

NICHE DIVERSITY IN FIVE SYMPATRIC SPECIES OF
INTERTIDAL AMPHIPODS (CRUSTACEA: HAUSTORIIDAE)¹

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INTRODUCTION

The presence of related sympatric species in various habitats has prompted biologists to determine differences between species. Although a relatively large amount of evidence gathered over the years exists for freshwater and terrestrial animals, and for birds (e.g. Lack, 1945, 1949; MacArthur, 1958; Mayr, 1963 for many references; Recher, 1966) studies on marine animals are fewer and more recent (e.g. Test, 1945; Kohn, 1959; King, 1962; Paine, 1963; Magnum, 1964; Bowers, 1964; Jeffries, 1966). For most well-studied situations, differences in the fundamental niches of species are apparent. For some marine animals, ecological isolation results in species distributions that differ especially with respect to zone occupied, relation to substratum or kind of food (Kohn, 1959). In non-marine animals, size or method of feeding (Dowdeswell, 1959; Mitchell, 1964) and heterogeneity of the environment, or staggering of breeding periods may be important (Skutch, 1954, 1960; Broadhead, 1958).

I will define the fundamental niche after Hutchinson (1957), as the cumulative abiotic and biotic factors permitting survival of a species. Sympatric is defined broadly to include species whose breeding individuals are within cruising range of each other,

regardless of spatial overlap of habitat (Cain, 1960; Mayr, 1963).

Relatively little information is available concerning the fauna of marine sand beaches (Hedgpeth, 1957), and since the malacostracan crustaceans either make up the bulk of the macrofauna, or are the only forms present (Dahl, 1953) this group appears to offer excellent material for studying a sympatric relationship of related species.

The Haustoriidae is a relatively ancient and morphologically primitive family of gammaridean Amphipoda with species in marine, brackish and fresh waters. The family is essentially a shallow-water, cold-temperate one, represented in the western Atlantic Ocean at high latitudes by the Sub-Family Pontoporeiinae including fresh water representatives. Another Sub-Family, the Haustoriinae, has radiated mainly along low latitude western Atlantic shores (Virginian and Carolinian zones). The two sub-families overlap in the Cape Cod region where New England haustoriids are essentially intertidal and shallow-water crustaceans. The most highly evolved, and most recent genera and species are the most southerly, while the most primitive are the most northerly (Bousfield, 1962, 1965, and personal communication). Early work on the Family Haustoriidae included the erroneous identification of the European species *Haustorius arenarius* on the Amer-

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ican Atlantic coast (Holmes, 1904; Paulmier, 1905; and Kunke, 1918), the description of *Lepidactylus dytiscus* from Georgia (Say, 1818), and the description of *H. americanus* (= *Pseudohaustorius americanus*) from Louisiana (Pearse, 1908). European work on the family includes studies on *H. arenarius*, *Urothoe marina*, and several species of *Bathyporeia* (Elmhirst, 1931; Dennell, 1933; Watkin, 1939, 1940, 1941a, 1941b; Remane, 1940; Schliek, 1943; Jones, 1948; Stopford, 1951; Stephen, 1953; and Dahl, 1953). Several American workers have provided habitat notes and quantitative data on haustoriid amphipods, usually however, without specific identification (Pearse *et al.*, 1942; Bishop, 1960; and Keith and Hulings, 1965).

This study concerns only the Sub-Family Haustoriinae recently described by Bousfield (1965), and species in seven genera including, *Haustorius* Müller 1775, *Protohaustorius* Bousfield 1965, *Parahaustorius* Bousfield 1965, *Neohaustorius* Bousfield 1965, *Pseudohaustorius* Bousfield 1965, *Acanthohaustorius* Bousfield 1965, and *Lepidactylus* Say 1818.

Seven species of haustoriids occur in the intertidal zone of Georgia beaches, but only five will be stressed here. The five species (with notes from Bousfield, 1965) are: 1) *Parahaustorius longimerus* Bousfield 1965, a very common species along surf-exposed or semi-protected sandy coasts and offshore banks from the south west shore of Cape Cod Bay to Georgia and northern Florida, 2) *Neohaustorius schmitzi* Bousfield 1965, ranging from the southeast side of Cape Cod Bay and outer coast of the Cape, southwards to Georgia and northern Florida, 3) *Lepidactylus dytiscus* Say 1818, a common intertidal estuarine species in Georgia and Florida currently being clarified by Bousfield, 4) *Haustorius*

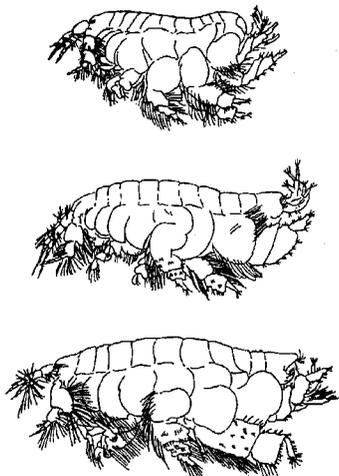


FIG. 1. Mature females of *N. schmitzi* (3.5 mm) top; *L. dytiscus* (4.5 mm) middle; *Acanthohaustorius* sp. (5.0 mm) bottom.

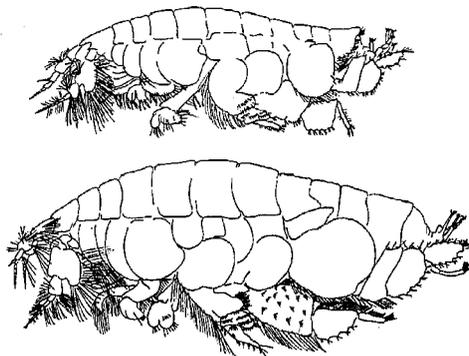


FIG. 2. Mature females of *Haustorius* sp. (7.0 mm) top; *Pa. longimerus* (10.0 mm) bottom.

sp., an undescribed long-rostrate species occurring southward from New England, and closely related to *H. canadensis* Bousfield 1962 (Bousfield, personal communication), and 5) *Acanthohaustorius* sp., an undescribed lower intertidal zone species closely related to *A. millsi* Bousfield 1965 (Bousfield, personal communication). Drawings of mature females of these five species are shown in Figures 1 and 2.

Two additional species will be briefly considered. *Pseudohaustorius carolinensis* Bousfield 1965 is restricted to surf-protected muddy sand kept moist by beach seeps or tidal runoff. The species was originally recorded from New England, but not since. It occurs in selected habitats of estuaries in the Carolinas and Georgia. *Protohaustorius deichmannae* Bousfield 1965, occurs mainly subtidally in shallow semi-protected inshore waters and estuaries from Cape Cod to Georgia, and is considered the most primitive and least specialized member of the sub-family (Bousfield, 1965).

Amphipod populations were sampled and observed during February 1964 through February 1966. Samples for most of the population data were obtained during four seasonal periods: mid-spring (April and May 1964); summer (July and August 1964); fall (November 1964); and early spring (March 1965). Additional population samples were obtained during the two year period. These will be described at the appropriate time. Laboratory experiments were performed during summers of 1964 and 1965.

SAND BEACH HABITATS

INTRODUCTION

A preliminary survey of intertidal beaches on Sapelo and Blackbeard Islands, Georgia, during winter 1964 (Fig. 3), led to the choice of three distinct habitat types for intensive sampling and observation where haustoriid amphipods were abundant. These were: 1) Dean Creek Beach, a relatively protected sand beach at the south end of Sapelo Island (Fig. 4); 2) Sapelo Beach, a moderately wave washed beach on the ocean side of Sapelo Island

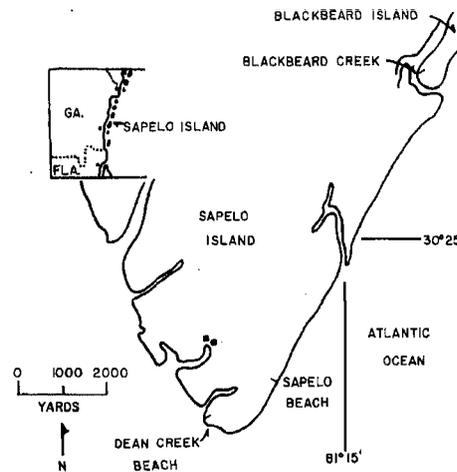


FIG. 3. Map of the Sapelo-Blackbeard area.



FIG. 4. Protected habitat, Dean Creek Beach, at low tide. Sampling transects were located at mid-picture, running from MHW (right, near wrack line) to LW level (left) on the day of sampling.

(Fig. 5); and 3) Blackbeard Creek, an extensive sand flat near the entrance of Blackbeard Creek into the ocean (Fig. 6). Additional observations were made during seasonal sampling periods, and at other times during the two year study period concerning habitat exposure to surf and tides, physical changes of beaches, general sediment characteristics, and frequency of occurrence of shore birds.

The three habitats were intertidal fine-grained sand beaches, with differences in exposure to surf, the silt, and debris content of sand, presence or absence of tide pools or seeps, and width and slope of beach. Georgia beach sands are well-sorted, with lower median grain size and carbonate content than those of beaches both north and south (Giles and Pilkey, 1965). Sand grain diameters are predominantly in the very fine (<0.125 mm) to fine (0.125–0.250 mm) categories (Hoyt, personal communication). Sapelo and Blackbeard Islands have less



FIG. 5. Exposed habitat, Sapelo Beach, at low tide. Sampling transects were located at mid-picture, running from MHW level (right) to LW level (left) on the day of sampling.



FIG. 6. Tidal creek habitat, Blackbeard Creek, at low tide with a tidal seep at LW level. Sampling transects ran from this spot to MHW level (left, out of sight).

violent surf as compared with other Atlantic coastal areas due to extensive nearshore shoals.

The habitats show exposure to: moderate surf (Sapelo Beach), exposure to ebb and flood movements of water from a tidal creek (Blackbeard Creek), and relatively little exposure to surf action (Dean Creek Beach). Ranges of mean and spring tides on Sapelo and Blackbeard Islands are 2.1, 2.4 and 2.1, 2.5 meters, respectively. Mean tide level for all habitats is 1.04 meters, based on the reference station at Savannah River Entrance, Georgia (U.S. Dept. Commerce, 1966). Average low tide heights during seasonal sampling trips to Sapelo Beach, Blackbeard Creek, and Dean Creek Beach were -0.03, 0.09, and 0.06 m, respectively.

GENERAL HABITAT CHARACTERISTICS AND OBSERVATIONS

SAPELO BEACH. This is a relatively flat sand beach about 180 m. wide from mean high tide level to mean low tide level. A tide pool was present at mid-beach (Fig. 5). The upper beach had little debris (except the drift line) and no silt, but the mid-region of

the beach near the tide pool had much silt and debris including bivalve shell fragments. Shell was present in the sand for some distance both seaward and landward from the mid-beach area. Burrows of the ghost shrimp, *Callinassa major* Say, and the polychaete, *Onuphis* sp. were present throughout the lower- and mid-beach areas. The lower beach also had more silt and debris than higher levels. The black reducing layer of the sand was always deeper than 15 cm. Except during storms, breaker heights at Sapelo Beach were never greater than about 0.6 m. This agrees with previous beach studies on Sapelo that reported typical wave heights as 0.3–0.6 m (Helle, 1958; Pilkey and Richter, 1964). The sea water at this habitat was generally very turbid due mainly to suspended detrital material from the adjacent marshes (Schelske and Odum, 1961; de la Cruz, 1965).

In November after two summer hurricanes a double tide pool straddled the location of the former tide pool. The berm at higher levels was flattened, as was the beach between mean and low tide levels. Immediately after the first hurricane in August, sand dunes bordering the upper beach were broken by fresh water and wind-driven sea water flowing from the adjacent marsh. Outflowing water scoured the upper beach, and joined the tide pool water before flowing seaward.

Shore birds seen in mixed, or monospecific flocks numbering 5 to hundreds on Sapelo Beach during all months except June were: Ruddy Turnstone, *Arenaria interpres*; Sanderling, *Crocethia alba*; Least Sandpiper, *Erolia minutilla*; Blackbellied Plover, *Squatrola squatarola*; Semi-palmated Plover, *Charadrius semipalmatus*; Semi-palmated Sandpiper, *Breumetes pusillus*; and Spotted Sandpiper, *Actitis macularia*. These birds are designated as winter residents (Teal, 1959). Several Wilson's Plover, *Charadrius wilsonia*, were seen during the summer months.

Sandpipers and plovers poked the sand on all parts of the beach, generally however in the wettest area above the water-line on a falling tide. Sandpipers and Sanderlings also worked the tide pool area where sand remained wet long after the falling tide passed.

Feces of shore birds were examined several times, but no amphipod remains were found. Richard Heard, formerly of The University of Georgia Marine Institute, reported (personal communication) finding haustoriid amphipod remains in guts of shore birds. Given the densities and distribution of the amphipods I will describe later, it seems likely that shore birds are responsible for some predation.

DEAN CREEK BEACH. This is a narrower, more sloping sand beach located at the south end of Sapelo Island, near the mouth of a tidal creek, and the entrance of Doby Sound into the ocean (Fig. 4). It was also protected from surf by a series of offshore bars in the ocean adjacent to the south end

of Sapelo Island. The beach measured about 60 m from mean high tide level to the mean low tide level. Higher levels were relatively free of silt and debris, as compared with lower levels, and burrows of the ghost shrimp, *C. major*, were common at lower levels. The reducing layer of the sand was closer to the surface than at Sapelo Beach, i.e. 5-8 cm deep at higher levels, and only 4-5 cm deep at lower levels. Waves were never higher than a few cm, and the sea water was as turbid, and sometimes more turbid than the surf at Sapelo Beach.

After hurricanes during summer 1964, shell was deposited at high tide level. A ridge was also out in the beach between mean- and high tide level. During spring 1965, considerably more silt and detritus was apparent at the entire habitat, and the reducing layer in the sand was closer to the surface (1.5–1.0 cm) at some areas near low tide level.

The only shore birds observed at this habitat were flocks of Least Sandpiper and Sanderling. These birds were seen during most of the year.

BLACKBEARD CREEK. This is a relatively flat sand beach located at the extreme south end of Blackbeard Island where Blackbeard Creek enters the ocean. It was protected from surf action by its location on the landward side of the southward-jutting island (Fig. 3). The beach measured about 150-180 m from mean high tide level to mean low tide level. A tidal seep crossed the beach at low tide level (Fig. 6) where there was more silt and debris than at higher levels. Burrows of *C. major* were present at low tide level. The reducing layer of the sand was always deeper than 15 cm. Waves were never higher than a few cm at this habitat, and the water in the adjacent creek was usually turbid. After the hurricanes during summer 1964, the tidal seep at low tide level was considerably scoured and widened, and numerous ridges and holes were present on the beach. The Sanderling was the only shore bird observed at this habitat, although observation time was limited due to the distance of the habitat from the laboratory.

TEMPERATURE, HUMIDITY, AND SALINITY

Temperature, humidity and salinity measurements were made during seasonal sampling trips at each habitat. Temperatures of the surf and air 13 cm above the sand surface were measured with either a Rochester dial thermometer, or a mercury thermometer. Interstitial temperatures of Sapelo Beach sand and air 0.5 cm above the sand surface were measured with a Yellow Springs electric, Tele-thermometer, and remote thermistors. Tele-thermometer readings were taken simultaneously at several tidal levels during a 6 hr period between low and high tides on several hot summer days at Sapelo Beach. Temperature profiles of the beach were obtained from these data and times of exposure to specific temperatures for each tidal level were then calculated. The relative humidity of air above the beach was measured with a portable Lab-Line Electrohy-

grometer. Humidity measurements of interstitial air in the sand were made with "humigraph" paper indicators.

Due to an unfortunate accident, surf salinity samples were ruined, and available equipment was not sufficient for taking interstitial salinities. Salinity records taken by Marine Institute personnel in areas near the three habitats were therefore used as indications of a probably salinity range for each habitat.

Air temperatures 13 cm above the beach ranged from 11-35°C during the year, with little difference between habitats. Similarly, water temperatures of surf adjacent to the three habitats ranged from 14-30°C. Air temperatures 0.5 cm above the sand surface however, reached as high as 40°C during the summer. Temperatures attained by intertidal sands during the summer depended on the tidal level. Data in Table 1 show exposure times of sands at

TABLE 1. Exposure time of intertidal sand at Sapelo Beach to summer temperatures during low tides August 13 and 14, 1965.

Tidal Level	% Water ¹	Hours Exposure to °C			
		34.0	34.4	35.0	35.5
High Between Mean & High	9.3	—	7	7	4
Low	20.2 20.5	— 3	5	5	
Depth cm		2.5, 5	5	2.5	2.5, 5

¹After exposure

three levels to the indicated temperatures during two hot August days. Prolonged contact of higher levels with air resulted in exposure of these levels to temperatures from 1-4 hours longer than sand at low tide level. The upper 2.5 cm layer of sand at both intermediate and high levels showed highest temperatures due to its contact with the heated layer of air just above the sand surface. Temperatures of low tide level sands did not increase above 34°C even on these hottest of summer days.

Relative humidity of the air above the beaches ranged from 25-60%. Relative humidity of interstitial air in the sand was always greater than 80% even at high tide levels after 6-7 hours exposure to high summer temperatures.

Salinities in Doby Sound near the protected habitat ranged from 18.5-31.9‰, and averaged 27.5‰ during August-March 1965-1966 (excepting February), while salinities off Sapelo Island near the exposed habitat, ranged from 26.5-32.0‰, and averaged 30.1‰ during the same period. Salinities at the mouth of Blackbeard Creek and nearby ranged from 23.2-28.2‰, and averaged 25.3‰ in February and March 1966, during a period of heavy fresh water runoff. In general, the salinity data for the Sapelo-Blackbeard area indicate more saline conditions go-

ing north from the south end of Sapelo Island, and away from the influence of fresh water from the Altamaha River system (Hoese, personal communication). Higher salinities probably occur interstitially due to evaporation on hot summer days, and very low salinities may be expected on the beach during heavy rains.

AMPHIPOD POPULATIONS

METHODS

Amphipod populations were sampled to provide data on: abundance, density, distribution, horizontal and vertical zonation, size, growth, sex ratio, reproductive cycles, fecundity, and pelagic presence.

The sampling method consisted of running two transects five m apart, from mean high tide level to low tide level on the day of sampling. Samples of sand were taken with a shovel designed to remove a constant volume of sand to a depth of 7.6 cm, with a surface area of about 0.1m². Samples were taken at various tidal levels with equal distances between them on each transect, giving a simple stratified sampling design. The number of tidal levels sampled at each location yielding duplicate 0.1 m² samples, depended on width of the beach, and sampling time available. Thus, at Sapelo Beach 5 and later 6 sample pairs were taken, while at Dean Creek Beach 4 sample pairs were taken. Three sample pairs were taken at Blackbeard Creek due to the short sampling time available at this flat beach. All population samples, except for those taken from a tide pool at Sapelo Beach, and a tidal seep at Blackbeard Creek, were taken when sands were exposed to the air during low tide. Sand was then passed through a 0.1 m² sieve with a mesh size of 1.5 mm². Amphipods were removed from the sieve with forceps, and preserved in 10% formalin buffered with hexamethylenamine.

Lengths of amphipods were measured to the nearest 0.25 mm from the base of the first antennae to the tip of the telson. Curled animals were extended with jewelers forceps to facilitate this measurement. Approximately 8500 amphipods were processed in this way.

To determine the kinds of size differences among the species, mean length of each on an annual basis was calculated for Sapelo Beach, weighting means for numbers of males and females present. Ratios of seasonal mean lengths, and an average annual ratio of mean lengths were then calculated for each species pair. Mean lengths of larger species were numerators of these ratios.

Densities of amphipods were expressed as: 1) a mean of numbers taken in pairs of 0.1 m² samples for each tidal level, and 2) the mean number/0.1 m² for each habitat by season. Densities of species were also determined for tidal levels where they occurred, and horizontal zonation diagrams were constructed for each season.

TABLE 2. Densities of amphipod species at three habitats, 1964-1965

Species	Mean Density/0.1m ²												
	Sapelo Beach				Dean Creek Beach				Blackbeard Creek				
	Number	Mid-Spring	Summer	Fall	Early Spring	Mid-Spring	Summer	Fall	Early Spring	Mid-Spring	Summer	Fall	Early Spring
<i>N. schmitzi</i>	2085	28.9	20.5	18.5	44.3	31.4	36.1	7.5	36.5	9.0	30.5	16.0	21.0
<i>Haustorius</i> sp.	529	4.1	4.3	5.0	3.1	17.1	10.5	4.0	3.6	13.3	0.3	—	2.5
<i>L. dytiscus</i>	3668	1.0	4.2	5.8	2.4	42.5	82.0	127.8	145.0	2.2	35.2	0.5	15.0
<i>Pa. longimerus</i>	561	26.0	0.0	3.3	13.0	—	—	—	—	0.8	—	0.2	3.5
<i>Acanthohaustorius</i> sp.	664	0.9	12.3	0.7	2.1	1.3	2.3	0.3	5.3	3.2	5.2	12.3	30.3
<i>Pr. deichmannae</i>	28	0.5	0.6	0.1	0.6	—	—	—	—	0.8	—	0.3	0.2
<i>Ps. caroliniensis</i>	3	0.1	—	—	—	—	—	—	—	0.3	—	—	—
TOTAL	8138												
TOTAL DENSITY 0.1m ²		60.0	54.4	33.4	65.5	92.3	131.5	139.6	191.3	34.6	71.2	20.3	72.5
SAMPLING VARIANCE		50.2	4.6	78.9	17.1	31.6	23.0	155.1	62.4	17.6	179.2	14.1	230.4
STANDARD ERROR		±7.1	±2.1	±8.9	±4.1	±5.6	±4.8	±12.2	±7.9	±4.2	±13.4	±3.8	±15.5
MEAN DENSITY 0.1m ² 1964-1965			55.6				138.7				51.9		

Sex of amphipods was determined by the presence of testicular papillae on the sternum of the last thoracic somite in males, or the presence of oostegites (brood plates) on the inner surface of coxopodites, proximal to the branchial plates in females. Animals lacking either pair of structures, but having definite adult morphology, were considered immature.

Female amphipods having either oostegites as small buds, or oostegites as flat lamellae, but lacking marginal setae, were designated as maturing females, while those possessing fully developed oostegites were designated as mature females.

For each ripe female the numbers of eggs were counted. This was defined as fecundity. Several eggs were found free in sample bottles; these were not included in fecundity determinations, but were noted.

Several population samples were taken at Sapelo Beach and Dean Creek Beach to determine the vertical distribution of amphipods by removing duplicate 0.1 m² areas of sand in 2.5 cm layers, to a depth where no haustoriids were present, and sieving sand as described above. Densities of amphipods within each 2.5 cm layer were expressed as a mean of the two 0.1 m² samples.

A series of 8 plankton tows was made at night, on a falling tide during summer 1964 to determine the presence of amphipods free in the water. The plankton net measured 31.8 cm across the mouth, and 0.3 mm mesh size. Duplicate tows were made parallel with the beach at four tidal levels, over a distance of approximately 91.4 meters. Plastic floats were tied to the net ring to assist buoyancy.

RESULTS

ABUNDANCE AND DENSITY. Data in Table 2 and Fig. 7 show total abundances and densities of all amphipods collected during seasonal sampling at each habitat. *N. schmitzi* and *L. dytiscus* made up 78.1% of 8138 amphipods collected, while *L. dytiscus* alone made up almost 50%. *Haustorius* sp., *Pa.*

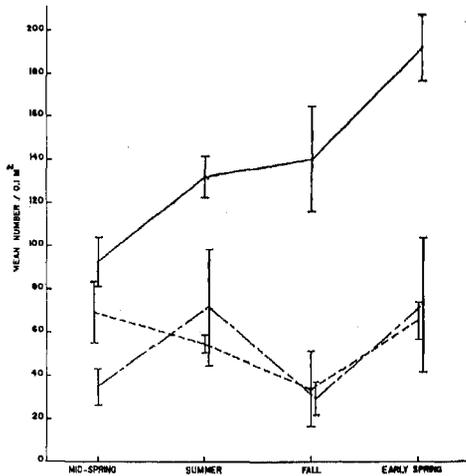


FIG. 7. Total density estimates of amphipod populations, 1964-1965. Solid line—Dean Creek Beach. Dashed line—Sapelo Beach. Dot-Dashed line—Blackbeard Creek. Vertical lines indicate 95 percent confidence limits for density estimates.

longimerus, and *Acanthohaustorius* sp. had similar relative abundances, and made up 21.6%. *Pr. deichmannae* and *Ps. caroliniensis* sp. made up less than one percent.

N. schmitzi was relatively abundant at all three habitats, while *Haustorius* sp. and particularly *L. dytiscus* were most abundant at the protected habitat (Dean Creek Beach). *Pa. longimerus* was most abundant at the exposed habitat (Sapelo Beach), present in small numbers at the tidal creek habitat (Blackbeard Creek), and was not collected at the protected habitat. *Acanthohaustorius* sp. was most abundant at the tidal creek habitat (Table 2).

The mean density of all amphipods on an annual basis was about two-and-one-half times greater at

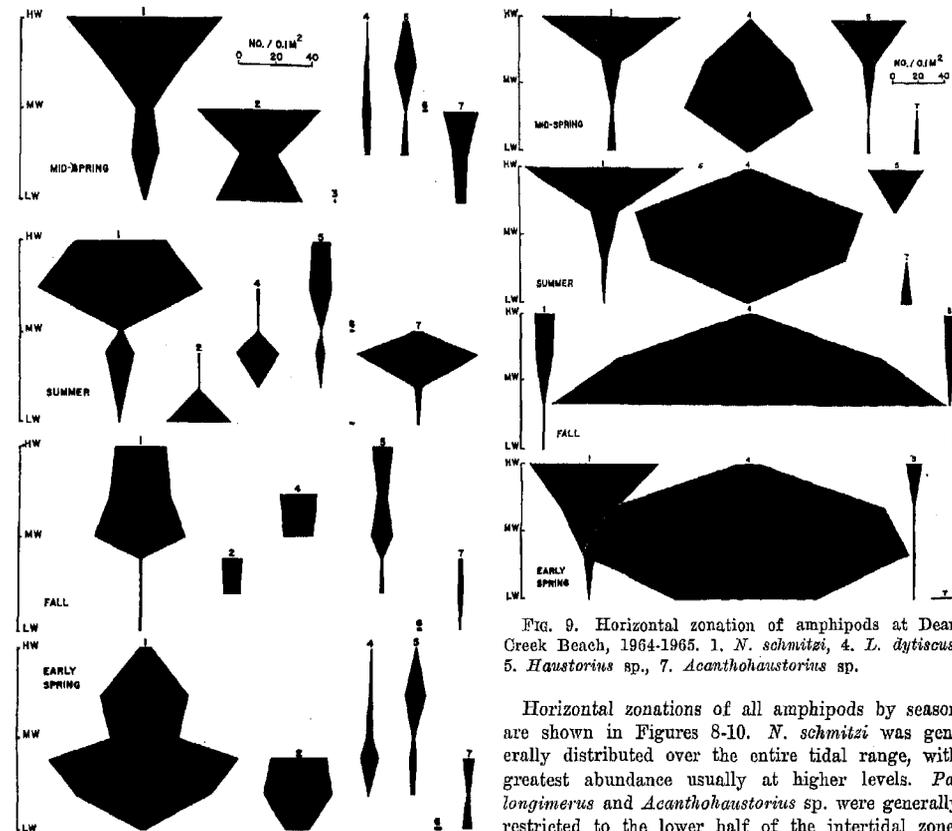


FIG. 8. Horizontal zonation of amphipods at Sapelo Beach, 1964-1965. 1. *N. schmitzi*, 2. *Pa. longimerus*, 3. *Ps. caroliniensis*, 4. *L. dytiscus*, 5. *Haustorius* sp., 6. *Pr. deichmannae*, 7. *Acanthohaustorius* sp.

the protected habitat as compared with the exposed and tidal creek habitats (Table 2, bottom). The range of seasonal densities, and mean density of all amphipods during the year were similar at these latter two habitats (Fig. 7). Population densities of amphipods fell to their lowest levels at these two habitats during the fall. On the other hand, the population density of all amphipods steadily increased through the year at the protected habitat (Fig. 7). This increase in density was contributed primarily by *L. dytiscus* (Table 2).

DISTRIBUTION AND ZONATION. Data in Table 2 show that except for *Pa. longimerus*, the five abundant species generally occurred at all three habitats. *Pa. longimerus* was not collected at the protected habitat, and was collected only rarely at the tidal creek habitat. The most consistent occurrence of the seven species was at the more exposed habitat, while only four species were collected at the protected habitat.

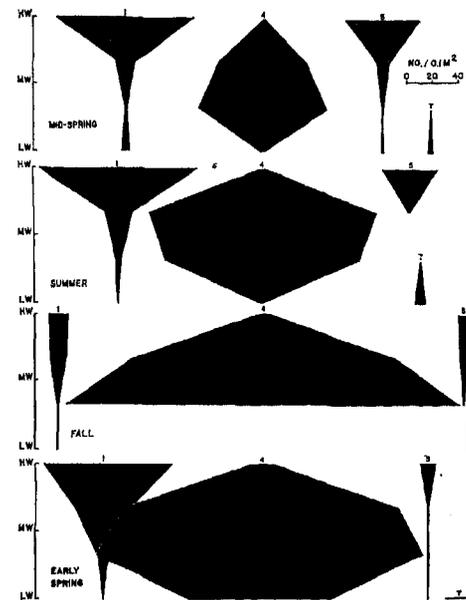


FIG. 9. Horizontal zonation of amphipods at Dean Creek Beach, 1964-1965. 1. *N. schmitzi*, 4. *L. dytiscus*, 5. *Haustorius* sp., 7. *Acanthohaustorius* sp.

Horizontal zonations of all amphipods by season are shown in Figures 8-10. *N. schmitzi* was generally distributed over the entire tidal range, with greatest abundance usually at higher levels. *Pa. longimerus* and *Acanthohaustorius* sp. were generally restricted to the lower half of the intertidal zone, while *L. dytiscus* was generally most abundant at mid-tide level with some extension both above and below this level. *Haustorius* sp. was generally restricted to the upper half of the intertidal zone, with some extension to lower levels. *Pr. deichmannae* and *Ps. caroliniensis* were restricted to either low tide level, or permanently wet tide pool areas.

Except for *N. schmitzi*, there was no significant difference between the horizontal distributions of males and females within any one species. Males of *N. schmitzi* were generally more abundant at higher levels. Except for *Haustorius* sp. there was no correlation of sizes of animals of any one species with horizontal distribution. There was a slight tendency for larger *Haustorius* sp. to live lower in the intertidal zone.

Figures 11 and 12 show vertical distributions of the amphipods at Sapelo Beach and Dean Creek Beach in summer, and at Sapelo Beach in winter. Most of the amphipods occurred at depths shallower than 4 cm, but they penetrated as deep as 12 cm. At both habitats *N. schmitzi* was generally more abundant in the upper 2.5 cm sand layer, while *Haustorius* sp. was more abundant at lower depths. This

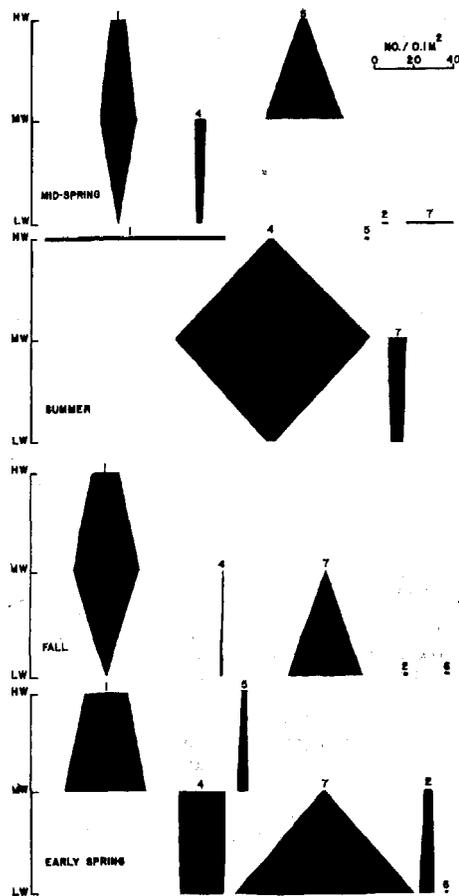


FIG. 10. Horizontal zonation of amphipods at Blackbeard Creek, 1964-1965. 1. *N. schmitzi*; 2. *Pa. longimerus*; 4. *L. dytiscus*; 5. *Haustorius* sp.; 6. *Pr. deichmannae*; 7. *Acanthohaustorius* sp.

is particularly evident at Sapelo Beach during summer (Fig. 11, A). There was a tendency for a similar distribution of *Acanthohaustorius* sp., and *Pa. longimerus* where they occurred together in abundance (Fig. 11, B). *L. dytiscus* was more abundant in the upper sand layers at the protected Dean Creek Beach (Fig. 11, C and D). In general, the data show 2-5 species living at the same depth at several habitat locations during the summer and winter. No amphipods were found in, or below the black reduction layer at the protected habitat during summer (Fig. 11, D and E).

N. schmitzi was the only amphipod to appear in plankton tow collections made during June 1964. Six juvenile animals were collected. Four of these animals were taken in the water at low tide level.

SEXUAL BIOLOGY. Fig. 13 shows the percentage of

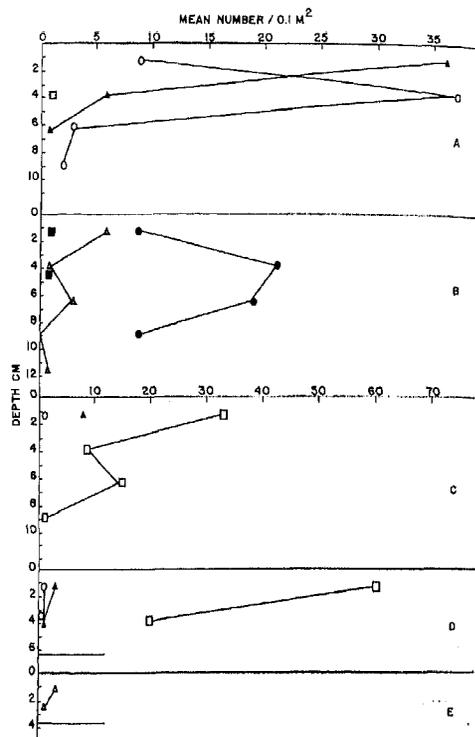


FIG. 11. Vertical zonation of amphipods, Summer 1965. A. Sapelo Beach, between HW and MW; B. Sapelo Beach, between MW and LW; C. Dean Creek Beach, HW; D. Dean Creek Beach, between HW and MW; E. Dean Creek Beach, LW. Closed triangles, *N. schmitzi*; open circles, *Haustorius* sp.; closed rectangles, *Pr. deichmannae*; open triangles, *Acanthohaustorius* sp.; closed circles, *Pa. longimerus*; open rectangles, *L. dytiscus*. Short horizontal lines on ordinate in D and E indicate upper limit of black reduction layer.

ripe females in all population samples during the year period. The data are based on a total of 5494 females including 198 animals collected at Sapelo Beach during winter 1965-1966. The maximum percentage of ripe females, or reproductive peaks for the five species were: *N. schmitzi*, mid-spring (April); *Haustorius* sp., early spring; *L. dytiscus*, mid-spring (May-June); *Pa. longimerus*, fall and winter; and *Acanthohaustorius* sp., winter.

Fecundities of the 5 abundant species are shown in Table 3. *Haustorius* sp. and *Pa. longimerus* showed highest fecundity with *Acanthohaustorius* sp. and *L. dytiscus* close behind. Except for spring-collected animals, the fecundity of *N. schmitzi* was considerably lower. *N. schmitzi* showed a decreasing fecundity from spring through fall, while the fecundity of *L. dytiscus* remained essentially the same during spring and summer, although fewer animals were ripe during summer as compared with

TABLE 3. Mean fecundity of amphipod species.

Season	Species	Habitat		
		SB	DC	BB
Mid-Spring	<i>N. schmitzi</i>	4.4±1.4 (287) ¹	3.8±1.3 (201)	4.7±0.3 (19)
	<i>Haustorius</i> sp.	6.0 (3)	5.7±3.5 (3)	0 ²
	<i>L. dytiscus</i>	5.3±0.8 (6)	4.5±1.5 (174)	3.0 (1)
	<i>Pa. longimerus</i>	9.0±4.5 (12)	—	0
	<i>Acanthohaustorius</i> sp.	6.5±3.8 (17)	4.0 (2)	4.0 (1)
Summer	<i>N. schmitzi</i>	2.2±1.1 (135)	2.0±0.6 (139)	2.0±0.3 (28)
	<i>Haustorius</i> sp.	0	0	0
	<i>Pa. longimerus</i>	4.2±1.5 (4)	4.3±1.1 (63)	4.3±1.9 (9)
	<i>Acanthohaustorius</i> sp.	0	—	—
	<i>L. dytiscus</i>	1.0 (1)	0	0
Fall	<i>N. schmitzi</i>	1.3±0.5 (4)	1.5 (2)	1.4±0.5 (9)
	<i>Haustorius</i> sp.	4.0 (1)	0	0
	<i>L. dytiscus</i>	0	0	0
	<i>Pa. longimerus</i>	8.2±3.4 (14)	—	—
	<i>Acanthohaustorius</i> sp.	5.3±1.9 (4)	0	2.0 (1)
Early Spring	<i>N. schmitzi</i>	3.0±0.9 (299)	3.2±1.1 (217)	5.6±1.2 (85)
	<i>Haustorius</i> sp.	6.3±3.3 (8)	5.7±2.3 (3)	6.0 (2)
	<i>L. dytiscus</i>	0	4.0±1.2 (162)	5.5±2.3 (31)
	<i>Pa. longimerus</i>	9.8±3.1 (4)	—	4.0 (1)
	<i>Acanthohaustorius</i> sp.	6.3±1.5 (6)	4.2±2.0 (10)	5.8±2.3 (32)

¹Number counted

²None ripe

³None collected

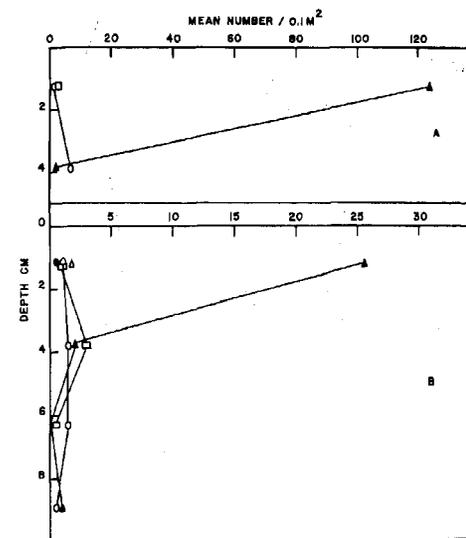


FIG. 12. Vertical zonation of amphipods, Winter 1966. A. Sapelo Beach, HW; B. Sapelo Beach, between MW and LW. Species code the same as Fig. 11.

N. schmitzi (Fig. 13). That this decrease in fecundity for *N. schmitzi* was not due wholly to differences in the mean size of female animals is evident by reference to Table 4.

Considering the sample sizes, there were no significant differences in fecundity within a species among habitats except for animals collected in the early spring. At this time, fecundities of *N. schmitzi* and *L. dytiscus* were higher at the tidal creek habitat

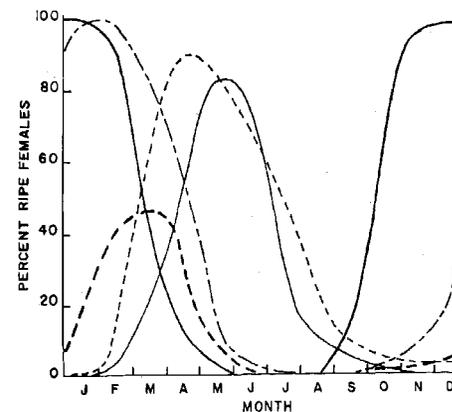


FIG. 13. Reproductive cycles of amphipods. Heavy solid line, *Pa. longimerus* n=166; light solid line, *L. dytiscus* n=2018; heavy dashed line, *Haustorius* sp. n=213; light dashed line, *N. schmitzi* n=2726; dot-dashed line, *Acanthohaustorius* sp. n=371.

than at the other two habitats. This difference was related to a difference in mean lengths of females in the population, i.e., females from Blackbeard Creek were larger than females from the other two habitats.

Sex ratios of species at the three habitats are shown in Table 5. Four types of sex ratios are apparent: 1) females greatly dominant for *N. schmitzi*, where as many as 57 of 58 animals were females, and where males were represented increasingly in the population during fall at two habitats; 2) males generally dominant in *Haustorius* sp., and

TABLE 4. Comparison of fecundities of two amphipod species within a selected size class during two seasons.

Species	Length in mm	Season	Total Number	Number Ripe	Mean Fecundity
<i>N. schmitzi</i>	3.00	Spring	38	33	3.70 ± 1.43 ¹
		Summer	154	42	2.17 ± 0.83 ¹
<i>L. dytiscus</i>	4.00	Spring	93	82	4.02 ± 1.23 ²
		Summer	75	41	4.41 ± 0.96 ²

¹Difference is significant at the 1% level (t=6.21, df=78)²No significant difference (t=0.96, df=121)

TABLE 5. Sex ratios (male:female) for amphipod species.

	Habitats		
	SB	DC	BB
<i>N. schmitzi</i>			
Mid-Spring.....	1:56.8 (290) ¹	1:21.7 (260)	1:4.0 (28)
Summer.....	1:52.0 (318)	1:47.0 (288)	no males (183)
Fall.....	1:13.9 (222)	1:11.0 (80)	1:47.0 (90)
Early Spring.....	1:14.6 (631)	1:26.4 (392)	1:7.4 (120)
<i>Haustorius</i> sp.			
Mid-Spring.....	1:0.70 (30)	1:0.48 (105)	1:0.41 (24)
Summer.....	1:0.96 (47)	1:1.08 (79)	1:0.5 (8)
Fall.....	1:1.81 (60)	1:0.58 (32)	—
Early Spring.....	1:0.80 (36)	1:0.54 (20)	1:1 (14)
<i>L. dytiscus</i>			
Mid-Spring.....	1:1.38 (19)	1:1.65 (339)	1:0.33 (8)
Summer.....	1:0.69 (49)	1:1.80 (600)	1:0.87 (211)
Fall.....	1:1 (70)	1:1.09 (1021)	no males (1)
Early Spring.....	1:1.64 (29)	1:1.05 (1167)	1:1.25 (90)
<i>Pa. longimerus</i>			
Mid-Spring.....	1:0.58 (108)	—	1:2 (3)
Summer.....	1:1.18 (72)	—	—
Fall.....	1:0.56 (39)	—	no males (1)
Early Spring.....	1:0.36 (122)	—	1:0.21 (17)
<i>Acanthohaustorius</i> sp.			
Mid-Spring.....	1:0.97 (69)	1:1 (10)	1:1.4 (48)
Summer.....	1:1.35 (152)	1:3.5 (18)	1:1.82 (31)
Fall.....	1:1.07 (8)	1:1 (2)	1:1.31 (74)
Early Spring.....	1:1.27 (25)	1:1.21 (42)	1:0.98 (178)

¹Number of animals

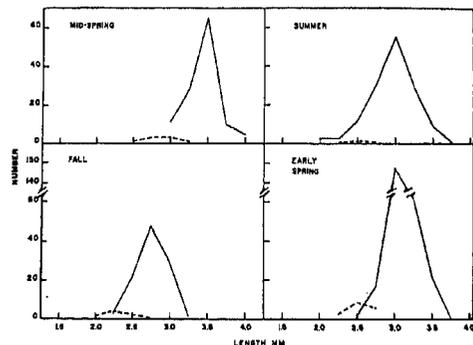
Pa. longimerus, except during summer or fall when females were more abundant; 3) females usually dominant in *L. dytiscus*, particularly during the spring reproductive period; and 4) females dominant during summer and fall, with about a 1:1 ratio during the remainder of the year—*Acanthohaustorius* sp.

Female *N. schmitzi* were identifiable at as small a size as 2.00 mm, and female *Acanthohaustorius* sp. at 2.25 mm, while the other three species were larger except for female *L. dytiscus* that were identifiable at 2.25 mm during the fall (Table 6). A similar size relationship is shown for the smallest ovigerous females of *N. schmitzi*, *L. dytiscus*, and *Acanthohaustorius* sp. that bear young at smaller sizes compared with *Pa. longimerus* and *Haustorius* sp.

SIZE AND GROWTH. Figures 14-18 show length frequencies of both sexes and some immature ani-

mals for the 5 abundant species during 1964-1965. Data for 4 species are from the population at Sapelo Beach, while data for the fifth species, *L. dytiscus*, are from the population at Dean Creek Beach. The data are typical for haustoriid populations in the Sapelo-Blackbeard area during 1964-1965, and show that males of each species were generally smaller than females. The data for each species will be considered in turn.

N. schmitzi (Fig. 14). A single mode is present for mid-spring males and females, indicating over-

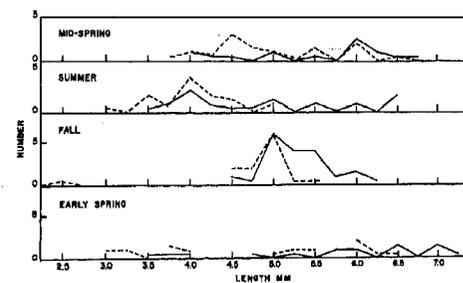
FIG. 14. Length frequency of *N. schmitzi* from Sapelo Beach, 1964-1965. Solid line, females; dashed line, males; n = 681.

wintering animals. Data for summer and fall show decreasing numbers of larger females, and recruitment of young females hatched during summer and fall. Females ranging in length from 2.25-3.75 mm were ripe during summer. Many of these animals were probably hatched the previous spring, although some overwintering females may have produced more than one brood during March-August. By fall, larger females were poorly represented in samples (by summer for larger males). Females hatched in late summer and fall overwintered, and were mostly ripe for the first time in late winter and early spring. Females can apparently live as long as 9-10 months, and perhaps for one yr, while males apparently live for 9-10 months.

Haustorius sp. (Fig. 15). Immature animals with a mode at 3.25 mm were present in mid-spring collections from Dean Creek Beach and Blackbeard Creek, but not in collections from Sapelo Beach

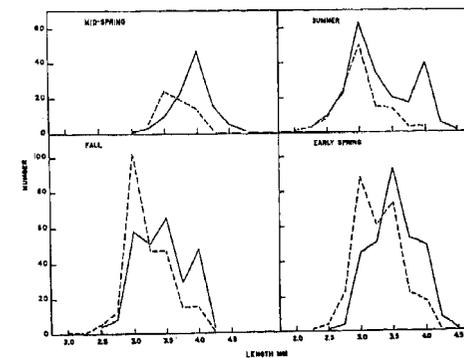
TABLE 6. Smallest sizes of maturing and ovigerous female amphipods collected at three habitats.

Species	Length of Smallest Female (mm)				Length When First Ripe (mm)			
	Mid-Spring	Summer	Fall	Early Spring	Mid-Spring	Summer	Fall	Early Spring
<i>N. schmitzi</i>	2.50	2.00	2.00	2.50	2.75	2.25	2.50	2.75
<i>Haustorius</i> sp.	3.00	3.50	3.50	3.50	6.00	0 ¹	5.75	5.25
<i>L. dytiscus</i>	3.00	2.50	2.25	2.50	3.25	3.25	0	3.25
<i>Pa. longimerus</i>	3.50	3.75	5.00	3.50	6.00	0	5.00	6.00
<i>Acanthohaustorius</i> sp.	2.25	2.25	2.50	2.50	3.50	3.50	3.00	3.00

¹None ripeFIG. 15. Length frequency of *Haustorius* sp. from Sapelo Beach, 1964-1965. Solid line, females; dashed line, males; n = 98.

population shown in the figure. This brood apparently attained a median length of about 4.0-4.25 mm by summer, and 5.00 mm by fall (Fig. 15). Few animals larger than 5.75 mm were present in fall collections. The following early spring, females hatched one year previous, and larger than 6.00 mm were ripe (also see Table 6). At this time, a smaller brood of maturing females was recruited with lengths 3.50-4.00 mm. In summary, reproducing females in the spring were probably one yr old, and may live for as long as 1.5 yr, while males may live equally as long.

L. dytiscus (Fig. 16). Animals present in mid-spring collections were primarily overwintering animals (no reproduction for the species during winter, see Fig. 13). In summer, a new brood with both sexes was apparent with a mode at 3.00 mm. Summer females were identifiable at 2.50 mm, but they were not ripe until 3.25 mm, and then only in small numbers. Thus, most females hatched in spring, overwintered and had their first brood at one yr of age, and their second brood that summer. Evidence for this is seen in the fact that almost all ripe females in the summer were 3.50 mm in length or longer. In fall, three groups of animals are apparent: 1) late summer and early fall young with a mode at 3.00 mm, 2) spring- and summer hatched adults that will overwinter, and 3) perhaps some older animals hatched one yr or more before. This latter group is probably mostly females, since most adult males in summer were animals hatched that

FIG. 16. Length frequency of *L. dytiscus* from Dean Creek Beach, 1964-1965. Solid line, females; dashed line, males; n = 1594.

spring, i.e. few males appear to live longer than one year.

Pa. longimerus (Fig. 17). Length frequency data for this species show a group of spring-hatched immature animals with a mode at 3.00-3.50 mm in mid-spring. Some of these animals probably develop oostegites at a length of 3.75 mm by summer (Table 6). Also present in mid-spring samples were young adults with lengths 3.75-5.75 mm, and older adults with lengths 5.75-7.50 mm. By summer many of these older animals were not represented in samples. In fall, a new brood of males appeared with a mode at 3.00 mm. Females with lengths 5.00-7.00 mm overwintered, and produced their first brood that winter, although some females produced fall broods when as small as 5.00 mm (Table 6). In early spring, the only ripe females were those animals larger than 6.00 mm. Females apparently may live for 1.5 yr, while males may live at least one yr.

Acanthohaustorius sp. (Fig. 18). In mid-spring, two groups of animals were apparent for this species, one, probably a winter brood at 3.00 mm, and older animals with an apparent mode at 4.00 mm for females. Most ripe females at this time were 3.75-4.75 mm long. By summer, spring and winter broods were not identifiable, and by fall most of the older animals were not represented in the samples. In fall, ripe females were 3.00-4.00 mm in length, rep-

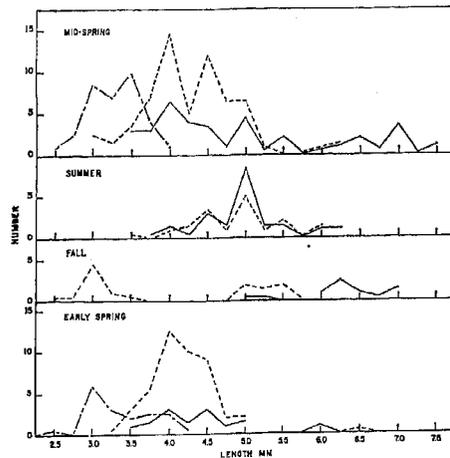


FIG. 17. Length frequency of *Pa. longimerus* from Sapelo Beach, 1964-1965. Solid line, females; dashed line, males; dot-dashed line, immatures; $n = 270$.

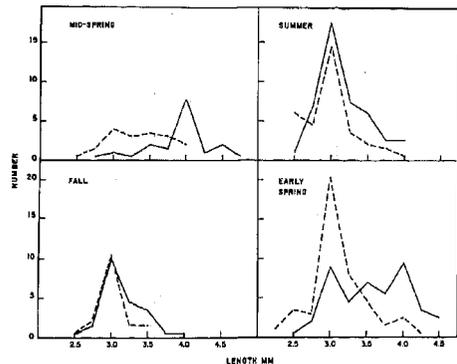


FIG. 18. Length frequency of *Acanthohaustorius* sp. from Sapelo Beach, 1964-1965. Solid line, females; dashed line, males; $n = 162$.

resenting animals hatched that previous spring or winter. In early spring, the winter brood with a mode at 3.00 mm was particularly evident. Both sexes apparently live for at least one yr, and perhaps for as long as 1.5 yr.

RATIOS OF MEAN LENGTHS. Seasonal ratios of mean lengths of species from Sapelo Beach ranged from 0.93-1.87, and the average ratio during 1964-1965 for all species pairs was 1.33 (Table 7). Data in the table show ratios were slightly higher for strongly co-occurring species pairs, and slightly lower for species pairs showing strong habitat isolation and/or highest densities in separate habitats.

ASSOCIATED FAUNA

METHODS

Animals living in association with haustoriids and retained by the sieve were preserved and brought

to the laboratory for identification and counting. Densities of associated fauna were calculated as mean numbers of each species taken in pairs of 0.1 m² samples at each tidal level. Seasonal mean densities for each species at a particular sampling location were then calculated on the basis of only those tidal levels where each species was actually collected. This procedure was followed since many associated species were restricted to certain tidal levels.

RESULTS

Animals of six phyla totalling 347 individuals were associated with haustoriid amphipod populations at the three habitats. The species, their taxa, tidal levels, and mean densities for 1964-1965 are shown in Table 8. Twenty-five species were collected, and of these, 16 were represented at Sapelo Beach, 12 at Dean Creek Beach, and 10 at Blackbeard Creek. Four species, *Donax variabilis*, *Nephtys pieta*, *Chiridotea caeca*, and *Monoculodes* sp. occurred at all three habitats. Two species, *Scoloplos* sp. at Dean Creek Beach, and *Chiridotea caeca* at Sapelo Beach, were collected at these habitats during all seasons. *Scoloplos* sp. exhibited the only significant change in zonation during the year, i.e. the population occurred at higher tidal levels during fall and early spring. Decapods were generally restricted to lower tidal levels, while only arthropods, molluscs, and annelids occurred above mid-tide level.

Mean densities of associated species ranged from 0.5-14.8 animals per 0.1 m² during the year. The 5 most abundant species were: *D. variabilis*, *Scoloplos* sp., *C. caeca*, *Scololepis* sp., and *Monoculodes* sp. The two most abundant species, *D. variabilis*, and *Scoloplos* sp. contributed to a general increase in density of associated fauna at Sapelo Beach and Dean Creek Beach from fall through early spring. Densities of faunal associates were generally higher at Sapelo Beach, and lowest at Blackbeard Creek (Fig. 19).

Most of the associated fauna either occurred from

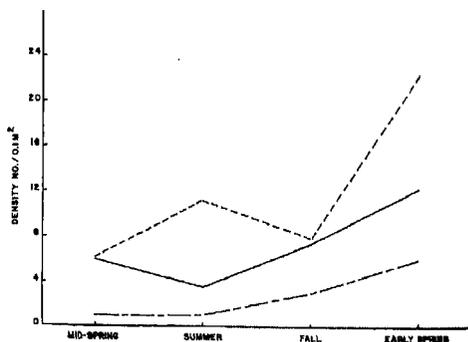


FIG. 19. Population density of faunal associates of amphipods, 1964-1965. Solid line, Dean Creek Beach; dashed line, Sapelo Beach; dot-dashed line, Blackbeard Creek.

TABLE 7. Ratios of mean lengths of amphipod species at Sapelo Beach, 1964-1965.

Species Pair	Ratios of Mean Lengths ¹		Species Pairs Characteristics		
	Range	Ave. 1964-65	Frequent Strong Co-occurrence	Strong Habitat Isolation	Highest Densities in Separate Habitats
<i>Haustorius</i> sp.	1.54-1.87	1.70	×		×
<i>N. schmitzi</i>					
<i>Pa. longimerus</i>	1.32-1.72	1.53		×	
<i>N. schmitzi</i>					
<i>Haustorius</i> sp.	1.45-1.56	1.49		×	×
<i>Acanthohaustorius</i> sp.					
<i>Haustorius</i> sp.	1.32-1.58	1.47	×		
<i>L. dytiscus</i>					
<i>Pa. longimerus</i>	1.19-1.58	1.34	×		×
<i>Acanthohaustorius</i> sp.					
<i>Pa. longimerus</i>	1.13-1.54	1.32		×	×
<i>L. dytiscus</i>					
<i>L. dytiscus</i>	1.12-1.23	1.16	×		×
<i>N. schmitzi</i>					
<i>Acanthohaustorius</i> sp.	1.06-1.26	1.14		×	×
<i>N. schmitzi</i>					
<i>Haustorius</i> sp.	0.93-1.30	1.13		×	×
<i>Pa. longimerus</i>					
<i>L. dytiscus</i>	0.98-1.10	1.02		×	×
<i>Acanthohaustorius</i> sp.					
Grand Mean		1.33	1.42	1.27	1.29

¹Weighted for numbers of males and females in each species

mean tide to low tide level, or had their highest abundance within this area of the intertidal zone. Only about 10% of associated fauna occurred over the full tidal range, while only 3% were abundant over the whole tidal range. Animals in the former category included *D. variabilis*, *Scoloplos* sp., *C. caeca*, and *Monoculodes* sp., while animals in the latter category included only *C. caeca* and *Monoculodes* sp. About one-third of associated fauna occurred, or were most abundant, at low tide level only (Table 9).

LABORATORY STUDIES

FOOD

Collections of amphipods were made at Sapelo Beach and Dean Creek Beach at tidal levels where each species was abundant. Animals were sieved from sand in the laboratory, and placed in small

finger bowls containing sea water of 21‰ salinity. Several animals of each species were sacrificed within 30 min after removal from their substratum. Intestinal tracts were removed and divided into fore-, mid-, and hind-gut portions. Intestinal contents were placed on glass slides, with a cover slip, and then examined under 430 power with a monocular microscope and ocular micrometer. A judgment of relative abundance of gut contents was then made, and representative sizes of contents in microns was noted.

Amphipods of each species were also placed in finger bowls containing sea water of 20-22‰ salinity at temperatures of 20-22°C. Attempts were then made to maintain amphipods on solid shrimp and fish parts, and various combinations of diatoms, *Calanassa major* feces, and beach sand with its included detritus and micro-organisms.

To further elucidate food selectivity, groups of

TABLE 8. Faunal associates of haustoriid amphipods.

Taxon	Species	Total No.	Occurrence		Mean Density /0.1m ² 1964-65		
			Habitat	Tidal Level			
Cnidaria.....	<i>Sagartia</i> sp.	1	BB	LW	0.13		
	<i>Cerabratulus lacteus</i>	2	BB	LW	0.13		
Nemertinea.....			SB	MW	0.13		
			DC	LW	0.13		
Sipunculoidea.....	<i>Micrura</i> sp.	1	DC	LW	0.13		
	Sipunculid	2	DC	MW	0.13		
Pelycepoidea.....	<i>Donax variabilis</i>	154	BB	HW-LW	0.88		
			DC	HW-MW	0.75		
			SB	HW-LW	6.15		
	<i>Macra fragilis</i>	4	DC	LW	0.25		
			SB	MW-LW	0.13		
	Oligochaeta.....	<i>Palinices duplicata</i>	1	DC	MW	0.13	
		<i>Tellina agilis</i>	1	BB	LW	0.13	
		Oligochaete	1	SB	MW	0.13	
		<i>Heteromastus</i> sp.	1	SB	LW	0.13	
		Polychaeta.....	<i>Laonereis culveri</i>	1	BB	HW	0.13
			<i>Nephtys picta</i>	7	BB	LW	0.25
				DC	LW	0.38	
			SB	MW	0.25		
			BB	LW	0.13		
			DC	MW	0.13		
		SB	HW-LW	0.88			
		DC	HW-MW	4.45			
		SB	HW-MW	0.85			
Cumacea.....	Bodotriid	2	DC	LW	0.25		
Isopoda.....	<i>Chiridotaea caeca</i>	58	BB	MW	0.75		
			DC	MW	0.13		
			SB	HW-LW	1.85		
Amphipoda.....	<i>Corophium</i> sp.	19	BB	LW	0.13		
			BB	LW	0.13		
			DC	HW-MW	0.38		
			SB	HW-LW	0.78		
Decapoda.....	<i>Talorchestia</i> sp.	1	SB	HW	0.13		
	<i>Emerita talpoida</i>	1	DC	LW	0.13		
	<i>Ogyrides alphaeostriis</i>	1	SB	LW	0.13		
	<i>Pagurus longicarpus</i>	1	SB	LW	0.13		
	<i>Pinnixa chaetopterana</i>	2	DC	LW	0.13		
			SB	LW	0.13		
	Xanthid crab	1	SB	MW	0.13		
Total.....		347					

TABLE 9. Intertidal distribution of faunal associates at three habitats.

Tidal Level	Occurrence		Highest Abundance	
	No.	%	No.	%
Full Range.....	6	9.2	2	3.2
HW.....	6	9.2	6	9.5
Above MW.....	9	13.9	8	12.7
MW.....	13	20.0	15	23.8
Below MW.....	10	15.4	9	14.3
LW.....	21	32.3	23	36.5
Total.....	65	100.0	63	100.0

each species were starved for one day, and then offered known food combinations. Animals were then sacrificed within one hour, and gut contents were examined as previously described.

All food studies on laboratory-maintained animals

were performed within one month after their collection, and usually within one to two weeks.

Data in Table 10 show gut contents of samples of amphipods collected during July 1965 and February 1966. Although the sample size is small, there were no large qualitative differences between species or seasons. There was a tendency for larger animals to ingest larger particles; this was especially true for detritus. Brownish detritus occupied most of the volume of gut contents of all species.

Attempts to feed solid shrimp and fish parts to all species were unsuccessful. The five abundant species did, however, feed on: 1) smaller materials present in beach sand from the field, and 2) a slurry made up of broken *C. major* fecal pellets, diatoms, and detritus from beach sand. Amphipods unselectively ingested these materials, and expelled feces. Individual *Pr. deichmannae* treated in the same way, did not ingest any combination of materials offered, and died after one week. No material was observed in their intestinal tracts at any time.

TABLE 10. Gut contents of amphipods during July 1965 and February 1966.

Species	Number	Month	Average Length mm	Size Range of Gut Contents (microns)					Gut Portion Examined
				Diatoms	Detritus	Algae	Protozoa	Other*	
<i>N. schmitzi</i>	2	July	3.09	12.8-48.0	1.2-25.0	—	—	8.0-32.0	Forc, Mid, Hind
	3	February	2.75	8.0-40.0	1.0-44.8	—	—	8.0-96.0	Fore
<i>Haustorius</i> sp.....	2	July	4.38	12.8-28.0	1.0-93.0	56.0	16.0	8.0-32.0	Fore
	2	February	5.03	9.0-64.0	1.3-201.0	17.3-48.0	—	19.2-88.0	Fore
<i>I. dytiscus</i>	2	July	4.00	18.0-24.0	1.0-80.0	10.2	—	8.0-82.0	Fore, Hind
	2	February	3.00	12.8-56.0	1.0-53.0	8.0-17.6	—	16.0-88.0	Fore
<i>Pa. longimerus</i>	2	July	5.75	16.0-48.0	1.0-260.0	16.0	—	3.2-56.0	Fore, Mid, Hind
	2	February	6.13	16.0-121.0	1.0-128.0	11.2-90.0	48.0	14.4-100.0	Fore
<i>Acanthohaustorius</i> sp.....	2	July	3.25	12.0-27.2	1.0-64.0	—	—	3.2-54.4	Fore, Mid, Hind
	2	February	2.63	8.0-48.0	1.0-48.0	9.0-22.4	—	11.2-73.6	Fore

*Razidarian fragments, flat particles (?), spicules, foraminiferans, sand, dinoflagellate tests.

BEHAVIOR

BURROWING AND SWIMMING. During summer 1965 amphipods of each species were brought into the laboratory and placed in finger bowls containing sea water of 20-22‰ salinity at temperatures of 20-22°C. No sand substratum was added at first, and the animals' general movements and swimming behavior were observed by eye in a partially darkened room. Usually 10-15 animals were observed at a time. All behavioral observations and experiments were performed on animals within 24 hours after their collection in the field.

To observe burrowing behavior, 2 or 3 amphipods of each species were placed in a petri dish with a large pipette, and a shallow layer of fine beach sand was introduced. Burrowing behavior was then observed with a dissecting microscope. Additional observations were made: 1) on animals placed on dry sand in a petri dish, and 2) after sea water was slowly added to the petri dish and dry sand to create varying moisture conditions of substratum.

The ability of amphipods to maintain their grasp on the substratum while burrowing was tested by trying to remove animals with a large pipette as they burrowed in a shallow sand substratum.

N. schmitzi and *Haustorius* sp. were extremely active in finger bowls containing only sea water. Both species attempted to dig into the bottom, and at intervals swam quickly to the surface where they lay upside down either remaining quietly in place, or swimming by beating their pleopods. They then quickly returned to the bottom of the bowl and resumed digging movements. *N. schmitzi* many times leaped over each other, landed on their dorsal sides and remained still, but finally righted themselves and resumed quick "walking" movements over the bottom of the bowl.

I. dytiscus lay mostly on its side in a finger bowl containing only sea water, although periodically this species "walked" as described above. The species spent less time swimming to and from the surface, or swimming upside down on the surface.

Pa. longimerus, *Acanthohaustorius* sp., and *Pr. deichmannae* were much less active. They generally

laid on their side on the bottom of the bowl, or simply floated motionless on the surface of the water (particularly *Pa. longimerus*). If the bowl was jarred, they attempted to dig into the bottom, but then just as quickly lay down again. The three species did not swim upside down, but *Acanthohaustorius* sp. sometimes swam in a slow spiral.

When a shallow sand substratum was presented to the six species in sea water, they either burrowed after making contact with sand, or they lay motionless, and then quickly burrowed. If the bowl was jarred while an amphipod lay motionless on the sand, the animal immediately burrowed. Burrowing in all species was accompanied by an arched body, the fifth peritopod held out posteriorly, some movement of antennae, and swift beating of pleopods to form the main water current used in loosening the sand. All species burrowed with such vigor that they were difficult to remove with a large pipette as they burrowed. Touching the animals on the abdomen or on the anterior end while they burrowed elicited an immediate withdrawal response by either moving deeper into the sand, or turning away from the direction of burrowing.

None of the species was able to burrow in dry sand. Under these conditions, either the animal lay still, or moved slightly. When a small amount of sea water was added to the side of the petri dish opposite from where the animal lay, there was no change in this behavior. Not until more sea water was added, and it had reached the animal to moisten the sand sufficiently was there any successful burrowing. If the animal was on its side, and moist sand was beneath it, the animal moved actively, and after gaining the proper position and hold on the substratum, it burrowed in.

FEEDING. Observations on feeding behavior were made in conjunction with food studies previously described. Amphipods were separated by species and starved for one day. Preferred food was added to finger bowls, and feeding behavior and rates were noted.

Feeding in the five abundant species was accomplished while the animals burrowed through sand containing detritus and associated microfauna and

flora. Currents produced by the pleopods and other appendages was followed by food entering the intestinal tract. Ingestion and movement of food through the intestinal tract was observed through the transparent dorsal body wall. As mentioned previously, *Pr. deichmannae* did not feed in the laboratory, although the animals moved through sand and exhibited the same general movements as the other species.

Starved animals of the five abundant species ingested some material from sand 4-5 min after sand was offered. After 10 min the mid-gut of most animals was full, and after 20-25 min the entire gut in some animals of all species was full.

Animals maintained in the laboratory exhibited movements associated with ingestion of food during most of the day.

SUBSTRATUM PREFERENCE. To determine substratum preference of amphipods, animals were collected in the field and separated by species. Thirty-six to 54 animals of each species were then placed in large finger bowls containing sand to a depth of 1.5 cm. One half of the finger bowl contained sand from the high beach, and was designated as "clean" sand; the other half contained sand from the lower beach with 1.4 to 2.8 times as much silt and debris, and was designated "silty" sand. A 0.5 cm layer of sea water of 23‰ salinity was introduced on top of the sand. Animals were introduced singly between two substratum types with a large pipette. A control was set up in the same way except that only clean sand was used. All finger bowls were protected from light, and kept under a constant 20.8°C temperature. After 24 hr, sand from each half of the experimental bowls, and from random halves of the control bowl was removed and sieved separately, and animals found within each substratum type were counted.

Data in Table 11 show results of the substratum preference experiments. *N. schmitzi* and *Haustorius* sp. preferred cleaner sand to sand containing more silt and debris ($P < 0.001$). No significant preference was shown for either of these two substrata types by *Pa. longimerus*, *L. dytiscus*, and *Acanthohaustorius* sp.

DIRECTIONAL LIGHT RESPONSE. To determine direction and relative strength of a phototactic response by the amphipods, 20 or 24 animals of each species were collected in the field and placed in small finger bowls containing sea water of 22 to 27‰ salinity, but no substratum. Room temperatures during these light experiments ranged from 20.8 to 25.2°C. To compare all species under comparable conditions, a finger bowl with animals of one species was covered around the sides, and placed in front of a window receiving sunlight. Animals were kept on the side of the bowl toward the light by a glass partition across the bowl. The partition and covering were then removed. The time in seconds for all animals to be repelled by sunlight to the side of the bowl away from the light source was then determined. This procedure was followed with both black and white

paper beneath the finger bowl in order to vary the albedo factor.

To determine species differences in movements of amphipods towards a more fully shaded environment, bowls were covered and partitioned with animals on the side of the bowl away from the light source. The covering was then removed on all sides except for a portion of the side toward the light source. Thus, a partially shaded area was present in the bowl with light filtering around the edges. After one minute the animals that moved to this shaded area of the bowl were counted. This procedure was repeated twice for each species, and with both white and black paper beneath the bowls. A mean number was determined for each run.

Covered finger bowls containing 10-15 animals of each species were observed from time to time and served as controls for both light experiments.

All light experiments were performed with adult animals during the time of either rising or high tide immediately following collection of animals in the field during July 1965. It was hoped that in this way the effect of any tidal rhythm would be partially eliminated.

Initial observations showed that *N. schmitzi*, *Haustorius* sp. and *L. dytiscus* were quickly repelled by artificial light, but that *Pa. longimerus*, *Acanthohaustorius* sp. and *Pr. deichmannae* were not. Combined with a size difference, speeds of the photonegative responses for the first three species made it possible to separate mixed collections of amphipods simply by exposing them to light. Data in Table 12 show speeds of the photonegative response. *N. schmitzi* showed the most rapid negative response to sunlight, while all *Haustorius* sp. and *L. dytiscus* were repelled within 35 sec. No consistent difference in response was noted for a black or white background with these species.

Responses of *Pa. longimerus*, *Acanthohaustorius* sp. and *Pr. deichmannae* to sunlight were considerably different. Although all *Acanthohaustorius* sp. were finally repelled by sunlight after 70 sec, their subsequent behavior was similar to several *Pa. longimerus*. Animals of both species exhibited random movements, and while some animals moved away from the light, others moved towards it. *Pr. deichmannae* showed some photonegative response with a black background, but some random movements were apparent. Even after 2 minutes, individuals of *Pa. longimerus* and *Pr. deichmannae* remained on the lighted side of the container.

The numbers of animals of all species moving away from light to a shaded area of the container are shown in Table 12. *N. schmitzi* and *Haustorius* sp. again exhibited a strong photonegative response, while *L. dytiscus* and *Pa. longimerus* were almost equally distributed between lighted and shaded portions of the container. The latter two species behaved differently, however, after one min, since individual *L. dytiscus* moving to the shade stayed there, while *Pa. longimerus* again showed random movements. After one

TABLE 11. Substratum preference of amphipods.

	No.	Percent Silt In Substratum		No. Animals In		χ^2	df	P	Control ¹
		Cleaner	Silty	Cleaner	Silty				
<i>N. schmitzi</i>	36	1.4	2.3	30	6	24.0	1	<0.001	20, 16
<i>Haustorius</i> sp.....	36	1.4	2.3	30	6	24.0	1	<0.001	19, 17
<i>Pa. longimerus</i>	48	1.4	1.9	25	23	0.1	1	N.S.	24, 24
<i>L. dytiscus</i>	54	1.1	3.1	32	22	1.9	1	N.S.	33, 21
<i>Acanthohaustorius</i> sp.....	50	1.4	1.9	26	24	0.1	1	N.S.	27, 23

¹Number of animals found in separate halves of containers; containers randomly halved.

TABLE 12. Speed and frequency of a photonegative response by amphipods.

	No.	Ave. length mm.	Color of Substratum	Mean Number of Animals in Shaded Area after 1 Minute	Time in Seconds for All Animals to be Repelled by Sunlight
<i>N. schmitzi</i>	24	2.77	White	24	20
			Black	24	8
<i>Haustorius</i> sp.....	24	4.52	White	20	30
			Black	24	35
<i>L. dytiscus</i>	24	2.81	White	14	28
			Black	14	28
<i>Pa. longimerus</i>	24	4.38	White	13	11 still on lighted side after 2 min.
			Black	13	4 still on lighted side after 2 min.
<i>Acanthohaustorius</i> sp.....	20	2.89	White	5	70 and random movements
			Black	3	70 and random movements
<i>Pr. deichmannae</i>	24	2.67	White	8	21 still on lighted side after 2 min.
			Black	9	10 still on lighted side after 2 min.

min, few *Acanthohaustorius* sp. and *Pr. deichmannae* were present in the shaded area of the container. No consistent difference in response was noted for a black and white background with the six species.

Amphipods of all species kept in covered finger bowls with no substratum, and used as controls, moved about randomly.

TOLERANCES

SURVIVAL IN DRY AIR. Tolerances of amphipods to dry air was investigated by performing comparison experiments using the closed sequential test design described by Cole (1962). This design is efficient for detecting gross differences between organisms, and is a standard nonparametric test. An animal of one species was chosen at random, and an animal from a second species was then matched with it for similar size. Each animal was lightly blotted and placed in a dry watch glass under a constant temperature of 26.5 ± 1.5°C and a relative humidity of 46.5%. Both animals were observed, and the time noted when no heartbeat could be detected under a dissecting microscope. The animal living the longest was considered to have "won". Either a specific number of wins, losses, and ties necessitated accepting the hypothesis of tolerance equality, or the number of comparisons

TABLE 13. Tolerances of amphipods to dry air.

Species Combinations	Ave. Length mm.	"Survival" time min.	Greater Tolerance	No. Comparisons Required ¹
<i>N. schmitzi</i> v. <i>Acanthohaustorius</i> sp.	2.74	15 ²	<i>N. Schmitzi</i>	7
v. <i>L. dytiscus</i>	2.46	9	Tie	17
<i>Haustorius</i> sp. v. <i>Pa. longimerus</i>	2.75 4.30 4.38	15 ³ 25 ² 20	<i>Haustorius</i> sp.	7

¹To accept or reject hypothesis of tolerance equality at $P = 0.05$

²But recovery of most animals after return to sea water

³Some animals exhibited heartbeat on return to sea water

required to reject the hypothesis of equality at $p = 0.05$ was noted.

Data in Table 13 show results of comparison experiments for the five abundant species. Average survival time appears to depend on the size of animals as indicated by their length. However, the comparison experiments do show that *N. schmitzi* and *Haustorius* sp. were more tolerant to drying than *Acanthohaustorius* sp. and *Pa. longimerus*, respectively. Only seven comparisons were necessary to reject the hypothesis of equality, i.e. the first two species "won" every time when compared against the second two species. *N. schmitzi* and *L. dytiscus* were equally tolerant of experimental conditions.

N. schmitzi, *Haustorius* sp. and *L. dytiscus* generally remained in a curled position until late in the experiment. *Pa. longimerus* and *Acanthohaustorius* sp. usually stretched out early during experimental runs, and were less active near the end of the experiments than the first three species. In addition, when individual *N. schmitzi* and *Haustorius* sp. had "died", i.e. there was no perceptible heartbeat, and were returned to sea water to check for sex, a heartbeat and movement of appendages resumed in most animals. One female *Haustorius* sp., 4.0 mm long, survived 18 min drying, was returned to sea water, and lived for one week. Similarly, several female *N. schmitzi*, 2.5-2.75 mm long, surviving an average of 20 min drying, were returned to sea water, and lived for several months.

HIGH TEMPERATURE. These experiments focused on investigating two phenomena: 1) the extension of *N. schmitzi* to extremely high levels on the beach where the species was exposed to considerably high temperatures during summer, and 2) the apparent movement of *Pa. longimerus* to lower tidal levels during summer months at Sapelo Beach. Experiments were performed in a controlled environment chamber manufactured by Sherer-Gillett Co. of Marshall, Michigan. Relative humidity was controlled by the strategic placement of shallow pans of fresh water. Humidity of the air in the chamber was maintained between 28 and 50%, closely paralleling the relative humidity of air on the beach during several summer sampling trips.

Two types of experiments were performed, one with substratum present, the second without substratum. The first type was performed only with *Pa. longimerus*. Twenty-four adult amphipods were divided into groups of 8, and introduced into 3 small finger bowls containing a 2.5 cm layer of beach sand and sufficient sea water of 27‰ salinity to saturate the sand. Two uncovered bowls were placed in the chamber under daylight strength illumination and an air temperature of $40 \pm 2.0^\circ\text{C}$ for 7 hours. Temperature of the substratum was measured with a Yellow Springs, electric, Tele-thermometer. One uncovered finger bowl was placed in a laboratory room with a constant temperature of 26.5°C , and served as a control. After 7 hours amphipods were sieved from each substratum, and percent mortality was calculated as a mean of the two experimental runs.

Percent water remaining after exposure to experimental conditions was calculated by subtracting the weight of substratum and water after exposure, from the weight of the same two factors before exposure, and knowing the weight of dry substratum alone. The weight of amphipods was disregarded.

To observe more closely the reactions of *N. schmitzi* and *Pa. longimerus* to high temperatures, several experiments were performed with amphipods in small finger bowls containing sea water only (27‰ salinity). Thirty individuals of the former, and 24 individuals of the latter species were divided into three groups. Two groups of each species were exposed to

TABLE 14. Temperature tolerance of *Pa. longimerus* exposed to a substratum temperature of 36°C for 6 hours.

No.	Percent Weight of Water		Substratum Relative Humidity after Exposure	Percent Mortality
	Start	Finish		
8	20	14.0	>80%	25
8	20	15.7	>80%	75

TABLE 15. Temperature tolerance of *N. schmitzi* and *Pa. longimerus* exposed to 40°C in sea water.

Species	No.	Temperature and Exposure Time	Percent Mortality
<i>N. schmitzi</i>	20	36°C (20 min.), 40°C (2 hr.)	0
<i>Pa. longimerus</i>	16	37°C (15 min.), 30°C (few min.)	100

$40 \pm 2.0^\circ\text{C}$ in the chamber, while a third group of each species was placed in a laboratory room with a temperature of $26.5 \pm 1.50^\circ\text{C}$, and served as a control. The experimental groups were observed throughout the exposure period. Temperature of the water in the finger bowls was measured with a Yellow Springs, electric, Tele-thermometer. Maximum duration of exposure time was two hours after the water temperature had attained $40 \pm 2.0^\circ\text{C}$.

Survivors of both types of experiments were transferred to fresh sea water, fed periodically, and observed for three weeks. Several eggs were shed by surviving females during this observation period. Eggs were removed from the parental bowl, observed for viability, and placed in a watch glass containing fresh sea water. Sea water was changed daily, and eggs were observed for hatching or mortality.

P. longimerus placed in the environmental chamber with an air temperature of 40°C , were exposed to a substratum temperature of 36°C for 6 hours (Table 14). An average of half of the animals did not survive. There was no mortality of control animals.

Data in Table 15 show results of experiments when *N. schmitzi* and *Pa. longimerus* were exposed to 40°C in sea water and without substratum. All *N. schmitzi* survived exposure to 40°C for 2 hr in sea water. Activity of the animals was reduced after they were exposed to 40°C for 14 min. None of the *Pa. longimerus* survived after exposure to 39°C after several minutes, and several were sluggish after 45 min exposure to 37°C . There was no mortality of control animals.

Twelve hours after termination of the experiment, surviving female *N. schmitzi* shed two young. One female also died overnight, and three viable eggs were removed from her brood pouch. Subsequently, 22 developing eggs were shed by experimental females. Of these, 18 were viable, and 4 hatched. Juveniles lived for 1-2 days after hatching, and ingested detri-

TABLE 16. Population changes of three amphipod species during 60 days in a closed container.

Species	Population	No.	Percent of Species Composition by				Species % of Indicated Population
			Immature	Maturing Female	Mature Female	Male	
<i>N. schmitzi</i>	Original	93	5.4	5.3	85.0	4.2	61.2
	Dead	250	10.0	34.8	43.6	11.6	90.9
	Survivors	90	13.3	21.1	58.9	6.7	74.4
<i>Haustorius</i> sp.....	Original	41	21.9	44.0	2.4	31.7	27.0
	Dead	12	16.7	66.7	8.3	8.3	4.4
	Survivors	29	24.1	31.3	3.4	41.4	24.0
<i>L. dytiscus</i>	Original	18	0	0	27.8	72.2	11.8
	Dead	17	0	0	29.5	70.5	4.7
	Survivors	2	0	50.0	0	50.0	1.6

tus. Fungi and the ciliate *Vorticella*, covered many developing eggs despite water changes, and were probably partly responsible for high mortality of eggs. Surviving females lived for several months and were subsequently sacrificed.

CROWDING. To investigate the effects of crowding on three common species of amphipods from the upper beach, approximately 100-200 animals were collected from Sapelo Beach during June 1964, and placed in a large finger bowl (0.03 m² surface area) containing 1.5 cm of sand, and 3 cm of sea water. Sand and sea water were renewed every 5-6 days during a subsequent holding period of 60 days. Animals were removed from sand to be discarded by passing sand through a sieve with a 1 mm² mesh. Dead animals were removed from the population daily, and were identified, measured, sexed, and counted.

Fig. 20 and Table 16 show results of confining *N. schmitzi*, *Haustorius* sp. and *L. dytiscus* together in a closed container. The experiment began with 152 animals and ended with 121. From the beginning of the experiment through 60 days, many animals were observed swimming. This indicated the population was dense, since under less crowded conditions animals were rarely observed swimming.

Three distinct groups of *N. schmitzi* females were identified during the course of the experiment, and after analyzing length frequency data of dead animals. These groups were: 1) a larger, mature group with a mode at 3.5 mm, most of which died during the first month, and that shed young during the first 10 days of the experiment, 2) survivors of the new brood with a mode at death of 3.0 mm, contributing to mortality during the last half of the experiment, and that shed young about one month after the experiment began, and finally 3) survivors of this second brood contributing to mortality during the last half of the experiment (insert, Fig. 20). The contribution of young of these two broods to mortality can be seen at 11 and 35 days of Fig. 20. Despite the total contribution of *N. schmitzi* to the population increasing from 61.2% of the original population to 74.4% of the survivors, the species made up 90.9% of the total mortality, while female *N. schmitzi* made up 70.3% of the total mortality.

The mortality experienced by *Haustorius* sp. oc-

curred during the first 30 days of the experiment, and almost all during the first 24 days (Fig. 20). There was no reproduction, and a slight decrease in percent contribution of this species to the total population of survivors (Table 16).

The mortality experienced by *L. dytiscus* occurred during the first 20 days of the experiment (Fig. 20) and the species did not reproduce.

DISCUSSION AND CONCLUSIONS

The results indicate several ecological, behavioral, and physiological differences among the haustoriid species. Most of the five abundant species occurred at the three habitats, but their horizontal and vertical zonation were different. Differences were more clear-cut for some species than others, e.g. *Haustorius* sp. with greatest abundance at higher tidal levels and deeper sand layers, while *N. schmitzi* living at the same high tide levels inhabited more shallow sand, as compared with overlapping horizontal and vertical

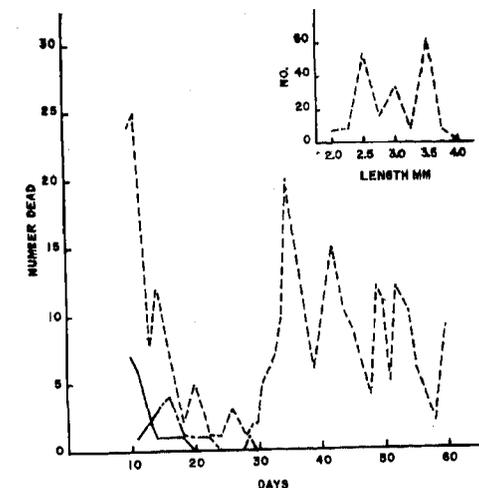


FIG. 20. Mortality of three amphipod species in a closed container, and length frequency of dead female *N. schmitzi* (insert). Solid line, *L. dytiscus*; dashed line, *N. schmitzi*; dot-dashed line, *Haustorius* sp.

distributions of *Pa. longimerus* and *Acanthohaustorius* sp. in the lower intertidal zone. The fact that zonation remained essentially the same throughout the year indicates that differences were real, and that the sampling design was adequate, since standard errors were low, ranging from ± 2.1 -15.5 during the year for mean density estimates of 29.3-191.3 amphipods per 0.1 m².

The time of low tide when haustoriids were collected is a period of inactivity for the infauna of tidal flats (Vader, 1964), and my experience showed that the presence of individual species could be predicted at a particular tidal level during the year. In addition, the only haustoriid species collected free in the water was *N. schmitzi*. This is one of the most active species, and it was collected only in small numbers. Dexter (personal communication) however, reported the occurrence of several haustoriid species in plankton collections from North Carolina inshore waters. The available evidence indicates that southeastern U.S. haustoriids spend most of their time in predictable areas of the sand substratum.

Pennak (1942) in his study of interstitial marine copepods near Woods Hole, reported the great majority of individuals of each species ($n=50$) were restricted to a relatively narrow strip of beach, and that average tidal and wave movements had little effect on these distributional patterns. Wider beaches showed correspondingly wider zonation of the copepods. Similarly, Sapelo Beach and Blackbeard Creek showed wider zonation of haustoriids as compared with the narrower Dean Creek Beach. Unlike haustoriids, the majority of Pennak's copepods occurred below the 4 cm sand depth, and at higher tidal levels density maxima were below the 12 cm depth. Only at low tide level were maximum numbers in the top 4 cm of sand. Keith and Hulings (1965) reported a maximum depth of penetration to 10 cm for *Acanthohaustorius* sp., and an optimum depth of 5 cm. This species penetrated to a depth of almost 12 cm at the exposed habitat during summer, while its optimum depth appears to depend on habitat.

Pennak (1942) showed that deepest penetration of copepod species was at an exposed beach. This was also true for haustoriids. Haustoriids at the protected habitat did not penetrate the shallow black reduction layer at lower tidal levels during summer. Finally, Pennak reported approximately the same vertical distribution for all species of copepods at a particular habitat. Data for haustoriids indicate that differences in vertical zonation exist for *N. schmitzi* and *Haustrorius* sp., and perhaps for *Pa. longimerus* and *Acanthohaustorius* sp. where they occur together in abundance.

With few exceptions, no significant segregation of amphipods by sex or size was apparent. This would indicate that life stages of individual species may be considered as an ecological unit, and that regions of the intertidal zone showing maximum densities for a particular species possess adequate environmental characteristics for that species.

Relative abundances of all haustoriids at the three habitats were high during the year, numbering 1565, 2132, 1693, and 2750 for mid-spring, summer, fall, and early spring, respectively. Newcombe (1935) reported large numbers of gammarid amphipods in sandy intertidal Canadian beaches during all seasons, and that seasonal fluctuations of infauna were not pronounced. MacGinitie (1939) believes marine littoral communities show a relatively low rate of change, but I believe that size and life span of individual species in a particular association should be considered before decisions are made concerning the presence or absence of significant fluctuations. This is especially important when attempting to correlate population changes with environmental changes.

Haustroriid populations showed lowest densities at the exposed and tidal creek habitats during fall (Table 2) while the population at the protected habitat steadily increased through the year. A decrease in densities at the exposed and tidal creek habitats followed passage of two hurricanes through the Sapelo-Blackbeard area. Obvious truncation of horizontal zonation of amphipod species occurred at this time at the exposed habitat. Truncation was not obvious at the other two habitats, although densities of *N. schmitzi* decreased considerably at all habitats from summer through fall. Any mortality due to storms was probably accompanied by a normal mortality of older female animals, since the life span of this species is one year or less. Normal mortality of other species must also be considered. Changes in beach morphology other than those due to severe storms are probably not important in determining the general pattern of distribution and abundance of haustoriid species on Georgia beaches. Seasonal changes in beach morphology are not significant, and may generally be similar to daily changes that correspond with changes in wind and tidal amplitude (Pilkey and Richter, 1964; Greaves, unpublished).

Lepidactylus dytiscus was most abundant at mid-tide levels, with some extension above and below and made up almost one-half of the total number of haustoriids collected at the three habitats. *N. schmitzi* and *L. dytiscus* together made up 78% of the total haustoriid fauna, and together with *Acanthohaustorius* sp. made up 86%. Each species exhibited highest densities at one habitat, and contributed to principal density variations of haustoriid populations at particular tidal levels during the year. Life history aspects of the three species were important for the events described. *N. schmitzi* and *L. dytiscus* produced broods in spring and summer, and abundances of both species remained high accordingly. *Acanthohaustorius* sp. produced fall and winter broods that increased the density of the haustoriid population in the lower intertidal zone. *L. dytiscus* and *Acanthohaustorius* sp. are southern species; their densities in the Georgia intertidal zone are at least average. *N. schmitzi* is near its southern geographic limit in the western Atlantic Ocean; its densities are at least not maximum. Dexter (personal communi-

cation) reports *N. schmitzi* may reach as high as 700 per 0.1 m², and averages about 70 per 0.1 m² through the year in the Beaufort, North Carolina area.

Pearse *et al.* (1942) reported haustoriids were more abundant on inundated shoals as compared with open sea beaches in the Beaufort, North Carolina area. On shoals maximum densities were found from mid- to high tide levels, while in ship channels, and on open sea beaches maximum densities were found at low tide level, or subtidally. Burbank (personal communication) reported abundant haustoriid populations on northern sandy shores of the estuarine Lake Pontchartrain, Louisiana. Bishop (1960) reported haustoriids were most abundant at two most brackish locations (to 138 per 0.1 m²) and near Hatters Inlet on the lee side of sand bars (75-80 per 0.1 m²). At fifteen other locations behind the outer banks of Pamlico Sound, haustoriid densities were less than 1.0 per 0.1 m². Bishop also reported haustoriids occurred commonly at high levels at locations with an average salinity greater than 17‰, and dominated the fauna over the whole tidal range, as well as subtidally, at highly brackish locations with an average salinity of 11‰. Lack of identification of haustoriid species in both these investigations precludes precise comparison with the present study, but several general comparisons can be made. Haustoriid densities in the Sapelo-Blackbeard area were highest at the protected, slightly more brackish habitat, and at higher tidal levels at this habitat. Higher densities were contributed primarily by *L. dytiscus*. The three habitats in Georgia probably all have yearly average salinities higher than 17‰ (Hoese, personal communication) and haustoriids dominated the macrofauna not only at high tide level, but over the whole tidal range.

The presence of silt and debris in sand at the three habitats indicated a departure from a typical ocean sand beach habitat and is reflected by the fauna. *D. variabilis*, the most abundant associated species especially at the more exposed habitat, is more abundant and reaches a larger size (up to 24 mm) on more surf-swept beaches. Fewer *Donax* are present on more protected beaches (Pearse *et al.*, 1942; Loesch, 1957). *D. variabilis* on Sapelo-Blackbeard beaches ranges in size from 2.0-11.0 mm, and most animals are smaller than 5.0 mm. These animals are apparently immature, and larger adult animals are rare. Fluctuations of this species are common, and except for the increased density of this species at the more exposed habitat during the fall through early spring, population densities of associated fauna at the three habitats were quite similar. *C. major*, the ghost shrimp, occurred at the three habitats, but was not represented in samples; the species is an indicator of muddy sand (Dahl, 1953). Southward (1965) mentioned the complete absence of molluscs on a European coarse sand beach, and the presence of the molluscs *Macoma baltica* and *Tellina tenuis*, as well as the polychaetes *Nereis diversicolor* and

Scoloplos armiger as additional associates of the haustoriid *Urothoe grimaldi* on a European muddy sand shore. On a coarse sand shore, four additional haustoriids (*Bathyporeia*) replaced *Urothoe*. Hartman (1945) listed *Nephtys picta* and *Laonereis culveri*, along with species of *Scoloplos* and *Heteromastus* as inhabitants of muddy, or debris-laden shores. Finally, the amphipod genus *Corophium* may indicate departure from a clean sand substratum (Elmhurst, 1931; Southward, 1965).

There is little information concerning macrofaunal associates of haustoriid amphipods in the western Atlantic Ocean. Species of genera previously reported as associates of haustoriids in North Carolina or Texas, and collected during this study include: *D. variabilis*, *Tellina*, *L. culveri*, *N. picta*, *Paraonis*, *Chiridotaea*, and *Emerita talpoida*. The bivalves *Mulinia* and *G. gemma* are associates of haustoriids in North Carolina, Georgia and Texas, but were not collected during this study (Pearse *et al.*, 1942; Bishop, 1960; Keith and Hulings, 1965).

Several feeding types are represented among faunal associates of haustoriids in Sapelo-Blackbeard sand beaches. Of the five abundant associated species, *D. variabilis*, and perhaps *Monoculodes* sp. are filter feeders, *Scoloplos* sp. and *Scololepis* sp. are deposit feeders, and *C. caeca* is a scavenger-chewer (Pearse *et al.*, 1942; Nicol, 1960). Although *D. variabilis* occurred from high- to low tide level, it was found primarily below mid-tide level. *Monoculodes* sp. was abundant over the whole tidal range. *Emerita talpoida*, *Ogyrides alphaerostris*, *Pinnixa chaetoptera*, *Corophium* sp., and *C. major* are filter feeders, and occurred either at low tide level, in tide pools, or in seepage areas. The remaining associates ($n=15$) occurred in small numbers (0.5-1.0 per 0.1 m²) and are either carnivores, scavengers, deposit feeders, or more subtidal filter feeders. Ninety-five % of these occurred below mid-tide level. Thus, by far the majority of associated species occurred in the lower half of the intertidal zone at the three habitats. The five abundant haustoriids are filter feeders, and considered as a group they showed quite a different zonation pattern. About 85 % of all haustoriids was contributed by *L. dytiscus*, *N. schmitzi*, and *Haustrorius* sp. These three species occurred primarily in the upper two-thirds of the intertidal zone at the three habitats. This relatively strong habitat isolation of filter feeding associates from three abundant haustoriid species, and partial isolation of higher and lower level haustoriids from each other, are interpreted as factors reducing competition for space and food. The differences between haustoriids are particularly important since haustoriids ingest similar types of food.

Instances where closely related animals are dependent on the same food are often accompanied by differences in animal size, or in the size of feeding appendages (Lack, 1944, 1949; Klopfer, 1962). Titmice (*Parus*) co-occur in the same habitat rarely, but when they do, one species is 1.6-2.0 times larger

than the other (Dixon, 1961). Hutchinson (1959) showed that ratios between the characters that determine the nature or size of food of co-occurring species of invertebrates and vertebrates ranged from 1.2-1.4, and that a mean ratio of about 1.3 may indicate the kind of difference permitting co-occurrence of two species at the same trophic level. The data for haustoriids show that a pair of species, one large and one small occurs primarily in the upper intertidal zone (*Haustorius* sp. and *N. schmitzi*), and in the lower intertidal zone (*Pa. longimerus* and *Acanthohaustorius* sp.), while an intermediate-sized species occurs primarily at mid-tide level (*L. dytiscus*). Ratios for mean lengths of haustoriid species pairs ranged from 0.93-1.87, and averaged 1.33 during the year. Average ratios were slightly higher for species pairs exhibiting frequent strong co-occurrence at particular tidal levels, and slightly lower for species pairs exhibiting strong habitat isolation and/or highest densities in different habitats. It should be stressed that horizontal zonations of all haustoriids overlapped to some degree during the year at the three habitats, and that lowered tolerances to high temperature or desiccation should be considered for certain species pairs, e.g. *Pa. longimerus*/*N. schmitzi*, *Haustorius* sp./*Acanthohaustorius* sp. The ratios may be tentatively used as an indication of the kinds of size differences permitting the co-occurrence of the haustoriid species at the same trophic level.

There is some indication that despite a considerable overlap in the types of food, that haustoriids ingested different sized particles. It would be expected that while smaller species might utilize smaller particles, that larger species might utilize small and large particles (MacArthur, personal communication). Lack (1961) discussed this phenomenon in his study of Darwin's finches, i.e. when two closely related species co-occur they do not usually take completely different foods, but it is sufficient if some of their foods are different. Studies on sympatric *N. schmitzi* and *Haustorius* sp. in North Carolina (Croker, in press) showed that both species ingested materials considerably larger than the internal dimensions of the filter apparatus, although *Haustorius* sp. ingested interstitial invertebrates and larger plant remains that the smaller *N. schmitzi* did not. Thus, size differences between these two co-occurring species at least, appear to be reflected in the size of the foods.

None of the haustoriid species were observed feeding on large solid food particles in laboratory experiments. Dennell (1933) reported similar observations for *H. arenarius*. Frankenberg et al. (1967) observed that *Pa. longimerus* and *N. schmitzi* did not extensively utilize solid *Callinassa* fecal pellets in laboratory experiments, while pagurid crabs did. Laboratory experiments performed during the present study leave little doubt that the five haustoriid species are filter feeders. Dennell (1933) came to the same conclusion for *H. arenarius*. This haustoriid fed grossly like Georgia haustoriids, i.e. the currents produced by the pleopods and other appendages was

followed by food entering the intestinal tract. Dennell (1933) reported that the flow of water entering and leaving the "food basin" was controlled by setae on the maxillae, with the maxillipeds removing food particles from the maxillae, and passing them forward to the mouth.

Size ratios of the five abundant haustoriids have additional implications for a potential reduction or avoidance of competition between the sympatric species. The maintenance of size differences and ratios is supported by the staggering of reproductive peaks. Hutchinson (1959) discussed the importance of this phenomenon for different animal groups. For birds or mammals, where the growth period is short compared with life span, he postulates that niche separation may be possible simply through genetic size differences, while in insects with relatively longer growth periods, a seasonal difference in reproduction might be important. For the maintenance of size ratios, the larger species must reproduce earlier and/or live longer to remain larger. Reference to the reproductive peaks shows that for the upper and lower intertidal co-occurring species pairs this is true, i.e. *Haustorius* sp. and *Pa. longimerus* reproduce earlier and live longer than the smaller *N. schmitzi* and *Acanthohaustorius* sp.

Actual interspecific competition is difficult to observe among animals, and the haustoriids are no exception. The importance of the staggering of peak reproductive periods in decreasing potential competition is illustrated however, in the laboratory crowding experiment. High mortality of reproducing *N. schmitzi* resulted while co-occurring with the larger *Haustorius* sp. and *L. dytiscus*. The shallow sand layer in the container did not permit the vertical separation between *Haustorius* sp. and *N. schmitzi* usually observed in the field. The species confronted each other in a shallow vertical niche dimension, and *N. schmitzi* was observed constantly coming up out of the sand. A confrontation of two or more species in peak reproductive condition might have resulted in even higher mortality of young females and immatures. The staggering of the reproductive periods may be considered as an additional safety factor since: 1) the horizontal and vertical distributions of some species overlap more than others, 2) some areas of the intertidal zone have restricted dimensions available for habitation due to accumulation of shell, the presence of a shallow black reduction layer, or the presence of otherwise unsuitable substrata.

The differences in fecundity and sex ratios between the five abundant species were discussed. Cole (1957) discussed several ways in which natural selection might alter the life history of a species to increase the biotic potential (r). For related sympatric species the operation of these factors are important. These factors and examples of their operation in the haustoriid populations are:

1) Larger broods—*Pa. longimerus*, *Haustorius* sp. and *Acanthohaustorius* sp.

2) Closer spacing of broods in time—*L. dytiscus* and *N. schmitzi*

3) Earlier maturation—*N. schmitzi*, *L. dytiscus*, and *Acanthohaustorius* sp.

4) Increased survival to the end of reproductive life—*Pa. longimerus* and *Haustorius* sp.

5) Increase in the number of females—*N. schmitzi* and *L. dytiscus*

Cole (1957) refers to the advantage gained by a species that increases brood size if it matures early. Reference was made to the fact that the spring fecundity of *N. schmitzi* was higher than subsequent seasonal fecundities. Here the species is not gaining greatest benefit from the fecundity increase since greatest benefit would be gained by initial small litter size. Perhaps with *N. schmitzi* the enormous increase in the number of females overweighs any possible disadvantage. Marshall (1949) described a similar situation where males were rare in populations of the marine copepod *Oithona similis* in Loch Striven. The females made up 87-98% of the population during the year, and males were almost absent in late winter. Similarly, Burbank (personal communication) reported the disappearance of males during the summer in populations of the estuarine isopod *Cyathura polita*.

The results of high temperature and desiccation tolerance experiments indicated different temperature tolerances for a lower—(*Pa. longimerus*) and higher (*N. schmitzi*) intertidal haustoriid. Their importance is strengthened by reference to the time-temperature profiles in the field. On hot summer days, temperatures at sand depths (2.5-5.0 cm) where *Pa. longimerus* lives never increased above 34°C for 3 hours in the lower intertidal zone. Temperatures of 39°C and above were regularly measured in the upper 2.5 cm of sand at high tide level. *N. schmitzi* remained at this depth during temperature measurements, as indicated by the collection of the species at this time. The importance of the experimental data for *Pa. longimerus* is further strengthened by reference to the complete absence of this species from the tidal creek habitat, and the indicated seaward movement of the species during summer at the exposed habitat.

Further work is needed for the haustoriids concerning the relationship between temperature tolerance and salinity. Present experiments were performed with one salinity (27‰) while Kinne (1959) discussed temperature tolerances, and stressed that time of survival depends on salinity, e.g. for *G. duebeni* survival is longer at higher salinities for a particular temperature. The experimental salinity for the temperature experiments described here was close to the probably average salinity at the three habitats (25.3-30.1‰). For this reason, the mortality data may be conservative, since even higher mortality might be expected at lower salinities.

Early work by Bruce (1928) and Linke (1939), and a recent paper by Johnson (1965) indicated

that sand substrata act as a buffer against marked temperature changes. Studies on sand beaches show a very sharp gradient in the upper 5.0 cm, with a very slow change after that (Moore, 1958; Croker, unpublished). Temperatures of sub-surface sands also varied less than air temperatures 0.5 cm above the sand during the present study. Also, as sand becomes wetter its heat capacity and thermal conductivity increases (Geiger, 1965). Thus, when wet sand at lower levels is exposed to a hot sun at low tide, temperatures can be higher (for short periods) than those measured in drier sands at higher levels (Croker, unpublished). Johnson's (1965) work indicates that temperature variations in intertidal sand flats resemble those observed in terrestrial soils, with those animals living in the upper one cm exposed to a daily temperature range as great as 3 times that experienced by subtidal individuals. Johnson reported that 70% of the animals on sand flats in Tomales Bay, California were found at depths greater than 5 cm, although his field samples included only those animals larger than 3 cm. The remarkable temperature tolerance of the upper intertidal haustoriids is indicated by the fact that the majority of the individuals of the three species, *N. schmitzi*, *L. dytiscus*, and *Haustorius* sp., ranging in length from 2-7 mm, inhabited sand depths less than 4 cm during summer where sand temperatures remained as high as 36°C for 2 hours.

In general, there is a tendency for those animals living highest on the shore, or those that are most terrestrial, to have the highest lethal temperatures (Broekhuysen, 1941; Evans, 1948; Southward, 1958; Edney, 1951). Broekhuysen (1941) described this relationship for South African gastropods, while Southward (1958) discussed the strong correlation between higher level occupied and higher tolerance to high temperatures for barnacles. As Southward (1958) stresses, although the temperatures on most shores appear to be well within the tolerance limits of most animals, extreme temperatures for longer periods of time can be lethal especially if a species is near its limit to high temperatures. The haustoriid *Pa. longimerus* is near its southern limit, and this may be important for the experimental results already described.

Field measurements indicated that relative humidities in the substratum were normally greater than 80 percent (maximum range of the paper indicators). The five haustoriid species inhabit an environment saturated with water vapor, but sand can be turned up by man, birds, or other foraging animals when the haustoriids would be exposed to potentially lower relative humidities. Desiccation tolerance experiments indicated that higher intertidal species are more capable of survival under these conditions than lower intertidal species. Furthermore, two important effects of desiccation, a failure to coordinate limb movements, and falling on one side (Williamson, 1951) were observed earliest for the

two lower intertidal species, *Acanthohaustorius* sp. and *Pa. longimerus*.

Behavioral experiments showed some similarities between the haustoriids: similar borrowing and feeding behavior (except for *Pr. deichmannae*), and inability of all species to burrow in dry sand; and some differences: 1) generally higher activity of *N. schmitzi* and *Haustorius* sp. as compared with other species, 2) choice of "cleaner" substratum over more silty substratum for *N. schmitzi* and *Haustorius* sp. as compared with no clear choice for *Pa. longimerus*, *L. dytiscus*, and *Acanthohaustorius* sp., and 3) relatively strong, and quicker photonegative response of *N. schmitzi*, *Haustorius* sp. and *L. dytiscus* to sunlight as compared with *Pa. longimerus*, *Acanthohaustorius* sp., and *Pr. deichmannae*. The results indicate a more stereotyped behavior pattern for the three lower intertidal species, *Pa. longimerus*, *Acanthohaustorius* sp., and *Pr. deichmannae*.

Klopfer (1962) interpreted behavioral stereotypy as a reduction in the size of the niche volume, i.e. the range of objects in the environment to which the animal responds is reduced. This hypothesis is supported by several other pieces of evidence concerning the three lower intertidal species. *Pr. deichmannae* is considered the most primitive member of the subfamily; any specialization it possesses is for subtidal, not intertidal existence. *Pa. longimerus* showed highest densities at the exposed habitat, rare occurrence at the tidal creek habitat, and complete absence at the protected habitat. The species is specialized for existence in the lower intertidal zone, and appears to require relatively more exposed surf habitats. *Acanthohaustorius* sp. occurred at all three habitats in the lower intertidal zone, but exhibited highest densities at the tidal creek habitat. This species also ranges sub-tidally, and rarely traverses the shore to mid-tide level unless permanently wet areas are available. These three species generally exhibited the narrowest horizontal zonation; a reduction in the spatial dimensions of their niches is also indicated.

Preference for cleaner sand over more silty and debris-laden sand (including shell) by *N. schmitzi* and *Haustorius* sp. observed in laboratory experiments, was paralleled by distribution in the field. Higher levels of habitats where abundant concentrations of these species occurred were relatively free of silt and debris. Meadows (1964) demonstrated contrasting preferences of the amphipods *Gorophium volutator* for mud, and *C. arenarium* for sand, each species choosing the type of substratum in which it was found abundantly in the field. Increased shell deposition at higher levels on Sapelo Beach may have been partly responsible for the decreased abundance of *N. schmitzi* at higher levels during early spring. The fact that *N. schmitzi* and *Haustorius* sp. were able to inhabit the intertidal zone from high tide level to below mid-tide level, in addition to any substratum preference, indicates that these two species were confronted with a relatively wide choice

of suitable substrata. Wieser (1956) commenting on factors influencing the choice of substratum by the eumacean, *Cumella vulgaris*, cited the importance of orthokinetic movements that kept animals agitated and swimming as long as suitable substrata were not present. Forsman (1938) reported that the eumacean, *Diastylis rathkei* seldom swam, but rather plowed through the substratum. The former behavior was observed for haustoriids in crowded populations, or when laboratory containers contained large quantities of shell or debris. The latter behavior was observed more frequently for all haustoriid species.

In regard to light, most crustaceans show positive or negative reactions; indifference is relatively rare. Although some crustaceans are positive or negative over a wide range of light intensities, the majority are positive in dim light, and negative in very bright light. At medium energy levels, some are positive and others are negative (Waterman, 1960). Dennell (1933) reported *H. arenarius* was positively phototactic when a light beam was directed at a swimming animal. *Haustorius* sp. and *N. schmitzi* exhibited strong negatively phototactic responses to sunlight during this study, while *L. dytiscus* exhibited a weaker negatively phototactic response. The three lower intertidal species, *Pa. longimerus*, *Acanthohaustorius* sp., and *Pr. deichmannae* exhibited some very weak negative responses, but mostly moved randomly. Further work at different light intensities is required.

The discussion considered some of the differences among sympatric haustoriids, and characteristics of their fundamental niches. Mayr (1963) discussed ways in which related sympatric species have either reduced or avoided competition, and considered two categories: conspicuous and subtle. Laock (1944), in an analysis of British songbirds, concluded that 21 sympatric situations had conspicuous differences (3 geographical, 18 habitat), while subtle differences were identified in 11-13 situations. Conspicuous factors as applied to haustoriids would include: presence in different habitats, temporal isolation of potentially competing life stages by staggering of the reproductive periods. Subtle factors would include: horizontal and vertical zonation, behavioral stereotypy, tolerances to high temperature and desiccation, substratum preferences, and fecundity and sex ratio differences acting to increase the biotic potential.

As Mayr (1963) stresses, it is tempting to say that differences between sympatric species are responsible for their coexistence. Differences shown for haustoriids probably have varying degrees of importance for reducing or avoiding competition, and further work is required to indicate their operation under varying environmental conditions and population densities. Continuing systematic and ecological work should also provide important evidence for lines of diversification within the Family Haustoriidae. Hopefully, this will provide some information concerning differences between sympatric species that are the result of divergence after establishment of sympatry, and those differences that were acquired during the

presumed preceding geographic separation. Despite overlap, differences may be considered as secondary isolating mechanisms that contribute to optimal adaptation to respective niches, and reinforce separation of species (Mayr, 1963). Within the framework of the flexible Huxelinsonian fundamental niche, one expects variable responses of species to environmental conditions with some habitats, or parts of a habitat optimum for occurrence of a particular species. Overlapping differences among haustoriids should be viewed in this way, so that any potential or actual competition for resources would be lessened by differences in habitat selection functioning through different physiological responses of species, and their small size allowing adaptation to micro-elements of the environment.

SUMMARY

1. Sympatric associations of seven haustoriid amphipod species were studied on Sapelo- and Blackbeard Island, Georgia marine sand beaches to determine differences among species. Five species were stressed: *Neohaustorius schmitzi*, *Lepidactylus dytiscus*, *Parahaustorius longimerus*, *Haustorius* sp., and *Acanthohaustorius* sp. Two other species briefly considered were: *Pseudohaustorius caroliniensis*, and *Protohaustorius deichmannae*.

2. Haustoriid populations at three intertidal sand beaches with varying degrees of exposure to surf were sampled during all seasons of the year yielding 8138 amphipods. The three habitats differed significantly from a typically clean sand beach, and this was reflected in faunal associates of the amphipods. Except for periodic severe storms, daily and seasonal changes in beach morphology at the three habitats were similar. Population fluctuations following passage of two hurricanes were also correlated with normal mortality of abundant species.

3. Haustoriid amphipods were numerically dominant members of the macrofauna at the three habitats. Densities of all haustoriids ranged from 29.3-191.3 per 0.1 m² during the year, and mean densities at a more brackish, protected habitat were about two- and one-half times greater than those at an exposed- and tidal creek habitat. Most haustoriids inhabited the upper 4 cm of sand.

4. Most of the five abundant species were present at the three habitats, but differed in horizontal zonation that remained relatively constant through the year. With few exceptions, no significant segregation of amphipods by size or sex was apparent. Differences in vertical zonation were most apparent for two pairs of species co-occurring in the upper- and lower intertidal zone. Haustoriids appear to spend most of their time in predictable areas of the sand beach; few were found swimming in the surf.

5. Three species, *L. dytiscus*, *N. schmitzi*, and *Acanthohaustorius* sp. made up 86% of the total haustoriid fauna, and *L. dytiscus* made up almost 50%. These species showed highest densities at the protected-, exposed-, and tidal creek habitats, re-

spectively, and strongly influenced population densities.

6. A total of 347 animals in 6 phyla, 25 genera, and 25 species were faunal associates of haustoriids. Mean densities of associates ranged from 0.5-14.8 per 0.1 m² during the year, with five species most abundant: *Donax variabilis*, *Scoloplos* sp., *Chiridotaea caeca*, *Scololepis* sp., and *Monoculodes* sp. Most associates occurred in the lower intertidal zone, and most filter feeding associates were restricted to low tide level, or permanently wet tide pool areas.

7. Three haustoriids, *L. dytiscus*, *N. schmitzi*, and *Haustorius* sp. made up 85% of the haustoriid fauna, and occurred primarily in the upper two-thirds of the intertidal zone. Partial habitat isolation of filter feeding associates, and of haustoriids from each other, were interpreted as factors reducing competition for space and food, since haustoriids are also filter feeders.

8. The majority of gut contents of haustoriids was contributed by *Spartina* detritus, with smaller amounts of diatoms, algae, and protozoans. There was a tendency for larger haustoriids to ingest larger detrital particles.

9. Size relationships among haustoriids were studied by calculating ratios of mean lengths of species. Ratios ranged from 0.93-1.87, and averaged 1.33 during the year. They were slightly higher for strongly co-occurring species pairs, and slightly lower for species pairs showing strong habitat isolation and/or highest densities in separate habitats. The ratios indicate the kinds of size differences permitting co-occurrence of haustoriids at the same trophic level.

10. Size ratios between haustoriids were maintained by staggered reproductive periods, with larger species in the upper and lower intertidal zone reproducing earlier than smaller species there. These factors are interpreted as supporting a temporal isolation of potentially competing life stages.

11. Haustoriids possess several different ways of increasing their biotic potential: larger broods, increased survival to the end of reproductive life, closer spacing of broods in time, earlier maturation, and increased number of females.

12. *N. schmitzi*, a high intertidal and smallest species, was tolerant of temperatures as high as 40°C for 2 hours, while *Pa. longimerus*, a low intertidal species near its southern geographic limit, experienced high mortality to temperatures of 36°C for 6 hours, and 39°C for several minutes. These results were correlated with time-temperature relationships in sand substrata where the two species live in the field.

13. Desiccation tolerance experiments indicated gross survival differences between high- and low intertidal haustoriids, with low intertidal species showing earliest mortality at 46.5% relative humidity and 26.5°C, no recovery after reimmersion in sea water, and earliest loss of coordination.

14. Behavioral observations and experiments indicated a more stereotyped behavioral pattern for three lower intertidal haustoriids: *Pa. longimerus*, *Acanthohaustorius* sp., and *Pr. deichmannae*. Phylogenetic, distribution, zonation, behavioral, and abundance data indicate a reduction in niche size for these species in the intertidal zone.

15. Substratum preference experiments indicated a choice of cleaner- over more silty substrata for two high intertidal species, *N. schmitzi* and *Haustrorius* sp., and no preference for three other species. The results are correlated with typically cleaner natural substrata of dense concentrations of the two species.

16. Three higher intertidal species, *N. schmitzi*, *L. dytiscus*, and *Haustrorius* sp. exhibited a stronger, and more frequent photonegative response to sunlight as compared with lower intertidal species.

17. Differences between haustoriid species are considered as secondary isolating mechanisms, contributing to optimal adaptation to respective niches, and reinforcing separation of species. Overlapping niche characteristics including: horizontal and vertical zonations, reproductive cycles, fecundity, size ratios, food, and general behavior, are considered to indicate variable responses of species to environmental conditions existing over the range of their fundamental niches.

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PRODUCTION OF JUVENILE STEELHEAD TROUT IN A FRESHWATER IMPOUNDMENT¹

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INTRODUCTION

The purpose of this study was to investigate the population dynamics of juvenile steelhead trout (*Salmo gairdneri* Richardson) in an artificial freshwater impoundment of 13.3 hectares situated in Western Oregon. Data were collected from May 1962 until May 1963. The specific objectives of the investigation were (a) to determine the limnological characteristics of the pond, and (b) to make a detailed study of the dynamics of survival, growth, and production of the fish population. In the study of fish population dynamics, data were obtained on population size, growth and mortality rates, net production, and total yield. The feeding habits of the fish were studied and related to the standing crop estimates of the available food organisms.

The concept of rearing fingerling steelhead trout and Pacific salmon (*Oncorhynchus* spp.) in controlled impoundments is relatively new. It originated a few years ago in the northwestern regions of the United States as a reaction against the increasing civilization pressure on the natural areas suitable for salmonid production. Fresh and saltwater areas were set aside for producing smolts in one-year cycles.

Information on the production of steelhead trout is almost entirely restricted to lotic environments. Some data are available for lakes concerning *S. gairdneri* Kamloops Jordan (Mottley, 1940; Larkin *et al.*, 1950) and the resident *S. gairdneri* (Johnson and Hasler, 1954). Schäperclaus (1933) dealt with the pond culture of the latter.

Other salmonid species more intensively studied in lentic environments are the brown trout (*S. trutta*), the brook trout (*Salvelinus fontinalis*), and the coho salmon (*O. kisutch*). The brown trout was studied in Europe, particularly in Great Britain (Allen, 1938; Frost and Smyly, 1952; Swift, 1955; Ball and Jones, 1960), in Germany (Schäperclaus, 1933), and in Sweden (Nilsson, 1955). Recently, studies on brook trout were reported from the eastern United States (Hatch and Webster, 1961; Flick and Webster, 1964). Adequate information about the Pacific salmon species reared in ponds has been obtained mostly in Oregon (Rutz, 1958; Haas and Willis, 1962; Hansen and Mullarkey, 1963; Higley, 1963).

The first factually-based estimate of the production of a fish population was made by Ricker and Foerster (1948) studying the production of juvenile sockeye salmon (*O. nerka*) in Cultus Lake, B. C. Allen (1951) published an excellent study on the dynamics of a brown trout population in a New Zealand stream. Later, Johnson and Hasler (1954)

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