ZONAL AND SEASONAL DISTRIBUTION OF INSECTS IN NORTH CAROLINA SALT MARSHES[1]

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INTRODUCTION

Although their obnoxious insect inhabitants have received much attention, it seems to not be generally recognized that salt marshes support a diverse insect fauna. For example, in summarizing reports of insects from marine habitats, Usinger (1957) merely remarked that "Grassy salt marshes and Pickleweed (*Salicornia*) marshes are the favorite habitats of salt marsh mosquitoes throughout the world. Also under these conditions, particularly near high tide mark, biting midges of the genera *Culicoides* and *Leptoconops* occur." Salt marsh midges and mosquitoes are certainly very common in some instances, but usually are far outnumbered by other species of insects. One purpose of this paper is to demonstrate that salt marshes are a type of marine-influenced habitat in which insects are present in both great variety and abundance.

The work described here began in June, 1959, and continued for fifteen months. The facilities of the Duke University Marine Laboratory and the salt marshes in Carteret County, North Carolina were utilized. The main objective was to provide a basic description of the insect assemblages of each of the major types of zonally distributed associations that comprise these salt marshes. Because the ecology of salt marsh insects is poorly known, their habits, interrelationships, and interactions with other types of organisms were observed and recorded whenever possible. Only the insects that inhabit the herbaceous strata are considered here.

The only previous investigation of zonal distribution of insects in intertidal phanerogamic communities was carried out in New Zealand by Paviour-Smith (1956). She took cylinder samples at six points on a transect that passed across four zones of vegetation, and obtained animals from both the vegetation and the soil down to the depth of one centimeter. Her samples contained a wide variety of terrestrial insects, but most of these were subterranean or surface-dwelling forms. Only one species (the coccid, *Trionymus* sp.) occurred consistently in the herbaceous strata, and it was present in all four zones.

Literature dealing with salt marsh insects is extremely scattered. Much of its consists of brief notes, species descriptions, check-lists, and scraps of information from various other sources. Only a few papers deal particularly with the ecology of insects from the herbaceous strata of marshes of the North American coasts, and these will be referred to later.

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PHYSICAL AND CLIMATIC FEATURES OF THE STUDY AREA

The study area, Carteret County, North Carolina, occupies the major portion of a peninsula situated between the estuaries of the Neuse River and the New River. Offshore bars, called Outer Banks, protect the mainland from wave action. The bars are broken at intervals by inlets which connect the ocean to the shallow sounds that separate the Outer Banks from the mainland. The mainland coast of Carteret County is deeply indented by the estuaries of the North and Newport Rivers. Many small bays and creeks increase the complexity of the coastline (Fig. 1).

According to United States Coast and Geodetic Survey Tide Tables (1960), the mean range of tides at Atlantic Beach, on the ocean side of Bogue Banks, is 1.15 meters. The tidal range is less in the sounds, averaging 0.76 meters at Beaufort and 0.85 meters at Morehead City. Tidal fluctuations occur in the levels of nearly all creeks and rivers in the county. The range of spring tides is usually from fifteen to thirty centimeters greater than the mean range. Because much of the land adjoining the sounds, estu-

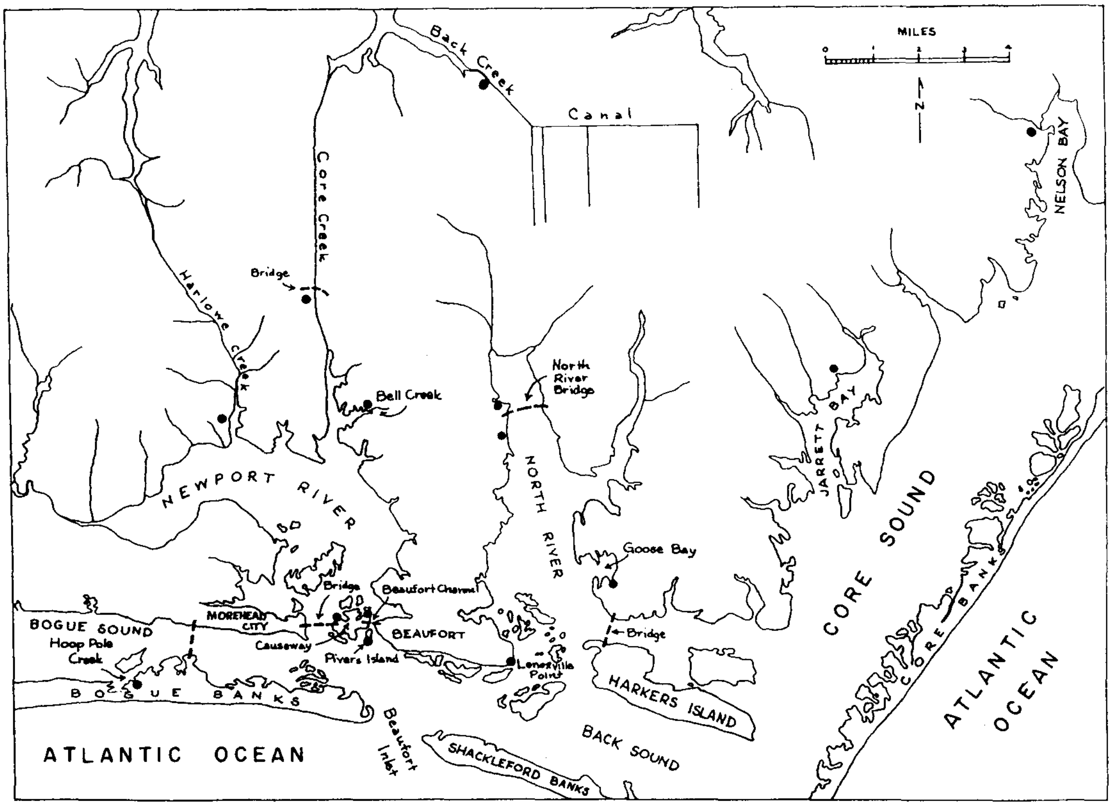

Fig. 1. Map of southeastern Carteret County, North Carolina, showing the locations of stations.

aries, and streams lies almost at sea level and is extremely flat, even this small increase in the tidal range floods much land that ordinarily remains dry at high tide.

The climate of the Beaufort area is classified by Trewartha (1954) as humid subtropical, with no dry season. United States Weather Bureau data (1960) reveal that the coolest months are usually January and February, with mean temperatures of about 7° C. However, in March, 1960, the mean temperature was only 5.6° C. Mid-summer temperatures average about 27° C. The total precipitation in 1959 at Morehead City was 131.85 cm, and in 1960 was 122.24 cm. Snowfall is infrequent, although three light accumulations of snow occurred in the winter of 1959-1960. Hurricanes strike the area frequently and cause unusually high tides, but none occurred while this study was in progress. During winter, strong northeast winds frequently push water down the sounds and flood thousands of acres of salt marshes.

SALT MARSH PLANT ASSOCIATIONS

Salt marshes cover a total area in Carteret County of nearly 56,000 acres (Perkins, 1938). Wave action prevents establishment of salt marshes on the ocean and estuaries, wherever there is sufficient deposition of mud, salt marsh usually gains a foothold. Almost every creek, canal, and small river is bordered by salt marsh to the limit of tidal influence.

The salt marsh associations of the North Carolina coast have been classified by Wells (1928) and Adams (1963). Adams' classification is more consistent with other studies of Atlantic coast salt marsh floras and is in much closer accord with our observations. He holds that there are three "low marsh" associations, and one "high marsh" association, all receiving their names from the dominant plants. The low marsh associations are: (1) *Spartina alterniflora*; (2) *Spartina alterniflora-Salicornia perennis-Limonium carolinianum,* hereafter referred to as *Spartina-Salicornia-Limonium*; and (3) *Juncus roemerianus.* The high marsh association is more complex and is named after its five dominants, *Aster tenuifolius-Distichlis spicata-Fimbristylis castanea-Borrichia frutescens-Spartina patens.* These associations form a zonal sequence, in the order given above, from below the mean high water level to above the level of the high spring tides. The distribution of the dominant salt marsh plants is determined primarily by the tide-elevation influences, especially hydroperiod, or the fraction of time during which the ground is inundated.

Adams' classification is simpler than the situation usually encountered in the field. To facilitate the discussion that follows, and to take into account the principal deviations from the ideal zonation given above, the tidal marshes of Carteret County are arranged in three sequences.

Along the borders of the sounds and estuaries, the slope of the shore in many places is comparatively steep because spoil from dredging operations has been dumped there. In such situations there is usually found a zonal sequence of *Spartina alterniflora* to *Spartina-Salicornia-Limonium* to high marsh dominated by *Spartina patens* (Fig. 2). Depending on the degree of shore slope, the *Spartina-Salicornia-Limonium* zone may be narrow or absent, and only a band of drift may separate the upper limit of *S. alterniflora* from *S. patens*. *S. patens* is always mixed with other plant species, especially *Borrichia frutescens*, *Strophostyles helvola*, and scattered bushes of *Iva frutescens*. This sequence is referred to hereafter as Sequence I.

Along the borders of many creeks, rivers, and canals, and occasionally along the borders of the sounds and estuaries, may be seen a second sequence (hereafter called Sequence II). This sequence consists of *S. alterniflora* to *Juncus roemerianus* to high marsh dominated by *Distichlis spicata*. The *Spartina-Salicornia-Limonium* zone is not ordinarily developed in this sequence except along the sounds and estuaries. The high marsh zone is often represented only by a very narrow belt located between extensive stands of *Juncus* and higher pine woods, but reaches its best development as enclaves on very low hummocks within *Juncus* stands. In areas of fresh-water seepage, stands of *Panicum virgatum*, *Cladium jamaicense*, or *Scirpus americanus* may occur immediately above *Juncus* and high marsh.

A third sequence is associated with creeks having low salinity and a high rate of silt deposition. *Spartina cynosuroides* replaces *S. alterniflora* in the lower zone of this sequence, and *J. roemerianus* occupies the higher zone. At these sites, high marsh is not ordinarily present.

The *Spartina alterniflora* association is intertidal, and occurs on ground that is regularly inundated twice daily. *S. alterniflora* is a grass, characterized by flat, succulent leaves, that often forms extensive pure stands in which conspicuous variation occurs

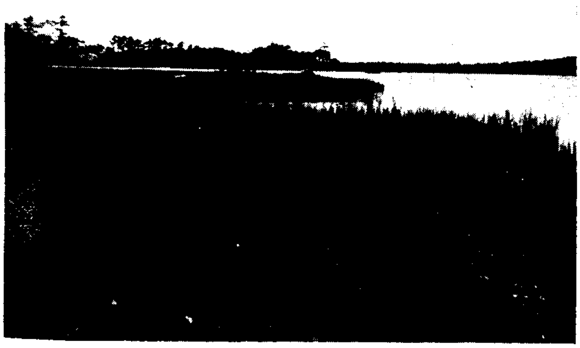

Fig. 2. Salt marsh zonal sequence showing *Spartina alterniflora* at the water's edge, and *Spartina patens* at the left. The intermediate area of short vegetation is the *Spartina-Salicornia-Limonium* zone.

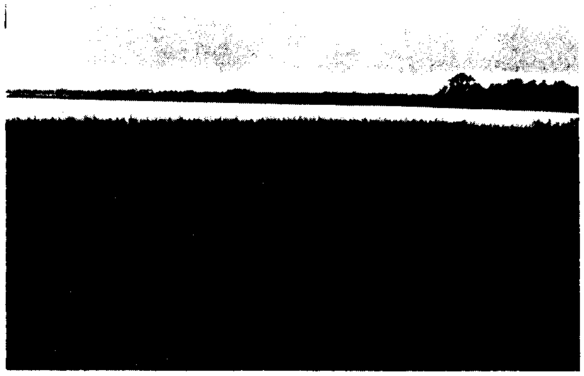

Fig. 3. A stand of *Spartina alterniflora*.

in the heights of culms growing at different elevations (Fig. 3). The extent to which the plants are submerged at high tide varies greatly, depending on the height of the culms, their elevation, and the level to which the tide rises. *S. alterniflora* is seldom entirely covered by water; usually the stems and leaves project fifty centimeters or more above the surface of the water even when the tide is highest.

S. alterniflora grades into the *Spartina-Salicornia-Limonium* association. *S. alterniflora* culms in this association are always quite short, less than fifty centimeters tall. *Salicornia* is a fleshy, leafless plant with branching green stems, and is usually less than thirty centimeters tall. *Limonium* is a branching herb with fibrous stems and sparse foliage; it is also usually less than fifty centimeters tall. This association occurs on ground that is inundated at irregular, but frequent, intervals. Spring tides often entirely submerge the vegetation.

The *J. roemerianus* association occupies extensive areas of flat ground that is reached by tides of above-average height. *J. roemerianus* is a tall (up to two meters) spike-tipped rush that forms nearly pure stands, but an understory of low herbs is sometimes present. The most extensive *Juncus* marshes in Carteret County are in the mainland coast above the *S. alterniflora* zone bordering Core Sound, and are a mile or so wide (Fig. 4). *Juncus* vegetation is

Fig. 4. An extensive stand of *Juncus roemerianus*.

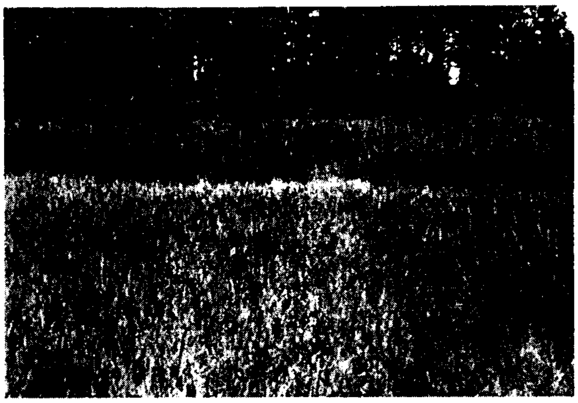

FIG. 5. A stand of *Distichlis spicata* (foreground), with *Juncus roemerianus* and pine woods in background.

seldom submerged for more than one-third of its height.

High marsh dominated by *Spartina patens* is reached only by exceptionally high tides, such as those caused by hurricanes. *S. patens* is usually distinguished from *S. alterniflora* by its more slender stems and leaves. High marsh dominated by *Distichlis spicata* occurs on ground that is inundated by spring tides, where the hydroperiod is slightly less than in *J. roemerianus* marsh. *D. spicata* is a short grass that often forms a carpet of uniform height, but is usually mixed with scattered clumps of *Fimbristylis castanea*, or sometimes with *S. patens* (Fig. 5). During high spring tides, the vegetation of *Distichlis* marsh may be almost entirely submerged.

Unfortunately, little information has been published concerning the length of time that the vegetation in these associations is actually submerged, or partially submerged. In the cases of vegetation that may be entirely submerged during spring tides (*Distichlis, Spartina-Salicornia-Limonium*), complete submergence would be limited to a few hours per month, and sometimes less. Northeast winds in the fall and winter may cause these same types of vegetation to be submerged for several hours daily for periods of two or three days; such conditions occurred less than half-a-dozen times during this study. Hurricanes may cause temporary complete submergence of all types of salt marsh vegetation. Adams (1963) provides considerable information concerning tide-elevation influences and the distribution of the dominant types of plants of the North Carolina salt marshes.

PROCEDURES

THE SAMPLING PROGRAM

The words "station" and "stand" are used here in accordance with the meanings assigned to them by Dice (1952), where a "station" is "each particular situation that is described in detail," and a "stand" is "a local example of an association composed of those individual plants and animals that live together in a particular situation." Each station mentioned here consisted of a stand, or part of a stand.

The criteria used in the selection of stations were: (1) degree of accessibility; (2) whether or not the stands appeared to be representative; (3) availability of satisfactory adjacent stands, since it was convenient to establish more than one station at each field locality that was visited.

The insects of all three low marsh associations, and of the two principal facies of the high marsh association, were studied. Several stations were established in each of the two principal low marsh associations, *Spartina alterniflora* and *Juncus roemerianus*. A single station in *Spartina-Salicornia-Limonium* was investigated. The *Distichlis spicata* and *Spartina patens* facies of the high marsh association were treated separately, and stations were set up in each.

Because summer is the season of greatest abundance and diversity of insect life, many stations were intensively sampled between June 1 and September 1, 1960. Ten visits were made to each of those stations during that period. Successive visits always occurred from five to ten days apart. Certain stations were also visited once each month between September 1, 1959, and June 1, 1960. The following outline summarizes the entire sampling program and gives the locations of all stations.

1. The summer sampling program. Locations of stands from which ten samples were obtained between June 1 and September 1, 1960.

   A. *Spartina alterniflora* association.
      - Bogue Banks
      - Piver's Island
      - Beaufort Channel
      - Bell Creek
      - Harlowe Creek

   B. *Spartina-Salicornia-Limonium* association.
      - Bogue Banks

   C. *Juncus roemerianus* association.
      - Bogue Banks
      - Core Creek
      - Bell Creek
      - Nelson Bay

   D. High marsh association.
      a. *Spartina patens* facies.
      - Bogue Banks
      - Piver's Island
      - Beaufort Channel
      - Harlowe Creek
      - Lennoxville Point

      b. *Distichlis spicata* facies.
      - Core Creek
      - Harlowe Creek
      - Lennoxville Point
      - Nelson Bay

2. Locations of stands from which monthly samples were obtained between September 1, 1959 and June 1, 1960.
   - A. *Spartina alterniflora* association.
     - Bogue Banks
     - Beaufort Channel
     - Goose Bay
     - North River B
   - B. *Spartina-Salicornia-Limonium* association.
     - Bogue Banks
   - C. *Juncus roemerianus* association.
     - Bogue Banks
     - Goose Bay
     - Core Creek
     - North River B
   - D. High marsh association.
     - a. *Spartina patens* facies.
       - Bogue Banks
       - Beaufort Channel
       - North River B
     - b. *Distichlis spicata* facies.
       - Core Creek
       - North River B
3. Locations of stands from which monthly samples were obtained in June, July, and August, 1960.
   - A. *Spartina alterniflora* association.
     - Core Creek
     - North River A
     - Goose Bay
     - North River B
   - B. *Juncus roemerianus* association.
     - Goose Bay
     - Harlowe Creek
     - North River A
     - Back Creek
     - North River B
     - Jarrett Bay
   - C. High marsh association.
     - A. *Spartina patens* facies.
       - Newport River
       - North River B
     - b. *Distichlis spicata* facies.
       - North River A
       - North River B

DESCRIPTIONS OF STATIONS

The localities of all stations are indicated on Figure 1. Each station was located on, or adjacent to, the geographic feature for which it is named. Stations were established at two locations (A and B in the preceding outline) along the west side of North River; location A is the more northerly of these two sites. Detailed descriptions of each station are not given here, but, with the exceptions noted in the following discussion, all were established in stands that appeared to be representative. The sizes and shapes of stands of these salt marsh associations vary greatly. To minimize these differences and make stations as comparable as possible, the sample size was standardized, and samples from a station were always obtained within a circumscribed area.

The salt marshes at Lennoxville Point, Piver's Island, and adjacent to Beaufort Channel, belong to Sequence I. In each case, *S. alterniflora* occupies the intertidal zone, *Spartina-Salicornia-Limonium* is poorly represented, and *S. patens*-dominated high marsh lies above a drift line on sloping, sandy ground. At Lennoxville Point, a small stand of *Distichlis* is present in a poorly drained depression behind the *S. patens* zone.

The marshes at Goose Bay, Bell Creek, Nelson Bay, Jarrett Bay, Back Creek, and Core Creek all belong to Sequence II. At all of these locations, except Nelson Bay and Core Creek, high marsh was too poorly represented for stations to be established. The *S. alterniflora* zone at Nelson Bay and Jarrett Bay was too inaccessible for study. At Back Creek the *S. alterniflora* zone was too narrow to be utilized.

Both zonal sequences are present at Bogue Banks and at Harlowe Creek. At Bogue Banks, Sequence II predominates, but the *Distichlis* facies is not developed, probably because of fresh-water seepage from nearby hills. A spoilbank is present in one part of this marsh, and a fine example of Sequence I occurs along its margin. The Harlowe Creek stations are located near the junction of that creek with Newport estuary. A small tributary empties into Harlowe Creek here. The tributary creek is bordered by marshes of Sequence II, and Harlowe Creek (at this point) is bordered by Sequence I marshes. Consequently, four stations could be established.

A stand of high marsh, dominated almost equally by *S. patens* and *Fimbristylis castanea* was studied. This station was located adjacent to the principal mouth of the Newport River on a damp, sandy area formed by the dumping of spoil.

Cattle-grazed marshes along the west side of North River were investigated. These marshes are heavily trampled, with many bare patches, poorly drained depressions, and small pools. *Distichlis* occupies the zone just above *S. alterniflora,* and below *Juncus.* This unusual situation probably results from the ability of *Distichlis* to tolerate highly saline conditions caused by evaporation of water from hoof tracks.

METHOD OF SAMPLING

DeLong (1932) and Gray and Treloar (1933) have pointed out that the sweep-net method is not suitable for making estimates of absolute insect density because an unknown portion of the population escapes the net. Beall (1935) concluded that the most legitimate use of the sweep-net was in comparing populations from one area at different times, or from different areas. The cylinder method, which involves placing a cylindrical trap over the vegetation and poisoning, collecting, and counting the insects caught within, has been used to sample insect populations, but has the disadvantages of being tedious, cumbersome, and of obtaining specimens from a very small area. Beall, Romney (1945), and Fenton and Howell (1957), have all compared the efficiency of the sweep-net to that of the cylinder, and other sampling methods.

The sweep-net method was chosen for use in this study because it gives a quantitative measure of the relative abundance of the insects, is not excessively time-consuming, and samples a relatively large area, thus eliminating errors caused by the irregular distribution of insects within the limits of a station. The sweep-net method has not been used here to determine absolute insect densities, but rather for obtaining density indices (estimates of the relative abundance of individuals of one, or more, species in different stands, or in the same stand at different times). If the limitations of the sweep-net method are understood, and the differing habits of the insects are taken into account when the data is examined, a great deal of useful information may be obtained in this way.

A beating net with a handle one inch in diameter and twenty-two inches long was used. The handle is an important feature because many so-called "sweeping nets" have slender handles and can not be effectively passed through resistant vegetation such as *Juncus*. A heavy metal ring fifteen inches in diameter supported the net bag. The bag itself was twenty-eight inches deep and made of muslin.

The handle of the net was grasped in both hands and swung vigorously back and forth, the net bag cutting a swath through approximately three feet of vegetation at each stroke. A step forward was taken with each swing, so that the same vegetation was not swept twice. It was necessary always to move upwind, while sampling, to prevent the net from being blown shut, but gusts of wind occasionally spoiled sets of sweeps.

Ninety strokes constituted a sample. This number was selected on the basis of preliminary summer studies, in which samples of several sizes were taken in representative stands of each association to be studied. The number of species obtained in samples of each size was plotted against the number of strokes. The resulting curves levelled off rapidly at sample sizes of sixty strokes or less, indicating that samples of that magnitude would obtain all common species. But to allow for the decrease of insect populations in winter, a larger sample was used.

The net was emptied three times during the taking of each sample, at intervals of thirty strokes. This practice reduced the escape rate of active insects from the net. Captured insects, along with the plant debris that accumulated in the bag, were transferred into large, wide-mouthed, cyanide killing-jars. Separation of insects from debris was performed in the laboratory, and the specimens were preserved in 70% alcohol in two-ounce specimen bottles. When necessary, specimens could be transferred from alcohol to pins by the method described by Oman and Cushman (1948).

Most of the difficulties encountered in the sampling program fell into three categories, the first including problems associated with daily changes in the environment. The effects of weather on insect activity are not well known. Menhinick (1963) found that sweep-net sampling of some kinds of insects is not greatly affected by the presence or absence of clouds, but ants and grasshoppers are not so frequently collected on overcast days. The problem is complex, especially when diverse species are sampled. It was not possible to restrict sampling to days of rigidly specified weather conditions, and still carry out an extensive program.

In this study, samples were taken only between the hours of 9:00 A.M. and 4:00 P.M. in summer, and between 10:00 A.M. and 3:00 P.M. at other seasons. No samples were taken during periods of tidal inundation, or when rain was falling. Humidity was determined by cog psychrometer, air temperature was measured, and other atmospheric conditions were noted, whenever samples were obtained. Attempts were made to correlate weather conditions with variations in the total size and composition of samples, but none was successful, and further consideration of this aspect is omitted.

Another sampling problem was caused by differences in the growth habits and structure of the vegetation. It is impossible to maintain an exact standard of sweeping in all stands of an association because of variations in both space and time of the height and density of the dominant plant species. Comparing samples from stands of different associations is even harder. For example, a stroke of the net cuts a much shorter swath through *Distichlis* than through *Juncus*, because the latter is a much taller plant. Comparison of sweep-net samples from different associations must be on a basis that does not require the samples to be from equal areas, or amounts of vegetation.

The third major sampling problem was caused by differences in the agility and tenacity of the insects. For example, grasshoppers frequently elude the net, but most species of planthoppers do not. A vigorous stroke of the net will dislodge and capture a greater proportion of the individuals of some kinds of insects. This selectivity can be compensated for only by supplementing the sampling process with observations of the behavior of the insects that appear in the samples.

A few other difficulties peculiar to the situation were encountered. In *S. alterniflora* stands the periwinkle, *Littorina irrorata*, occurs on the leaf blades in large numbers. When the vegetation was struck by the net, these snails tumbled into the bag along with insects and other animals, and the subsequent shifting about of the snails pulverized the softer bodied insects and sometimes prevented accurate counting and identification.

RESULTS AND DISCUSSION

THE SUMMER ASPECT: ORDINAL COMPOSITION AND VARIATION

Table 1 shows the ordinal composition of the insect aggregations at those stations, twenty in all, that were included in the summer sampling program. The Homoptera were first in abundance at fourteen stations, and the Diptera were preponderant at the other six. The Diptera were second in abundance at eight stations, Homoptera at five, Orthoptera at four, and Hemiptera at three. Thus, the Homoptera ranked either first or second at all but one of the twenty stations. Coleoptera and Hymenoptera occurred at practically all stations, but never in large numbers, and other orders of insects were represented very meagerly.

The total number of insects per sample varied greatly in *S. alterniflora*. Samples from the most productive *S. alterniflora* station, at Harlowe Creek, contained (on the average) forty-two times more insects than samples from the least productive station, at Beaufort Channel. Homoptera (principally the delphacid, *Prokelisia marginata*) comprised 30% or more of the insects from each of the six stations. Variations in the population growth of *P. marginata*, discussed in another section, are responsible for the large differences in average sample size from different stands of *S. alterniflora*.

TABLE 1. Ordinal composition of sets of ten samples taken in five types of salt marsh vegetation in the summer of 1960.

Stations	MEAN PERCENTAGE COMPOSITION							Average number of insects per sample
	Homoptera	Diptera	Hemiptera	Orthoptera	Coleoptera	Hymenoptera	Other orders	
Spartina alterniflora								
Bogue Banks*	75.15	9.27	12.31	2.05	0.46	0.61	0.08	1316
Piver's Island	53.47	40.28	0.70	0.70	2.78	2.08		288
Beaufort Channel	55.09	30.94	5.28	3.02	3.02	2.26	0.38	265
Bell Creek*	87.74	10.20	0.16	1.22	0.26	0.37	0.05	1893
Harlowe Creek**	95.73	3.07	0.68	0.13	0.21	0.16	0.02	11095
Lennoxville Point	31.65	52.23	3.16	7.91	2.22	2.53	0.32	316
All stations	90.11	6.72	1.76	0.66	0.38	0.37	0.04	2529
Spartina-Salicornia-Limonium								
Bogue Banks	78.10	13.41	3.89	2.67	0.98	0.73	0.24	411
Juncus roemerianus								
Bogue Banks	85.61	5.30	1.52	5.30		2.27		132
Core Creek	30.00	15.00	20.00	20.00		10.00	2.27	20
Nelson Bay	73.17	7.32	1.22	15.85	1.22	1.22		82
Bell Creek	16.66	50.00		22.22	11.11	11.11		18
All stations	72.22	9.92	2.78	11.11	0.79	2.78	0.40	63
Distichlis spicata								
Lennoxville Point	60.83	13.64	21.83	2.35	0.51	0.78	0.06	1782
Core Creek	72.29	14.13	9.45	0.39	3.04	0.62	0.08	1281
Nelson Bay	38.41	40.71	14.60	1.50	3.54	1.15	0.09	1130
Harlowe Creek	54.32	10.12	30.19	2.36	1.85	1.18	0.08	1186
All stations	57.32	18.66	19.18	1.17	2.04	0.91	0.07	1345
Spartina patens								
Bogue Banks	41.06	25.17	17.22	2.65	9.27	3.31	1.32	115
Piver's Island	19.90	61.22	4.59	2.04	3.07	7.65	1.53	196
Beaufort Channel	28.65	40.00	10.81	3.24	5.41	10.81	1.08	185
Harlowe Creek	43.90	31.22	6.83	4.39	1.95	11.22	0.49	205
Lennoxville Point	22.04	54.69	6.94	2.45	3.67	9.39	0.80	245
All stations	30.41	43.88	8.78	2.96	4.39	8.78	1.02	196

**Prokelisia marginata* (Homoptera) estimated in two samples.
***P. marginata* estimated in four samples.

There was also considerable variation in the average number of insects per sample from *Juncus* stations, caused largely by differences in the population size of *Keyflana hasta* (Homoptera: Delphacidae). This planthopper occurred at all *Juncus* stations, usually in small numbers, but abundantly at Bogue Banks and Nelson Bay.

The two facies of the high marsh associations support insect assemblages that are quite unlike in size and composition. The average number of insects per sample from four *Distichlis* stations was almost seven times greater than from five *S. patens* stations. All *Distichlis* stands supported a very large insect fauna, of which 80% or more consisted of four species: *Delphacodes detecta* (Homoptera: Delphacidae); *Amphicephalus littoralis* (Homoptera: Cicadellidae); *Trigonotylus americanus* (Hemiptera: Miridae); and *Conioscinella infesta* (Diptera: Chloropidae). Approximately 35% of *S. patens* insects were *C. infesta*, but no other species comprised a large percentage of the catch. Both of the high marsh facies differed from *Juncus* and *S. alterniflora* in that the average number of insects per sample from different stations did not vary greatly.

Hydroperiod and other tidal effects do not limit the total size of the insect aggregations of the five types of marshes included in this study. Of the five, *Distichlis*, which has a short hydroperiod, but is almost submerged by spring tides, supports the largest insect assemblage. *Juncus* has a similar hydroperiod, and is seldom more than one-fourth submerged, yet sustains a very sparse insect fauna. *S. alterniflora* and *Spartina-Salicornia-Limonium* are reached most frequently by the tides, but support more insects than *S. patens*, which is flooded only during storms.

Shelter and food are factors that affect the size of these insect assemblages more than tidal influences. *Juncus* marsh supports few insects because the vegetation consists of slender, fibrous stems that provide little protection from predators or wind, and a scant food supply for primary consumers. By contrast, *Distichlis* forms a dense carpet that gives ample cover and food for a large number of herbivorous insects. Of the two Spartinas, *S. alterniflora* has larger and more succulent culms and supports more herbivores. *S. alterniflora* forms stands that are much more open than those of *Distichlis*, and probably for that reason does not sustain as large an insect fauna.

It is evident from Table 1 that the Homoptera decrease in importance as zone elevation increases, while other orders show just the reverse trend. There

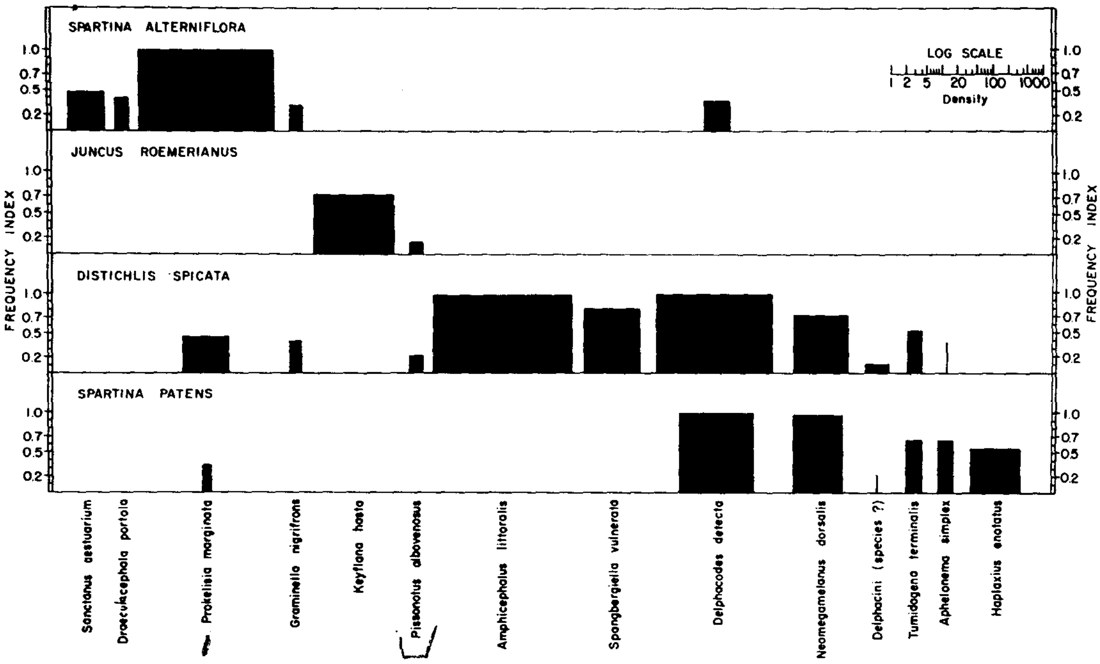

Fig. 6. Frequency-density diagram of the principal species of Homoptera from the herbaceous strata of four zones of salt marsh vegetation, based on samples taken during the summer of 1960.

are some exceptions to this rule, the most obvious being that the Orthoptera constitute a much greater proportion of the insects of *Juncus* than of the high marshes. It appears that Orthoptera are relatively most successful in those salt marshes (particularly *Juncus*) that consist of open stands of coarse vegetation, probably because they can utilize tough plant tissues for food better than most other insects.

Hymenoptera are best represented in *S. patens*, where several species of ants occur commonly. Ant hills were frequently seen in the sandy soil in which *S. patens* grows, whereas ants that nest in the ground are excluded by the tide from the other types of salt marshes, except as occasional visitors.

THE SUMMER ASPECT: SPECIFIC COMPOSITION AND ZONAL DISTRIBUTION

Two important features of insect aggregations that can be described from sweep-net samples are the *frequencies* and *densities* of the component species. The *frequency* of a species is the fraction of samples in which it is present. *Density* refers to the average number of specimens per sample. Frequencies and densities of the same species in different types of marshes, and of different species in the same or in different types of marshes, can be validly compared, but are subject to the errors described previously.

Figures 6-11 are frequency-density diagrams, in each of which the four principal salt marsh associations and facies are represented vertically, in their proper zonal order. Ideally, in each diagram, the insect assemblage of each zone should intergrade with the assemblages of the zones just above and below it. However, this ideal pattern is modified by two factors: (1) the marshes actually occur in two sequences, instead of in a simple zonal pattern; (2) the food of herbivorous insects is frequently restricted to two or more closely related plant species, and in one instance here, dominant plants of different zones (*S. alterniflora* and *S. patens*) belong to the same genus. Results of sampling from *Spartina-Salicornia-Limonium* are not included in these diagrams because only one station in that association was studied.

Figure 6 shows the frequencies and densities of common salt marsh homopterans. Several species belong to the family Cicadellidae (*Sanctanus aestuarium, Draeculacephala portola, Amphicephalus littoralis, Spangbergiella vulnerata, Graminella nigrifrons*); except for *Haplaxius enotatus* (Cixiidae) and *Aphelonema simplex* (Issidae), the others are delphacids. *Rhynchomitra microrhina* (Dictyopharidae) is a characteristic inhabitant of *Juncus*, but does not appear in the diagram because it is elusive and often avoided capture.

Both kinds of high marsh support a greater diversity of Homoptera than do either *Juncus* or *S. alterniflora*, and have more species in common with each other than with these low marsh associations. The same species of homopterans occur in *Spartina-Salicornia-Limonium* as in *S. alterniflora*, with the addition of *Sanctanus sanctus* (Cicadellidae).

The homopterans have a more nearly zonal distribution pattern than do members of the other insect orders, but two major departures from the ideal are evident. *Prokelisia marginata*, although principally associated with *S. alterniflora*, frequently occurred in all marsh types except *Juncus*. *P. marginata* speci-

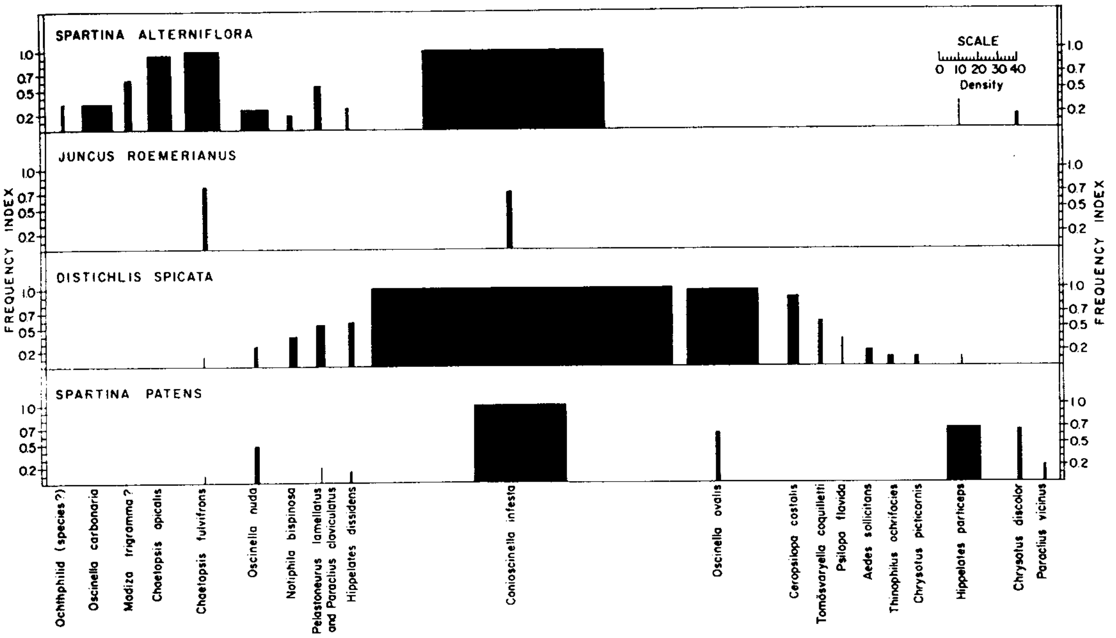

Fig. 7. Frequency-density diagram of the principal species of Diptera from the herbaceous strata of four zones of salt marsh vegetation, based on samples taken during the summer of 1960.

mens collected in *Distichlis* and *S. patens* were probably strays from the huge *S. alterniflora* populations. *Delphacodes detecta* is more widely distributed than any other homopteran, being very abundant in *S. patens* and *Distichlis* in summer, and equally common in *S. alterniflora* in autumn. *D. detecta* from *S. patens* and *Distichlis* bear markings that differ from those of specimens collected in *S. alterniflora*, so it is possible that these are two species currently called by one name.

Most of the common salt marsh dipterans (Fig. 7) belong to three families, the Chloropidae (*Oscinella carbonaria, O. nuda, O. ovalis, Hippelates particeps, H. dissidens, Madiza trigramma, Conioscinella infesta*), Dolichopodidae (*Chrysotus discolor, C. picticornis, Paraclius vicinus, P. claviculatus, Pelastoneurus lamellatus, Thinophilus ochrifacies*), and Ephydridae (*Psilopa flavida, Ceropsilopa costalis, Notiphila bispinosa*). Other families represented are the Otitidae (*Chaetopsis fulvifrons, C. apicalis*), the Pipunculidae (*Tomösvaryella coquilletti*), the Culicidae (*Aedes sollicitans*), and the Ochthiphilidae.

S. alterniflora and *Distichlis* both accommodate large and diverse dipteran assemblages. The fly fauna of *Spartina-Salicornia-Limonium* usually includes the ephydrid, *Dimecoenia austrina* (Ephydridae), but is otherwise similar to that of *S. alterniflora*. The small fly assemblage of *Juncus* is composed of strays from other types of vegetation. Flies comprise a larger proportion of the *S. patens* insect fauna than any other group, but fewer common species occur there than in *Distichlis* or *S. alterniflora*. *Conioscinella infesta* is the commonest fly species in all five types of salt marshes.

Only six species of Hemiptera were abundant (Fig. 8), and these belong to three families, the Miridae (*Tytthus vagus, Trigonotylus uhleri, T. americanus*), the Lygaeidae (*Ischnodemus badius, Cymus breviceps*), and the Pentatomidae (*Rhytidolomia saucia*). Four species (*T. vagus, T. americanus, I. badius, R. saucia*) are restricted to one marsh type. *T. uhleri* occurred in both *S. patens and S. alterniflora,* but not in other zones, indicating that its distribution is related to the occurrence of *Spartina. T. uhleri* was most common in *S. patens* in late spring and early summer, and in *S. alterniflora* in late summer. *Cymus breviceps* occurred in all five types of salt marshes, and also in adjoining stands of *Panicum virgatum,* being most abundant in the higher marsh zones.

The species of Orthoptera included in Figure 9 belong to three families, the Tettigoniidae (*Orchelimum fidicinium, Conocephalus* spp.), the Acrididae (*Paroxya clavuliger, Orphulella olivacea, Clinocephalus elegans, Mermiria intertexta*), and the Gryllidae (*Anaxipha scia, Cycloptilum antillarum, Oecanthus quadripunctatus, Nemobius sparsalsus. O. fidicinium* is restricted to *S. alterniflora, N. sparsalsus* to *Distichlis*, and *P. clavuliger* to *Juncus*. The other orthopterans are not limited to any single type of vegetation. *O. olivacea*, abundant in *Distichlis*, is also common in *Spartina-Salicornia-Limonium*. *C. elegans* and *M. intertexta* are characteristic of high marsh, the former occurring most often in *Distichlis,* and the latter mainly in *S. patens.* At least four species of *Conocephalus* are common, but unfortunately they are hard to distinguish, especially in the nymphal stages. Enough identifications were made to show

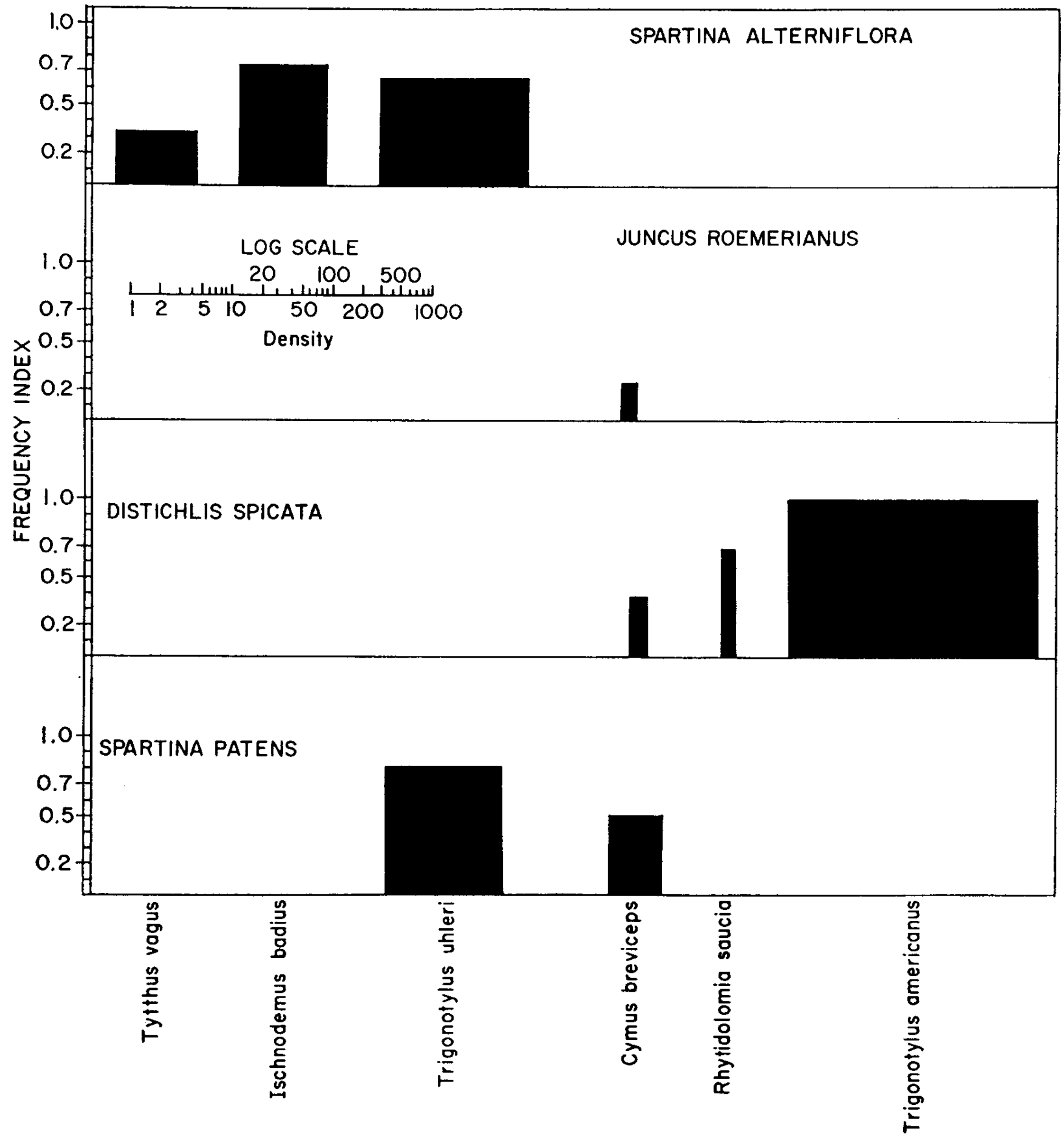

Fig. 8. Frequency-density diagram of the principal species of Hemiptera from the herbaceous strata of four zones of salt marsh vegetation, based on samples taken during the summer of 1960.

that none of these species is restricted to any one kind of marsh.

Six families of Coleoptera are represented by the species included in Figure 10. These are the Coccinellidae (*Naemia serriata*), the Cleridae (*Isohydnocera tabida*, *I. aegra*), the Malachiidae (*Collops nigriceps*), the Mordellidae (*Mordellistena* spp.), the Elateridae (*Glyphonyx* sp.), and the Chrysomelidae (*Chaetocnema* sp., *Pachybrachys atomarius*, *Cryptocephalus venustus*). Most common salt marsh beetles are restricted to one type of marsh. Exceptions are *C. nigriceps*, which occurs in *S. alterniflora* and *Spartina-Salicornia-Limonium*, and *N. serriata*, found in *Distichlis* and *S. alterniflora*. The distribution of *N. serriata* in *S. alterniflora* is very erratic; it is absent from most stands, but extremely abundant in a few.

All of the common Hymenoptera (Fig. 11) are ants (*Crematogaster clara*, *Pseudomyrmex pallida*, *Formica* sp., *Monomorium minimum*, *Iridomyrmex pruinosus*, *Dorymyrmex pyramicus*, *Tapinoma sessile*), or belong to parasitic groups (chalcids, Braconidae, Tiphiidae, Scelionidae). *C. clara* is the only one of these ant species that occurs in the lower marsh zones; it nests in upright, dead, hollow stems of *S. alterniflora*.

The following outline (based on frequencies, densities, field observations, and special collections) indi-

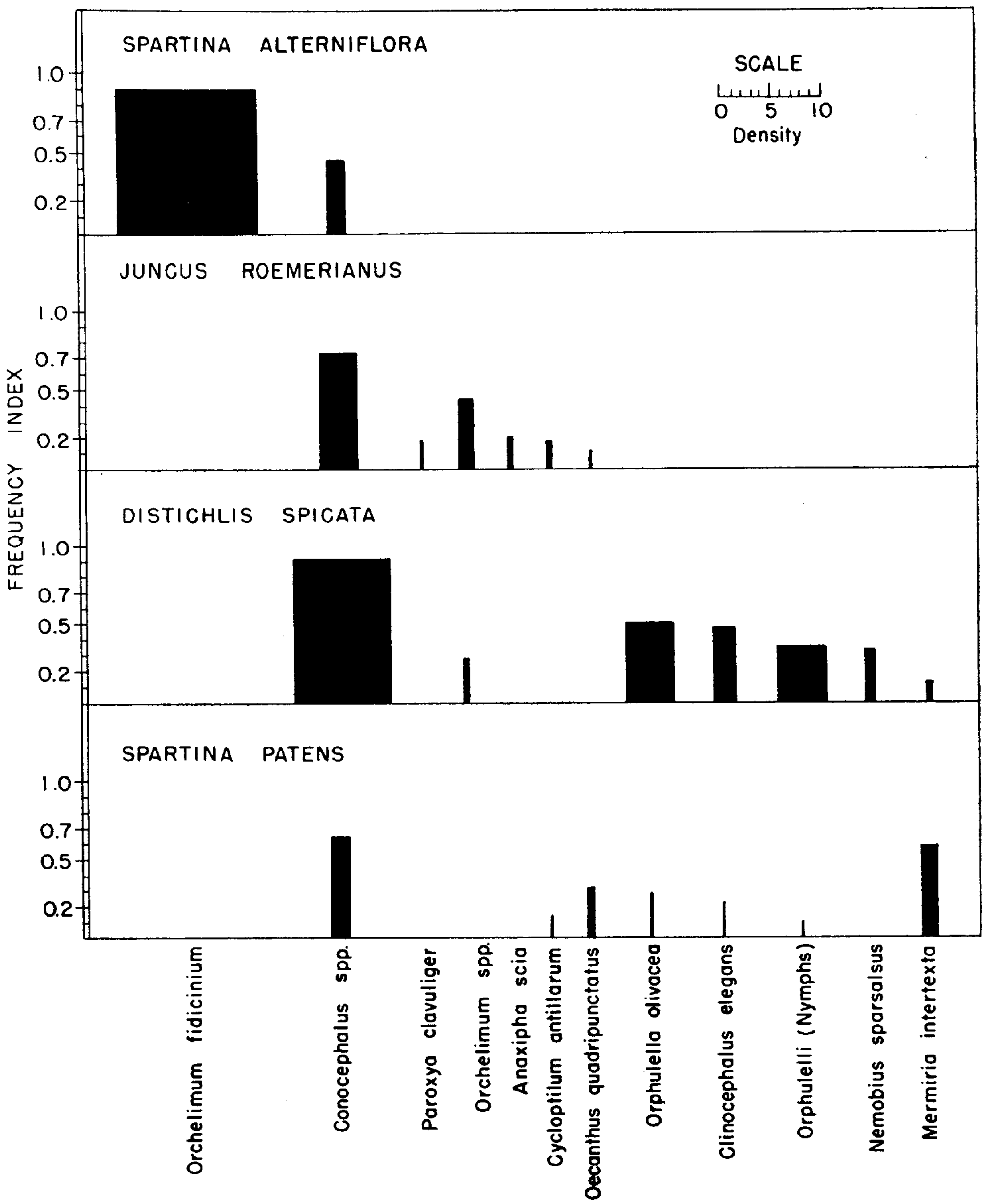

Fig. 9. Frequency-density diagram of the principal species of Orthoptera from the herbaceous strata of four zones of salt marsh vegetation, based on samples taken during the summer of 1960.

cates the characteristic insect inhabitants of each of the five types of salt marshes included in this study. These are the insects that comprised the great majority of the individuals obtained in samples, plus others that were conspicuous, but able to avoid capture.

Spartina alterniflora association

Prokelisia marginata (Homoptera: Delphacidae)
Sanctanus aestuarium (Homoptera: Cicadellidae)
Draeculacephala portola (Homoptera: Cicadellidae)
Chaetopsis apicalis (Diptera: Otitidae)
Chaetopsis fulvifrons (Diptera: Otitidae)
Conioscinella infesta (Diptera: Chloropidae)
Ischnodemus badius (Hemiptera: Lygaeidae)
Trigonotylus uhleri (Hemiptera: Miridae)

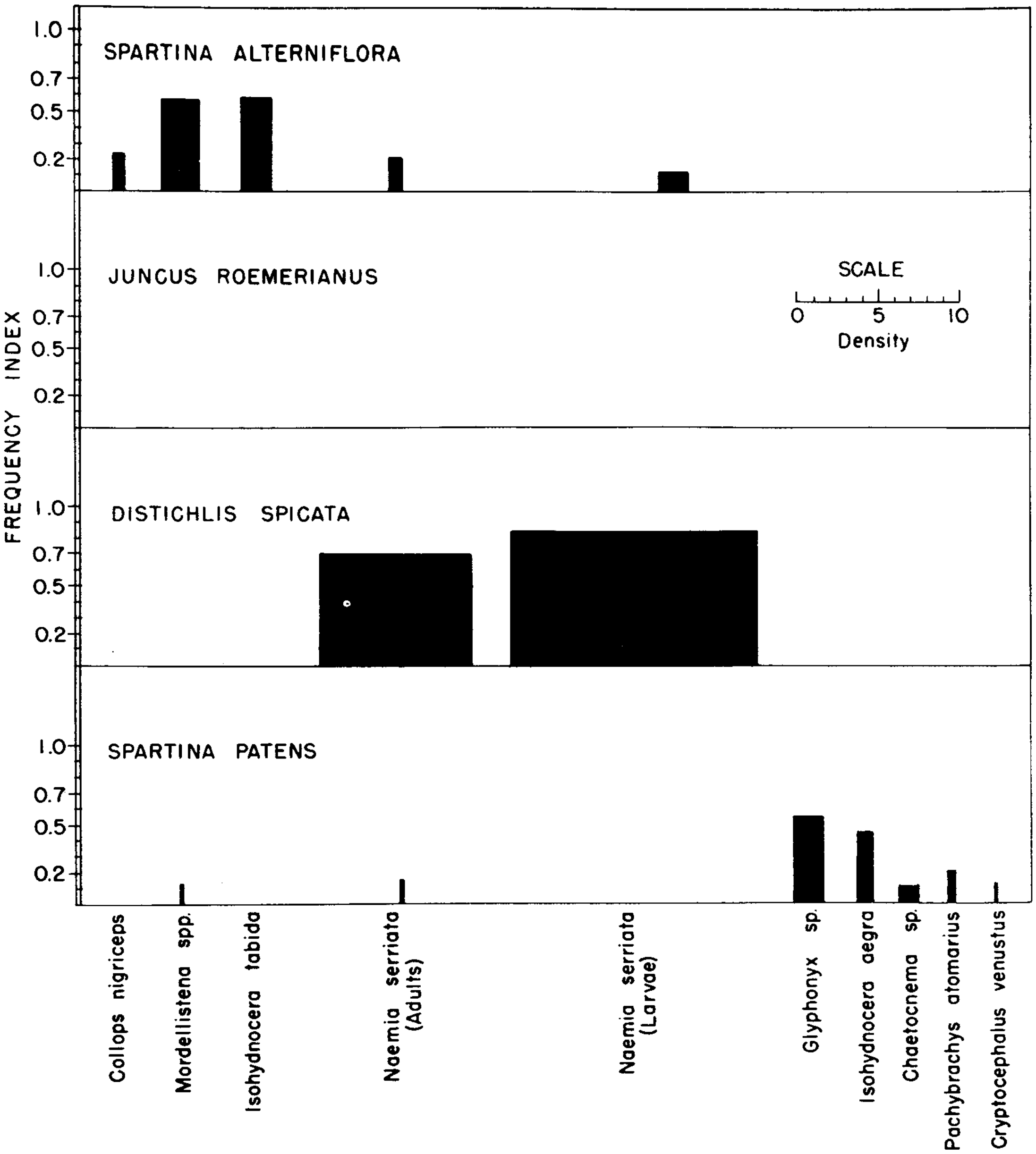

Fig. 10. Frequency-density diagram of the principal species of Coleoptera from the herbaceous strata of four zones of salt marsh vegetation, based on samples taken during the summer of 1960.

Orchelimum fidicinium (Orthoptera: Tettigoniidae)
Conocephalus spp. (Orthoptera: Tettigoniidae)
Isohydnocera tabida (Coleoptera: Cleridae)
Mordellistena spp. (Coleoptera: Mordellidae)
Collops nigriceps (Coleoptera: Malachiidae)

Spartina-Salicornia-Limonium association
Prokelisia marginata (Homoptera: Delphacidae)
Sanctanus sanctus (Homoptera: Cicadellidae)
Conioscinella infesta (Diptera: Chloropidae)
Chaetopsis apicalis (Diptera: Otitidae)
Chaetopsis fulvifrons (Diptera: Otitidae)
Dimecoenia austrina (Diptera: Ephydridae)
Pelastoneurus lamellatus (Diptera: Dolichopodidae)
Orphulella olivacea (Orthoptera: Acrididae)

Juncus roemerianus association
Keyflana hasta (Homoptera: Delphacidae)
Rhynchomitra microrhina (Homoptera: Dictyopharidae)
Paroxya clavuliger (Orthoptera: Acrididae)
Conocephalus spp. (Orthoptera: Tettigoniidae)
Erythrodiplax berenice (Odonata: Libellulidae)

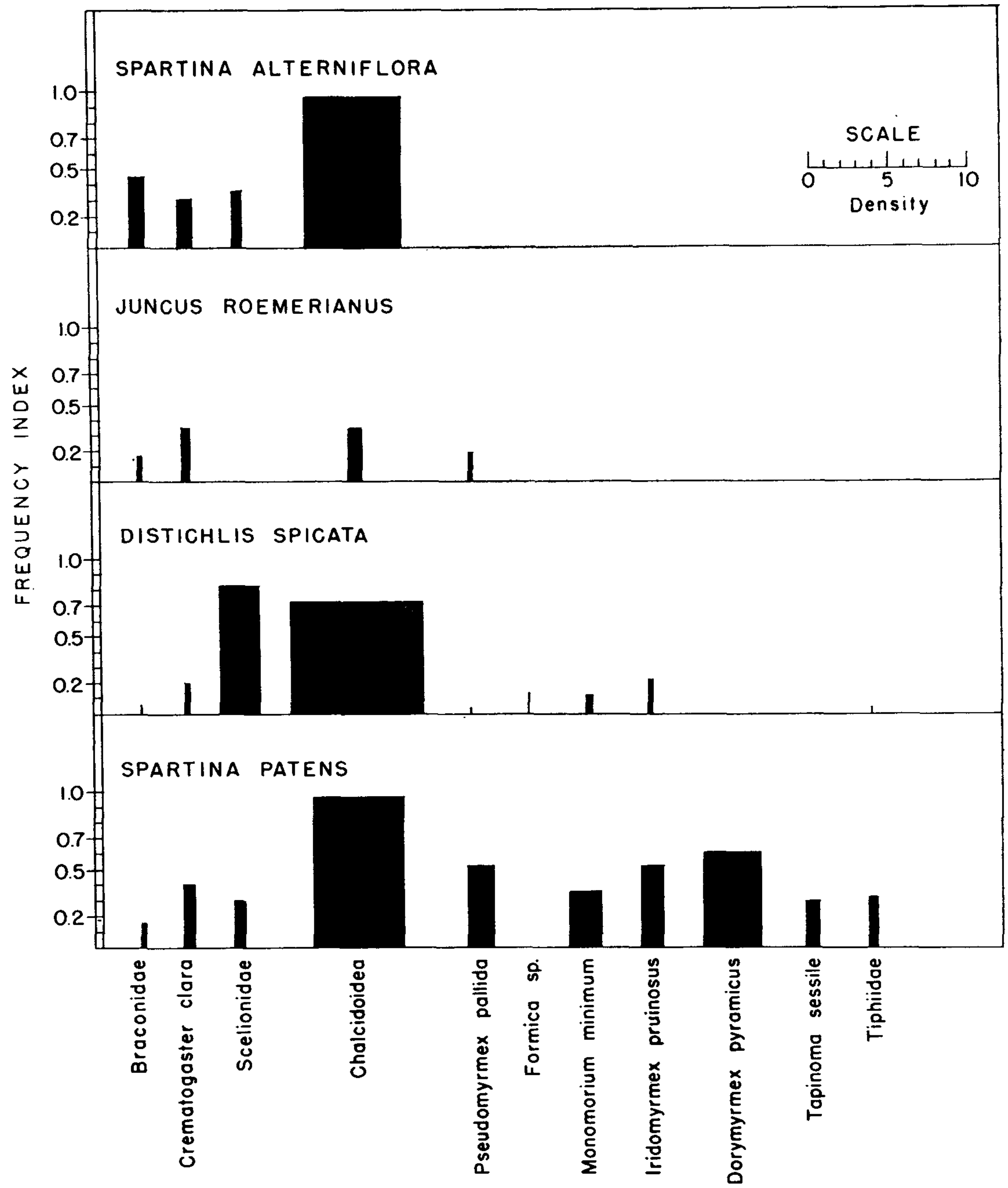

Fig. 11. Frequency-density diagram of the principal species of Hymenoptera from the herbaceous strata of four zones of salt marsh vegetation, based on samples taken during the summer of 1960.

High marsh association, *Distichlis spicata* facies
- *Amphicephalus littoralis* (Homoptera: Cicadellidae)
- Spangbergiella vulnerata (Homoptera: Cicadellidae)
- *Delphacodes detecta* (Homoptera: Delphacidae)
- *Tumidagena terminalis* (Homoptera: Delphacidae)
- *Neomegamelanus dorsalis* (Homoptera: Delphacidae)
- *Conioscinella infesta* (Diptera: Chloropidae)
- *Oscinella ovalis* (Diptera: Chloropidae)
- *Ceropsilopa costalis* (Diptera: Ephydridae)
- *Tomösvaryella coquilletti* (Diptera: Pipunculidae)
- *Trigonotylus americanus* (Hemiptera: Miridae)
- *Rhytidolomia saucia* (Hemiptera: Pentatomidae)
- *Cymus breviceps* (Hemiptera: Lygaeidae)
- *Nemobius sparsalsus* (Orthoptera: Gryllidae)
- *Conocephalus* spp. (Orthoptera: Tettigoniidae)

Orphulella olivacea (Orthoptera: Acrididae)
Clinocephalus elegans (Orthoptera: Acrididae)
Naemia serriata (Coleoptera: Coccinellidae)

High marsh association, *Spartina patens* facies
Delphacodes detecta (Homoptera: Delphacidae)
Tumidagena terminalis (Homoptera: Delphacidae)
Neomegamelanus dorsalis (Homoptera: Delphacidae)
Haplaxius enotatus (Homoptera: Cixiidae)
Aphelonema simplex (Homoptera: Issidae)
Conioscinella infesta (Diptera: Chloropidae
Oscinella ovalis (Diptera: Chloropidae)
Hippelates particeps (Diptera: Chloropidae)
Trigonotylus uhleri (Hemiptera: Miridae)
Cymus breviceps (Hemiptera: Lygaeidae)
Mermiria intertexta (Orthoptera: Acrididae)
Conocephalus spp. (Orthoptera: Tettigoniidae)
Isohydnocera aegra (Coleoptera: Cleridae)
Glyphonyx sp. (Coleoptera: Elateridae)
Dorymyrmex pyramicus (Hymenoptera: Formicidae)
Pseudomyrmex pallida (Hymenoptera: Formicidae)
Iridomyrmex pruinosus (Hymenoptera: Formicidae)

From the preceding outline, the following species are under-represented, or not represented, in the frequency-density diagrams because of their ability to evade the sweep-net: *Erythrodiplax berenice* (dragonfly); *Draeculacephala portola* (leafhopper); *Rhynchomitra microrhina* (planthopper); *Orchelinum fidicinium, Orphulella olivacea, Conocephalus* spp., *Clinocephalus elegans,* and *Mermiria intertexta* (all grasshoppers). Not included in the outline are some ephydrids, culicids, dolichopodids, and other dipterans, and a few other species (such as the mirid, *Tytthus vagus*), that were occasionally very abundant in one or more marsh types, but did not appear with high frequency.

Most of these characteristic insect species are restricted to salt marshes, or at least to maritime and submaritime habitats. Some occur in fresh-water marshes and other hydric environments, and a few are found in a wide range of terrestrial conditions. Individuals belonging to numerous other, uncharacteristic, species were collected; most of these were strays from adjoining mesic habitats. Space does not permit presentation here of a full list of the insect species that were represented, but 252 kinds were collected and determined to species, and 74 others to genus. Between 50 and 100 kinds were recognized, but identified only to family.

TROPHIC RELATIONSHIPS

On the basis of their feeding habits, salt marsh insects (adults unless otherwise stated) are divided into the categories of herbivores, carnivores, omnivores, and parasites. It is difficult to draw clear distinctions between those insects that are external plant parasites, and those that are free-living herbivores, because many herbivorous insects are sharply restricted in their diets and live virtually their entire lives on the "host" plants. Difficulties are also encountered in trying to distinguish between some so-called insect parasites of animals, such as mosquitoes, and predaceous insects. Therefore the term "parasitic" is restricted here to insects that invade the bodies of their hosts, and the terms "carnivorous" and "herbivorous" will refer to both free-living and "ectoparasitic" forms. The important omnivorous salt marsh insects are all scavengers, feeding mostly on detritus.

In Table 2, the herbivores are divided into three groups, according to the type of plant food that they use. The first group, those that feed on plant tissues, are all insects with chewing mouthparts. The principal herbivorous chewing insects in all five types of salt marshes are grasshoppers, but several species of ants, all presumably herbivorous, are common in *S. patens.* The second group are those that feed on plant sap, and possess piercing mouthparts that enable them to penetrate plant tissues. These sap feeders are abundant in all types of marshes except *Juncus,* and include all of the common species of homopterans and hemipterans. The third group are those that principally subsist on fluids secreted by marsh plants, although it is possible that bacteria, detritus, and other materials on the leaf blade surfaces, also contribute to their diet. Included here are several common species of dipterans, particularly *Chaetopsis fulvifrons, C. apicalis,* and *Conioscinella infesta.* These flies were often seen to feed by holding their sponging mouthparts against plant surfaces, while walking along blades or stems.

Smalley (1959, 1960) studied the energy flow from *S. alterniflora* to the two principal primary consumers of the living plant, *Prokelisia marginata* and *Orchelimum fidicinium. P. marginata* assimilated more than 6%, and *O. fidicinium* less than 1% of the annual *S. alterniflora* production.. Energy flow in other types of salt marshes has not been reported.

In Table 2, the predaceous arthropods are divided into two groups: (1) those that feed on solid tissues primarily; (2) those that suck out the body fluids of their prey. Belonging to the first group are the dragonflies, *Erythrodiplax berenice, Pachydiplax longipennis,* and *Erythemis simplicicollis,* individuals of which were often seen fluttering about *Juncus* marsh, feeding on small flying insects. The malachiid beetle, *Collops nigriceps,* was seen to feed on injured flies, and will probably eat any small insects that it can get. The clerids, *Isohydnocera tabida* and *I. aegra* (from *S. alterniflora* and *S. patens* marshes respectively), and the coccinellid, *Naemia serriata* (from *Distichlis*), are assumed to be predaceous, because most other clerids and coccinellids are, but their feeding habits were not actually observed.

Belonging to the second group of predators are the asilid flies that were sometimes seen preying upon grasshoppers. Midges and culicids are locally abundant in poorly drained marshes, especially *Dis-*

TABLE 2. Trophic relationships of characteristic invertebrates from the herbaceous strata of five types of North Carolina salt marshes.

Feeding Habits	FOOD	DOMINANT PLANTS				
		Spartina alterniflora	*Spartina-Salicornia-Limonium*	*Juncus roemerianus*	*Distichlis spicata*	*Spartina patens*
Herbivorous	Plant Tissues	*Orchelimum fidicinium* *Conocephalus* spp. *Mordellistena* spp.	*Orphulella olivacea*	*Paroxya clavuliger* *Conocephalus* spp.	*Orphulella olivacea* *Conocephalus* spp. *Clinocephalus elegans* *Nemobius sparsalsus*	*Conocephalus* spp. *Mermiria intertexta* *Glyphonyx* sp. *Dorymyrmex pyramicus* *Pseudomyrmex pallida* *Iridomyrmex pruinosus*
	Plant Sap	*Prokelisia marginata* *Sanctanus aestuarium* *Draeculacephala portola* *Ischnodemus badius* *Trigonotylus uhleri*	*Prokelisia marginata* *Sanctanus sanctus*	*Keyflana hasta* *Rhynchomitra microrhina*	*Amphicephalus littoralis* *Spangbergiella vulnerata* *Delphacodes detecta* *Tumidagena terminalis* *Neomegamelanus dorsalis* *Trigonotylus americanus* *Rhytidolomia saucia* *Cymus breviceps*	*Delphacodes detecta* *Tumidagena terminalis* *Neomegamelanus dorsalis* *Haplaxius enotatus* *Aphelonema simplex* *Trigonotylus uhleri* *Cymus breviceps*
	Plant Secretions	*Chaetopsis apicalis* *Chaetopsis fulvifrons* *Conioscinella infesta*	*Chaetopsis apicalis* *Chaetopsis fulvifrons* *Conioscinella infesta*		*Conioscinella infesta* *Oscinella ovalis*	*Conioscinella infesta* *Oscinella ovalis* *Hippelates particeps*
Carnivorous	Animal Tissues	*Isohydnocera tabida* *Collops nigriceps*	Spiders	*Erythrodiplax berenice* Spiders	*Naemia serriata* Spiders	*Isohydnocera aegra* Spiders
	Animal Body Fluids	*Dictya oxybeles* *Hoplodictya spinicornis* Spiders	*Dictya oxybeles* *Hoplodictya spinicornis* Spiders	Reduviids Asilids Spiders	*Tomosvaryella coquilletti* Reduviids Culicids Asilids Spiders	Reduviids Asilids Spiders
Omnivorous	Detritus	Ephydrids Dolichopodids *Littorina irrorata*	Ephydrids Dolichopodids		Ephydrids Dolichopodids	
Parasitic	Plant Tissues and Sap	Dipterous larvae	Dipterous larvae		Dipterous larvae	Dipterous larvae
	Animal Tissues and Body Fluids	Larvae of parasitic Hymenoptera	Larvae of parasitic Hymenoptera	Larvae of parasitic Hymenoptera	Larvae of parasitic Hymenoptera	Larvae of parasitic Hymenoptera

tichlis. Sciomyzid flies (*Dictya oxybeles, Hoplodictya spinicornis*), although never abundant, were widely encountered in *S. alterniflora* and *Spartina-Salicornia-Limonium.* It has been suggested that all sciomyzid larvae attack snails (Berg, Karlin and Mackiewicz, 1955). If so, it is likely that the larvae of *D. oxybeles* and *H. spinicornis* feed upon the marsh periwinkle, *Littorina irrorata.* Predaceous bugs (the reduviids, *Doldina interjungens, Sinea diadema, Zelus cervicalis,* and the nabid, *Nabis capsiformis*) are widely distributed, but not numerous, in the higher marsh zones.

Marples and Odum (1964) reported that spiders are the principal carnivores in *S. alterniflora.* Barnes (1953) collected, from the herbaceous strata, 22 species of spiders in *S. alterniflora,* twelve in *Juncus,* and eight in *S. patens.* Our observations indicate that spiders are important predators upon insects in all the kinds of salt marshes included in this study. Comparison of our data with those of Barnes shows that spiders usually outnumber carnivorous insects in all types of marshes, except *Distichlis,* which Barnes did not study.

Detritus, derived principally from plant tissues, is an abundant source of food in *S. alterniflora* (Teal, 1959). Marples and Odum (1964) report that the dolichopodids and ephydrids that inhabit *S. alterniflora* feed on detritus. These flies are often abundant in other types of marshes, in spring and early autumn, often occurring in a stand in large numbers for a short time, and then disappearing for weeks or months. At North River, where the marshes are modified by the presence of cattle, dolichopodids and ephydrids were seen on the bare ground, undoubtedly feeding on the rich detritus supply. Another important detritus feeder, in *S. alterniflora* marshes, is *Littorina irrorata* (Odum and Smalley, 1959). These snails spend part of their time in the herbaceous stratum, but feed while on the ground and surfaces of the lower parts of the plants.

The marsh plants, especially *S. alterniflora,* are attacked by dipterous larvae, which live in the stems.

The adults of parasitic Hymenoptera (chalcids, braconids, ichneumonids, tiphiids, scelionids) occurred in all types of vegetation, and their larvae undoubtedly infect various types of salt marsh insects.

Tidal Inundation

Tidal inundation is the feature of salt marshes that most distinguishes them from other insect environments. The insects of the herbaceous strata are fundamentally terrestrial, and evidently lack aquatic adaptations. A question then arises as to how they survive periods of high water. Do they retreat to higher ground, or do they remain in their usual habitat? In an attempt to answer this question, observations and simple experiments were performed.

The behavior of salt marsh insects was observed in the field during all stages of the tidal cycle, including spring high tides. However, field observations of animals that are as small as most insects are difficult to make, so attempts were made to simulate conditions of rising water and high tide in the laboratory. In these, clumps of marsh vegetation, still embedded in soil, were placed in large glass battery jars. Insects of any desired type were placed on, or with, the plants, and the jar then covered. Sea water was introduced through a notch in the cover, into a tube that extended down to the surface of the soil. The reactions of the insects were noted as the water level was slowly raised. The results of this work follow.

(1) *Prokelisia marginata.* Arndt (1914) reported that *Megamelus marginatus* (now called *Prokelisia marginata*) in *S. alterniflora* marsh at Cold Spring Harbor Bay, New York, clings to grass blades during periods of inundation, and can remain under water for two days without suffering ill effects. Despite many efforts to do so, we are unable to confirm this statement. In the field, *P. marginata* was never found to occur on submerged plants. But the conjecture of Metcalf and Osborn (1920) that *P. marginata* lays its eggs in leaves or stems that are frequently submerged is verified. The eggs are laid in *S. alterniflora* leaf blades that are often under water, although the effect of inundation on the eggs is still questionable.

The reactions of *P. marginata* to rising water were observed in the laboratory. Individuals responded to slowly rising water by retreating up the stems of the plants, and hopping over the surface film to any available dry surface. However, it was possible to submerge feeding individuals by putting them in test tubes with pieces of *Spartina* and, after feeding activities began, filling the tubes rapidly with water. In these experiments, the open ends of the tubes were covered with gauze, and the closed ends were embedded in a layer of sand in the bottom of a glass aquarium filled with water. This procedure insured the submergence of individuals that released their grasps, for the duration of the test. Twelve of eighteen *P. marginata* survived four hours of immersion at water temperatures of 22-25° C. No individuals, including those that retained their grasps on the grass blades, successfully withstood submergence for five hours.

It is likely that *P. marginata* individuals in natural surroundings are seldom submerged. They bound over the surface film to taller plants, when menaced by rising water. In the field, it was observed that if they are knocked onto the water, they then hop toward any nearby object, and leap up onto it. This behavior should be an effective response when they are swept from their holds by waves, or otherwise dislodged.

(2) *Amphicephalus littoralis.* Metcalf and Osborn (1920) speculated that *Deltocephalus littoralis* (now called *A. littoralis*) is unable to avoid high water, and therefore must be able to withstand submergence. We are not able to substantiate this hypothesis. Clumps of the host plant, *Distichlis,* were examined in the field during periods of flood, but no specimens were found on them. If *A. littoralis* individuals are pushed beneath the water surface, they will seize any available grass blade, hold on briefly, then lose their holds and rise to the surface. Like *P. marginata,* they readily hop over the surface film, and can easily escape rising water in this way.

(3) *Trigonotylus americanus* and *T. uhleri.* When subjected in the laboratory to slowly rising water, these plant bugs retreated to the ends of the grass blades. As the water approached, they either flew away or walked over the surface film to taller blades. However, they sometimes broke through the film, adhered to it, and were helpless.

(4) *Ischnodemus badius.* This lygaeid, having rudimentary wings, cannot escape high water by flying. In the laboratory, individuals left their holds whenever rising water approached, and swam to new perches. They are efficient swimmers, and probably always avoid submergence in natural surroundings.

(5) *Rhytidolomia saucia.* This pentatomid is too large and heavy to walk on the surface film. In the laboratory, *R. saucia* first reacts to rising water by climbing to the highest available hold. When it can no longer remain above water, it climbs down the grass stem to which it is holding, and enters the water. As it continues to climb downward, it may encounter another stem and ascend it, or descend to the ground, walk about, and then select a new stem to ascend. These aquatic explorations last for six to eight minutes, or less, and are often terminated by a sudden rapid climb to the surface on any stem that is available, even the one previously used for descent. *R. saucia* will not usually submerge until its original hold is untenable. Individuals cling awkwardly to the ends of leaf blades even when only two of their spiracles are exposed to the air. If an individual loses its grasp while under water, it rises to the surface and struggles in the surface film until it encounters a solid object by which it can climb out, or until it drowns.

(6) *Orchelimum fidicinium.* Smalley (1960) reported that *O. fidicinium* "will dive under water readily at the approach of man or boat. . . ." This

behavior was not observed by us in the field, but in laboratory experiments, individuals left their perches when menaced by rising water, and swam by vigorous strokes of the posterior legs to new positions.

(7) *Orphulella olivacea.* Like *O. fidicinium*, this grasshopper swims strongly, but will only momentarily hold to vegetation while submerged.

(8) *Chaetopsis apicalis* and *C. fulvifrons.* These dipterans avoid rising water by flying away. They are completely helpless in water; their large, membranous wings adhere to the surface film and prevent effective movement.

(9) *Collops nigriceps.* These beetles first responded to rising water by moving about nervously, and then flew away. They are clumsy and often fell into the water and struggled ineffectually. If forcibly submerged for long periods, they may survive. Five individuals that were kept under water for an hour each resumed normal activity in from three to twenty minutes. Two of four individuals that were submerged for four hours recovered.

(10) *Naemia serriata.* These coccinellid beetles climbed grass blades to avoid rising water, but did not attempt to fly. When overtaken by the water, they floated quietly at the surface for two to five minutes, struggled briefly, became motionless again, and repeated this behavior until drowned.

The hypothesis that salt marsh insects are frequently inundated has appeared several times in the older literature (Arndt, 1914; Metcalf and Osborn, 1920; Metcalf, 1920; Osborn and Metcalf, 1920), and again more recently (Shelford, 1963, p. 85). Our observations show that this is a highly improbable happening, except possibly for salt marsh coccids found in *S. alterniflora* (Sasscer, 1907), and in New Zealand salt meadows (Paviour-Smith, 1956). Coccids were rarely encountered during our study.

Many insect species have been able to successfully colonize salt marshes because of their ability to escape high water, either by flying or swimming, or by walking or hopping on the surface film. Some of these kinds of insects can endure prolonged submergence, but it is not known if they differ in this capacity from insects of other habitats. Some insects, such as large, clumsy beetles, are at an obvious disadvantage in salt marsh vegetation. However, most insects that occur in other communities dominated by herbaceous plants would be as capable of avoiding inundation as those that live in salt marshes.

SEASONAL DISTRIBUTION

Samples were taken in stands of all five types of salt marshes throughout the year. The seasonal variations of the salt marsh insect fauna are summed up below, with each aspect considered separately. Most of the trends referred to are shown in Table 3. Of course, when based on the results of a one year study, as here, this type of information will be strongly biased by the weather conditions of the study period. The only notable deviation from "average" weather was the occurrence of unusually low temperatures in March, the effects of which are apparent in Table 3.

Winter Aspect. At this season, the stems and leaves of the dominant types of salt marsh plants, except *Juncus roemerianus*, were brownish or yellowish in appearance, and dead. *J. roemerianus* showed little outward change throughout the year. Homopterans of the family Delphacidae (*Prokelisia marginata, Delphacodes detecta, Tumidagena terminalis, Neomegamelanus dorsalis, Megamelus lobatus, Pissonotus albovenosus, Pentagramma vittatifrons*), and the issid, *Aphelonema simplex*, occurred in moderate numbers until March, and then virtually disappeared. Occasionally a few members of typical summer species were seen, especially in *S. patens* on warm days; for example, adult grasshoppers (*Melanoplus femur-rubrum*, family Acrididae) were collected in January. The hemipteran, *Ischnodemus badius*, occurred in small numbers in *S. alterniflora* throughout the winter; individuals were sometimes found beneath the bases of leaves, even in the midst of the coldest periods of weather. The predaceous sciomyzid flies, *Dictya oxybeles*, and less commonly *Hoplodictya spinicornis*, were present, their numbers apparently little diminished from the summer. Ephydrid flies, particularly *Neoscatella obscuriceps* and *Dimecoenia austrina*, were often present in *Salicornia-Spartina-Limonium* and *Distichlis*. In some localities, the chironomid *Hydrobaenus* sp. appeared in January, and was extremely abundant during February and March, gradually decreasing in the spring. *Hydrobaenus* was not restricted to any particular type of vegetation; wherever it appeared, as at North River, it occurred impartially in all types of marshes.

Most species of salt marsh insects pass the winter in the egg stage. Dead stems of *S. alterniflora* and other types of salt marsh plants were examined, and eggs were found within. Individuals of some insect species probably deposit their eggs in the ground, for example *Orphulella olivacea, Clinocephalus elegans*, and other acridids. The specific details of the reproductive habits of salt marsh insects were not investigated.

Spring Aspect. In 1960, the growing season for salt marsh plants began in mid-April. Insect populations were very small in all communities until late April, grew rapidly in May, and reached summer levels in June. No species of Homoptera became abundant until June, when *Keyflana hasta* in *Juncus*, and *Delphacodes detecta* and *Neomegamelanus dorsalis* in *Distichlis*, reached summer population sizes. Several species of the dipteran families Dolichopodidae and Ephydridae were temporarily abundant in *Distichlis* and *Salicornia-Spartina-Limonium* in late April and May. These flies were very erratic in occurrence, and probably emerge in short-lived broods; some of these same dolichopodids and ephydrids were also present briefly in late summer and fall. The hemipterans, *Trigonotylus uhleri* and *T. americanus*, appeared in late April, reached their numerical peaks in May, and continued to be common throughout the summer. Nymphs of all the common salt marsh grasshoppers hatched in April and May, and therefore the numerical peaks for each grasshopper species occurred in late spring. Several species of Coleoptera (*Pachybrachys atomarius*, *Chaetocnema* sp., and *Cryptocephalus venustus*, all chrysomelids) were most common in *S. patens* marsh in May and June.

TABLE 3. Seasonal distribution of dominant species of insects from salt marsh herbaceous strata. Symbols: x— presence; xx— period of peak abundance; numbers— dates of first or last collections of season.

Insect species and types of vegetation	January	February	March	April	May	June	July	August	September	October	November	December
HOMOPTERA												
from *Spartina alterniflora*												
Prokelisia marginata	x	x	x	x	x	x	xx	xx	xx	xx	xx	x
Sanctanus aestuarium					9x	x	xx	xx	x	16x		
Draeculacephala portola					13x	x	x	xx	xx	x	15x	
Graminella nigrifrons					11x	x	x	xx	xx	x	x	11x
Delphacodes detecta	xx	x	15x		16x	x	x	x	x	x	xx	xx
from *Spartina-Salicornia-Limonium*												
Prokelisia marginata	x	10x		8x	x	x	x	x	x	xx	xx	xx
Sanctanus sanctus					24x	x	x	xx	x	x	24x	
Delphacodes detecta	x	10x			24x	x	x	x	x	x	xx	xx
from *Juncus roemerianus*												
Keyflana hasta	11x				7x	xx	xx	x	x	x	x	x
Pissonotus albovenosus	x	10x		9x	x	x	x	x	x	x	x	x
Rhynchomitra microrhina				9x	x	x	xx	x	12x			
from *Distichlis spicata*												
Amphicephalus littoralis				15x	x	x	xx	xx	x	x	x	9x
Spangbergiella vulnerata				9x	x	x	xx	xx	x	13x		
Delphacodes detecta	14x		19x	x	x	xx	xx	xx	x	x	x	x
Tumidagena terminalis					18x	x	xx	xx	x	17x		
Neomegamelanus dorsalis				9x	x	xx	xx	x	1x			
Megamelus lobatus				10x	x	x	x	x	x	xx	xx	9x
Graminella nigrifrons					4x	x	x	xx	xx	x	12x	
Pissonotus albovenosus					11x	x	x	x	x	x	13x	
from *Spartina patens*												
Delphacodes detecta	xx	x	x	x	x	x	x	x	x	xx	xx	xx
Tumidagena terminalis	x	x	x	x	x	x	x	x	x	x	x	x
Neomegamelanus dorsalis	x	10x		8x	x	x	x	x	x	x	x	x
Haplaxius enotatus						14x	x	x	x	x	12x	
Aphelonema simplex	xx	11x		27x	x	x	x	x	x	xx	xx	xx
Pentagramma vittatifrons	xx	10x				27x	x	x	x	x	xx	xx
DIPTERA												
from *Spartina alterniflora*												
Chaetopsis apicalis	x	12x		8x	x	xx	xx	xx	xx	x	x	x
Chaetopsis fulvifrons				8x	x	xx	xx	xx	xx	x	x	11x
Conioscinella infesta	14x			11x	x	xx	xx	xx	xx	x	x	x
Oscinella carbonaria				23x	x	x	x	xx	17x			
Madiza trigramma?					4x	x	x	x	xx	xx	14x	
Oscinella nuda						6x	x	xx	x	12x		
Dictya oxybeles	x	x	x	x	x	x	x	x	x	x	x	x
from *Spartina-Salicornia-Limonium*												
Dimecoenia austrina	x	x	x	x	x	x	x	x	x	x	x	x
from *Distichlis spicata*												
Conioscinella infesta			9x	x	x	xx	xx	xx	xx	xx	x	13x
Oscinella ovalis					4x	x	xx	xx	x	13x		
Ceropsilopa costalis				27x	x	x	x	x	17x			
Psilopa flavida	x	12x		11x	x	x	x	x	x	x	x	x
Notiphila bispinosa				26x	x	x	x	x	x	x	13x	
Neoscatella obscuriceps	x	xx	xx	xx	6x							
Thinophilus ochrifacies				14x	x	x	x	x	x	x	x	x
Chrysotus picticornis					10xx	x	x	27x				
Tomösvaryella coquilletti					18x	x	x	x	17x			
from *Spartina patens*												
Conioscinella infesta				27x	x	x	x	x	x	x	14x	
Oscinella ovalis					6x	x	x	x	6x			
Oscinella nuda					13x	x	x	xx	4x			
Hippelates particeps					6x	x	x	x	17x			
Hippelates dissidens					13x	x	x	x	x	x	14x	
Chrysotus discolor					4xx	x	x	x	4x			
Paraclius vicinus					9x	x	x	17x				
from all types of vegetation												
Aedes sollicitans				25x	x	x	x	x	xx	xx	x	10x
Hydrobaenus sp.	14x	xx	xx	x	13x							
*Pelastoneurus lamellatus**				8x	xx	x	x	x	xx	x	11x	

TABLE 3. continued.

Insect species and Types of vegetation	January	February	March	April	May	June	July	August	September	October	November	December
HEMIPTERA												
from *Spartina alterniflora*												
Trigonotylus uhleri					6xx	xx	xx	xx	x	x	14x	
Ischnodemus badius	x	x	x	x	x	x	x	x	xx	xx	x	x
Tylthus vagus	13x				10x	x	x	xx	xx	x	x	x
from *Juncus roemerianus*												
Cymus breviceps				9xx	xx	23x						
from *Distichlis spicata*												
Trigonotylus americanus				23x	xx	xx	xx	xx	x	17x		
Rhytidolomia saucia				9x	x	x	x	x	5x			
Cymus breviceps				11xx	xx	x	x	18x				
from *Spartina patens*												
Trigonotylus uhleri				27x	xx	xx	xx	x	x	x	11x	
Cymus breviceps						6xx	xx	27x				
ORTHOPTERA												
from *Spartina alterniflora*												
Orchelimum fidicinium				26x	xx	xx	xx	x	16x			
from *Spartina-Salicornia-Limonium*												
Orphulella olivacea					24x	xx	x	x	x	13x		
from *Juncus roemerianus*												
Paroxya clavuliger						10x	x	x	x	13x		
Anaxipha scia						10x	x	x	x	x	12x	
from *Distichlis spicata*												
Nemobius sparsalsus						29x	x	x	x	17x		
*Orphulella olivacea***					13x	x	x	x	17x			
*Clinocephalus elegans***					x	x	x	26x				
from *Spartina patens*												
Mermiria intertexta					13x	x	x	x	x	16x		
from all types of vegetation												
Cycloptilum antillarum						18x	x	x	x	17x		
Oecanthus quadripunctatus					16x	x	x	x	x	17x		
Conocephalus spp.					10x	xx	x	x	x	17x		
COLEOPTERA												
from *Spartina alterniflora*												
Collops nigriceps					27x	x	x	8x				
Isohydnocera tabida					4x	x	x	x	x	12x		
Mordellistena spp.				26x	x	x	x	x	14x			
from *Distichlis spicata*												
Naemia serriata (adults)				11x	x	x	x	xx	x	x	13x	
Naemia serriata (larvae)					4x	x	x	xx	x	17x		
from *Spartina patens*												
Glyphonyx sp.						11x	x	30x				
Isohydnocera aegra				27x	x	x	x	27x				
Chaetocnema sp.						13xx	x	x	17x			
Pachybrachys atomarius						11xx	x	21x				
Cryptocephalus venustus						18xx	x	11x				
HYMENOPTERA												
from *Spartina patens*												
Tapinoma sessile					11x	x	x	x	15x			
Dorymyrmex pyramicus						12x	x	x	14x			
Iridomyrmex pruinosus				27x	x	x	x	x	14x			
Pseudomyrmex pallida					6x	x	x	x	x	x	x	11x
Monomorium minimum					11x	x	x	x	x	12x		
from all types of vegetation												
Crematogaster clara	15x			8x	x	x	x	x	x	x	x	x

*Entry probably includes specimens of *Paraclius claviculatus*.
**Young nymphs of *Orphulella olivacea* and *Clinocephalus elegans* are indistinguishable.

Summer Aspect. All types of salt marsh vegetation attained maximum development during the summer. Most of the discussion in previous sections of this paper deals especially with the summer insect assemblages. The population levels of most species did not remain constant during this season. The orthopterans and hemipterans gradually declined, several common summer species becoming rare by September. Most of the homopterans that were abundant in the summer had a definite peak period. Of special interest is *Prokelisia marginata*, in which the populations occurring in different stands of *S. alterniflora* increased to various levels. In some stands of *S. alterniflora*, one sweep-net sample taken during the peak period was sufficient to obtain tens of thousands of adults and nymphs; in other stands, only a very modest peak occurred. The time of population increase of *P. marginata* in the same stand can vary considerably from year-to-year; for instance, at Bogue Banks in 1959 the *P. marginata* population did not enlarge until October, but in 1960 it grew tremendously in August.

Fall Aspect. The salt marshes stayed green until late fall. Some insects that were common in the summer remained abundant throughout most of this season, particularly several species of Homoptera (family Delphacidae) and Diptera. Three species of Homoptera attained their peak population level in the fall; these were *Pentagramma vittatifrons*, *Delphacodes detecta* (in *S. patens* only), and *Aphelonema simplex*. The salt marsh mosquito, *Aedes sollicitans*, reached its maximum abundance in September and October, and was collected then in large numbers in all types of salt marshes. Only occasional specimens of *A. sollicitans* were obtained at other seasons.

SUMMARY

1. The main purpose of this study was to describe the zonal and seasonal distribution of the principal species of insects from the herbaceous strata of the major types of salt marshes in Carteret County, North Carolina. The responses of these insects to flood conditions, and their trophic relationships, were also observed.
2. The salt marshes of the study area are classified as follows: (1) the *Spartina alterniflora* association, which occurs on substratum inundated at each high tide; (2) the *Spartina-Salicornia-Limonium* association, which occurs on substratum inundated at each high tide; (2) the *Spartina-Salicornia-Limonium* association, which occurs on slightly higher ground, and forms a narrow zone just above *S. alterniflora*; (3) the *Juncus roemerianus* association, which grows on flats inundated by spring tides, and occurs just above *Spartina-Salicornia-Limonium*; (4) the high marsh association, of which there are two principal facies, the first dominated by *Distichlis spicata* and occurring principally within or on the margin of *Juncus* marshes and at about the same elevation, and the second dominated by *Spartina patens* and usually occurring on sandy ground above the *Spartina-Salicornia-Limonium* zone, at a level seldom reached by high tides.
3. The insect assemblages of each type of marsh were sampled by sweeping the vegetation. The period of most intense sampling was June, July, and August, 1960, when sets of ten samples were obtained from twenty stations, of which six were established in *S. alterniflora*, one in *Spartina-Salicornia-Limonium*, four in *Juncus*, four in *Distichlis*, and five in *S. patens*. Samples were also taken monthly from one or more stands of each type of marsh from September 1, 1959, to June 1, 1960.
4. The ordinal composition of samples from stations included in the summer sampling program was determined. Homoptera predominated at fourteen stations, of which five were in *S. alterniflora*, one in *Spartina-Salicornia-Limonium*, three in *Juncus*, three in *Distichlis*, and two in *S. patens*. Diptera were most abundant at the other six stations, and were second in abundance in samples from most stations at which Homoptera were predominant. Hemiptera, Orthoptera, Coleoptera, and Hymenoptera were also present at all stations, usually in much smaller numbers. Homoptera decrease, and other orders increase, in abundance as zone elevation increases.
5. The specific composition of the insect assemblages of each type of marsh was determined. The zonal distribution, frequencies, and densities of the principal insect species are illustrated in diagrams.
6. Frequencies, densities, field observations, and special collections, were used to construct an outline of the characteristic insect species of the summer aspect of each type of marsh.
7. Most of the characteristic insect species from all types of marshes are herbivores, and fall into these three categories: (1) those with chewing mouthparts, the most important of which are grasshoppers, feed on plant tissues; (2) those with piercing and sucking mouthparts, the homopterans and most hemipterans, feed on plant sap; (3) those with sponging mouthparts, mainly species of Diptera, feed on plant secretions.
8. The principal carnivores in all types of marshes are spiders. The most abundant carnivorous insects are beetles, asilids, mosquitoes, and reduviids. Detritus-feeding ephydrid and dolichopodid flies are common in *S. alterniflora*, *Spartina-Salicornia-Limonium* and *Distichlis*. Dipterous larvae parasitize salt marsh plants, and the larvae of parasitic hymenopterans undoubtedly infect many species of salt marsh insects.
9. There is no evidence that members of any insect species encountered in this study ordinarily allow themselves to be inundated by rising water. Some kinds of salt marsh insects can swim, walk, or hop over the surface film, and others escape high water by flying.
10. The seasonal distribution of the predominant types of insects, as indicated by their presence or absence in samples, is given. Several species of fulgorids and other homopterans, some dipterans, and a lygaeid, occur throughout the year in the adult stage. Orthopterans, beetles, most species of ants, parasitic hymenopterans, most cicadellids, and most kinds of hemipterans and dipterans are absent in winter.

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