

## Population dynamics of the tanaid *Hargeria rapax* (Crustacea: Peracarida) in a tidal marsh

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**Abstract.** The tanaidacean *Hargeria rapax* (Harger, 1879) was sampled along intertidal transects semi-monthly at one site and quarterly at two other sites in salt marshes on Sapelo Island, Georgia, USA, from July 1985 to July 1986. Tanaids were most abundant near the mean high-water line and became progressively less abundant at lower intertidal elevations. Population density was greatest in the winter (December to February) when there were >29 000 individuals/m<sup>2</sup> at one high intertidal station. Although reproductive individuals were present most of the year, peaks in reproductive activity occurred in autumn (late August to early November) and spring (early March to mid June). An increase in population density coincided with increased reproductive activity only in autumn. Tanaid cohorts produced in the spring and summer rarely survived beyond 6 to 8 wk, but those produced in the autumn overwintered and lived 22 to 26 wk. The sex ratio among mature individuals was 2.8:1 (females:males). Mature females ranged in size from 2.2 to 3.9 mm total length (TL) and mature males were 2.3 to 4.1 mm TL; there was no significant sexual difference (Student's *t*-test,  $P > 0.05$ ) in the mean TL of mature individuals. The mean ( $\pm$ SD) size of brooding females was  $2.9 \pm 0.32$  mm TL and the mean ( $\pm$ SD) number of offspring/brood was  $8.3 \pm 4.99$  young/female. The timing of tanaid reproduction together with the effects of predation by juvenile fish and crustaceans may account for most of the spatial and temporal patterns of tanaid abundance observed in this study. There was a significant linear relationship ( $P < 0.001$ ,  $r^2 = 0.54$ ) between the growth rate (GR, mm/d) of individuals and average daily air temperature ( $^{\circ}$ C) described by the equation:  $GR = 0.00178 (^{\circ}\text{C}) - 0.00971$ . The potential annual contribution of tanaid production to higher trophic levels, estimated from knowledge of standing stocks, growth rates and fecundity, was 5.71, 0.91 and 0.46 g dry wt/m<sup>2</sup> for high, mid and low intertidal areas, respectively. The high intertidal marsh, which supports the largest and most persistent standing stock of *H. rapax*, provides a rich foraging area for aquatic predators at high tide and an important source of recruits from which tanaid popu-

lations at lower intertidal elevations are recolonized after periods of intense predation pressure.

### Introduction

Tanaidaceans are a diverse and cosmopolitan group of small (1 to 37 mm) peracarid crustaceans that are common in marine benthic communities from the intertidal zone to abyssal habitats (Ogle et al. 1982, Sieg 1986). In shallow subtidal and intertidal habitats, densities of tanaids often exceed 10 000 individuals m<sup>-2</sup> (Woodin 1974, Johnson and Attramadal 1982, Modlin and Harris 1989), yet detailed studies of ecological interactions involving tanaids are rare (Sieg 1986). In some benthic invertebrate assemblages, tanaids may have a significant influence on benthic community structure by consuming the larvae and juveniles of other infaunal species (Highsmith 1983, Oliver and Slattery 1985). However, most tanaids are deposit-feeders and, because they commonly occur in the diets of many fishes and larger crustaceans, are characterized more often as prey than predators (Ogle et al. 1982).

The tanaid, *Hargeria rapax* (Harger, 1879) (= *Leptochelia rapax*), is a tubicolous species commonly found in benthic macrofaunal assemblages of shallow estuarine environments along the Atlantic and Gulf coasts of the USA from Massachusetts to Texas (Heard 1982, Ogle et al. 1982). Unlike most other tanaids, which occur primarily in marine habitats (Sieg 1986), *H. rapax* is euryhaline (Boesch and Diaz 1974) and occurs in a variety of estuarine habitat types including subtidal seagrass beds (Stoner 1983, Virnstein et al. 1983), tidal creeks (McBee and Brehm 1979, Horlick and Subrahmanyam 1983), tide pools (Modlin and Harris 1989) and vegetated intertidal marshes (Subrahmanyam et al. 1976, Kneib 1984a, Wenner and Beatty 1988, LaSalle and Rozas 1991).

Reproduction in *Hargeria rapax* follows that reported for tanaids in general. Females typically carry the eggs and young in a ventral pouch or marsupium formed by

one or more pairs of oöstegites, which develop at a molt just prior to brood production (Ogle et al. 1982). After hatching, the young remain with their mother through two larval (manca) stages until molting into a juvenile or neuter stage (Ogle et al. 1982, Masunari 1983). The sexes are difficult to distinguish in non-reproductive individuals, but are strongly dimorphic at maturity (Heard 1982); adult males, which have greatly elongated gnathopods, either develop directly from the neutral (juvenile) stage or result from the sex reversal of a previously reproductive female (Modlin and Harris 1989). In either case, the molt to the male form is terminal because the mouthparts of the male are greatly reduced or fused, ultimately resulting in starvation.

*Hargeria rapax* feeds primarily on diatoms and fine organic particles (Heard 1982) and, in turn, is consumed by a variety of predators, including many species that use marsh habitats as nurseries. For example, most of the benthic prey taken by juvenile spot (*Leiostomus xanthurus*) in a North Carolina salt marsh consisted of *H. rapax* (Hodson et al. 1981). Tanaids constitute a major component of the diets of small resident species (e.g. *Fundulus heteroclitus* and *F. grandis*) that numerically dominate the fish assemblages of the Atlantic and Gulf coast salt marshes of the USA (Valiela et al. 1977, Meredith and Lotrich 1979, Kneib 1986, Rozas and LaSalle 1990). Predatory decapod crustaceans, including caridean and penaeid shrimp, also feed on tanaids in salt marshes (Mayer 1985) and have reduced *H. rapax* densities in experimental studies (Nelson 1981, Kneib 1985).

This paper describes the population dynamics of the tanaid *Hargeria rapax* from a salt marsh in the southeastern USA. I consider the potential importance of several factors, especially predation, in determining patterns of intertidal distribution and abundance of *H. rapax*, and suggest that high marsh habitats are an important source of recruits which sustain populations of tanaids at lower intertidal elevations where predation pressure is most intense.

## Materials and methods

### Study sites

Specimens of *Hargeria rapax* (Harger, 1879) were collected from three vegetated intertidal marsh sites along the Duplin River, a tidal lagoon on the west side of Sapelo Island, Georgia, USA, from July 1985 to July 1986. The sampling sites included the upper, middle and lower portions of the Duplin River drainage (Fig. 1). At each principal site, three sampling stations were established along a tidal gradient representing high, mid and low intertidal elevations. Each station was a 5 m × 2 m plot with the long axis perpendicular to the elevation gradient. The plots were divided into ten 1 m<sup>2</sup> subplots, which were marked at the corners with short wooden stakes. Because there were site-specific differences in the absolute elevations of the marshes (sites) above mean low water (MLW), stations included a range of relative intertidal elevations within but not between sampling sites. The ranges in elevation above MLW covered by the intertidal stations at each sampling site (Fig. 1) were: +185 to +204 cm (Upper Duplin Site), +170 to +201 cm (Middle Duplin Site), and +208 to +225 cm (Lower Duplin Site). Mean tidal range in the area is ~210 cm.

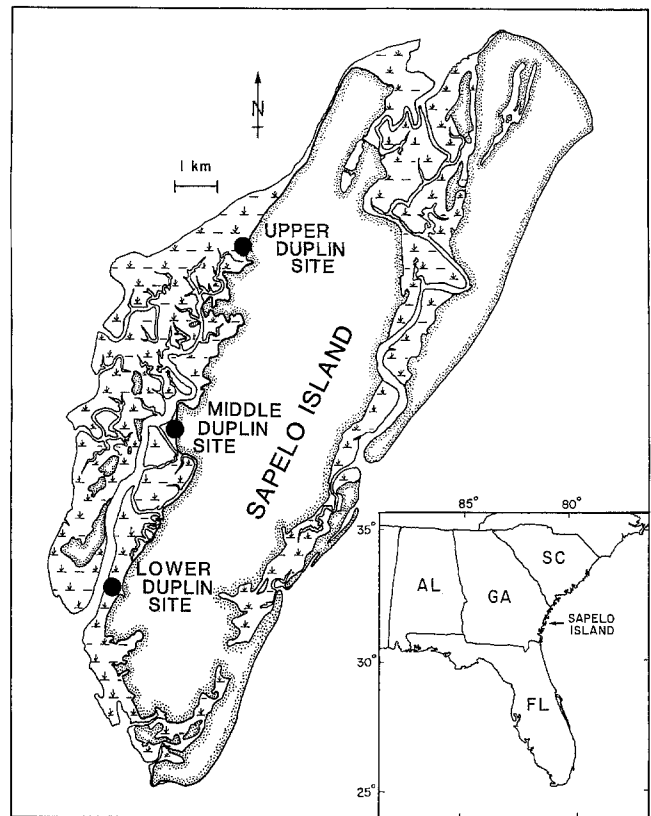


Fig. 1. Locations of the three sampling sites along the Duplin River. Inset shows location of Sapelo Island, Georgia, on southeastern coast of USA

The physical and structural characteristics (e.g. sediment composition, vegetation cover, etc.) of each station were not quantified. However, the substratum was generally firmer at the high stations because the sediments contained more sand and there was a denser root mat than at either the low or intermediate intertidal stations. *Spartina alterniflora* (smooth cordgrass) was the dominant vascular plant at all stations, but was shorter and exhibited higher stem density in the upper intertidal zone than at lower stations. The needlerush *Juncus roemarianus* grew in a band at the upland border of the high intertidal stations. Semimonthly measurements of salinity and water temperature were taken at the Middle Duplin Site; salinity was measured with an optical refractometer. Average daily air temperatures were recorded at a meteorological monitoring station within 5 km of the Middle Duplin Site.

### Sampling

A 6.2 cm-diam (30 cm<sup>2</sup>) stainless steel tube was used to remove a core of marsh substratum to a depth of 2.5 cm. In the laboratory, tanaids were washed from the cores with a stream of freshwater and collected on a 0.25 mm-mesh sieve. This method extracted 98.0% of the *Hargeria rapax* (Kneib unpublished data). Samples were preserved in a 10% solution of buffered (sodium borate) formalin in freshwater. All tanaids were later sorted from the debris retained by the sieve, sexed, counted and measured [total body length (TL) = tip of cephalothorax to the end of the urosome] to the nearest 0.1 mm with an ocular micrometer mounted in a stereomicroscope (25 × magnification).

Cores were collected quarterly at all sites to determine large-scale distribution patterns of *Hargeria rapax* along the Duplin River. Each quarterly sample included a core taken haphazardly from each of the ten 1-m<sup>2</sup> subplots at every station (a total of 90 cores/

sampling date). Detailed monitoring of the population dynamics was conducted only at the Middle Site (Fig. 1), which was sampled at 2 wk intervals for one year beginning 8 July 1985. These semi-monthly samples included cores from 5 of the 10 subplots at each intertidal station (a total of 15 cores/sampling date). To insure interspersed samples at each station, the cores were taken from every other subplot in a pattern that alternated between even-numbered subplots on one sampling date and odd-numbered subplots on the next.

In addition to the semi-monthly and quarterly core samples, separate monthly collections of tanaids were taken near the high intertidal station at the Middle Site for determination of length-weight relationships. Usually 100 to 110 fresh specimens were measured live, washed in distilled water, dried to constant weight (3 to 4 d) at 60°C and weighed to the nearest 0.1 µg.

### Reproductive activity and fecundity

The morphological changes that occur in sexually mature *Hargeria rapax* (i.e., development of a marsupium in females and enlarged gnathopods in males) were used to identify reproductively active individuals in the population. The proportions of mature males and brooding females in the samples were used as measures of reproductive activity in the population. Females with distinctly developed oostegites were considered reproductively active even if no eggs or young were present, as these could have been dislodged from the marsupium during sample processing. When eggs or young were present, they were counted to provide an estimate of fecundity.

### Growth rate

On any given sampling date, length-frequency histograms for *Hargeria rapax* were multimodal, containing up to five apparent modal size classes. Growth-rate estimates were based on the assumption that the observed distributions resulted from a mixture of normal size distributions, each representing a distinct size-cohort of tanaids. I used the interactive computer program MIX (Release 3.0, distributed by Ichthus Data Systems) to fit mixtures of normal distributions to the data and estimate the mean length of the individuals in each of the component cohorts (for details of this procedure, see Macdonald and Pitcher 1979). The most reasonable growth trajectory for individuals in each cohort was established by plotting the means at each sampling date and connecting the points along a time axis in such a way that: (1) a positive growth rate was maintained (except in the cooler months when growth apparently ceased) and (2) the resultant lines did not intersect (see Fig. 4). The difference between the mean size of individuals within a cohort on consecutive sampling dates (time  $t$  to  $t + 1$ ) was the average growth increment of the individuals in that cohort for the 2 wk interval between  $t$  and  $t + 1$ . The growth rates are expressed in mm/day by dividing the incremental growth by the number of days in the sampling interval. The overall mean growth rate for a given sampling interval was determined by averaging the growth rates of all cohorts present during that sampling interval (mean number of cohorts per interval was 3.7 with a range of 2 to 5). If the overall mean growth increment was negative, growth rate was taken as zero.

I used linear regression (Sokal and Rohlf 1981) to derive an equation describing the relationship between temperature and growth rate by regressing the average growth rate of tanaids during each sampling interval on average daily air temperature during the same intervals. I used air temperature instead of water temperature because in any given 24 h period, the intertidal marsh is exposed to air longer than it is inundated by tidal water.

### Observed and expected standing stocks

The monthly length-weight regression equations were used to estimate the dry weight of all tanaids collected from each station and

sampling date ( $t$ ). The observed standing stock biomass was the mean total dry weight of tanaids per 30 cm<sup>2</sup> for a given location and date. I estimated an expected standing stock at time  $t + 1$  by augmenting the observed standing stock at time  $t$  with the expected increase in biomass due to growth and reproduction during the 2 wk interval prior to  $t + 1$ . Growth was estimated from the regression equation relating growth rate to temperature. The contribution from reproduction was estimated by multiplying the mean number of reproductive females per 30 cm<sup>2</sup> at time  $t$  by the mean number of offspring per female and assuming that the young entered the population at a mean size of 1 mm (see Fig. 4) at time  $t + 1$ . The expected standing-stock biomass should match the observed biomass on each sampling date as long as there are no significant losses due to emigration (or mortality) nor gains due to immigration during the 2 wk interval.

### Statistical analyses

All statistical procedures used in this study are described in Sokal and Rohlf (1981) and were calculated using Version 4.0 of the statistical package SPSS PC+ (Norusis 1990). In the absence of serious violations of underlying assumptions, parametric statistical analyses were used. If the restrictive assumptions of parametric procedures were seriously violated and could not be corrected by mathematical transformation of the data, an appropriate nonparametric statistical procedure was applied.

## Results

### Physical factors

The annual ranges of water temperature and salinity at the Middle Duplin Site were 9.0 to 37.5°C and 15.5 to 30.0‰, respectively. These physical variables tended to covary so that the highest values of both occurred in the summer (June to September) and the lowest in the winter (January to March). This is a normal annual temperature pattern for the area but the salinity, which is usually 15 to 20‰ at the Middle Site (own personal observation), was higher than normal during this study because the area received lower than normal amounts of rainfall during the summers of 1985 and 1986.

Although the intertidal marsh surface usually was inundated by the tide twice daily, on any given day it was exposed to the air three times longer than it was flooded by the tides (Kneib unpublished data). Between periods of tidal inundation, the temperature of the surface sediments often was higher than the water temperature and could exceed 40°C on clear summer afternoons.

### Spatial distribution patterns

Annual mean densities of *Hargeria rapax*, obtained by pooling the quarterly samples at each sampling station, show that tanaids were not evenly distributed in the marshes along the Duplin River (Table 1). *H. rapax* were generally less abundant at the Lower Duplin Site than at the two other sampling sites. The results of a nonparametric multiple comparison test using the STP (simultaneous test procedure) method (Sokal and Rohlf 1981) showed that tanaid densities were significantly greater at

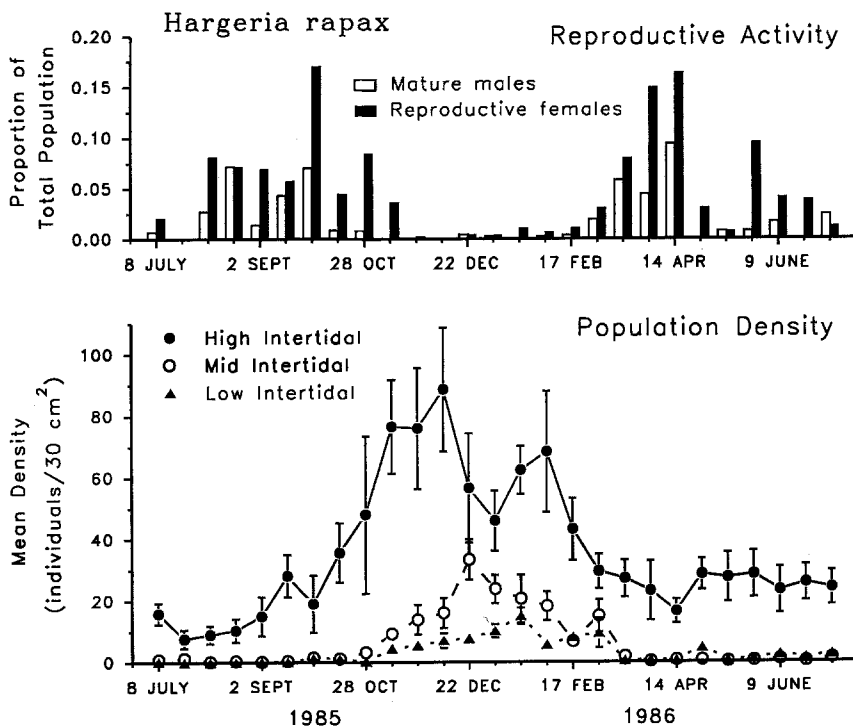


Fig. 2. *Hargeria rapax*. Temporal patterns in reproductive activity and population density at three intertidal stations in Middle Duplin Site

Table 1. *Hargeria rapax*. Mean densities ( $\pm 1$  SE) of tanaids from 40 cores ( $30 \text{ cm}^2$ ) at each of nine intertidal sampling stations along Duplin River, Sapelo Island, Georgia, USA. Superscripts give the results of nonparametric multiple-comparison tests by the STP (simultaneous test procedure) method; stations that share a common letter do not differ significantly ( $\alpha=0.05$ )

Sampling	Relative elevation		
	High intertidal	Mid intertidal	Low intertidal
Upper Duplin	$35.2 \pm 5.68^a$	$0.4 \pm 0.15^{b,c}$	$0.4 \pm 0.20^{b,c}$
Middle Duplin	$29.8 \pm 4.21^a$	$6.6 \pm 1.95^e$	$3.0 \pm 0.85^{c,e}$
Lower Duplin	$0.2 \pm 0.10^{b,d}$	$0.0 \pm 0.02^{b,d}$	$0.0 \pm 0.00^{b,d}$

the high intertidal stations than at the lower intertidal stations of the Upper and Middle Duplin Sites (Table 1). Although there appeared to be a similar pattern of intertidal distribution at the Lower Duplin Site, the differences among stations were not statistically significant (at  $\alpha = 0.05$ ).

#### Temporal patterns of abundance and reproductive activity

Seasonal changes in density and reproductive activity within the *Hargeria rapax* population were apparent in the semimonthly samples from the Middle Duplin Site (Fig. 2). Tanaid density was greatest in the winter (December to February), when it reached a maximum mean of 88.6 individuals/ $30 \text{ cm}^2$  (29 533 individuals/ $\text{m}^2$ ) at the high intertidal station. Tanaids were not abundant ( $< 2$  individuals/ $30 \text{ cm}^2$ ) at the mid and low intertidal stations from March to October, but exhibited respective winter

maxima of 33.4 and 15 individuals/ $30 \text{ cm}^2$  at these stations. Density maxima were not temporally coincident at all intertidal stations, but occurred in early-December, late-December and late-January at the high, mid and low intertidal stations, respectively (Fig. 2).

There were weak negative correlations between tanaid densities and salinity at all intertidal elevations (Pearson correlation coefficients for high, mid- and low intertidal stations were  $-0.37$ ,  $-0.58$  and  $-0.60$ , respectively). The weakest correlation occurred at the high intertidal station, where tanaids were most abundant, and there were apparent differences among intertidal elevations in the salinity at which density maxima occurred. At the mid and low intertidal stations, tanaids were most abundant when salinity was 17 to 18‰, but at the high intertidal station tanaid density was greatest when salinity was 21 to 23‰ and densities at salinities of 15 to 17‰ were similar to those at 25 to 28‰ (Fig. 3).

Some reproductive individuals occurred in the population throughout the year, but reproductive activity was most evident in autumn (late-August to early-November) and spring (early-March to mid-June). Even during these periods of maximum reproductive activity, a relatively small proportion of the population ( $< 0.25$ ) was involved in reproduction. A major increase in population density coincided with the reproductive episode in autumn, but population density remained low and unchanged during the spring reproductive period (Fig. 2).

The sex ratio among reproductively active individuals strongly favored females (2.8:1, females:males). Mature female *Hargeria rapax* ranged in size from 2.2 to 3.9 mm TL and mature males from 2.3 to 4.1 mm TL. There was no significant difference (Student's *t*-test,  $P = 0.24$ ) between the mean sizes of mature males (3.0 mm TL) and females (2.9 mm TL).

There was a statistically significant linear relationship ( $F, P < 0.001$ ) between number of young (eggs or larvae) in a brood and size (TL, mm) of female tanaids. However, the high variance associated with the data made the regression equation a poor predictor of fecundity ( $r^2 = 0.14, N = 101$ ). Given that there was relatively little variance (expressed  $\pm$ SD) around the mean size ( $2.9 \pm 0.32$  mm TL) of brooding females and considering the relatively poor relationship between size and number of offspring, it seems reasonable simply to use the mean ( $\pm$ SD) number of young ( $8.3 \pm 4.99$  young/female) per brood as the best measure of individual fecundity in this tanaid population.

Growth rates, survival and length-weight relationships

The population of *Hargeria rapax* at the Middle Duplin Site (high intertidal station) comprised 2 to 5 distinct size cohorts on each sampling date. From July 1985 to July

1986, a total of 17 cohorts were followed for at least 45 wk (Fig. 4). There was a seasonal pattern in the growth and survival of tanaids that had an apparent relationship to temperature (Fig. 4). When average daily temperatures were  $> 15^\circ\text{C}$ , growth was relatively rapid and few cohorts of tanaids survived beyond 6 to 8 wk. Although growth slowed when temperatures fell in the late-autumn and winter months, survival was highest at this time of the year and cohorts could be followed for 22 to 26 wk (Fig. 4).

A comparison of the mean growth increments exhibited by individuals from cohorts of the smallest and largest tanaids in each sampling interval provided no evidence for a size-specific difference in growth rate (paired  $t$ -test,  $P = 0.22, df = 25$ ). Consequently, I used the average growth increment from all cohorts within a sampling interval to describe the mean growth rate within that interval. There was a significant ( $F, P < 0.001$ ) relationship between mean growth rate and average daily temperature (Fig. 5).

The slopes of the regression lines describing the length-weight relationship in *Hargeria rapax* (Table 2) differed among months (analysis of covariance,  $F, P < 0.05$ ) and therefore it is inappropriate to make statistical comparisons of monthly mean weights adjusted for length. However, visual inspection of the monthly relationships (Fig. 6) suggests that tanaids of a given length generally weighed more in winter and early-spring (December to March) and less in autumn (October in particular) than at other times of the year.

Standing-stock biomass

There was a positive relationship between the standing stock biomass of *Hargeria rapax* and intertidal elevation (Fig. 7). At the high intertidal station, tanaid biomass ranged from 0.26 to 1.3 mg/30 cm<sup>2</sup> in late-April to October, but was greater (3.2 to 5.2 mg/30 cm<sup>2</sup>) from late-November to mid-February and was greatest in mid-January. At the mid and low intertidal stations, tanaid stand-

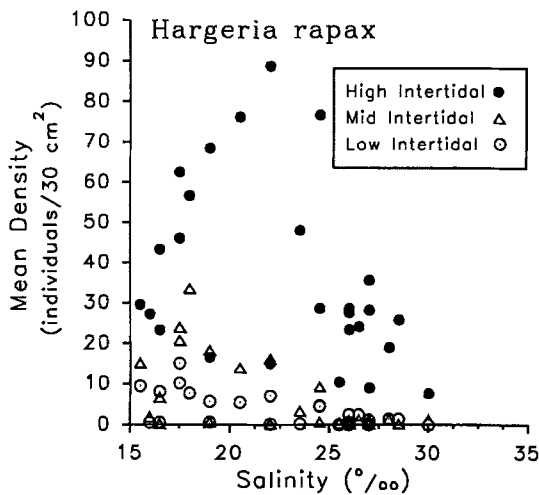


Fig. 3. *Hargeria rapax*. Scatter-plot relating salinity and tanaid densities at three intertidal stations in Middle Duplin Site

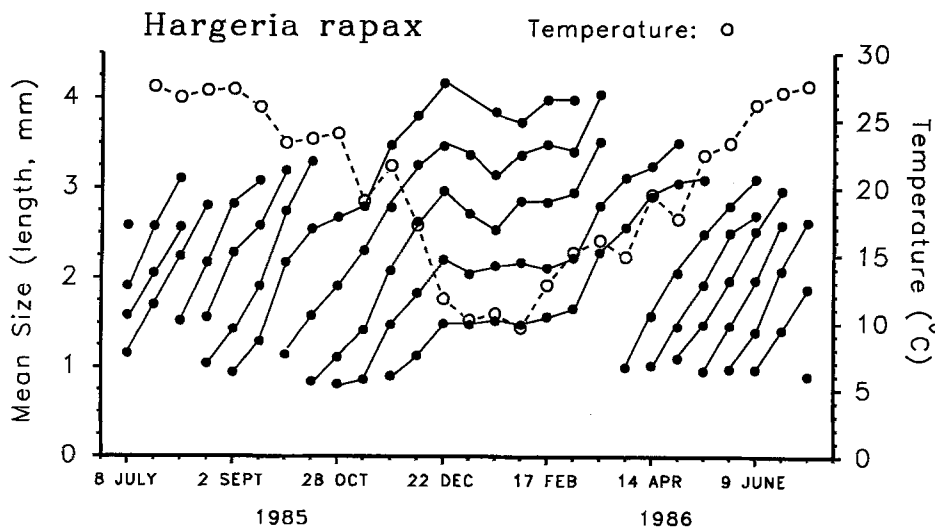


Fig. 4. *Hargeria rapax*. Estimated growth trajectories of tanaids from cohorts collected at high intertidal station of Middle Duplin Site. Average daily air temperatures are superimposed over growth curves

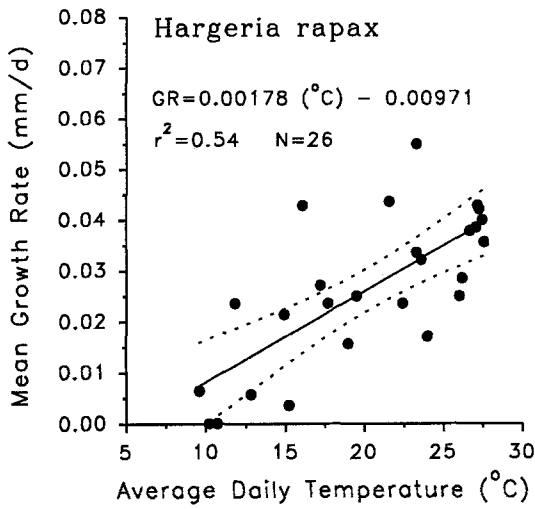


Fig. 5. *Hargeria rapax*. Relationship between average daily air temperature and average growth rate (GR) of tanaids. Dashed lines are 95% confidence limits for regression line

Table 2. *Hargeria rapax*. Regression constants describing monthly relationships between total length (TL, mm) and dry weight (DW, µg). Dry weight (µg) was calculated by substituting appropriate table values into the following equation:  $DW = a(TL)^b$ . (N): number of observations (tanaids) used to estimate coefficients;  $r^2$ : coefficient of determination

Month	b	a	(N)	r <sup>2</sup>
1985				
July	2.858	3.741	(56)	0.912
August <sup>a</sup>	2.792	3.908	(-)	-
September	2.726	4.111	(105)	0.914
October	2.580	4.178	(124)	0.946
November	2.634	4.550	(122)	0.936
December	3.011	3.516	(113)	0.914
1986				
January	2.784	5.140	(118)	0.929
February	2.956	4.018	(119)	0.909
March	2.904	4.236	(135)	0.844
April	2.817	4.093	(113)	0.918
May	2.889	3.819	(118)	0.905
June	2.942	3.564	(116)	0.913

<sup>a</sup> Data were unavailable for August; constants were estimated by averaging values from July and September

ing stocks ranged from 0.0 to 1.3 mg/30 cm<sup>2</sup> for much of the year (mid-March to late-October). However, at both of these stations standing stocks began to increase in early November to maxima of 2.1 mg/30 cm<sup>2</sup> in late-December at the mid intertidal and 1.2 mg/30 cm<sup>2</sup> in early March at the low intertidal station.

Expected standing stock biomass usually was greater than the observed biomass at the high intertidal station (21 of 26 comparisons), but often either matched or underestimated the observed values at the mid (12 of 26 comparisons) and low (13 of 26 comparisons) intertidal elevations, especially in the autumn and early winter months (Fig. 7). The results of a nonparametric sign test (Sokal and Rohlf 1981) showed that the proportion of

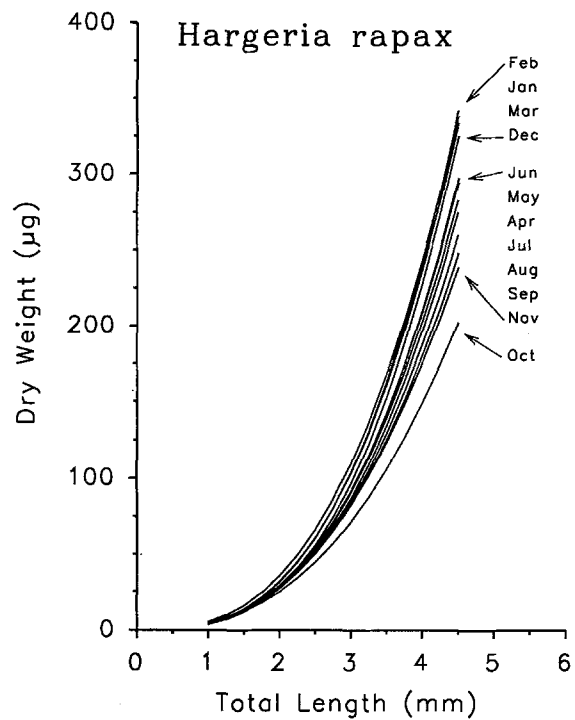


Fig. 6. *Hargeria rapax*. Monthly length-weight relationships for tanaids from Middle Duplin Site. Regression constants and coefficients are given in Table 2

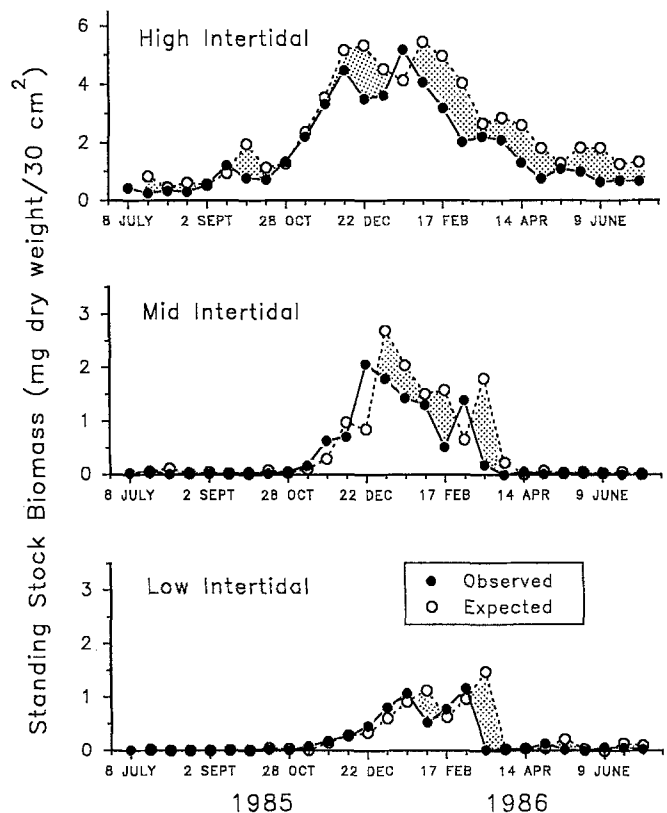


Fig. 7. *Hargeria rapax*. Observed and expected standing stocks of tanaids on each sampling date at three intertidal stations in Middle Duplin Site. Shaded areas between lines indicate amount by which observed standing stocks were less than would be expected from growth and reproduction. Note that scale of ordinate is not same for all intertidal elevations

times the expected exceeded the observed standing stocks differed significantly from 0.5 (a ratio of 1:1) in the high intertidal ( $P = 0.003$ ), but not in either the mid ( $P = 0.690$ ) or low ( $P = 0.839$ ) intertidal.

Assuming that differences between the observed and expected standing stocks reflect net losses (expected > observed) or gains (observed > expected) in each sampling interval, summing the differences across all sampling intervals yields an estimate of the annual net losses or gains at each intertidal elevation. Although there was an annual net loss of biomass from all stations, there was a considerable difference in the magnitude of those losses, which totalled 17.13, 2.73 and 1.38 mg/30 cm<sup>2</sup> from the high, mid and low intertidal stations, respectively.

## Discussion

The abundance of *Hargeria rapax* in the marshes on Sapelo Island varied on two spatial scales: (1) densities were greater at the Upper and Middle Duplin Sites than at the Lower Duplin Site, and (2) there were more tanaids at the high intertidal than at lower intertidal elevations (Table 1). The larger-scale distribution pattern may be related to site-specific differences in substrate. Members of the family Paratanaidae, of which *H. rapax* is one, are found primarily in sandy or sandy mud substrates (Sieg 1986). The Lower Duplin Site has a poor drainage system with fewer intertidal creek channels, and is flooded less frequently than the other sites. In most respects, this site is characteristic of an old marsh (Frey and Basan 1978) but, instead of the sandy sediments expected in a marsh at this developmental stage, a layer (2 to 5 cm deep) of fine silt and clay overlies the substrate at the Lower Duplin Site (own personal observations). Surface sediments at the other two sites, which were more isolated from the influence of mainland river drainages, contain more sand and less clay (own personal observations).

The results of the present study confirm the report by Kneib (1984a) that densities of *Hargeria rapax* follow a gradient of intertidal elevation through the *Spartina alterniflora*-dominated marshes of Sapelo Island, with the greatest densities at the higher intertidal elevations. A similar intertidal distribution of tanaids occurs in a North Carolina salt marsh (Reice and Stiven 1983), but the distribution of *H. rapax* is different in marshes of northern Florida, where densities are greater in low than in high marsh zones (Subrahmanyam et al. 1976). Such regional differences in intertidal distribution may be related to regional differences in the tidal regime. The distribution of vegetation types often reflects characteristics of local tidal patterns. In marshes of the southeastern USA, the mean high-water line is located near the border between stands of *S. alterniflora* and *Juncus roemarianus* (Gallagher 1977). At the Georgia and North Carolina sites, this line was near the upland boundary of the high intertidal stations, but was at the edge of tidal creeks in the "low" marsh in the northern Florida site (Subrahmanyam et al. 1976). References to "low" and "high" marsh sites are relative and may lead to confusion when attempting to make comparisons among studies in different tidal regimes. Considered in terms of regional tidal

regimes, densities of *H. rapax* seem to be greatest near the mean high-water line in vegetated intertidal marshes of the southeastern USA.

The intertidal distribution of tanaids conforms to a hypothetical scheme proposed by Kneib (1984a) to describe the relative effects of different factors on the abundance of benthic marsh invertebrates along an intertidal elevation gradient. Under that model, natant predators control the densities of benthic invertebrates at relatively low intertidal marsh elevations. Densities of invertebrates are expected to increase with intertidal elevation because the foraging time of aquatic predators is limited by the frequency and duration of tidal inundation. At some point above the mean high-water level, the infrequency of tidal inundation and the effects of desiccation place an upper limit on the distribution of marsh benthos, perhaps explaining the low densities of tanaids in the "high" marsh sites studied by Subrahmanyam et al. (1976) in northern Florida. Near the mean high-water level, between the effects of predation at low intertidal elevations and desiccation at high elevations, the model predicts high densities of benthic invertebrates controlled primarily by density-dependent processes.

The temporal pattern of abundance in the population of *Hargeria rapax* at the Middle Duplin Site was similar to that observed in some other marshes (Subrahmanyam et al. 1976, Reice and Stiven 1983) and in seagrass beds (Stoner 1983), but differed markedly from the pattern observed in marshes of the northern Gulf of Mexico, where the populations exhibit density maxima in the spring and summer months (Modlin and Harris 1989, LaSalle and Rozas 1991). Sieg et al. (1982) suggested that physical conditions, particularly the moisture and oxygen content of the substratum, were more favorable for tanaids in the cooler months than in the warm summer months. Modlin and Harris argued that seasonal changes in salinity could explain temporal patterns in tanaid abundance and suggested that tanaids respond to high salinity (> 20‰) by migrating to less saline areas; Modlin and Harris did not suggest a mechanism for such mass migrations of a small, benthic tubicolous organism.

Subrahmanyam and Coultas (1980) found no correlation between tanaid density and either temperature or oxygen and suggested that temporal variation in reproductive activity and recruitment had a greater effect on densities and composition of the macrofaunal community in general. My findings do not support the contention that salinity has a strong effect on tanaid abundance. I suggest that seasonal variation in salinity has little effect on densities of *Hargeria rapax*. However, at sites such as the marsh tide pool studied by Modlin and Harris (1989), salinity values may covary with the effect of other factors, perhaps biological agents, that underlie changes in tanaid abundance. For example, predators can influence the abundance of *H. rapax* (Stoner 1983, Virnstein et al. 1983, Kneib 1985), and tanaids commonly occur in the diets of fishes and crustaceans that use salt marshes as nurseries during the spring and summer months (Hodson et al. 1981, Mayer 1985, Kneib 1986).

The seasonal abundance of tanaids in the present study can be explained by the timing of both reproductive

activity and predation pressure. Nektonic predators, which occur at high densities during much of the time that tanaids are reproductive, may regulate the population density of *Hargeria rapax*. Spot (*Leiostomus xanthurus*) are abundant in the marsh during the spring (Hodson et al. 1981, Hettler 1989), and are followed by high densities of killifishes (*Fundulus* spp.) and juvenile penaeid shrimp (*Penaeus* spp.) in the summer and early-autumn months (Kneib 1984 b, Zimmerman and Minello 1984, Hettler 1989). It is not until the densities of these predators decline in September–October that the tanaid population begins to increase. Population growth terminates with the cessation of reproductive activity in the winter months. The seasonal pattern in the survival of tanaids also is consistent with the predation hypothesis.

*Hargeria rapax* was relatively abundant at the mid and low intertidal stations only in late autumn and winter, when predation pressure was least. Increases in tanaid densities at lower intertidal elevations were associated with a winter decline in the density of tanaids at the high intertidal station. I suggest that the tanaid population in the high intertidal zone served as a source from which lower intertidal areas, depleted by predators in the warmer months, were repopulated in the winter. The mechanism may involve either active migration (Borowsky 1983), perhaps in response to density-dependent agonistic encounters (Highsmith 1983, Kneib 1984 a), or a physical disturbance such as rainfall which may dislodge and move individuals to lower intertidal areas (Mendoza 1982).

A comparison of observed and expected (based on estimates of growth and reproduction) standing stocks of tanaids at each intertidal elevation supports the hypothesis that the maintainence of tanaid populations at lower intertidal elevations is dependent on the population in the high intertidal marsh. At the high intertidal station, the expected almost always exceeded the observed biomass, suggesting that the net loss of biomass was a consistent characteristic of the high intertidal population. Losses were evident at the mid and low intertidal elevations only when biomass was declining at these sites, but when standing stocks were increasing (October–December) the observed biomass usually exceeded that expected from growth and reproduction. The chronological sequence of density and biomass maxima at each of the intertidal stations also suggests a net movement of individuals from the high to the lower intertidal zones.

Assuming that all the estimated annual net loss of tanaid biomass from the high ( $5.71 \text{ g dry wt m}^{-2}$ ), mid ( $0.91 \text{ g dry wt m}^{-2}$ ) and low ( $0.46 \text{ g dry wt m}^{-2}$ ) intertidal zones is ultimately consumed by predators, *Hargeria rapax* plays an important role in the production dynamics of intertidal marshes by contributing to the food resources of juvenile fishes and crustaceans that use marshes as nurseries. High marsh sites, even though relatively inaccessible to nektonic predators, can be particularly important to fisheries production as a source of recruits from which benthic prey populations at lower intertidal elevations are maintained and repopulated after periods of intense predation pressure.

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