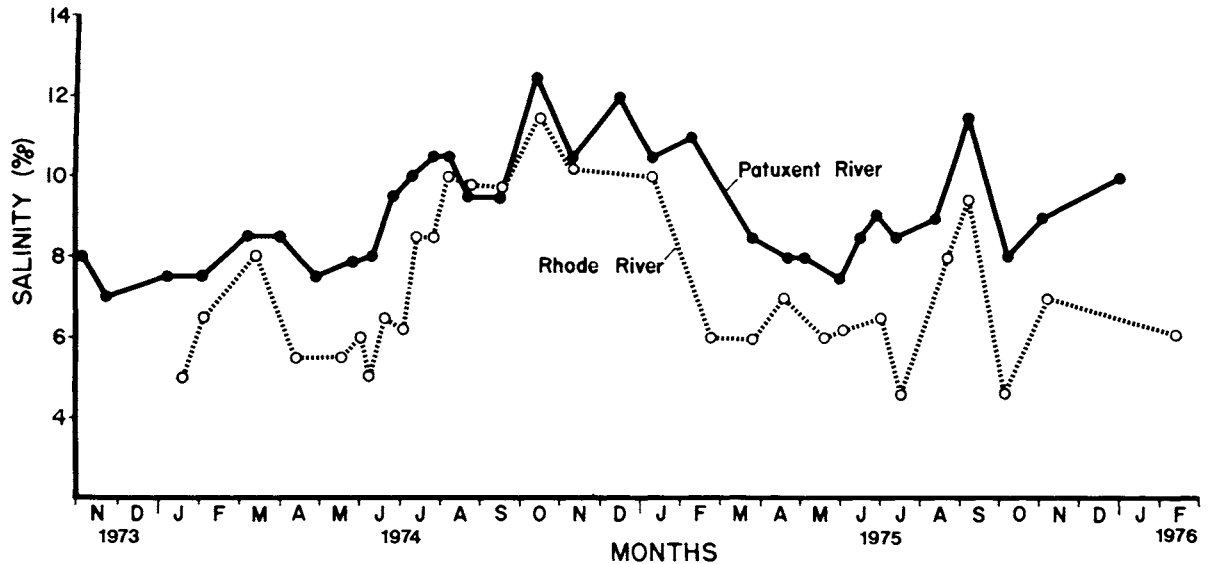
FIG. 15.   Seasonal variations in salinity from 1973 to 1976 at the Patuxent and Rhode River study sites.

Salinity tolerance

Bousfield (1973) considers *G. palustris* a euryhaline species capable of tolerating short exposures to freshwater and extended exposures to 5‰. Gable (1972) observed the salinity tolerance of this species to vary with temperature and generation period although there were no differences in tolerance with age or sex within a generation. He concluded that *G. palustris* mortality may occur when low-salinity/low-temperature conditions prevail. As salinity decreases are partially correlated with declines in amphipod abundance in both

FIG. 16.   Salinity tolerance of *Gammarus palustris* at 10 and 20°C (±2°C). Dots represent mean values and bar lines represent standard error. Controls represent ambient salinity at the time of amphipod collection.

rivers (Figs. 2, 3 and 15), I conducted salinity tolerance tests on *G. palustris* at 2 temperatures (10 and 20°C) with salinities ranging from 0.2 to 10‰.

Methods.—All tests were conducted under controlled lighting (12 h/day), and at each test of salinity, 3 replicate jars containing 20 amphipods in 600 ml of water were monitored over a 7-day period. Dead amphipods were removed daily with death determined by the lack of peraeopod or pleopod movements when disturbed. Test salinities were measured by a Beckman model RB-3 Solubridge™ salinometer and consisted of aged tap water mixed with natural brackish water. Salinities in the control replicates were equivalent to river salinity at the time of amphipod collection. The jars were aerated and covered during the course of the experiments and test salinities measured at the end of the experiments showed no significant change.

Results.—Survival of this species for short periods (2 days) in low salinity is very high at both temperatures, with survival at 1‰ equivalent to the higher control salinities (Fig. 16). After 1 wk, survival is still very high in the low salinities as compared with the controls. These results indicate that the low salinities present in my study areas are not a significant source of mortality for the *G. palustris* populations.

Seasonal temperature fluctuations

Water temperature ranged from a winter low of 4°C in both rivers to a summer high of 28.5°C in the Patuxent River and 30°C in the Rhode River (Fig. 17). Cory and Nauman (1970) reported water temperature ranging from −1° to 32°C in the Patuxent River and R. L. Cory (*personal communication*) noted water temperature in the Rhode River ranging from 0.5° to
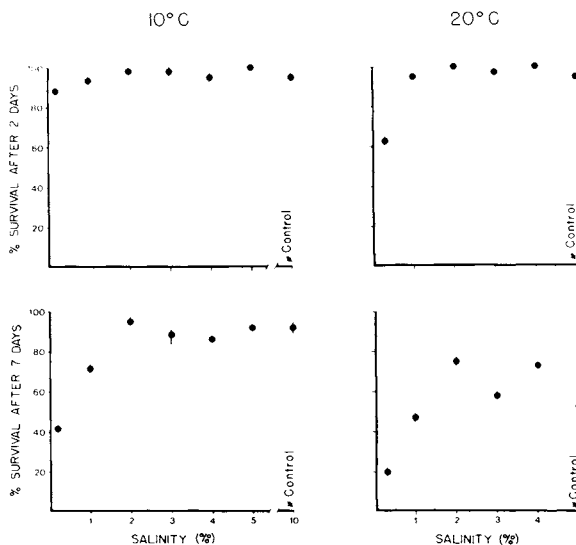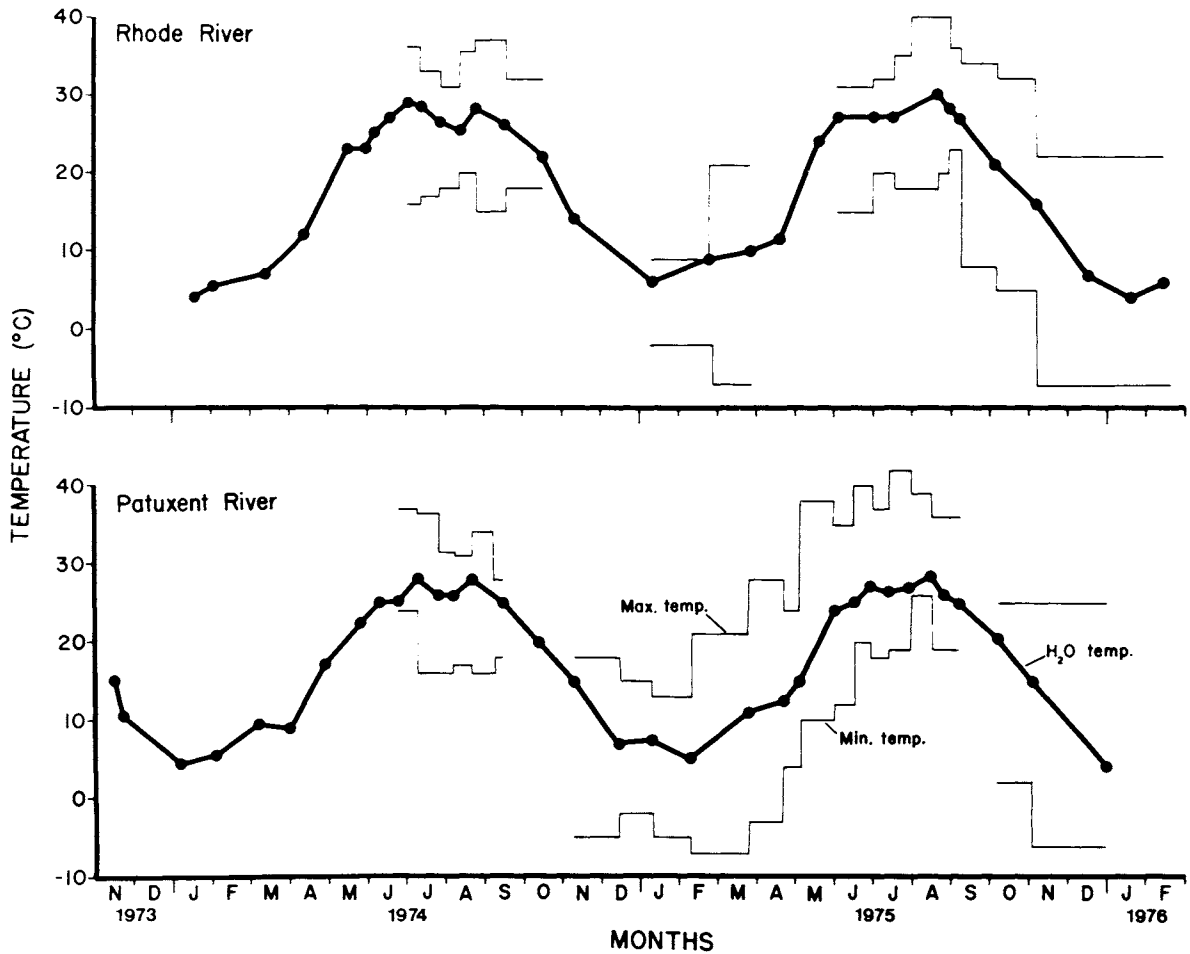
FIG. 17. Seasonal variation in water temperature as well as minimum and maximum air or water temperatures at the Patuxent and Rhode River study sites. Horizontal lines for min–max temperatures indicate lowest or highest temperatures observed intertidally between sampling periods. Gaps in data are due to loss of thermometers.

32.5°C. However, the general trend of seasonal temperature fluctuations that I observed was similar to those noted by Cory and Nauman (1970).

The minimum and maximum temperatures on the intertidal shelf ranged from −7° to 42°C in the Patuxent River and −7° to 40°C in the Rhode River (Fig. 17). The difference in maximum temperatures observed is probably due to the denser *Spartina* growth in the Rhode River providing increased shading effects. As these temperature extremes coincide with periods of decreased intertidal amphipod density (Figs. 2, 3, and 17), the freezing and high-temperature tolerance of *G. palustris* was examined in the laboratory.

Freezing tolerance

Methods.—Amphipods were collected from subtidal traps during the winter and maintained in the lab at a temperature and salinity equivalent to that observed at the time of collection (8 ± 3°C, 10‰). At all test temperatures (8° to −8°C), 25 adults were placed in each of 4 replicate finger bowls filled with natural peat

substratum and 800 ml of estuarine water. After 2 h, the water was slowly removed to simulate low tide and the containers transferred to an incubator for 22 h. This low-tide duration was selected as frequently only 1 high tide inundated the intertidal shelf during a 24-h period in the winter. Following the low-tide simulation, the containers were refilled with estuarine water and, after a 24-h recovery period at 8°C, the number of *G. palustris* surviving were noted. Control replicates were treated similarly but with an 8°C low-tide temperature.

Results.—Even with the 22-h exposure period, these amphipods are capable of withstanding freezing temperatures (Fig. 18). However, at −8°C *G. palustris* experienced 100% mortality and −7°C is the estimated LD$_{50}$ (mean lethal dose) temperature for this species. Therefore, significant mortality would occur in populations remaining intertidally during the winter as I observed minimal temperatures of −7°C at my study sites (Fig. 17).

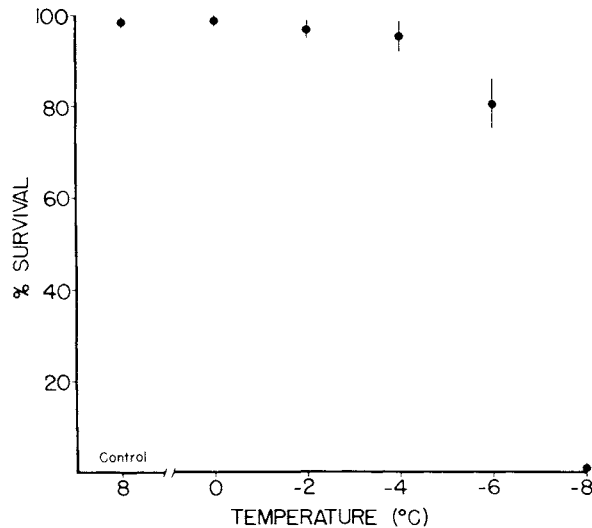The use of natural substratum in these experiments

FIG. 18.   Freezing tolerance of *Gammarus palustris*. Dots represent mean values and bar lines indicate standard error. The estimated LD$_{50}$ (mean lethal dose) temperature for this species is $-7°C$.

aids in amphipod survival as I noted 100% mortality in preliminary experiments without substratum at -1 $\pm$ 2°C (12-h exposure). Thus, the substratum must act as a buffer due to the time lag before it equilibrates with the ambient air temperature. Unfortunately, a remote thermistor was unavailable to determine the actual time amphipods were at the test temperature. Despite this, it is reasonable to assume that substratum surface temperatures were equivalent to the test temperatures by the end of the 22-h exposure due to the small amount of peat used in these tests.

High-temperature tolerance

Methods.—Thermal and desiccation tolerance of *G. palustris* at high temperatures was tested using an experimental design similar to the freezing tolerance tests. Twenty amphipods were placed in each of 3 replicate finger bowls with natural substratum and estuarine water equivalent in temperature and salinity to that at the time of amphipod collection (25 $\pm$ 3°C, 11‰). After 2 h, the water was removed and the containers transferred to an incubator with circulating air at various test temperatures (35–47°C, low humidity). Twenty-two h later, the containers were refilled with 25°C water and the amphipods allowed to recover for 6 h. Preliminary experiments indicated no significant difference ($P > .1$, chi-square contingency test) in survival rates between 6- and 24-h recovery periods (40°C, low humidity). Adults and juveniles were tested separately and amphipods in control replicates were subjected to a 25°C low-tide temperature. Adult tolerance was further tested under high-humidity conditions at 39° and 43°C by placing large pans of water in the incubator during the test period.
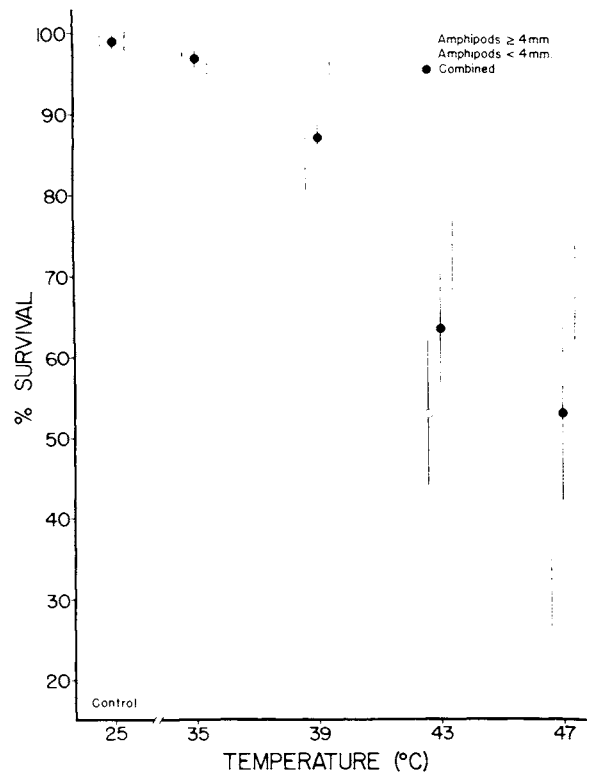

FIG. 19.   High-temperature tolerance of *Gammarus palustris*. Dots represent mean values and bar lines denote standard error. The LD$_{50}$ (mean lethal dose) temperature for the adults and juveniles combined is $>47°C$. This is a much higher temperature than ever observed intertidally at all study sites.

Results.—Juveniles appear to be slightly more tolerant than adults at all test temperatures (Fig. 19) although only significantly so at 47°C ($P < .001$, chi-square contingency test). This greater tolerance of juveniles may be due to increased physiological tolerance or simply that their smaller size enables them to utilize the small crevices in the peat more effectively, thereby decreasing desiccation stress. However, even under the low-humidity conditions of these experiments, the combined results of adult and juvenile survival show an LD$_{50}$ temperature in excess of 47°C. Furthermore, they endured these temperatures for 22 h of simulated low tide and I only rarely observed the intertidal shelf exposed for this length of time in the summer months. Thus, the maximum observed temperatures of 40° and 42°C (Fig. 17) are unlikely to cause significant mortality in natural populations.

The results of the high-humidity tolerance tests indicate that survival is even better at high humidity as the mean percent survival at both 39° and 43°C was 93.3%. This survival rate is not significantly different from the low-humidity test at 39°C ($P > .05$) but is significantly greater than the low-humidity test at 43°C ($P < .001$, chi-square contingency test). In my study
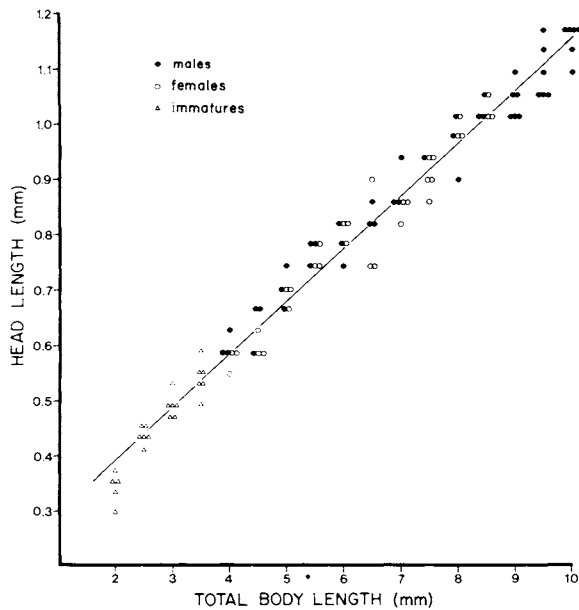
FIG. 20. Relationship of head length to total body length for *Gammarus palustris*. $Y = 0.199 + 0.96X$, $r = .99$, $N = 101$.
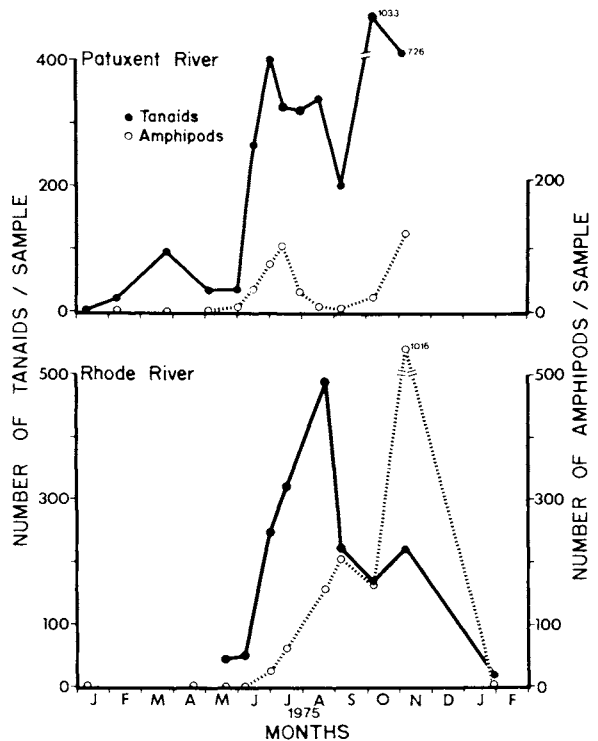

FIG. 21. Seasonal variation in the intertidal density of the tanaid *Leptochelia rapax* and the amphipod *Corophium lacustre*. Dots represent mean values. *Leoptochelia rapax* densities were computed from the lowest 3 sampling levels. *Corophium lacustre* densities were computed from the lowest sampling level only.

areas, the hot summer days are generally very humid. Therefore, it is even less likely that heat or desiccation stress causes significant mortality in the *G. palustris* populations.

BIOLOGICAL FACTORS

Biological factors which might account for the observed fluctuations in amphipod numbers include intraspecific and interspecific competition for food or space, and predation.

Associated fauna

Sampling method.—Quantitative estimates for the majority of associated fauna were obtained through the analysis of the suction-pump samples. These include other amphipod species, tanaids, isopods, polychaetes, oligochaetes and mud crabs. The larger and more mobile grass shrimp *Palaemonetes pugio* were not effectively sampled using the suction technique. Therefore, monthly quantitative estimates of this species were obtained by vigorously scraping a D-net over a 4.54-m² area of the intertidal zone at each site.

Attempts to obtain quantitative estimates of the dominant fish populations in these areas (*Fundulus* spp.) proved unsuccessful. However, observations on each sampling date determined their presence or absence and seine hauls were periodically collected throughout the summer in each river for a gut analysis of the fish present. All seining was done in the late high-tide or early low-tide periods to insure that the fish were able to feed intertidally. The seining procedure was similar to that used by Myers (1976).

All gammarid amphipods found in the guts were counted and identified if possible. *Gammarus palustris* were also measured in length for size-selective predation analysis. When *G. palustris* were found in pieces, only the heads were counted and the length of the cephalon measured.

Estimates of total body length from cephalon length were made by measuring 101 *G. palustris* in total body length to the nearest 0.5 mm and in cephalon length using an ocular micrometer. The results (Fig. 20) show a high correlation between cephalon length and body length.

Sampling results

Competitors.—Though *G. palustris* is the dominant intertidal amphipod species in my study areas, other epifaunal amphipod species were occasionally observed. These include *Gammarus mucronatus*, *Gammarus tigrinus*, *Melita nitida* and *Orchestia uhleri*. *Gammarus mucronatus* and *M. nitida* were rarely collected and then only during the spring and summer months. *Gammarus tigrinus* was found intertidally at area A of the Rhode River during the spring and only attained moderate density on 1 sampling date (15 May 1975) when *G. palustris* density was low.
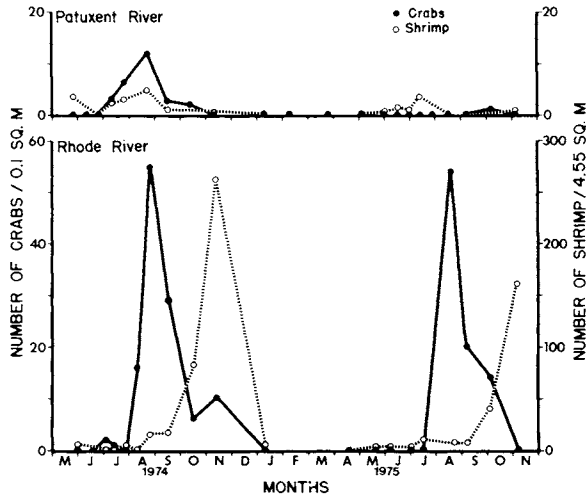
FIG. 22.   Seasonal variation in the density of the mud crab *Rhithropanopeus harrisii* and the grass shrimp *Palaemonetes pugio*. Dots represent mean values and *R. harrisii* densities were computed from the lowest 3 sampling levels only.

TABLE 5.   Seasonal variation in the ratio of ovigerous ♀♀ to nonovigerous ♀♀ and average brood size (ABS) of *Gammarus palustris*. Ratios were computed from the combined total of all ♀♀ in the samples collected on each date. N = no ovigerous females

Patuxent River			Rhode River		
	Ovig. ♀♀			Ovig. ♀♀	
Date	♀♀	ABS	Date	♀♀	ABS
21 Nov 1973	0.02	0.03	19 Jan 1974	N	0
7 Jan 1974	N	0	2 Feb	N	0
3 Feb	0.02	0.07	2 Apr	3.33	7.33
31 Mar	1.43	2.55	15 May	0.31	1.36
28 Apr	2.14	4.42	30 May	0.53	0.68
26 May	0.91	1.14	18 Jun	0.25	0.34
10 Jun	0.45	0.36	2 Jul	0.50	0.65
24 Jun	1.07	0.82	12 Jul	0.38	0.28
9 Jul	0.21	0.17	26 Jul	0.51	0.47
24 Jul	0.29	0.28	8 Aug	0.37	0.39
21 Aug	0.43	0.52	23 Aug	0.40	0.59
15 Sep	0.89	0.80	16 Sep	0.39	0.59
12 Oct	0.28	0.45	5 Oct	0.43	0.60
10 Nov	N	0	2 Nov	N	0
9 Jan 1975	N	0	10 Jan 1975	N	0
8 Feb	N	0	18 Apr	1.55	6.58
24 Mar	0.82	1.97	19 May	0.16	0.92
3 May	1.90	3.23	6 Jun	0.98	0.94
30 May	0.60	0.72	1 Jul	0.31	0.49
15 Jun	1.29	0.96	15 Jul	0.35	0.48
29 Jun	0.15	0.13	20 Aug	0.74	0.62
12 Jul	0.50	0.38	5 Sep	0.96	0.77
27 Jul	0.46	0.44	3 Oct	0.76	0.85
14 Aug	0.58	0.44	5 Nov	N	0
6 Sep	1.09	0.91	13 Feb 1975	N	0
5 Oct	1.04	1.21			
2 Nov	N	0			

Orchestia uhleri was observed in low densities throughout the spring, summer and fall in levels 3 and 4. This species was not collected during the winter but I was rarely able to sample level 4 at this time.

Infaunal species present intertidally included the polychaete *Nereis succinea*, an oligochaete species, the tanaid *Leptochelia rapax* and the amphipod *Corophium lacustre*. *Nereis succinea* was observed throughout the year in both rivers but the oligochaete species was usually present in the spring only. Neither of these species were ever abundant although my sampling technique probably underestimates their density due to their ability to burrow deeply in the peat substratum. *Leptochelia rapax* and *C. lacustre* attained much higher intertidal densities. *Leptochelia rapax* was most abundant in the lower 3 levels in both rivers. Within these levels, the population abundance of tanaids was greatest during the early summer and fall in the Patuxent River whereas in the Rhode River, tanaids reached maximum abundance by August and declined throughout the remainder of the year (Fig. 21). As increases in tanaid density are partially correlated with declines in *G. palustris* densities (compare Figs. 2, 3 and 21), *Leptochelia rapax* may be an important competitor. *Corophium lacustre* was rarely found above the lowest level in either river and never attained high densities in the Patuxent River (Fig. 21). *Corophium lacustre* density was much higher in the Rhode River with maximum abundance in level 1 occurring in November (Fig. 21). This difference between rivers, combined with the lack of an autumn increase in *G. palustris* density in the Rhode River, suggests that *C. lacustre* may also be an important competitor.

Predators.—The mud crab *Rhithropanopeus harrisii* and the grass shrimp *Palaemonetes pugio* might also compete with *G. palustris*, as these species injest detritus (Odum and Heald 1972, Welsh 1975). However, experimental evidence (presented later) demonstrates that both species consume amphipods. Hence, it is reasonable to assume that if resources are limiting, mud crabs and grass shrimp would prey on amphipods as well as compete with them.

Mud crabs were never abundant in the Patuxent River, with only a small increase in density occurring in July and August, 1974 (Fig. 22). In the Rhode River, mud crabs were rarely collected during the early summer months. However, by August of both years, their density had increased substantially, followed by a decline in abundance during September and October. This rapid increase in the crab population coincides with the decline in *G. palustris* density observed in both years (Fig. 3). Increases in the intertidal crab population were probably due to immigration from subtidal areas because (1) a large proportion of the crabs sampled at this time were adults, and (2) *R. harrisii* was present subtidally (Van Dolah 1977). Mud crabs which occupied the intertidal zone were usually found only in the lower 3 levels during high tides. At
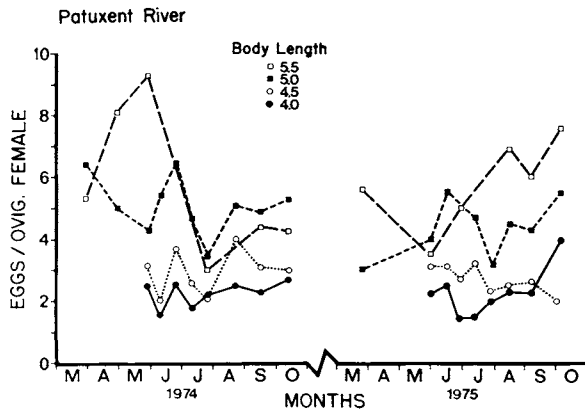
FIG. 23. Seasonal variation in the average brood size of ovigerous *Gammarus palustris* collected at the Patuxent River site. Dots represent mean values for each size class.
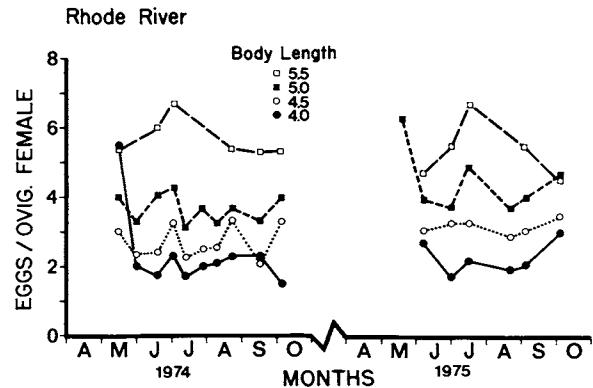

FIG. 24. Seasonal variation in the average brood size of ovigerous *Gammarus palustris* collected at the Rhode River sites. Dots represent mean values for each size class.

low tide, this species was most abundant in level 1 or below the peat shelf.

Grass shrimp densities were low throughout the study period in the Patuxent River, whereas they were quite abundant during the autumn months in the Rhode River (Fig. 22). This difference in *P. pugio* density between rivers may account for the lack of an autumn increase in *G. palustris* populations (Fig. 3) and suggests the importance of this species as a potential predator or competitor.

The observed densities of both *R. harrisii* and *P. pugio* are undoubtedly underestimates due to the ability of mud crabs to burrow deeply and the extremely quick escape movements of shrimp from the dip-net sweeps.

Fish observed in the intertidal zone of these salt marshes include *Fundulus heteroclitus, Fundulus diaphanus, Fundulus majalis* and *Menidia* spp. The results of the seine hauls collected during the summer indicate that *F. heteroclitus* is (1) the dominant *Fundulus* species present at this time, and (2) the dominant fish feeding on *G. palustris* (Van Dolah 1977). During the winter and early spring, no *Fundulus* were observed intertidally in either river. Fraser (1973) observed *F. heteroclitus* at Broomes Island from May through September and noted that it was the dominant species from May through July. A. K. Myers (*personal communication*) observed *F. heteroclitus* to be the predominant *Fundulus* species in the Rhode River from May through October.

As the evidence presented previously indicates that biological factors may be important in regulating *G. palustris* populations, the following competition and predation studies were conducted.

Food competition

Gammarus palustris consumes detritus and algae (Gable 1972). If this species utilizes detritus as its primary energy source, then food should not be a limiting

resource in the detritus-rich peat beds. However, if *G. palustris* feed on the microorganisms associated with the detritus, as shown in other detritus-feeding amphipods (Hargrave 1970, Odum and Heald 1972) then the high amphipod densities in the summer may result in intraspecific competition for food. Interspecific food competition may also be important as *R. harrisii, P. pugio* and *L. rapax* are known detritivores (Odum and Heald 1972, Welsh 1975), and as mentioned previously, increases in the abundance of these species correlate with decreases in *G. palustris* abundance.

The egg-ratio analysis provides possible evidence of food limitation during the summer due to the decrease in birth rates (Figs. 8 and 9). Further support is obtained upon examination of the average brood size (ABS) = (0.5) (total number of eggs) ÷ (total number of adult females). This reproductive index is believed to be correlated with food availability (Hall 1964) with low values (<1) indicating insufficient female replacement. The ABS showed a decline from high values during the spring to low values by late May or June and remained low (<1) throughout the remainder of the breeding season (Table 5). However, this decline in ABS may simply be due to the concurrent decline in the ratio of ovigerous:nonovigerous females (Table 5) rather than food limitation. To confirm this, the seasonal change in the average brood size of ovigerous females was examined (Figs. 23 and 24). The results indicated that food was not limiting as no significant change in the average brood size occurred throughout the breeding season in either river. The declines observed in the 5.5-mm females (Patuxent River, 1974) and the 4.0-mm females (Rhode River, 1974) probably result from the small sample size obtained for these size classes on 24 July and 15 May respectively.

Although the above evidence indicates that competition for food did not account for the summer declines in *G. palustris* abundance, competition for space may be important in determining amphipod den-
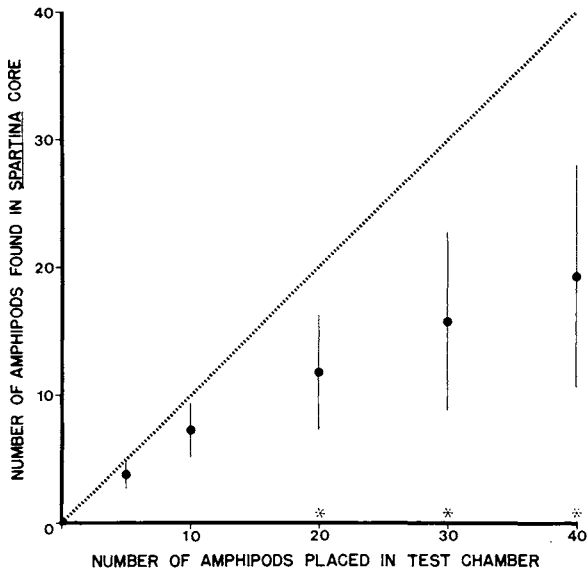
FIG. 25. Results of the culm limitation competition experiments. The dotted line represents the theoretical number of *Gammarus palustris* which would be found on the core if competitive displacement did not occur. The solid dots represent the actual results obtained with dots representing the mean number of amphipods found on the core after 48 h. The bar lines represent the 95% confidence intervals and the * indicates significant differences at the .05 level (*t*-test).

sity and distribution. The following experiments were designed to test this possibility.

Space competition—crowding experiments

Laboratory observations indicated that amphipods of the same sex which contacted each other usually responded by active avoidance. However, I occasionally observed adult males grappling in an apparent fight, and though I never observed one amphipod kill another, cannibalism on dead amphipods was common. This behavior suggests that when *G. palustris* densities are high, intraspecific aggression for the limiting resource may occur, resulting in decreased densities through cannibalism (see Fox 1977) or at least defense of a limited preferred substratum.

Methods.—To determine whether high amphipod densities induce aggressive lethal interactions, crowd-

TABLE 6. Results of the crowding experiments on *Gammarus palustris* after 1 wk at experimental densities. All cores had 3 to 4 stalks of *Spartina alterniflora*. See text for details

Amphipods on enclosed cores (n)	Replicates (n)	Alive after 7 days (n)		Missing after 7 days (n)	
		$\bar{x} \pm$ SD	%	$\bar{x} \pm$ SD	%
20	4	18.3 ± 2.1	91.3	1.7 ± 2.1	8.3
60	3	57.7 ± 2.1	96.1	2.3 ± 2.1	3.9

ing experiments were conducted by placing 8 cores (4 cm in diameter) of peat with *S. alterniflora* in a large plastic pan containing 6 litres of estuarine water (25°C, 8.5‰). Each core was tightly enclosed by a plastic cylinder (8 cm high) which had large holes in the side covered with 140-μm mesh screening to allow adequate water circulation. Sixty amphipods were placed in 4 of the cores and represented a high amphipod density as compared with intertidal populations in areas of similar *S. alterniflora* density. The other 4 cores contained 20 amphipods which served as low-density controls. Amphipod survival was noted after 7 days under controlled lighting (12 h/day) and simulated tides. During high-tide periods, the water was circulated, filtered and aerated using a Dynaflo® model 425 aquarium filter. Dye studies indicated a complete changeover of water every 10 min. All amphipods used were randomly selected from stock aquaria and no food was added during the 7-day period.

Results.—The mean percent survival of amphipods in the high-density chambers was higher than the control densities, indicating minimal mortality due to intraspecific aggression (Table 6). Although mortality at high densities might increase with increased trial time due to starvation, this experiment suggests that space limitations do not induce aggressive behavior in *G. palustris* which would result in the observed population declines (Figs. 2 and 3). Rather, avoidance was the general reaction as a large proportion of amphipods were observed clinging to the sides of the high-density chambers. This behavior was rarely observed in the control chambers, which indicates that sufficient space was available for the majority of amphipods at this density.

Space competition—culm limitation experiments

Intraspecific competition for space is still potentially important in determining the distribution of *G. palustris* within the intertidal zone because *Spartina* culms (the preferred substratum) may be a limiting resource when amphipod densities are high. This situation may result in competitive displacement.

Methods.—To test this, various densities of amphipods were randomly picked from stock aquaria and placed in pans (32 × 32 cm) containing a centrally placed core (4-cm diameter) of peat with *S. alterniflora* surrounded by sand (a nonpreferred substratum, Fig. 14) and 3 litres of estuarine water (25°C, 7‰). After 48 h under controlled lighting (12 h/day), the core was isolated by a plastic cylinder and the number of amphipods found on the core and sand noted. Three series of displacement experiments were completed as follows: 3 replicates with 1 culm/core at amphipod densities of 20 and 100; 3 replicates with 2 culms/core at amphipod densities of 20 and 100; and 5 replicates with 3–4 culms/core at amphipod densities of 5, 10, 20, 30, and 40. Experiments lasting 72 h (100 am-

TABLE 7. Results of the culm limitation competition experiments. Differences between core and sand ratios were tested by chi-square contingency test using combined total of replicates

Amphipods/ replicate in chamber	Test duration (hr)	*Spartina* stalks/core	Amphipods on core		Amphipods on sand		Adult:juvenile ratio			χ^2 value	Prob- ability (P)
			$\bar{x} \pm SD$	%	$\bar{x} \pm SD$	%	Total	Core	Sand		
20	48	1	14.7 ± 5.2	73.3	5.3 ± 5.2	26.7	1.9	1.4	6.0	2.3	<.5
100	48	1	21.7 ± 3.5	22.0	76.3 ± 3.5	78.0	7.9	20.7	6.6	2.9	<.1
20	48	2	10.7 ± 1.2	55.3	8.7 ± 0.6	44.7	1.3	0.8	2.7	3.9	<.05
100	48	2	46.3 ± 12.6	47.7	50.3 ± 11.7	52.3	2.5	2.9	2.3	0.5	<.5
100	72	2	58.7 ± 3.2	58.0	42.7 ± 4.1	42.0	2.4	2.6	2.1	0.7	<.5

phipods, 2 culms/core) were also conducted to insure that 48 h was a sufficient trial time.

Results.—The results of the experimental series using 5–40 amphipods support the culm-limitation hypothesis. If *G. palustris* are unable to displace conspecifics, then the density of amphipods found on the highly preferred substratum should be equivalent to the increased density placed in the test chamber, up to some reasonable limit (Fig. 25, dashed line). If competitive displacement occurs, the numbers found on the core should not rise proportionally with increasing amphipod density. The experimental results (Fig. 25, solid dots) demonstrate the latter effect. Although the number of amphipods found on the core increases, the numbers are significantly lower than expected at densities > 10 ($P < .05$, t-test) and the percent of the total population found on the core decreases with increasing amphipod density. Therefore, it appears that space limitation is occurring. The possibility that the trials using high amphipod numbers represent unreasonably high densities is very unlikely because >40 amphipods/core were observed in other trials using 100 individuals (Table 7).

An analysis of the adult:juvenile ratio in the high density trials (100/container) shows that this ratio is greater for those amphipods found on the preferred substratum although only significantly so in the container having 1 culm/core (Table 7). This suggests that adults can displace juveniles from *Spartina* culms when this preferred substratum is a limiting resource. Further support for this hypothesis is obtained from the low-density trials (20/container) as the adult:juvenile ratio is much lower for those amphipods found on the core *versus* those on the sand.

Finally, the results of the high-density trials lasting 72 h (Table 7) indicate that increased trial time does not alter the experimental findings because the mean number of amphipods found on the culm substratum was not significantly greater than the equivalent 48-h trial ($P > 0.1$, t-test), and the adult:juvenile ratios were similar.

Laboratory predation experiments

Methods.—Predation on *G. palustris* by *F. heteroclitus* was examined using 3 types of substratum: peat with no culms, peat with a low culm density (2 culms/

dish), and peat with a high culm density (10–14/dish). For each test, a finger bowl (10.5-cm diameter) filled with substratum was centrally placed in a 9.5-litre covered aquarium and surrounded by sand (5 cm deep). The finger bowl was isolated by a plastic cylinder and the aquarium filled with aerated estuarine water (25°–28°C, 8–10‰). Twelve h prior to each test, 40 amphipods (20 adults, 20 juveniles) were placed in the finger bowl and 1 adult *F. heteroclitus* was placed in the other portion of the aquarium. This (1) insured that the predators were equally starved, and (2) allowed both amphipods and fish to acclimate to the experimental environment. The isolation barrier was then removed and the fish allowed to feed for 6 h. Following this, the number of amphipods found alive in the aquarium were noted using a standardized search procedure which included gently rinsing the peat and sand as well as shocking the amphipods on the peat with probes connected to a Staco[*] model #1010 variable autotransformer. Three replicates were tested for each substratum type under constant light. Control replicates were treated similarly but did not contain predators.

Predation on *G. palustris* by *R. harrisii* and *P. pugio* was tested using a similar experimental design for all substratum types except that the predators and amphipods were confined to the isolated finger bowl during the 6-h feeding period and 2 adult predators were used per replicate.

Forty amphipods per finger bowl represents a relatively low amphipod density (≈ 60 amphipods/sample) as compared with the summer intertidal amphipod populations. Therefore, I tested the effects of predation by *R. harrisii* and *P. pugio* on substratum with a high culm density and 150 amphipods/finger bowl (50 adults, 100 juveniles), using the above experimental technique but with 4 rather than 3 replicates for each predator type and controls. The density and adult:juvenile ratio of amphipods used in these experiments were roughly equivalent to the density and ratio of amphipods observed in the study sites during the early summer (equivalent to 230 amphipods/ sample).

Results.—In the experiments using 40 amphipods/ replicate, *F. heteroclitus* consumed more *G. palustris* than *R. harrisii* and *P. pugio* (Fig. 26). Predation by
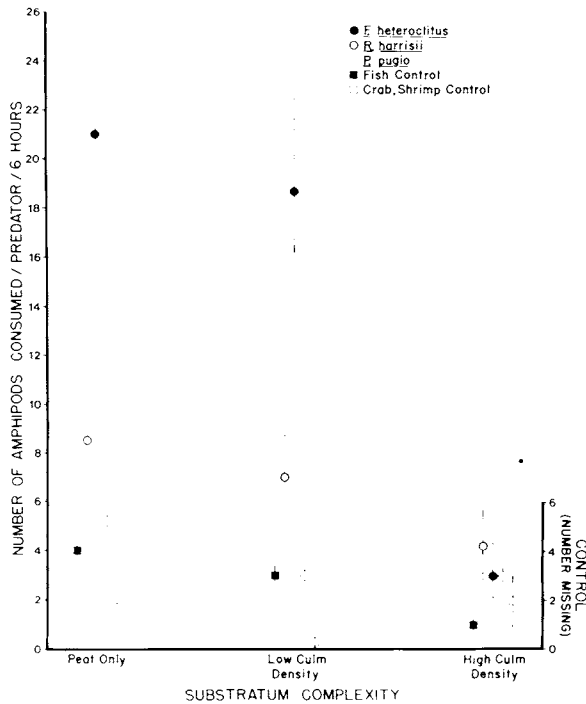
FIG. 26. Results of predation experiments on various substratum types for 3 predator species (*Fundulus heteroclitus*, *Rhithropanopeus harrisii*, and *Palaemonetes pugio*). Dots represent mean values and bar lines represent standard error.
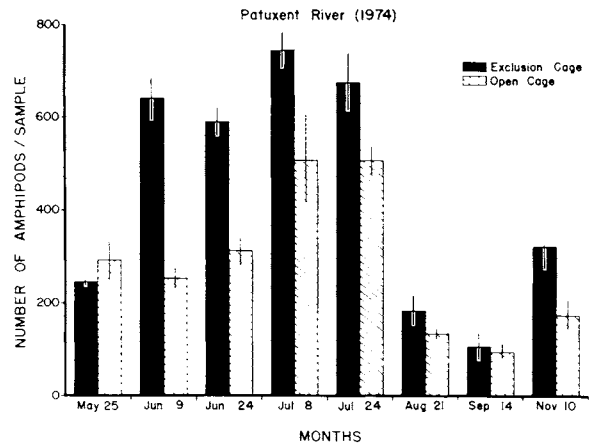

FIG. 27. Comparison of *Gammarus palustris* densities between cages at the Patuxent River site, 1974. Values represent mean numbers present and bar lines indicate standard error.

these fish decreased significantly with increased substratum complexity ($P < .001$, analysis of variance test) to the extent that no significant predation of amphipods occurred at high culm densities ($P > .05$, S-N-K test). *Rhithropanopeus harrisii* showed a slight but not significant decrease in amphipod consumption with increased substratum complexity by an analysis of variance test ($P > .05$). However, crab predation was significant on peat and low culm substrata as compared to controls ($P < .05$) and not significant on the high culm substratum ($P > .05$, S-N-K test). *Palaemonetes pugio* predation was not significant on any of the substratum types at this amphipod density ($P > .05$, S-N-K test).

At the higher amphipod density (150/replicate), both invertebrate predators consumed a significant number of amphipods on high culm substratum as compared to control replicates (Table 8). The density of grass used in these replicates was comparable to that found in the Rhode River. Similar experiments were not performed using fish because of experimental problems in recovering all uneaten amphipods at this density.

Field predation experiments

Methods.—The impact of these predators on the summer populations of *G. palustris* was assessed by caging experiments. In the spring of 1974, 2 large cages

(3.2-mm Vexar[k] plastic) were constructed in the lower portion of the intertidal zone (levels 1 and 2) near the Patuxent River study site. These cages were ≈2.4 m long, 1.2 m wide and 0.7 m high. The cages were open at the top to reduce cage effects and the sides were high enough to prevent aquatic predators from entering the top during high tides. Birds were never observed feeding intertidally at the study sites. One cage was designed to exclude all predators while the other had large holes in the sides which allowed predators to forage within. Throughout the summer, 3 replicate samples were collected biweekly from each cage using the suction technique.

The caging experiments were repeated in both rivers during the summer of 1975. These cages had similar dimensions but were constructed of 3.2-mm wire mesh and spanned the entire width of the intertidal zone. As in 1974, 1 cage at each study site was designed to exclude all predators while the other allowed the predators to forage within. Three replicate samples were collected monthly from each cage using the suction technique.

Results.—The 1974 caging experiments (Fig. 27) in the Patuxent River indicate that fish and shrimp predation limited the population density of *G. palustris* during the summer as the mean density in the exclusion cage was significantly greater than in the open cage from 9 July to 24 July ($P < .05$, analysis of variance test). I was unable to exclude *R. harrisii* in any of the caging experiments, but mud-crab densities were low in the Patuxent River at this time (Fig. 22). Comparison of amphipod densities in both cages at the beginning of this manipulation indicates that the difference in amphipod abundance observed is not an artifact of cage location, as the densities were not significantly different on 25 May ($P > .05$, Mann-Whitney U-test) when the cages were constructed.

TABLE 8. Results of the predation experiments using invertebrate predators at high amphipod and culm density. A significant difference was observed in the total number missing between treatments and controls by an analysis of variance test ($P < .001$). a, b. Treatments with different superscripts are significantly different ($P < .01$) using the S-N-K multiple range test

Predator	Replicates (n)	*Gammarus palustris* remaining $\bar{x} \pm SD$
Palaemonetes pugio[a]	4	131.2 ± 3.95
Rhithropanopeus harrisii[a]	4	138.0 ± 3.56
Control[b]	4	148.0 ± 2.00

After 24 July, the densities in both cages declined substantially, which suggests that the summer crash in amphipod abundance observed in the Patuxent River was not due to predation pressures. However, previous results (Fig. 11) show that, at this time, the intertidal distribution of *G. palustris* had shifted to the highest intertidal levels. As the cage mesh was too large to prevent amphipods from moving shoreward, the decreased densities within both cages may be an artifact of cage location and migration. Thus, predation may still be the important factor causing the summer decline in amphipod abundance. To test this, the caging experiments were repeated in 1975 but with cages which spanned the entire width of the intertidal zone as previously described.

The results of these manipulations (Fig. 28) show a substantial decrease in amphipod density in the open cage relative to the exclusion cage so that by July there was a significant difference in densities between cages ($P < .05$, analysis of variance test). Following this, amphipod density increased in the open cage during August. This may be due to reduced predation pressure, as I was unable to collect any *Fundulus* (the major predator) at this time after repeated seine hauls. No significant difference in amphipod densities between cages was observed from August to November ($P > .05$, analysis of variance test). However, note that from July to October, amphipod densities were always lower in the open cage whereas they were higher than the predator-exclusion cage densities at the beginning of the summer and in the fall when *Fundulus* densities were low. Thus, even though differences were only significant on 1 sampling date, the general trend towards lower densities in the open cage, combined with the 1974 results, indicates that predation probably limits intertidal *G. palustris* populations during the summer months in the Patuxent River.

The results of the Rhode River caging experiments (Fig. 29) show amphipod densities decreasing in both cages throughout the summer and fall with no significant difference in densities between cages at any time ($P > .05$, analysis of variance test). This suggests that predation by fish and shrimp is not limiting intertidal *G. palustris* populations in this river. However, as
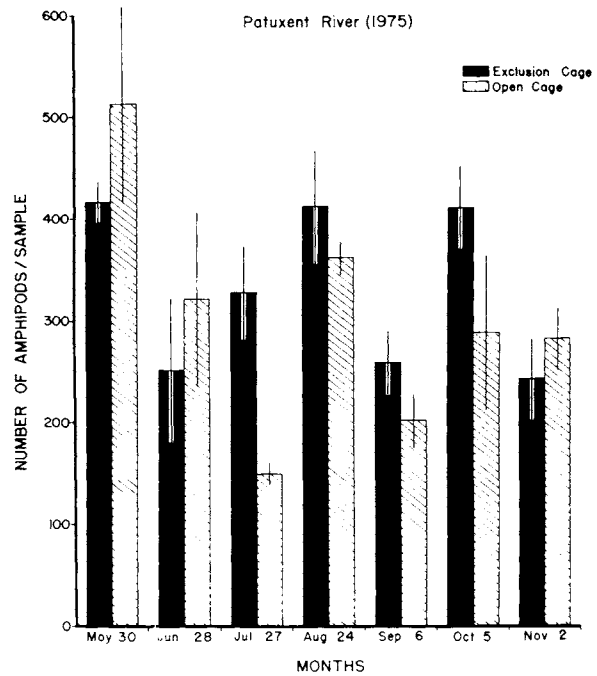

FIG. 28. Comparison of *Gammarus palustris* densities between cages at the Patuxent River site, 1975. Values represent mean numbers and bar lines indicate standard error.

stated previously, *R. harrisii* density increased substantially during the summer (Fig. 22) and I was unable to exclude these predators from the caged area.

The Patuxent River cages were constructed in areas having greater *Spartina* densities than the regular study site. As areas of equivalent grass density were not present outside the cages, control samples were
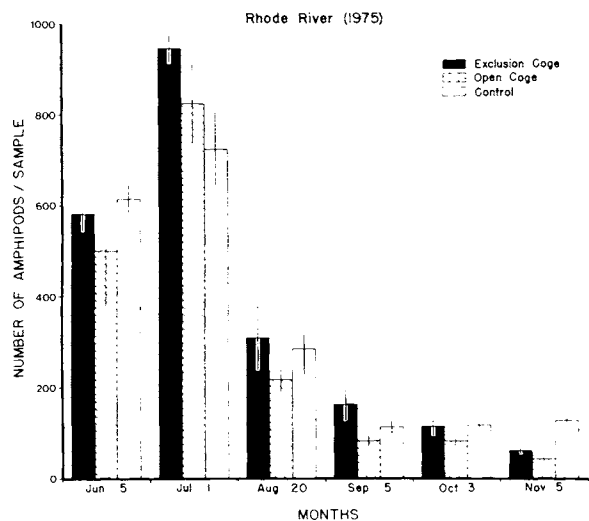

FIG. 29. Comparison of *Gammarus palustris* densities between cages at the Rhode River Site B, 1975. Values represent mean numbers and bar lines indicate standard error. Control samples represent densities found at regular sampling site.

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TABLE 9. Size selective predation results in the laboratory experiments. The combined total of amphipods in all replicates were used in chi-square tests. Analysis of variance in the experiments using natural substratum represents comparisons of adult:juvenile ratios in treatments *versus* appropriate controls. Predators include *Fundulus heteroclitus*, *Rhithropanopeus harrisii*, and *Palaemonetes pugio*

Experiment using no natural substratum:

		Number of amphipods remaining				
Predator type		$\geq$4.0 mm	<4.0 mm	Total	χ^{2a}	Probability
F. heteroclitus (adults)		33	55	88	11.14	$P < .001$
R. harrisii (adults)		9	40	49	31.04	$P < .001$
(juveniles)		46	41	87	0.67	$.3 < P < .5$
P. pugio (adults)		45	38	83	1.41	$.2 < P < .3$
(juveniles)		59	54	113	–	–
Controls (for crabs & shrimp)		60	60	120	–	–

Experiments using natural substratum:

		Mean number of amphipods remaining			
	Predator type	$\geq$4.0 mm	<4.0 mm	F^{b}	Probability
	F. heteroclitus (adults)	9.33	9.67	2.11	$.25 < P < .5$
Peat[c]	Fish controls	19.50	17.50		
(no culms)	*R. harrisii* (adults)	10.33	12.67	12.90	$.025 < P < .05$
	Crab controls	20.00	18.00		
	F. heteroclitus (adults)	11.00	10.33	6.47	$.05 < P < .1$
Peat[c]	Fish controls	20.00	17.00		
(low culm)	*R. harrisii* (adults)	10.33	12.67	30.41	$.005 < P < .01$
	Crab controls	20.00	18.50		
		$\geq$5.0 mm	<5.0 mm		
Peat[d]	*R. harrissi* (adults)	42.25	95.50	0.45	$.50 < P < .75$
(high culm)	*P. pugio* (adults)	38.25	93.00		
	Control	44.75	103.25		

[a] By chi-square contingency.

[b] By analysis of variance analysis of adult/juvenile proportions (coded using arcsine transformation).

[c] 40 amphipods/replicate.

[d] 150 amphipods/replicate.

not collected in this river to test for possible cage effects. The grass density in the cages and regular sampling site were equivalent in the Rhode River and comparison of amphipod densities (Fig. 29) showed no significant differences between the regular sampling area (control) and the open cage ($P > .05$, t-test). Furthermore, with the exception of the 1 July samples, the relationship of amphipod density in the control vs. open cage areas was comparable to that observed on 5 June when the cages were constructed (Fig. 29). Thus, cage effects on amphipod densities were minimal.

Size-selective predation studies

A number of studies have demonstrated that predators are often size selective for large prey items (Ivlev 1961, Brooks and Dodson 1965, Cooper 1965, Werner and Hall 1974). If *G. palustris* populations are subjected to similar predation pressures, adults may have a higher mortality rate than juveniles.

Methods.—To determine which, if any, of the 3 predator species are size selective, predation experiments without natural substratum present were conducted in the laboratory. *Fundulus heteroclitus* predation was tested by placing 1 adult fish in each of 4

white pans (32 × 23 cm) containing 4 litres of aerated water (27°C, 9‰) and starved for 12 h. Forty amphipods (20 $\geq$ 4.0 mm, 20 < 4.0 mm) were then placed in the container and the order of amphipod consumption noted for the next 5 min. Following this, the fish were removed and preserved for stomach analysis. The remaining amphipods were also counted and sized. *Rhithropanopeus harrisii* and *P. pugio* predation was tested by placing predators in white plastic jars containing 1 litre of aerated water. After 12 h. 40 amphipods (20 $\geq$ 4.0 mm, 20 < 4.0 mm) were added and left for 6 h. The predators were then removed and the number and size of the remaining amphipods noted. Three replicates for both adult and juvenile predators were tested using 2 adults/replicate and 4 juveniles/replicate. Control replicates contained no predators. Size-selective predation effects were also analyzed in the previously described predation experiments using natural substratum since the number of adults and juveniles used in these experiments was controlled.

Results.—The results indicate that predator size selectivity varies for the different species (Table 9). Adult *F. heteroclitus* and *R. harrisii* showed significant selection for large amphipods ($P < .001$). Obser-

TABLE 10. Ratio of large to small *Gammarus palustris* collected from the Patuxent River cages. All numbers represent the mean number of amphipods per sample in each cage

	Exclusion cage			Open cage				
Date	≥4.0 mm	<4.0 mm	≥4.0 <4.0	≥4.0 mm	<4.0 mm	≥4.0 <4.0	F[a]	Probability
				1974				
25 May	79.33	164.67	0.48	124.00	109.00	1.14	1.44	.25 < P < .5
9 Jun	181.33	459.33	0.39	110.67	198.67	0.56	1.53	.25 < P < .5
24 Jun	201.33	386.67	0.52	77.33	232.00	0.33	5.87	.05 < P < .1
8 Jul	304.00	442.67	0.69	165.33	344.00	0.48	1.81	.1 < P < .25
24 Jul	288.88	390.00	0.74	188.00	321.33	0.59	0.42	.5 < P < .75
21 Aug	79.33	120.00	0.66	46.67	88.67	0.53	2.40	.1 < P < .25
				1975				
30 May	137.33	278.67	0.49	238.67	274.67	0.87	9.31	.025 < P < .05

[a] By analysis of variance of adult/juvenile proportions (coded using arcsine transformation).

vations on the order of amphipod consumption by fish provides additional support as, of the first 10 amphipods consumed, a mean of 8.75 (SD = ±0.50) were adults. Juvenile *R. harrisii* and adult *P. pugio* showed no significant size selection and juvenile *P. pugio* consumed too few amphipods for analysis.

In the experiments using natural substratum, *F. heteroclitus* showed a slight preference for large amphipods (Table 9). The lack of significant size selectivity by these fish may, in part, be due to the large number of amphipods consumed in these replicates which would reduce the availability of preferred prey. *Rhrithropanopeus harrisii* predation in the peat and low culm replicates was significantly size selective for large amphipods but at higher amphipod and culm densities, predation by *R. harrisii* and *P. pugio* was not significantly size selective (Table 9).

Fundulus heteroclitus size-selection experiments at high amphipod densities were not tested but an analysis of the 1974 caging experiments in which *Fundulus* were the dominant predators indicate that predation pressure was greater on adult amphipods (Table 10). When the cages were constructed (25 May), there was no significant difference in the large:small amphipod

ratio between cages. As time progressed, this ratio increased in the exclusion cage and decreased in the open cage with the ratios being significantly different by 24 June (.05 < P < .1). A similar analysis of the 1975 caging experiments was not done due to initial significant differences in this ratio between cages in the Patuxent River (Table 10) and a lack of significant predation by *Fundulus* in the Rhode River. The gut-content analysis (Table 11) provides additional support that *Fundulus* are size selective as, in all but 1 instance, the proportion of large amphipods consumed was greater than the proportion of large amphipods observed in the intertidal zone.

DISCUSSION

An examination of *G. palustris* population structure (Figs. 4–7) combined with the egg-ratio analysis (Figs. 8 and 9) reveals that population growth during the spring (both rivers) and autumn (Patuxent River) is primarily due to pulses in reproductive activity. However, increased birth rates observed during the autumn (Rhode River) and mid-summer (both rivers) did not result in greater amphipod densities. Instead, all ages of *G. palustris* declined to low intertidal densities at

TABLE 11. Body lengths of *Gammarus* consumed by *Fundulus* spp. The percent >4.0 mm of total from sampling sites represents a mean percentage computed from all samples collected on that date in 1974. If fish were not collected on the same date (in 1974) as the amphipod samples, the closest possible date was used for comparison

Date	Number of amphipods measured	$\bar{x}$	SD	% ≥4.0 mm of total consumed	% ≥4.0 mm of total from sampling sites	River
25 Jun	5	6·0	1·4	100	28	Patuxent
24 Jul	15	5·0	1·7	87	43	
18 Jun	22	4·6	1·2	82	23	
27 Jul	218	3·4	1·0	36	31	
15 May	13	5·7	1·9	92	30	Rhode
6 Jun	15	4·2	1·7	67	27	
12 Jul	42	3·5	1·5	38	38	
18 Aug	41	4·8	1·7	60	55	
19 May	21	6·1	2·1	86	20	

these times as well as during the winter months. Therefore, physical and/or biological factors must be regulating the amphipod populations.

Salinity stress undoubtedly influences *G. palustris* at the limits of its range, as is the case for other estuarine amphipods (Kinne 1971, Feeley and Wass 1971). Gable (1972) reported experimental evidence which suggests that low-temperature/low-salinity effects may cause mortality in populations of *G. palustris* when these conditions prevail. However, he does not present quantitative data to document seasonal declines in the abundance of this species correlated with salinity stress. My salinity-tolerance experiments (Fig. 16) demonstrate that low salinities observed at the study sites would not cause significant mortality. Furthermore, C. P. Rees (*personal communication*) noted abundant populations of *G. palustris* in areas of the Patuxent River which had much lower salinities than those I normally observed. While the effects of high-temperature/high-salinity combinations were not experimentally evaluated, they also should not be stressful because the populations were located at the lower end of their salinity range and *G. palustris* is a very euryhaline species (Gable 1972).

Heat and/or desiccation stress usually determines the upper range limits of intertidal organisms (Newell 1970, Connell 1972), but there is conflicting evidence on the impact of these environmental parameters on the seasonal abundance of epifaunal populations. Evans (1948), Fraenkel (1960) and Wolcott (1973) noted species with tolerances which exceeded the temperatures present in their study areas whereas Frank (1965), Sutherland (1970) and Branch (1975) observed substantial mortalities of intertidal species during seasonal hot weather. Croker (1967) and Sameoto (1969*a*) have examined the heat/desiccation tolerance of infaunal amphipods but the effects of this stress have not been previously tested on epifaunal amphipod species. My results (Fig. 19) demonstrate that the summer crash in population abundance of *G. palustris* was not due to heat or desiccation mortality. In fact, survival tolerance of this species to high-temperature/desiccation conditions was much greater than has been reported for other amphipod species (Croker 1967, Sameoto 1969*a*). The peat substratum used in these experiments undoubtedly aided in the high survival observed. This substratum retains water well and was always found to be moist at the study sites during low tides. Thus, considerable evaporative cooling must occur when the intertidal shelf is exposed creating high-humidity conditions which enhance the desiccation tolerance of *G. palustris* (see results) as well as other intertidal invertebrates (Wolcott 1973).

Freezing temperatures are also known to influence many intertidal invertebrates either directly through physiological stress (Kanwisher 1955, Williams 1970, Prosser 1973, Murphy and Pierce 1975) or indirectly through ice shear effects (Frank 1965). However, as with high-temperature stress, the effects of freezing on epifaunal amphipods have not been studied previously. My results (Fig. 18) demonstrate that *G. palustris* is not tolerant enough to survive the lowest freezing temperatures observed intertidally. Even so, this parameter is not a major source of mortality for this species, due to the subtidal migration which occurs in late autumn (Table 4).

Because freezing temperatures represent the only environmental factor which significantly influences the distribution of these epifaunal amphipods by necessitating a subtidal migration to avoid mortality, biological factors must be controlling the distribution and abundance of *G. palustris* at other times of the year. The experimental evidence presented in this study supports this hypothesis.

Competition represents an important regulatory mechanism for many intertidal epifaunal populations (Sutherland 1970, Connell 1972, 1975, Haven 1973, Paine 1974, Menge 1976). If competitive interactions for food resources regulate *G. palustris,* the effects should be maximized when amphipods are very dense in the marsh beds (Figs. 2 and 3) or when the abundance of other detritivores increases (Figs. 21 and 22). However, no significant declines in the ovigerous female brood size occurred at these times (Figs. 23 and 24) as might be expected if food resources were limiting (Slobodkin 1954, Hall 1964). The decreases in average brood size (Table 5) of the total adult female population can be attributed to a reduction in the mean size of ovigerous females through a die-off of the overwintering generation, combined with a reduction in the ratio of ovigerous to nonovigerous females. Furthermore, increases in competitor density (intra- or interspecific) at other times during the breeding season were not correlated with decreases in average brood size (Figs. 2, 3, 21; Table 5). Thus, it is unlikely that food limitation influenced amphipod densities.

Competition for space, however, does influence intertidal *G. palustris* populations through competitive displacement for *Spartina* culms rather than mortality through aggressive interactions (Table 6, Fig. 25). Field collections support this competitive displacement hypothesis as I observed *G. palustris* inhabiting the peat between *Spartina* culms in both rivers (Fig. 13B, personal observations), even though culms are a highly preferred substratum (Fig. 14). In addition, the laboratory data suggest that adults can partially displace juveniles from *Spartina* culms when they are a limiting resource (Table 7). Similar instances of competitive dominance by large amphipods relative to smaller ones have been reported for other species (Connell 1963, Nagle 1968). Thus, intraspecific competition for *Spartina* affects the distribution and population structure of *G. palustris* within the intertidal zone but does not directly cause the declines in amphipod abundance observed (Figs. 2 and 3).

As *G. palustris* is the only epifaunal species prevalent in the marsh beds studied, interspecific interactions for space should be minimal. Competitive interactions with the infaunal amphipod *Corophium lacustre* might explain the relatively lower densities of *G. palustris* found in level 1 during the summer (Fig. 11) but would not result in the overall decrease in amphipod abundance which occurred because *C. lacustre* was primarily restricted to level 1. Interactions for space with the tanaid *Leptochelia rapax* may also affect *G. palustris* populations. Technical difficulties in working with these tanaids precluded explicit tests of this hypothesis. However, one would not expect the observed increases in amphipod density at times of high tanaid density if competition for space between these species was critical (compare Figs. 2 and 21).

Based on the negative evidence obtained from the environmental and competition studies, predation represents the most likely alternative hypothesis to explain the declines in amphipod abundance during the summer in the Patuxent River and summer and fall in the Rhode River. Gable (1972) contends that predation on intertidal *G. palustris* populations is minimal at the northern limit of its range, but did not experimentally document this hypothesis. The results of the caging experiments, along with correlative evidence, indicate that the opposite is true in the Chesapeake Bay.

The Patuxent River caging experiments demonstrate that a significantly greater number of amphipods were present in cages which excluded predators during the summer months (Figs. 27 and 28). The primary predator limiting *G. palustris* at this time was *Fundulus heteroclitus*. Fraser (1973), A. K. Myers (*personal communication*) and I have observed that *Fundulus* spp. leave the marsh beds during the autumn months. This would relieve amphipods from predation pressure because invertebrate predators were not abundant at this site. The subsequent increase in amphipod density resulting from the increased birth rate also substantiates the predation hypothesis because nearly equivalent rises in b during the summer produced only slight increases in amphipod density.

Although similar caging results were not obtained from the Rhode River study area (Fig. 29), difficulties arise in assessing the effects of predation on epifaunal amphipods via caging experiments due to their ability to exit or enter a cage. The small size of this species precluded forcing inclusion within a cage because a finer mesh would quickly clog. Thus, it is possible that amphipod movements within the intertidal zone may obscure results. Furthermore, I was unable to exclude *Rhithropanopeus harrisii* and small *Palaemonetes pugio* from the cages. A comparison of the invertebrate predator abundance between rivers (Fig. 22) shows that these species were much more abundant in the Rhode River from midsummer to late fall. A similar comparison of total amphipod abundance (Figs. 2 and 3) demonstrates that amphipod density was decreasing

throughout this time in the Rhode River with no autumn increases, even though birth rates increased to values comparable with those observed in the Patuxent River (Figs. 8 and 9). As *R. harrisii* and *P. pugio* are capable of consuming amphipods in dense beds of *Spartina* such as those present in the Rhode River (Table 8), it is probable that predation is the cause for the *G. palustris* mortality in this river as well.

The predation hypothesis also explains the strong preference of *G. palustris* for *Spartina* culms (Fig. 14) because the experiments using varying substratum types (Fig. 26) demonstrate that these amphipods can utilize *Spartina* as a refuge. Thus, this behavioral preference represents an effective predator-avoidance mechanism and accounts for the high amphipod densities found in areas of greatest culm density (Figs. 11, 12, 13A). Similar cases of differential survival in refuges have been noted for other intertidal salt-marsh amphipods (Vince et al. 1976) as well as subtidal populations (Nagle 1968, Orth 1975).

Cooper (1965), Strong (1971) and Vince et al. (1976) have shown that size-selective predation can affect the structure and behavior of amphipod populations. The preference for large amphipods by *Fundulus* and *Rhithropanopeus* noted in this study (Tables 9–11) would explain the competitive behavior of adults displacing juveniles for *Spartina* culms because this would position the most preferred prey in the least accessible areas. This would, in turn, account for the high mortality of juveniles observed in both rivers (Figs. 4 and 5) as competitive displacement would result in increased predation pressure on juveniles by fish and the nonselective invertebrate predators. However, competitive displacement does not completely protect large amphipods from predators as noted by the declines in adult abundance during the summer (Figs. 4 and 5). Therefore, size-selective predation may also account for the preponderance of females in the adult sex ratio (Table 3) because males represent the largest size classes (Figs. 6 and 7) and would be preferentially selected when refuges are limiting.

Connell (1975) and Menge and Sutherland (1976) present models which predict that predation is the principle structuring agent operating on communities in relatively benign environments. Furthermore, at least in the rocky intertidal system, predation may affect the dominant species most severely (Paine 1966, 1969, Dayton 1971, Menge 1976). The evidence presented in this study supports the above models because salt marshes represent a relatively benign environment for the predominant epifaunal species (*G. palustris*) throughout most of the year. Furthermore, predation best explains the seasonal changes in the distribution and abundance of these amphipods during this period.

Competition, however, plays a weaker role in regulating population and community structure in this system as (1) intraspecific competition among *G. pal-*

ustris only indirectly influenced population abundance by determining which size classes of amphipods were exposed to predation, and (2) interspecific competitive effects were minimal. These results differ from the conclusions obtained in other studies of trophically simple intertidal communities where competition was a dominant structuring agent (Croker 1967, Woodin 1974, Menge 1976). This discrepancy may be due to the mobility of epifaunal amphipods which permits avoidance of lethal competitive interactions. Mobility also accounts for the absence of mortality from freezing stress, even though this factor is indirectly important in regulating the winter distribution of *G. palustris*.

In summary, this study demonstrates that both biological and environmental factors regulate *G. palustris* populations inhabiting intertidal marsh beds. Very few previous studies have experimentally determined the relative influence of these factors on intertidal epifaunal amphipods, or for that matter, on any invertebrates inhabiting estuarine salt marshes. The comparatively dominant effects of biological factors operating in this system correlate well with the increasing evidence that biotic factors represent a major structuring force in intertidal systems.

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