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Intertidal distribution, population dynamics and production of the amphipod *Uhlorchestia spartinophila* in a Georgia, USA, salt marsh

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Abstract The talitrid amphipod *Uhlorchestia spartinophila* Bousfield and Heard occurs in close association with the smooth cordgrass *Spartina alterniflora* Loisel in salt marshes along the U.S. Atlantic coast. In order to assess its potential as a prey resource for secondary consumers, we followed the population and production dynamics of this amphipod from 3 November 1990 to 2 October 1991 in a salt marsh on Sapelo Island, Georgia. Semimonthly samples were taken along an intertidal transect, which extended from a vegetated creekbank levee landward 140 m to a site near the upland edge of the marsh. Amphipod densities ranged from 9 to 826 ind m^{-2} and were greatest in the levee and high marsh habitats at opposite ends of the transect. The highest densities occurred in March to May and the lowest in November and December. Specific growth rates, which ranged from 0.001 to 0.024 mm mm^{-1} d^{-1} length and 0.003 to 0.068 mg mg^{-1} d^{-1} AFDW (ash-free dry weight), were least in winter and decreased with increasing amphipod size. Although some reproduction occurred year-round, most of the population's reproductive output was from January to May, when adults had the greatest size-specific mass. Sex ratio usually favored females, which were larger than males. Minimum adult female size was 5.4 mm total length (TL). Broods included from 1 to 28 eggs or young and increased with increasing body size, averaging 7.4 young for an average-size female of 7.6 mm TL. Annual production, which ranged from 0.769 to 1.444 g AFDW m^{-2}, was least in the low marsh and greatest in the levee habitat. Production:biomass ratios were 15.4 to 17.3 in different habitats. Such high turnover rates, together with the population's broad intertidal distribution, suggest a greater contribution to trophic dynamics than is implied by the relatively low standing stock biomass of *U. spartinophila* in this marsh system.

Introduction

The gammaridean amphipod superfamily Talitroidea is unique in that several species in this group have adopted a semi- or fully terrestrial existence (Wildish 1988). Talitridae is the largest talitroid family, comprising over 200 species (Bousfield 1982, 1984). Studies of life histories and production dynamics of talitrids, have focused primarily on species associated with wrack in the supralittoral zone of sandy beaches and rocky shores (e.g. Venables 1981; Behbehani and Croker 1982; Van Sensus and McLachlan 1986; Marsden 1991 a). Talitrid amphipods feed on detrital material and so contribute to decomposition of the mats of decaying vegetation with which they are usually associated (Lopez et al. 1977; Robertson and Lucas 1983). In turn, they are consumed by a variety of vertebrate and invertebrate predators (Wildish 1988). Although recognizing their trophic importance on a local scale, Wildish (1988) suggested that talitroids do not contribute significantly to trophic transfers in most marine and estuarine environments because they are confined to narrow littoral and supralittoral habitats.

Uhlorchestia spartinophila occurs in salt marshes along the U.S. Atlantic coast where it inhabits culms and stems of the smooth cordgrass *Spartina alterniflora*. Unlike many other talitrids, this amphipod species is broadly distributed within the intertidal zone (Bousfield and Heard 1986). Earlier studies of salt marsh talitrids (e.g. Averill 1976; Vince et al. 1976; Phillips 1978; Kneib 1982) were conducted prior to the publication of a formal description of *U. spartinophila* by Bousfield and Heard (1986), and so some confusion over the habits of different species within this group is possible. In previous studies, *U. spartinophila* has been identified as *Orchestia spartinophila* (Phillips 1978) or *Orchestia* sp. (Kneib 1982) and may have been

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confused with *Orchestia uhleri* (Averill 1976) and *O. grillus* (Vince et al. 1976). With benefit of taxonomic clarification, we examined the population and production dynamics of *U. spartinophila* in order to assess its potential as a prey resource for secondary consumers in an intertidal marsh on Sapelo Island, Georgia (USA).

Materials and methods

We collected amphipods twice monthly from 3 November 1990 to 2 October 1991 in a marsh near the upper reaches of the Duplin River, a tidal lagoon along the western border of Sapelo Island. Tides in the area were semidiurnal with a range of ca. 137 to 320 cm and a mean of ca. 210 cm (Ragotzkie and Bryson 1955). The predominant emergent vegetation was *Spartina alterniflora* Loisel, which grew >1.5 m tall along the creek banks and became increasingly shorter with increasing intertidal elevation to a height of < 25 cm in the high marsh. We estimated elevations above mean low water (MLW) by measuring relative elevations of sampling locations and major topographic features with a surveying transit and stadia rod and relating the measurements to detailed tide data recorded at the site from March 1988 to December 1991 (Kneib unpublished data). At that time, duration and depth of tidal inundation were measured on the marsh surface at 10-min intervals using a Druck Model PDCR 10/D (175 mbar range) pressure transducer connected to an electronic datalogger (Easylogger Model EL-824, Omnidata International Inc.). Average daily air temperatures were calculated from measurements recorded during the study at 10-min intervals by a temperature probe (Model ES-060, Omnidata International, Inc.) attached to the on-site datalogger.

Amphipod samples were collected at four locations (levee, back-levee, low marsh and high marsh) along a 140-m transect extending from an intertidal creek channel to the upland border of the marsh (Fig. 1). At each location we installed a series of wooden trestles (20 cm tall) on 2-m centers to define 4×60 m sampling grids, which were oriented with the long axis perpendicular to the transect line. The trestles supported removable wooden boards (0.145 m wide and 2.0 m long) that allowed temporary access to any point within the sampling grid without disturbing the marsh substratum. We estimated mean stem density of *Spartina alterniflora* in March 1991 at each location by counting the number of stems in 15 randomly selected 0.25 m^2 quadrats within each sampling grid.

Uhlorchestia spartinophila Bousfield and Heard 1986 were closely associated with the marsh vegetation, so we collected them by clipping five haphazardly selected cordgrass stem sections (the sampling unit) 25 cm long from ten randomly selected 2×2 m plots at each transection location. Stem sections were cut at the marsh surface and quickly placed in sealable plastic bags. In the laboratory, hot (ca. 60 to 65 °C) tap water added to the bags killed the amphipods before they were sorted from the vegetative debris and placed in a 10% solution of buffered freshwater formalin. Multiplying the number of amphipods $stem^{-1}$ by the site-specific mean stem density gave estimates of amphipod density. Sampling dates coincided with the peak spring tide period and the following neap tide (1 wk later) each month so that we could have monthly paired samples to assess effects of the lunar tidal cycle on intertidal distribution and estimates of amphipod abundance.

In July 1990 and March 1991 we evaluated the effectiveness of our sampling method by comparing the numbers of amphipods collected using the following sampling techniques: (1) 6.2 cm diameter benthic core (5 cm deep) from between cordgrass stems (core only); (2) the same size benthic core but including stems (core + stems); and (3) clipped stems without a core tube (stems only). There were 20 and 24 replicates of each sample type in the July and March samples, respectively. The number of stems in the stems-only samples matched the number in the cores + stems samples.

Using an ocular micrometer mounted in a stereomicroscope (12× magnification), we measured amphipod total length (TL) to the nearest 0.1 mm from the head at the base of the first antenna to the end of the telson. Ash-free dry weights (AFDW) were determined for 50 individuals from each sampling date; individuals were selected to represent the range of sizes taken on each date. These were rinsed in deionized water, dried to constant weight (4 to 5 d) at 60 °C, weighed to the nearest 0.01 mg, ashed at 400 °C for 6 h and reweighed. Slopes and intercepts of amphipod length-weight regression lines were compared among different stages of the tidal cycle (spring, neap) and seasons (spring, summer, winter, autumn) using analysis of covariance (Snedecor and Cochran 1980). Standing stock biomass at each transect location and sampling date was calculated by using seasonal length-weight regression equations to estimate the mean AFDW of amphipods $stem^{-1}$ and by multiplying that value by the mean number of stems at the transect location for each date.

We identified the following categories of *Uhlorchestia spartinophila*: (1) juveniles were < 5 mm TL and of undetermined sex; (2) adult males were identified by their enlarged subchelate second gnathopod; (3) adult females were larger than males but gnathopod 2 was not enlarged. We subdivided females into the following two categories: (a) reproductively active females which had setose oostegites on pereiopods 2 to 4 forming a ventral brood pouch or marsupium often containing eggs or embryos; and (b) reproductively inactive females in which the marsupium was absent. We measured individual fecundity as the number of eggs or embryos carried by gravid females. Population fecundity was estimated from the total number of eggs and embryos carried by all females in a sample. The average number of eggs and embryos $stem^{-1}$ multiplied by the number of stems m^{-2} at a location was expressed as egg density.

Growth rates were estimated from changes in the size frequency distributions with time. Length frequency histograms constructed on 1 mm length intervals were multimodal and included two to four cohorts on each sampling date. We assumed that distributions represented overlapping, but normally distributed cohorts and used the interactive computer program MIX (version 3.0, Ichthus Data Systems) to estimate the mean size of individuals within each cohort on each sampling date. The growth of individuals within each cohort

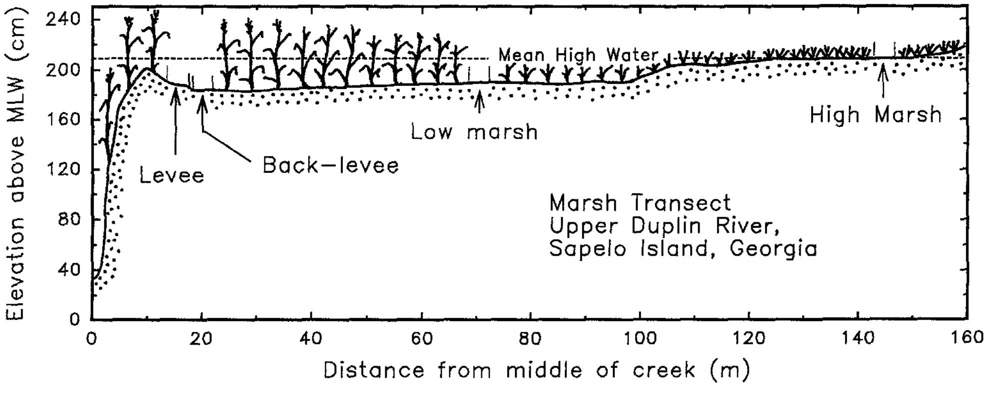

Fig. 1 Transect through the intertidal marsh sampling site showing location of the four sampling grids. Emergent vegetation, though not drawn to scale, depicts the general pattern in stem height and density of *Spartina alterniflora* along the transect. (*MLW* mean low water)

was estimated by plotting the means by sampling date and connecting the points so that positive growth occurred (except in the colder winter months). We chose to estimate growth rates from spring and neap tide samples separately for two reasons: (1) it provided two independent estimates of growth based on monthly intervals; and (2) we did not expect to estimate growth accurately over the 1-wk interval between spring and neap tide samples each month.

Specific growth rates were estimated by the following generalized equation:

$$g = \ln (s_{x+1}/s_x)/(t_{x+1}-t_x)\,, \tag{1}$$

where s_x and s_{x+1} are the mean sizes (total length in mm or mass in mg) of the individuals in a cohort at the beginning (t_x) and end (t_{x+1}) of the time interval in days between samples. Separate specific growth rates were estimated for amphipods 2.0 to 3.9 mm, 4.0 to 5.9 mm, and 6.0 to 8.0 mm TL. Larger amphipods were too few to accurately estimate growth from the size-cohort analysis; we assumed they grew at the same rate as individuals in the 6- to 8-mm size class.

Habitat-specific production within a sampling interval was estimated separately for each size class then summed across size classes using the following formula:

$$P_i = \Sigma\, g_y(t_i)\,(b_y)\,, \tag{2}$$

where g_y is the daily specific growth rate (mg mg^{-1} d^{-1}) for size class y, t_i is the number of days in the interval and b_y is the average biomass of size class y at the midpoint of the interval. Annual production was the sum of the production estimates (P_i) across all sampling intervals. Neap and spring tide samples were treated separately to provide two independent estimates of production for each habitat along the marsh transect.

Results

Physical variables and vegetation density

The pattern of tidal inundation at each sampling location was largely a function of intertidal elevation and tidal amplitude. The back-levee and high marsh were the most and least flooded transect locations, respectively (Table 1). There were also semilunar and seasonal differences in tidal flooding. Mean daily flooding durations in the 2 d prior to each amphipod collection were significantly higher (paired $t_{11\mathrm{df}}=3.70$ to 4.89 for different locations, $P<0.005$) on spring than neap tides at all transect locations. Semilunar differences in flooding duration were most pronounced from December 1990 to June 1991 and were greatest at the high marsh and least at the back-levee location.

Mean daily air temperatures during the study ranged from –0.3 to 29.1 °C and were more variable in the winter (December to March) than at other times of the year (Fig. 2). There was no significant difference (paired $t_{8\mathrm{df}}=0.83$, $P=0.43$) in temperatures between the monthly pairs of spring and neap tide dates on which amphipods were collected.

The height and diameter of *Spartina alterniflora* stems generally decreased with increasing distance from the tidal creek (Fig. 1). Stem densities increased with distance from the tidal creek channel to a maximum in the high marsh (Table 1). A logarithmic transformation ($\log_{10} x$) was applied to the stem density data so that they conformed to the assumption of variance homogeneity prior to the application of a one-way analysis of variance. Results of the analysis indicated a difference in stem density ($F_{3,56}=161.3$, $P<0.001$) among transect locations. The Scheffé procedure ($\alpha=0.05$), used to determine which means differed significantly, detected differences among all locations except the levee and back-levee.

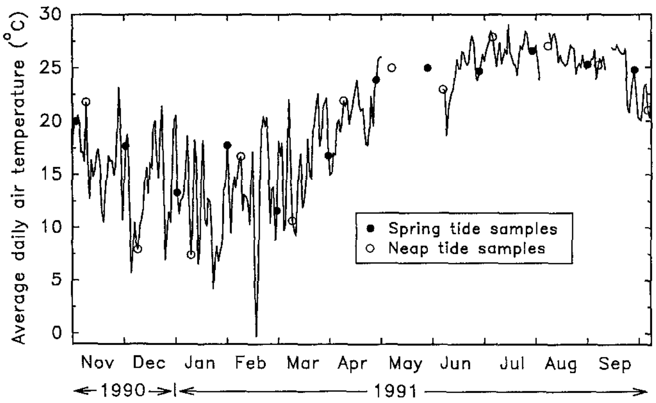

Fig. 2 Temporal variation in average daily air temperature at intertidal study site shown in relation to the spring and neap tide sampling dates

Table 1 Intertidal elevation, flooding duration and vegetation density at each sampling location along the marsh transect at the Upper Duplin River study area. (*MLW* mean low water; *N* number of observations). Means ± SD

Sampling location	Mean elevation above MLW (cm) (N=14)	Mean daily duration of tidal flooding (h) (N=338)	Mean number of *Spartina alterniflora* stems 0.25 m^{-2} (N=15)
High marsh	209±2.1	3.8±2.50	116±21.8
Low marsh	190±1.8	6.5±2.50	54±7.3
Back-levee	184±2.2	7.7±2.50	41±6.9
Levee	188±5.7	6.7±2.45	38±4.6

Table 2 *Uhlorchestia spartinophila*. Comparison of sampling methods for estimating amphipod densities. Mean (±SD) no. ind sample^{-1} shown with no. replicates (N) treatment^{-1}

Sampling date	N	Sampling treatment		
		Core only	Stems + core	Stems only
Jul 1990	20	0.2±0.13	1.0±0.22	1.4±0.27
Mar 1991	24	0.1±0.10	3.5±0.34	3.7±0.44

Density and intertidal distribution of amphipods

The test of our sampling method confirmed that *Uhlorchestia spartinophila* was closely associated with *Spartina alterniflora* stems (Table 2). Samples of the substratum between stems (core only) contained few amphipods and there was little difference between samples of only stems and those that also included the surrounding substratum

Table 3 *Uhlorchestia spartinophila*. Overall mean (±SE, $N=240$) density of amphipods at each sampling location. Neap and spring tide samples pooled

	Sampling location			
	High marsh	Low marsh	Back-levee	Levee
Ind stem^{-1}	0.7± 0.05	0.7±0.05	1.3± 0.08	2.3± 0.11
Ind m^{-2}	331.4±24.04	156.1±9.74	218.7±12.52	350.2±16.89

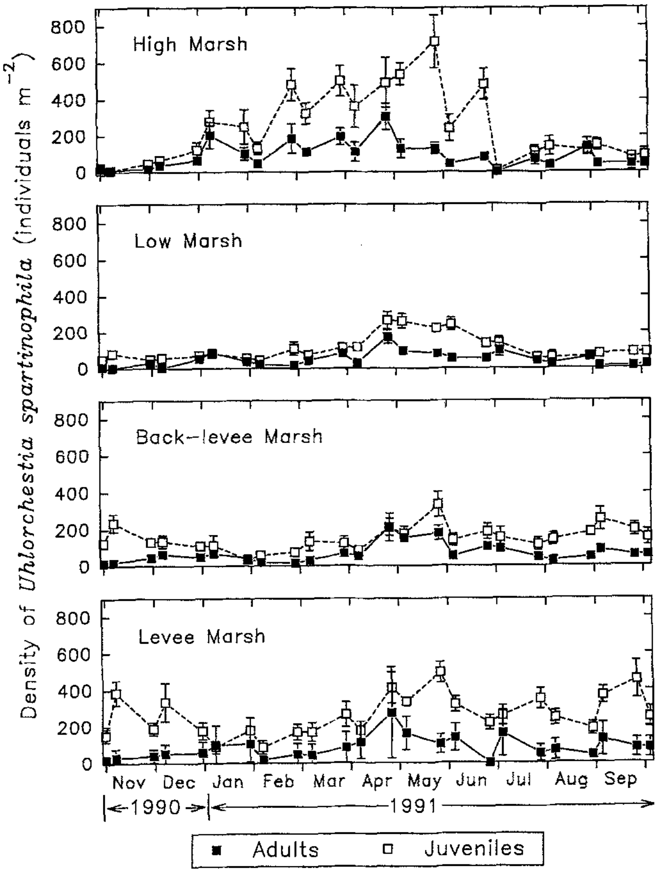

Fig. 3 *Uhlorchestia spartinophila*. Temporal variation in mean (±SE, $N=10$) densities of adults and juveniles at each sampling location along the intertidal marsh transect

(stems + core). Although a *t*-test indicated a significant difference ($t_{38df}=5.14$, $P<0.001$) between the two sample types containing stems in July 1990, this was because there were more, not fewer, amphipods in the stems only samples. There was no significant difference ($t_{46df}=1.76$, $P>0.05$) in the mean number of amphipods between sample types with stems in March 1991.

Problems of variance heterogeneity, which could not be resolved with mathematical transformations, prohibited the use of parametric statistical analysis of the amphipod density data. However, a nonparametric Kruskal–Wallis one-way analysis of variance detected highly significant differences among sampling locations when density was expressed as either individuals stem^{-1} ($\chi^2_{3df}=46.5$, $P<0.001$) or individuals m^{-2} ($\chi^2_{3df}=21.7$, $P<0.001$). The mean number of amphipods stem^{-1} was highest on the levee and appeared to decrease with increasing distance from the tidal creek (Table 3). However, the estimated number of amphipods m^{-2} was influenced by stem density, which increased with increasing distance from the creek (Table 1). Consequently, areal densities (ind m^{-2}) of amphipods were similar and greatest in the high and levee marsh habitats at opposite ends of the sampling transect (Table 3).

The seasonal pattern of amphipod abundance was not the same across the marsh transect. At most locations, abundance increased to a maximum sometime during March to May, then declined and remained low from June to December, but substantial numbers of juveniles persisted in the levee habitat for most of the year (Fig. 3). Seasonal variation in density was greatest in the high marsh where both adults and juveniles were more abundant than elsewhere from January to June. Short-term (i.e., semilunar) density oscillations in the high marsh, and to a lesser degree the levee marsh, were suggested by a saw-tooth pattern in the plots of density with time in these habitats (Fig. 3).

Length-weight relationships

We used ash-free dry weight (mg, AFDW) as a measure of amphipod mass, but to facilitate comparisons with other studies that used dry weight (mg, DW) we provide the following conversion equation for *Uhlorchestia spartinophila*:

$$\mathrm{DW}=1.232(\mathrm{AFDW})-0.00523. \tag{3}$$

This predictive equation was derived from a significant ($F_{1,540}=95\,857.8$, $P\ll0.001$; $r^2=0.997$) linear regression of DW on AFDW based on 543 amphipods for which both DW and AFDW were measured.

Analysis of covariance (ANCOVA) did not detect significant differences in either the slopes ($F_{1,1187}=1.05$, $P=0.305$) or intercepts ($F_{1,1188}=2.55$, $P=0.110$) of relationships between $\log_{10}$(AFDW) and $\log_{10}$(length) of amphipods collected from different stages of the tidal cycle, and so monthly spring and neap tide samples were pooled in subsequent analyses. However, there was a significant difference (ANCOVA, $F_{1,1180}=6.18$, $P<0.001$) in the slopes of the length-weight relationships when the data were grouped by season. This indicated that separate seasonal equations were required to estimate amphipod mass from length measurements. An inspection of regression equation slopes for each season suggested that amphipods had greater size-specific mass in the spring than at other times of the year (Table 4).

Sex ratio, reproduction and fecundity

Females were 2.25 times more abundant than males overall. However, sex ratio varied seasonally, favoring females

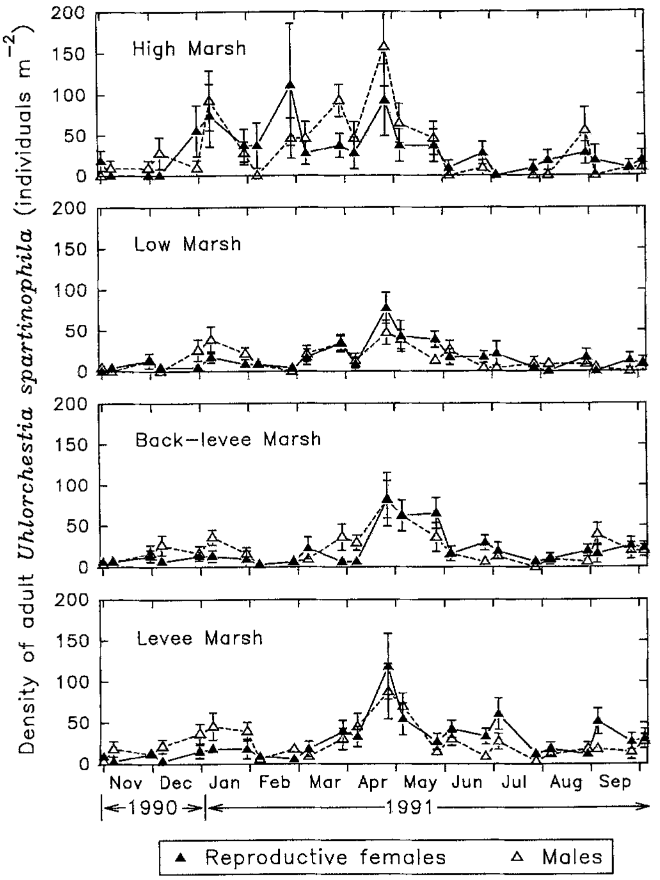

Fig. 4 *Uhlorchestia spartinophila.* Site-specific temporal variation in the mean (±SE, $N=10$) densities of adult males and reproductively active females

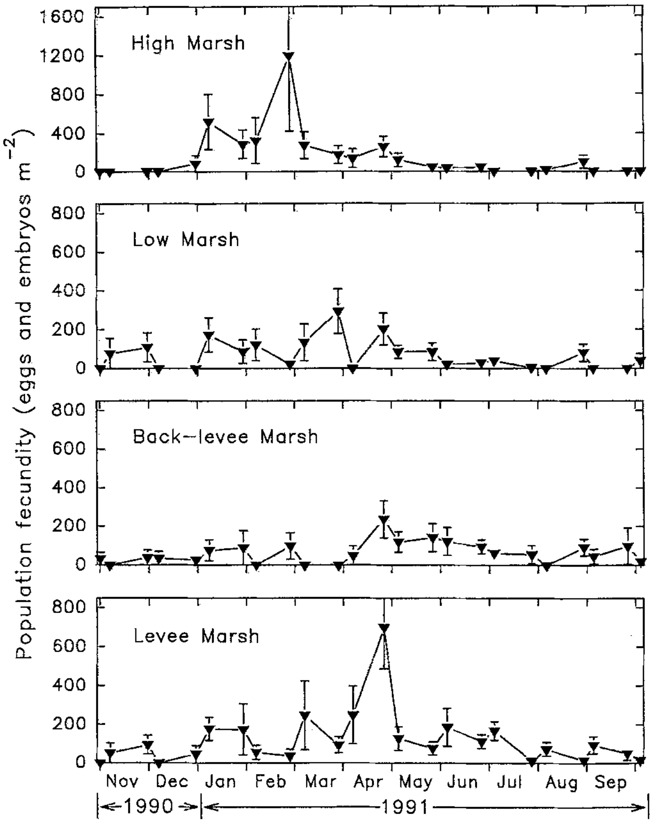

Fig. 5 *Uhlorchestia spartinophila.* Site-specific temporal variation in mean (±SE, $N=10$) population fecundity (density of eggs and embryos)

Table 4 *Uhlorchestia spartinophila.* Calculated coefficients for estimating amphipod mass (mg, AFDW) from measurements of total length (mm, TL) at different times of the year. Form of the linear regression equations is: $\log_{10}(\text{AFDW})=b[\log_{10}(\text{TL})]-a$. [*N* no. of amphipods used in the calculation of each equation; r^2 square of the correlation coefficient (estimate of the proportion of variation in AFDW explained by variation in TL)]. Sampling periods included in each season shown in parentheses

Season	*N*	*b*	*a*	r^2
Spring (30 Mar to 5 Jun 1991)	299	3.181	2.842	0.956
Summer (26 Jun to 3 Sep 1991)	298	2.967	2.580	0.947
Autumn (24 Sep to 2 Oct 1991 and 3 Nov to 9 Dec 1990)	291	2.975	2.713	0.952
Winter (1 Jan to 9 Mar 1991)	296	3.018	2.758	0.961

more strongly in June (4.2 ♀ : 1 ♂) and July (7.4 ♀ : 1 ♂) than at other times of the year (1.1 ♀ : 1 ♂). Gravid females were present year-round (Fig. 4) but were most abundant from January to April, particularly in the high marsh. Individual fecundity also was greatest at this time because more large females were present in the population, and there was a positive linear relationship between brood size and female size as described in the following regression ($F_{1,292}=339.3$, $P \ll 0.001$, $r^2=0.54$) equation:

$$BS=2.59\,(TL)-12.32\,, \qquad (4)$$

where BS = brood size (number of eggs or embryos) and TL = total length (mm). The smallest gravid female was 5.4 mm TL, but the mean size was 7.6 mm TL, with a mean *BS* of 7.4 young.

Site-specific population fecundity as measured by the number of eggs and embryos m^{-2} at each sampling location showed that most of the population's reproductive potential was in the high marsh in February but shifted toward the levee marsh in April (Fig. 5).

Growth and survival

The size-cohort analysis produced similar results when independently conducted on spring and neap tide samples (Fig. 6). Growth was slowest in winter when temperatures were low (Fig. 2), but during most of the year absolute growth rates, estimated from temporal changes in mean sizes of individuals within cohorts (Fig. 6), averaged 0.081 mm d^{-1} length and 0.012 mg d^{-1} AFDW, respectively. Mean specific growth rates decreased with increasing am-

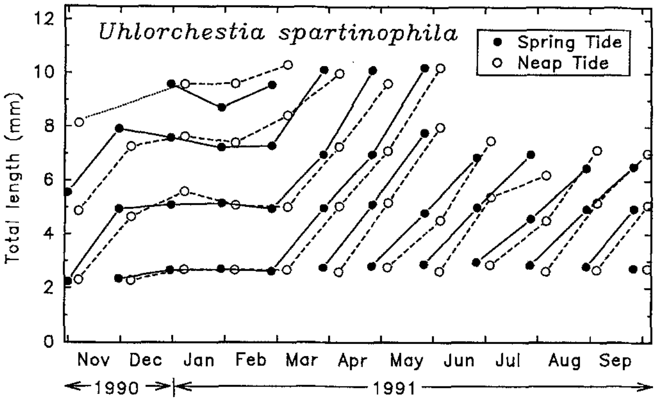

Fig. 6 *Uhlorchestia spartinophila*. Estimated growth trajectories of amphipod cohorts. Estimates based on spring and neap tide samples were independent

Table 5 *Uhlorchestia spartinophila*. Mean (±SD) specific growth rates for three size classes of amphipods expressed in terms of both length (mm mm^{-1} d^{-1}) and ash-free dry mass (mg mg^{-1} d^{-1}). [*N* no. or intervals from the size-cohort analysis (Fig. 6) used in the estimate of each mean.] Spring and neap tide samples treated as independent measures

Season	*N*	Size class (total length)		
		2.0–3.9 mm	4.0–5.9 mm	6.0–8.0 mm
Growth in length (mm mm^{-1} d^{-1})				
Autumn	4	0.024±0.0026	0.011±0.0015	–
Winter	6	0.002±0.0023	0.001±0.0023	0.001±0.0017
Spring	6	0.020±0.0047	0.012±0.0012	0.011±0.0026
Summer	6	0.019±0.0048	0.012±0.0046	–
Growth in mass (mg mg^{-1} d^{-1})				
Autumn	4	0.068±0.0093	0.033±0.0057	–
Winter	6	0.004±0.0058	0.003±0.0063	0.003±0.0045
Spring	6	0.065±0.0085	0.041±0.0036	0.036±0.0071
Summer	6	0.057±0.0151	0.035±0.0137	–

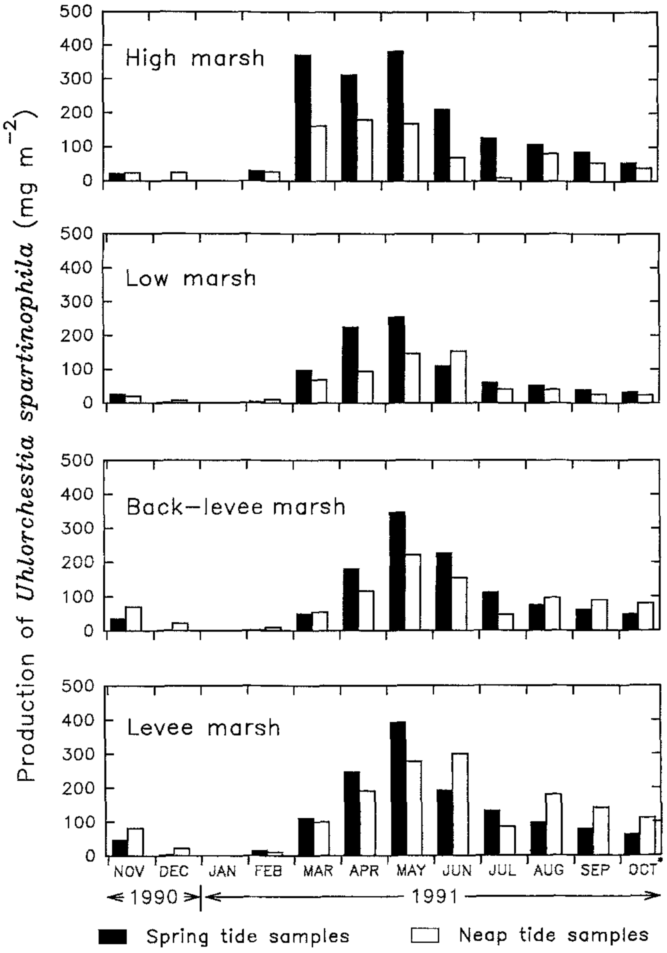

Fig. 7 *Uhlorchestia spartinophila*. Site-specific temporal variation in production of amphipods. Independent estimates of production calculated from neap and spring tide samples. Oct*: production estimates for October obtained by averaging values from September 1991 and November 1990

Table 6 *Uhlorchestia spartinophila*. Annual production estimates at four sampling locations along a transect through the intertidal marsh at the upper reaches of the Duplin River, Sapelo Island, Georgia, USA. Values from spring and neap tide samples averaged

Sampling location	Annual production (*P*) (g AFDW m^{-2})	Mean annual biomass (B) (g AFDW m^{-2})	P:B
High marsh	1.277	0.083	15.4
Low marsh	0.769	0.047	16.4
Back-levee	1.055	0.061	17.3
Levee	1.444	0.085	17.0

phipod size (Table 5). Growth could not be estimated for amphipods >8 mm total length because there were too few large individuals for an accurate analysis.

The cohort analysis also suggested a seasonal pattern of mortality in the amphipod population. Survival within cohorts present in November and December was likely high because the population size did not decline during winter, even though few new individuals were added to the population (Fig. 3), and the cohorts remained large enough to follow for up to 28 wk (Fig. 6). As growth rates increased during the warmer months (May to September), mortality in adult size classes probably also increased because, despite a higher reproductive output, the adult population did not increase (Fig. 3) and no cohorts remained abundant enough to follow for more than 8 wk (Fig. 6).

Production

Most of the production in this population of *Uhlorchestia spartinophila* occurred from March to July (Fig. 7). Production during October 1991 could not be calculated because our final sample was collected 2 October 1991. However, we estimated October production as the average of the values from September 1991 and November 1990. There was almost no production in winter when mean individual growth rates were lowest (Table 5) and population size was relatively stable (Fig. 3).

Monthly estimates of production based on spring tide samples were usually higher than those from neap tide. However, the neap tide samples often yielded higher estimates in the levee and back-levee locations from June to November. We averaged the neap and spring tide estimates for each monthly interval and summed across months to estimate the average annual production at each sampling location (Table 6). The greatest annual production was in the levee habitat and lowest in the low marsh. Average standing stock biomass did not exceed 0.085 g AFDW m^{-2} in any habitat and so turnover rates [production biomass (P: B) ratios] were relatively high, ranging from ca. 15 to 17.

Discussion

Several environmental factors are known to affect the survival and distribution of talitrids in estuaries (Wildish 1979, 1988), but moisture seems to be among the most important for intertidal species (Moore and Francis 1985; Spicer and Taylor 1987; Marsden 1991 a, b). Averill (1976) found that *Uhlorchestia spartinophila* (identified as *Orchestia uhleri*) densities in a Delaware (USA) marsh were greatest near the middle of the *Spartina alterniflora* vegetation zone. Phillips (1978) later suggested that desiccation stress restricted the intertidal distribution of this species to frequently flooded habitats. Experiments conducted in a North Carolina (USA) salt marsh (Kneib 1982) showed that *U. spartinophila* (identified as *Orchestia* sp.) preferred conditions that were neither too wet nor too dry.

In the present study, the highest densities of *Uhlorchestia spartinophila* occurred at opposite ends of our transect, which seemed inconsistent with previous observations on the intertidal distribution of this species. However, tidal range at Sapelo Island was greater than at the marsh sites where previous studies of *U. spartinophila* were conducted. Our highest intertidal sampling location (i.e., high marsh) was inundated by ca. 74% of all high tides and so may be comparable to the mid-elevation marsh sites of the other studies. If so, then the distribution of amphipods with respect to tidal flooding frequency was similar in all of the marshes, except for the high densities of amphipods we observed at the levee location. This exception suggested that elevation was not the only factor that determined the intertidal distribution of *U. spartinophila* because the levee was at the same relative elevation as the low marsh site where amphipod density was lowest. We believe an explanation for the apparent anomaly of the levee may lie in the characteristics of the vegetation and topography at this location. The levee is a narrow (10 m wide) depositional environment forming an elevated border along tidal creek channels adjacent to the most frequently flooded habitats. Here stems of *Spartina alterniflora* were larger in diameter and grew taller than elsewhere. This provided amphipods the option of climbing stems to escape submergence when the marsh was tidally inundated. Also, the acute slope of the levee allowed better drainage of the marsh substratum than occurred at comparable relative elevations in the low marsh. Consequently, amphipods in the levee marsh may experience a moisture regime similar to that at higher intertidal elevations. If so, the seemingly anomalous high density of amphipods on the levee may be consistent with the hypothesis that *U. spartinophila* preferred a moisture regime intermediate to that of the most and least frequently flooded habitats of the intertidal marsh.

Tides induce gradients in biotic as well as abiotic in factors (Kneib 1984) that may have influenced the distribution of amphipods along the intertidal marsh transect. Aquatic predators have a greater impact on density and size structure of amphipods (Vince et al. 1976; Van Dolah 1978) and other prey species (Schindler et al. 1994) in the most frequently flooded marsh habitats. This could explain the differences in amphipod densities we observed in the low and high marsh locations, but again the levee seems to be an exception. However, there are at least two ways that the levee habitat may function as a predator refuge for amphipods.

First, most aquatic predators access the intertidal marsh by following narrow rivulets that connect to larger channels or embayments (Rozas et al. 1988; Hettler 1989). Rivulets provide breaches in creekbank levees that otherwise block the movement of nekton into the intertidal marsh (Peterson and Turner 1994). Once around the levee, many aquatic predators may follow the rising tide to forage further into the interior of the marsh (Kneib and Wagner 1994), functionally ignoring the levee habitat and its occupants.

Second, the structural refuge value of *Spartina alterniflora* stems may be greater on the levee than in other habitats because stem height and diameter both increased toward the creek. Microspatial patterns of distribution on vegetation can influence predation risk for some aquatic insects (Wellborn and Robinson 1987). The larger *S. alterniflora* stems on the levee and creekbank may offer more places for amphipods to hide from their predators. Our data showed that stems on the levee harbored more amphipods than those in other habitats (Table 3). If amphipods compete for space on individual stems, larger stems should support more amphipods. Where individual stems are smaller, larger adult amphipods may displace juveniles, forcing them into microhabitats associated with greater predation risk (e.g. Wilson 1989). Although additional work will be required to establish cause, there appears to be something unusual about the levee habitat that supports higher *U. spartinophila* densities than occur in other areas of the marsh at similar intertidal elevations.

The original description of *Uhlorchestia spartinophila* indicated that the species had an annual life cycle with ovigerous females present from April to July (Bousfield and Heard 1986). Although this may be true of populations at higher latitudes, reproductive individuals were found year-round on Sapelo Island and the life cycle appeared to be semiannual, much like that reported for other talitrids in subtropical and tropical climates (Ali and Salman 1987; Wildish 1988). There was, however, a peak in abundance of juveniles during April and May that was consistent with previous observations.

Although sex ratio followed the usual pattern of favoring females during much of the year, *Uhlorchestia spartinophila* differed from many other talitrids in that the ratio was most strongly biased toward females just after the major reproductive season. In other talitrids the sex ratio often shifts in favor of males following peak periods of reproductive activity (Venables 1981; Behbehani and Croker 1982; Morritt and Stevenson 1993), presumably because males grow faster and enter the adult population before females (Van Senus 1988). This hypothesis is consistent with the observation that males of most talitrids are larger than females (Bousfield 1973). However, females are the larger sex in *U. spartinophila*. If they grow faster than the males, they may be the first to enter the adult population.

Larger female size should confer a reproductive advantage in addition to that gained by the female biased sex ratio (Wildish 1988) because brood size increases with increasing female body size in many amphipods (Nelson 1980). Brood size varies considerably within and between many families of gammaridean amphipods but tends to be greater in epifaunal than in infaunal species (Nelson 1980; Van Dolah and Bird 1980). The production of large broods at relatively small sizes may compensate for a higher risk of adult mortality due to predation in epifaunal species (Nelson 1980; Van Dolah and Bird 1980). Although *Uhlorchestia spartinophila* and many other talitrids are relatively large and epifaunal, their brood sizes tend to be small. Multiple small broods of relatively large young produced over a long reproductive season, as was the case for *U. spartinophila* in our study, is consistent with a reproductive pattern that diffuses mortality risk for the young in a fluctuating environment (Schaffer 1974; Stearns 1977). The salt marsh exemplifies a fluctuating environment on many temporal scales from seasonal changes in temperature and tidal flooding regime to the semi-diurnal tidal fluctuations that alter both the moisture conditions and predation risk to which intertidal amphipods are exposed.

Annual production of *Uhlorchestia spartinophila* varied among marsh habitats from 0.94 to 1.77 g DW m^{-2} but was within the range of the few estimates available for other talitrid species (Ali and Salman 1987; Wildish 1988). Our production estimates were on average ca. 39% greater than the 1.0 g DW m^{-2} estimated by Phillips (1978) for this species in a marsh at 6 to 7° higher latitude. However, the mean standing stock biomass (0.18 g DW m^{-2}) of amphipods at the higher-latitude site was greater than that in our study (Table 6), suggesting that the *U. spartinophila* population on Sapelo Island turned over ca. three times faster than the population studied by Phillips (1978). To our knowledge, the only talitrid population with a higher turnover rate was a population of *Talorchestia margaritae* from a beach in Venezuela (at ca. 10° N latitude), where Venables (1981) estimated a P: B ratio of ca. 30.

Uhlorchestia spartinophila standing stocks are small compared to the total macrofauna biomass of 15 g C m^{-2} that was estimated for marshes on Sapelo Island (Montague et al. 1981). However, most of the macroconsumer biomass in this system comprises bivalves (e.g. mussels *Geukensia demissa*, oysters *Crassostrea virginica*), gastropods (e.g. marsh periwinkle *Littoraria irrorata*, mud snails *Ilyanassa obsoleta*) and fiddler crabs (*Uca* spp.) that are too large to be included in the diets of small fishes and crustaceans, which are the most abundant aquatic predators in the salt marsh (Kneib and Wagner 1994). Amphipods, however, are commonly consumed by the small aquatic predators of intertidal marshes (Vince et al. 1976; Van Dolah 1978).

Unlike many other talitrid amphipods, whose distributions are restricted largely to narrow supralittoral zones (Wildish 1988), *Uhlorchestia spartinophila* is broadly distributed through the vegetated intertidal marshes of the U.S. Atlantic coast (Phillips 1978; Kneib 1982; Bousfield and Heard 1986; present study). Its intertidal distribution, accessibility to aquatic predators and high turnover rate suggest this amphipod may contribute more to trophic dynamics in Georgia marshes than might be expected from its modest standing stock biomass. Assuming an annual production of 1.0 g C m^{-2}, the population of *U. spartinophila* in marshes of the Duplin River (Sapelo Island) drainage alone (ca. 16 km^2) may contribute 16.0 metric tons C to this estuarine system. The small absolute contribution of *U. spartinophila* to total secondary production may belie this species' importance as a functional link between the production of intertidal marshes and adjacent open waters of the estuary.

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