Winter 1985

Bionomics of *Culicoides* Spp. (Diptera: Ceratopogonidae) from a Coastal Georgia Barrier Island

George J. Magnon

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submitted by

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B.S., The Citadel 1976

A thesis Submitted to the Graduate Faculty of

Georgia Southern College in Partial

Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE IN BIOLOGY

Statesboro, Georgia

1985

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ACKNOWLEDGEMENTS

The author wishes to express his appreciation to Dr. Daniel V. Hagan, Chairman of his advisory committee, for his guidance and encouragement throughout this study. Gratitude is also expressed by the author to other members of his advisory committee, Drs. W. Keith Hartberg, and Richard L. Osburn for critical review of this manuscript.

Sincere thanks are extended to Dr. D. L. Kline (USDA, Insects Affecting Man and Animals Laboratory, Gainesville, FL) for his advice during the planning of this study; to Dr. J. A. Rafter (GSC), for his assistance with statistical analysis of the data; to Dr. W. W. Wirth (Smithsonian Institute, U.S. National Museum, Washington, DC) for confirmation of identifications of the Culicoides species collected; to Dr. D. J. Drapalik (GSC) for identification of plant species from the research site; to Michele Owsley for her invaluable technical support in identifying and counting Culicoides; and to Karen Corsetti for her help in the conduct of the field work.

The author additionally wishes to gratefully acknowledge the support from the biology faculty and staff, fellow graduate students and research assistants. Appreciation is also expressed to the Sapelo Island Research Foundation for financial support which made this research possible, and to Mr. Ralph Graham for providing access and cooperation in this research effort.

Finally, the author wishes to extend his warmest gratitude to his beloved parents whose enduring faith, love and support make no task insurmountable.

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ABSTRACT

The seasonal abundance of adult *Culicoides* spp. on a coastal Georgia barrier island was determined during a 20-month period, September 1983 through May 1985 by CO_2-baited CDC miniature light traps and sticky cylinder traps.

A total of 220,670 adult biting midges representing nineteen species and including the first report of *C. loughnani* Edwards in Georgia was collected. *Culicoides furens* (Poey), *C. hollensis* (Melander and Brues), and *C. melleus* (Coquillett) were the most abundant. *Culicoides furens* was abundant from early spring to late fall. *Culicoides hollensis* and *C. melleus* were bimodal with spring and fall abundance, but *C. melleus* appeared later in the spring and disappeared sooner in the fall. Adult light trap catches were statistically significant for temperature, but not for rainfall, wind velocity or moon phase.

Culicoides spp. larvae (5717) were recovered from salt marsh substrate and correlated with vegetation type, elevation, soil pH and soil mineral content of calcium, magnesium, phosphorus and potassium. Larvae of *C. furens* were most abundant in areas dominated by *Spartina alterniflora* Loisel (<1.2 m) and at an intermediate elevation between the low and high water mark. Larvae of *C. hollensis* were most abundant in areas dominated by tall *S. alterniflora* (>1.2 m) at an elevation located near the mean low

water mark. Larvae of this species were found to be statistically significant for elevation and phosphorus. Larvae of C. melleus were found mostly in areas characterized by Distichlis spicata L. and at an elevation located near the high water mark. Soil was found to be acidic with a mean value for all species of pH 5.6. Characteristics of larval habitat and adult emergence sites coincided well by species for environmental parameters measured.

Substrate samples from the coastal Georgia salt marsh were also found to provide habitat for other ceratopogonid Diptera, Dasyhelea atlantis Wirth and Williams, D. mutabilis (Coquillett) and Leptoconops linleyi Wirth and Atchley. This is the first report of L. linleyi from the state of Georgia.

Larval head capsule measurements were made and head ratios calculated to determine instar number for the three dominant salt marsh species. Analysis of variance for headlength, headwidth and head ratio values revealed statistically significant differences for inter- and intraspecific instars. Dyar's growth progression factors were 1.34 for C. furens, 1.49 for C. hollensis and 1.25 for C. melleus.

Seasonal incidence of larval instars was compared with adult abundance to predict life cycle and development. Lower larval densities of C. hollensis and C. melleus were present in spring and fall, coinciding with periods of adult abundance. High larval densities in winter and summer may indicate that these species have two generations per year. A majority of third-instar C. furens may indicate both autogenous and anautogenous races in the population.

INTRODUCTION

Small bloodsucking Diptera of the genus *Culicoides* (comprised of over one thousand species) belong to the family Ceratopogonidae, suborder Nematocera. Of the 60 genera of Ceratopogonidae, *Culicoides* is one of four genera (*Leptoconops*, *Austroconops*, *Forcipomyia*) known to feed on warm-blooded vertebrates (Linley et al. 1983). *Culicoides*, known more commonly as biting midges, sand flies or sand gnats, are notorious in all tropical and temperate zones of the world (Arnaud and Wirth 1964), with the exception of New Zealand (Macfie 1932), Patagonia, and southern Chile (Ingram and Macfie 1931, cited by Hill 1947).

The importance of biting midges is the irritation and annoyance associated with the biting habits of female midges who need a bloodmeal to complete egg maturation. This biting habit may interfere with development of industry and tourism (Dove et al. 1932, Linley and Davies 1971). The primary medical importance of *Culicoides* is as a disease vector. Sand flies were once thought to be incapable of transmitting parasitic diseases because of their small size and presumed short life span (Lee 1963). However, at least 37 species of *Culicoides* are known to transmit viral diseases and filarial and protozoan parasites to man and animals (Karstad et al. 1957, Kettle 1965, Ah 1968).

The first association of Culicoides with filarial transmission was by Sharp (1928) who identified C. austeni Carter, Ingram and Macfie as intermediate host of the filarial worm Acanthocheilonema perstans Manson in west Africa. Buckley (1934) later observed larval development of Mansonella ozzardi Manson in females of C. furens Poey.

The role of Culicoides as vector for filariasis in animals was first demonstrated by Steward (1933) who traced development of Onchocera cervicalis Leuckardt microfilariae in C. nubeculosus Miegen that had fed on horses affected with fistulous withers. Biting midges have also been associated with filarial transmission in cattle (Buckley 1938), numerous avian groups (Robinson 1971 and Soulsby 1965, cited by Braverman and Galun 1973), and in monkeys (Lowrie et al. 1978 and Eberhard et al. 1979, cited by Linley et al. 1983).

Ghosh (1925) was first to note the role of Culicoides in transmission of protozoa when he reported the cilate Balantidium knowlesi in C. peregrinus Kieffer. Development of Haemoproteus nettionis (Johnson and Cleland), a malaria parasite of ducks was observed in Culicoides by Fallis and Wood (1957). Leucocytozoonosis, a disease of considerable economic importance for poultry in Southeast Asia and Japan is transmitted by C. arakawai (Arakawa) (Akiba et al. 1959, 1960, cited by Braverman and Galun 1973).

The ability of Culicoides to transmit pathogenic viruses to vertebrates was first recorded by DuToit (1944) in South Africa who proved that bluetongue virus of sheep and African horse sickness virus can be transmitted by C. pallidipennis Carter, Ingram and Macfie. Other arthropod-borne viruses associated with Culicoides include Eastern Equine Encephalomyelitis (EEE) (Karstad et al. 1957), Venezuelan Equine Encephalitis (VEE) (Jones et al. 1972), Epizootic hemorrhagic disease (EHD) (Jones et al. 1977) and the viruses Buttonwillow, Lokern and Main Drain (Nelson and Scrivani 1972). Oropouche, an important human viral disease transmitted by C. paraensis (Goeldi), occurs in the Amazon region of Brazil and causes febrile illness with fever, chills, headache and dizziness persisting two to seven days (Linley et al. 1983). Growing awareness of the role of Culicoides spp. in disease transmission and their impact on tourism has resulted in research efforts to determine distribution, seasonal fluctuations, life cycle and larval habitats.

Biting midges have been known to breed in a variety of aquatic and semi-aquatic environments (Blanton and Wirth 1979). Early accounts of their life history were made in sermons by Derham (1713, cited by Hill 1947). The availablity of moisture, ranging from the thin film between leaves on the forest floor, the decaying parts of a banana tree stump or the mud of a tidal salt marsh, seems to be the primary requirement for Culicoides development.

Early investigations of Culicoides larval habitats revealed that some species had adapted to a wide range of physical, chemical and nutritional conditions (Smith 1966, Kardatzke and Rowley 1971, Battle 1971, Battle and Turner 1972, Lubega and Khamala 1976).

Certain species had definite limitations in their habitats, favoring soils with specific nutrients and pH.

Differences in seasonal abundance of biting midge larvae from various habitats have been linked to one or more environmental factors such as temperature, sunlight, tide-elevation levels and vegetation (Hull et al. 1934).

Dove et al.(1932) found the longevity increased substantially in sand fly larvae maintained in water at a low temperature (10°C) increased substantially over those kept at a high temperature (32°C). In temperature gradient experiments, second to fourth-instar larvae of C. melleus (Coquillett) prefered an 18-25°C range (Linley and Adams 1972). Williams (1951) found 13°C to be the optimum temperature for both larval and pupal development. Kettle (1956) found higher air temperatures were associated with decreased larval abundance.

Hull et al. (1934) found a higher incidence of larvae in the shade of trees during summer, while in winter more larvae were collected in the open (unshaded) marsh. Dove et al. (1932) found larvae most abundant in areas protected from direct sunlight. Collections from emergence traps in a mangrove swamp (Davies 1969) revealed dense populations of C. barbosai Wirth and Blanton in shaded areas, while populations of C. insignis Lutz and C. furens were unaffected by shading.

The influence of tides and elevation on Culicoides spp. larval habitats has diverse effects depending on geographic location, species involved, seasonal change in mean sea level and monthly pattern of spring tide flooding (Blanton and Wirth 1979). Location of larvae at different elevations along depressions, ditches and barriers within the marsh was attributed by Hull et al. (1934) to transport of larvae by seepage of subsurface water. In a study of tidal influence on Culicoides adults, Reye and Lee (1972) found peak collections were correlated with neap-tide periods and meagre catches with spring tides. Elevations attained by tidal water affect location of larval and pupal zones for Culicoides (Linley 1966, Linley and Adams 1972).

Tidewater plants occur in regular patterns related to tidal flooding, and serve as indicators for elevation on the marsh (Ranwell 1972). A detailed study by Kettle (1961) found Culicoides habitats associated with distinct flora and larval species prefered specific vegetative zones. Kline and Axtell (1977), in a North Carolina salt marsh, also found larval species associated with certain plant types and found correlations with percentage of time marsh was flooded and soil characteristics.

The life cycle of Culicoides species varies considerably with climatic as well as other ecological factors. Many species have a single generation a year, while others are capable of annually producing ten or more generations under controlled laboratory conditions (Hair and Turner 1966).

Feeding activity studies reveal many species to be crepuscular in biting activity, although some species are nocturnal and others diurnal. Population dynamics of adult Culicoides spp. have been monitored by various trapping techniques. Methods range from light traps and animal-baited traps to less biased sticky cylinder traps and vacuum devices. Emergence traps of various designs have also been used to determine larval distribution.

In Georgia, few studies of Culicoides spp. have been conducted and none have surveyed coastal species for an extended length of time. Some studies (Foote and Pratt 1954, Williams 1955a, Karstad et al. 1957, and Ah 1968) have focused on non-coastal species. Wright (1985) surveyed Culicoides of Sea Island, but collected insufficient specimens to measure population fluctuations.

Foote and Pratt (1954), in their work on Culicoides of the eastern United States, reported 17 species from Georgia which included fresh-water, salt-water and tree hole breeding sand gnats.

In Baker County, Georgia, Williams (1955a) investigated species occurring from August 1952 through January 1953 and established laboratory colonies for studies of disease transmission and immature stages. In Wayne County, Georgia, Karstad et al. (1957) reported eastern equine encephalomyelitis virus from an unknown species of Culicoides.

Ah (1968), from June 1966 to June 1968, conducted a study of the systematics, bionomics and vector potential of Culicoides primarily from Clarke County, Georgia. He collected a total of 14,011 adults, representing 34 species of seven subgenera.

Various authors mentioned that the salt marsh not only provides excellent habitat but also produces the most pestiferous species of biting midges (Williams 1962, Lee 1963, Hair et al. 1966, Blanton and Wirth 1979). Many observations on life history and activity of

Nearctic species (Jamnback and Wall 1958, Khalaf 1969, Linley et al. 1970, Koch and Axtell 1979) have been conducted in coastal areas since salt marsh species are present in tremendous numbers much of the year.

Studies on immatures of these species have involved larval distribution (Carpenter 1951, Blanton et al. 1955, Bidlingmayer 1957, Kline and Axtell 1977), control (Jamnback et al. 1958, Fox et al. 1968), behavior (Linley 1966, Linley and Adams 1972) and growth and survival of laboratory colonies (Linley 1969a). Factors which affect larval habitat preference and distribution within a salt marsh remain poorly understood and have not been examined in coastal Georgia.

The objectives of this study of ceratopogonids in coastal Georgia were twofold. The study involved an examination of adult Culicoides species present, seasonal incidence and distribution of species on the coast of Georgia. The second part of the investigation concerned the bionomics of the three most common salt marsh species. It focused on larval habitat preferences (biotic and abiotic factors), seasonal distribution of larval instars, and larval morphometrics of the four instars.

MATERIALS AND METHODS

Description of the Research Site

The research area, located in Glynn County, Sea Island and St. Simons Island, Georgia (81^{o} 20' 30" longitude, 30^{o} 11' 30" latitude), is a coastal barrier island 7.9 km long with a maritime forest community located on the beach ridges (Figure 1). The island is bordered on the east by the Atlantic Ocean and on the west by a 2.3 km wide salt marsh interspersed with numerous tidal creeks and waterways. Sea Island is 1.6 km wide at the north end and narrows to about 0.5 km to the south. Sea Island is separated from St. Simons Island by Goulds Inlet to the south and from Little St. Simons Island by the Hampton River to the north. The climate on Sea Island is moderate the year around with an average summer temperature of $32^{o}C$ and average winter temperature of $17^{o}C$. The average annual rainfall is 137 cm.

The major components of the maritime forest are: *Quercus virginiana* Miller (live oak), *Pinus elliottia* Engelm (slash pine), *Myrica cerifera* L. (wax myrtle), *Juniperus virginiana* L. (red cedar), *Sabal palmetto* Lodd ex. Schultes (cabbage palmetto), *Serenoa repens* Hooker F. (saw palmetto) and *Ilex* spp. (hollies). The salt marsh vegetation was dominated by *Spartina alterniflora* Loisel (smooth cordgrass) in the low marsh areas. The higher marsh associations included the less abundant species: *Spartina patens*

Ait. (saltmeadow cordgrass), Salicornia virginiana L. (glassworts Batis maritima L. (saltwort), Juncus roemerianus Scheele (black needlerush), Distichlis spicata L. (seashore saltgrass), Borrichia frutescens L. (sea ox-eye), Iva frutescens L. (marsh elder) and Baccharis halmifolia L. (sea myrtle).

Seasonal Incidence

Population levels of adult Culicoides were monitored by the use of three trapping techniques: (1) sticky cylinder traps (SCT), (2) light traps operated in the scotophase (LT) and (3) light traps operated in the photophase (LTP). The SCT's, modified after those described by Kline and Axtell (1977), captured adult gnats in flight or as they landed on the surface. Traps were made from sections of white plastic PVC (polyvinyl chloride) pipe, 3.1 m high x 10.1 cm diam. which were placed 46 cm into the ground. Sheets of cellulose acetate (26 cm x 35 cm) coated with Tangle-Trap (Tanglefoot Co., Grand Rapids, MI) were wrapped around the outside of the plastic pipe and attached with metal clips, thus providing a white cylinder background behind the trapping area. Sheets were placed with centers 0.6 m, 1.2 m, and 1.8 m above ground level. Sticky cylinder traps were positioned at five of the six collection sites and were in continuous operation from 23 September 1983 through 31 May 1985. Collection and replacement of sticky sheets was carried out once every two weeks. Sticky sheets were transported to the laboratory and Culicoides were counted and identified as to sex and species.

Center for Disease Control (CDC) miniature light traps (John

W. Hock and Co., Gainesville, FL) were equipped with a photoswitch (model LCS-2) designed to turn the traps on at dusk and off at dawn to accurately determine those species active during the hours of darkness (scotophase). The level of light intensity at which traps operated was <7.72 foot-candle. A small incandescent lamp (0.52 foot-candle) model CM 47 (Chicago Miniature Lamp Works, Chicago, IL) was located at the top of the trap. A suction fan, operated by a 6 volt battery, pulled gnats attracted to the light into an 80 mesh collection bag. Below the fan, air-actuated gates opened during trap operation and closed automatically when the fan shut off. A 16 mesh screen was secured at the trap opening to prevent collection of mosquitoes or other larger insects.

Light traps were additionally modified as described by Floore (1982) for dry ice (CO_2) dispersal. A dry ice chamber constructed from a 3.8 liter paint can was suspended over the trap. The dry ice was cut into blocks of ca. 0.9 kg each at the East Coast Ice Co., Brunswick, GA and transported to the field in an insulated cooler. Prior to placement in the chamber, the dry ice was wrapped in a brown paper bag containing a small hole to allow CO_2 to escape. The lid of the paint can was taped on with duct tape to reduce CO_2 loss. Sublimation rates varied with ambient weather conditions, but one 0.9 kg block of dry ice provided adequate CO_2 release for about 12 hours. A 12-15 cm section of 1.3 cm plastic tubing inserted through a hole at the bottom of the paint can directed the CO_2 down to the entrance of the light trap. Light traps were operated at a height of about 1.8 m above ground level. A single light trap was located at each of the six locations. Weekly scotophase light trap collections were made from 23 September 1983 through 31 May 1985. Collection nights varied slightly from week to week.

To determine daylight (photophase) activity of Culicoides spp., a study was conducted utilizing light trap catches from 7 January 1984 through 29 December 1984. Collection sites were identical to those used in the scotophase collections. Photophase collections were made once every two weeks from two hours after sunrise until two hours prior to sunset. All light trap collections (both scotophase and photophase) were brought to the laboratory, preserved in 70 percent ethanol, counted and identified as to sex and species.

The first collection site (Fig. 1) was an area near the Cloister, a hotel-restaurant complex. This site is an area of high human density and outdoor activity since it is located adjacent to tennis courts. A LT was positioned 2 m behind the tennis courts in a canopy formed by Viburnum spp. which was approximately 7 m tall. A SCT was located behind a storage building surrounded by Pittosporum tobira Ait., Nerium oleander L. and Pinus spp., 7 m from the tennis courts.

The second collection site (Fig. 1) was a beach site selected to examine effects of beach exposure to gnat abundance. A LT was attached to a branch of Quercus virginiana 9 m from the south side of a residence and 50 m from the sea wall facing the Atlantic Ocean. A SCT surrounded by Myrica cerifera and Baccharis halmifolia was located 11 m behind the sea wall. A second SCT was positioned on the north corner, 20 m from the residence and 50 m from the sea wall. This SCT was surrounded by surrounded by *Pittosporum tobira* and *Nerium oleander*.

Collection site 3 was on the marsh side of the island on a peninsula projecting into the marsh (Fig. 1). A LT was attached to a branch of *Quercus virginiana* 80 m from a residence and at the extreme northwest end of the peninsula. This site was an undisturbed area with no lights to compete with the trap light. Three SCT's were placed in the following habitats: (1) intermediate form of *S. alterniflora* in the salt marsh flat, (2) *J. roemerianus*, *Q. virginiana*, *B. frutescens*, *I. frutescens*, *B. maritima* and *Juniperus* spp. at the northwest end of the peninsula, and (3) *S. repens*, *J. roemerianus*, *B. maritima* and *Juniperus* spp. 30 m from the residence.

The fourth collection site was an area of *Q. virginiana* and *S. repens* about 500 m from the marsh (Fig. 1). This was a forested area and a LT was attached to a branch of *Q. virginiana*. A single SCT was also placed here.

The fifth collection site was at the north end of the island with the Hampton River to the north and Village Creek to the west (Fig. 1). This area was free from human disturbance and development. A LT was attached to a branch of *Q. virginiana* 22 m from the river and 15 m from a large salt marsh area. Three SCT's were positioned in the following habitats: (1) adjacent (4 m) to *Q. virginiana* and *Juniperus* spp. trees, with *Distichlis spicata* at its base, 15 m from high tide level, (2) a mound 0.15 m above the salt marsh flat covered by *Spartina patens*, *Salicornia virginica*, *B.*

maritima and I. frutescens, and (3) on the marsh flat 45 m from the mound location above intermediate and short growth of S. alterniflora.

The sixth collection site was at the Sea Island horse stables, located on St. Simons Island 3 km northwest of Sea Island and about 100 m northwest of the Sea Island Causeway and Frederica Road intersection (Fig. 1). Selection of this site was prompted by the presence of horses in unsheltered stables which might influence gnat abundance. A LT was attached to the outside of a corner stable directly across from another row of stables. Numerous chickens were also common in the area. Major vegetation types present were Q. virginiana, Q. nigra L. and S. repens. A large deposit site of horse manure (4-6 m in height) was located 5 m from the trap.

Larval Habitat Site and Sampling Methods

Site selection for the study of environmental factors that influence distribution of Culicoides larvae within the marsh was based on diversity of vegetation and degree of the tide-elevation influence. A 14,600 m^2 area of salt marsh located on the north end of the island was selected. The marsh research site ranged in elevation from 0.6 m below mean sea level (MSL) to 0.6 m above MSL (Figure 2). Water margins along the river, tidal creeks and several ditches were dominated by a tall form of Spartina alterniflora (>1.2 m). Progressing from these low-lying areas toward the upland, a band of intermediate form of S. alterniflora (0.3 m-1.2 m) was present. This area of the marsh was designated as zone I with an elevation $\leq$-0.15 m. Zone II, the largest area of the marsh with elevations from -0.15 m to 0.3 m was dominated by a short form of S. alterniflora (<0.3 m). The variety of vegetation forms of S. alterniflora probably indicates the difference in degree of inundation by salt water (Adams 1963). Most of the research site was flooded by tides once each 12 hour period. A distinctive zone of Juncus roemerianus separated the marsh from the upland forested area. This is designated as Zone III and is characterized by a number of shrubs (Fig.2) including Borrichia frutescens and Baccharis halmifolia at higher elevations ($\geq$0.3 m). Vegetative zones and corresponding tide/ elevation influence are depicted in Figure 2.

A topographical survey was conducted using a theodolite (Wild model T16) with readings recorded at 10 m intervals (Fig. 3). Each of the 146 (10 m x 10 m) plots was marked at the southwest corner of the plot with labeled 1 m sections of 5.08 cm diameter white PVC pipe driven about 0.6 m into the substrate.

Paired substrate samples of marsh soil were collected from 20 different plots each two weeks from 28 April 1984 to 31 May 1985. Plots to be sampled were systematically selected so that all plots were sampled once in each of four sampling cycles. The four sampling cycles were: 28 April 1984 to 28 July 1984, 28 July 1984 to 17 November 1984, 17 November 1984 to 8 March 1985 and 8 March 1985 to 31 May 1985. Soil samples were taken only during periods of low tide and daylight. Samples were obtained from the top 5 cm of substrate using a gardener's hand trowel. Soil samples (ca. 1300

cm^3) from each plot were placed in labeled individual plastic containers (16 cm x 11 cm), (Sweetheart Plastics Inc., Wilmington, MA) and transported to the laboratory. In the laboratory one of each paired sample was processed with the agar method outlined by Kline et al. (1981) for extraction of Culicoides larvae. Larvae collected were placed in 70 percent ethanol for later examination.

The second soil sample was retained for a period of 60 days for collection of emerging adult gnats. Containers were opened three times weekly on alternate days inside a small cage (40 cm x 26.6 cm x 26 cm). Adult gnats which had emerged from a sample were aspirated with a mechanical aspirator (Hausherr's Machine Works, Toms River, NJ) and transferred to 70 percent ethanol for later identification.

Identification of Larvae

A diagnostic key for the three species of Culicoides larvae studied was constructed from descriptions by Carter et al. (1920), Painter (1926), Hill (1947), Williams (1951), Wirth (1952), Jamnback et al. (1958) and Linley and Kettle (1964). Larvae were examined on a depression slide containing 100 percent liquified phenol (Wirth 1952). Larvae so treated were easily relaxed, cleared and manipulated for observation of distinguishing characters. Dimensions of the head in all larvae were expressed by two measurements, length and width. Head length (HL) was measured along the mid-dorsal line, from anterior edge of the transparent labrum to posterior edge of the post-occipital ridge. Head width (HW) was measured at the widest point, located about one third of the total length of the head from the posterior end (Linley and Kettle 1964). Head ratio (HR), the ratio of HL to HW described by Kettle and Lawson (1952) was calculated for all larvae. Measurements were made with a Nikon (Model S) compound microscope with an ocular micrometer.

Measurements of HL and HW were expressed in micrometers. Dyar's Law (1890) was used with larval head capsule measurements to determine instar number by species.

<u>Environmental Measurements</u>

Meteorological data was obtained from the FAA Weather Station, McKinnon Airport, St. Simons Island, GA by way of the National Climatic Data Center, Asheville, NC. Daily rainfall was recorded by a cooperative observer (Miss Terrell Thomas) residing on Sea Island.

A botanical survey including plant height was made and vegetation mapped giving a distribution of plant communities within the larval study site. At each site, soil pH was tested using a Kelway soil tester (model HB-2, Kel Instruments Co., Clifton, NJ). Soil samples to a depth of 5 cm from each plot were also collected and analysed by the Soil Testing Laboratory, Cooperative Extension Service, University of Georgia, Athens, GA for calcium, magnesium, phosphorus and potassium. Contour lines for the study site were determined as previously described.

Environmental conditions (temperature, wind velocity, rainfall and moon phase) for collections by LT's for September 1983 to May

1985 were compared with monthly totals of Culicoides collected to determine statistical significance. Collection data was recorded and processed on an Apple IIe microcomputer by means of the relational data base program, dBase II (Ashton and Tate, 1982). Vegetation type, soil pH, soil mineral content and elevation were compared to number of larvae/ plot to determine larval habitat preference by species.

Data were tested for statistical significance by multiple linear regression, analysis of variance (ANOVA), chi-square, or Duncan's multiple range test using the Statistical Program for Social Science (SPSS) and were analyzed with the University System of Georgia CYBER 74 computer.

RESULTS

Species Present

A total of 220,670 adult Culicoides comprised of nineteen species was collected by LT, LTP and SCT from the research area on Sea Island and St. Simons Island during the 20-month period, September 1983 through May 1985 (Table 1). The three most abundant species, from most to least in abundance, were C. hollensis (50%), C. furens (39%) and C. melleus (11%) and were obtained by all trapping methods from all locations. Two apparently new species (Table 1) are awaiting further taxanomic study (W.W. Wirth, personal communication). The largest number of species (16) was obtained by light traps operated in the scotophase, followed by sticky cylinder traps (10 species) and light traps operated in the photophase (8 species). Seasonal distribution for each species by month is presented in Table 2. Greatest species diversity occurred in April and May 1984 (Fig. 4), when 12 different species were collected. Fifty-three percent of the total collection was obtained by LT, 45 percent by SCT and two percent by LTP.

Seasonal Incidence of Dominant Species

The seasonal incidence of C. furens from SCT's and LT's is shown in Figure 5.

On SCT's C. furens was collected during each of the collection periods with exceptions of January and December 1984 and January through February of 1985. Peaks of abundance occurred through the spring-summer-fall period, diminishing during the colder months (November-February). One gnat/ trap period or less was collected during the November 1984 through mid-March 1985 time period. A small peak of activity (<10 gnats/ trap period) was recorded in early February of 1984. Males comprised 28 percent of the SCT collection of C. furens. SCT collections of C. furens (Table 3) were not significantly different for the three trap heights. The greatest total number of this species was collected at the trap height of 1.2 m. SCT collections comprised 25 percent of the total collection by all methods for this species.

The pattern for LT collections indicates that incidence of C. furens was greatest during similar months for the 20-month period of the study. This species first appeared in LT collections in late March 1984 and was collected through early December 1984. The highest peak attained in months sampled for 1983 occurred in late September. During the March-December 1984 period, higher peaks occurred in mid-April, mid-May and mid-August. A spring peak occurred in late May 1985. An average of one gnat/ trap night or less was caught by LT from early December 1984 to late March 1985. The percentage of males caught was low (<1% of total C. furens collected by LT). LT catches comprised 72 percent of the total collection by all methods for this species.

Photophase light trap collections of C. furens (Table 4) revealed two peaks, spring (April) and fall (October) over the one year (1984) collection period. No gnats of this species were collected in July and August 1984. These results, though similar to maximum periods of gnat abundance indicated in 1984 scotophase collections (Fig. 5), show different minimum periods of gnat activity. Photophase collections reached a maximum in the spring when 48 percent of the total collection was present. No male C. furens was collected by LTP.

A comparison of trapping methods showed similar trends in seasonal incidence. However, the detailed seasonal fluctuations indicated by LT collections was not shown in SCT collections. Few males were collected in LT's and a ratio of less than 1:1 males to females was attained in SCT collections. A greater percentage (72%) of C. furens adults was collected by LT's than with SCT's. LTP collections of C. furens indicate a slightly different seasonal pattern of activity from that revealed by LT collections.

The seasonal incidence of C. hollensis from SCT's and LT's is shown in Figure 6.

On SCT's C. hollensis was collected during each of the trap periods with the exception of early to mid-August 1984. A spring peak occurred in early March 1984 and late March to early April 1985. Fall peaks occurred in early November 1983 and early October 1984. One gnat/ trap period or less was collected from June through August 1984. Spring and fall peaks were similar in size. Males comprised 47 percent of C. hollensis caught by SCT. SCT collections of C. hollensis were not significantly different for the three trap heights (Table 3). The greatest total number for this species was collected at the trap height of 1.8 m. SCT's comprised 61 percent of the total collection by all methods for this species.

The pattern for scotophase light trap collections indicates that incidence of C. hollensis was greatest during similar months for the 20-month period. This species first appeared in LT collections in mid-February 1984 reaching a peak in the spring and almost disappearing in the summer. From mid-June 1984 to early September 1984 one gnat/ trap night, or less was caught. A second major peak in population occurred in the fall (September-December 1984) with numbers diminishing in the winter. These spring and fall peaks occurred in early to mid-April of 1984 and 1985 for the spring and mid-November 1983 and early October 1984 for the fall. The spring peak of 1984 exceeded that of the preceding fall with the opposite occurring in the spring of 1985. The percentage of males collected was low (<1% of C. hollensis caught by LT). LT collections comprised 37 percent of the total collection by all methods for this species.

Photophase light trap collections of C. hollensis (Table 4) indicate greater activity occurring from April to December with peaks occurring in June and September 1984. No gnats of this species were collected in January, February and March 1984. These results do not correspond with 1984 peaks of gnat activity indicated in scotophase collections (Fig. 6). The largest photophase collections were made in summer (June) when 40 percent of the total caught was present. No male C. hollensis were collected by LTP.

A comparison of trapping methods showed that though seasonal trends indicated by LT collections were similar to those of SCT method, they differed in the periods of spring peaks for 1984 (Fig. 6). More detailed fluctuations of seasonal incidence were revealed in LT data. Another dissimilarity between LT and SCT data was that the proportion of males in LT's was low, but comprised nearly half of the SCT collection. A greater percentage of C. hollensis adults (61%) was caught with SCT's than with LT's. LTP collections indicated different seasonal patterns from the LT collections, in that months of peak activity differed.

Seasonal incidence of C. melleus by SCT's and LT's is shown in Figure 7.

On SCT's C. melleus was collected during each of the collection periods with exception of January 1984 and January through February of 1985. Spring peaks occurred in mid-April of 1984 and 1985 with fall peaks also occurring in each of the preceeding years. Collections were lowest (10 gnats/ trap period or less) during the summer (June through August) and winter (November through late March), but disappeared only in the winter. Males comprised 10 percent of the SCT collection of C. melleus. SCT collections of C. melleus (Table 3) were not significantly different for the three trap heights. The greatest total number of this species was collected at the SCT height of 0.6 m. SCT collections comprised 42 percent of the total collection by all methods for this species.

Scotophase light trap collections indicate that incidence of C. melleus was greatest during similar months for the 20-month period. This species first appeared in LT catches in early March 1984 and late February 1985, reaching a spring peak in mid-April of both years and diminishing during the summer months. One gnat/ trap night or less was caught from mid-June through July 1984. Fall peaks occurred in early October of 1983 and 1984 with collections dwindling and then disappearing during the coldest months (January through early March) of each year. The spring peak of 1984 exceeded that of the preceding fall with the opposite occurring in the spring of 1985. Few males were collected by LT (<1% of C. melleus). LT collections represented 55 percent of the total for this species.

Photophase LT collections of C. melleus (Table 4) indicate spring (April) and fall (October) peaks of abundance over the collection period. No C. melleus were collected during the photophase in January, February and August, which corresponds well with 1984 gnat activity indicated in scotophase collections (Fig. 7). Photophase collections reached a maximum in spring when 82 percent of the total for the year were collected. No male C. melleus was collected by LTP.

A comparison of trapping methods reveal that data from each collection method coincided well. Males of C. melleus were not attracted to LT's (<1%) and were caught in only moderate numbers (10%) with SCT's. A slightly higher percentage (55%) of C. melleus adults was recovered by LT than by the SCT (42%) method.

Influence of Environmental Variables

A comparison of effects of various environmental variables on seasonal incidence (by LT collections) of the dominant species of adult Culicoides is presented in Table 5.

Climatological data obtained for LT collections indicate that 98 percent of the mean number/ trap night of C. furens was collected on nights with a mean air temperature between 16.4°C and 28.8°C. Ninety-eight percent of the mean number/ trap night of C. hollensis and C.melleus was collected on nights with a mean air temperature range of 9.1°C - 24.6°C and 13.4°C - 27.2°C respectively (Table 5). Analysis of variance of mean nightly air temperature for species activity revealed the mean temperature for C. hollensis to be significantly different from that of other species at the 0.05 level of probability using Duncan's multiple range test. Analysis by multiple linear regression also indicated mean air temperature for C. hollensis to be statistically significant at the 0.05 level.

The mean nightly wind speed below which $\geq$99 percent of the mean number of gnats/ trap night was collected was 11.3 kts for both C. furens and C. hollensis and 9.3 kts, for C. melleus (Table 5). Windspeed was not found to be correlated to LT collections of Culicoides when analyzed by multiple linear regression.

Light trap collections (Table 5), when compared with moon phases, indicated that 41.6% of the total C. furens was collected during the full moon. The lowest percentage (28.5%) occurred during the new moon. Activity of C. hollensis was greatest (39.1%) also during those nights in which the moon was full and least (25.5%) during the new moon. LT collections of C. melleus were greatest (46.0%) during periods of first or last quarter moon and least (14.8%) during the new moon.

Rainfall was not found to be correlated to LT collections of Culicoides when analyzed by multiple linear regression, nor were there any apparent trends of pre-collection rainfall (7, 14 and 28 day intervals) affecting collections of biting midges. Rainfall data was not included in Table 5.

Distribution of Larvae

A total of 5717 larvae was recovered from the salt marsh habitat. Larvae of each species, C. furens (26%), C. hollensis (53%) and C. melleus (21%) were found throughout the marsh. Distribution of larvae by the environmental variables of elevation, soil pH, and soil mineral composition is presented in Table 6. The dominant vegetation and the larvae present in sampled plots is presented in Table 7.

Larvae of C. furens, though present throughout the marsh, were found mostly (greatest mean number of larvae/ plot/ sample) in habitat characterized by: pH of 5.6, vegetation dominated by short ($\leq$0.3 m) to intermediate height (<1.2 m) S. alterniflora (Table 7), and an elevation (-0.060 m) between the low and high water mark for daily tides (Table 6). Substrate in this intermediate elevation zone remained soft and moist between daily occurrences of the tide.

Larvae of C. hollensis were found throughout the marsh, but were found mostly (greatest mean number of larvae/ plot/ sample) in habitat characterized by: pH of 5.6, vegetation dominated by tall (>1.2 m) S. alterniflora, an elevation (-0.066 m) located near the low water mark along the creek and river margins, and remaining flooded longer.

Larvae of C. melleus were also recovered from throughout the marsh, but were found mostly (greatest mean number of larvae/ plot/ sample) in habitat characterized by: pH of 5.6, vegetation dominated by D. spicata, and an elevation (0.041 m) located near the high elevation zone. This area was flooded for a shorter period of time than areas preferred by C. furens and C. hollensis. Substrate in this zone was a mixture of fine sand with mud.

Mean number of Culicoides larvae/ plot present at each elevation zone is depicted in Figure 8. Mean number of C. furens larvae/ plot (13.2) was greatest at the intermediate elevation zone. Mean number of C. hollensis larvae/ plot (35.6) was greatest at the low elevation zone. Mean number of C. melleus larvae/ plot (10.8) was greatest at the intermediate elevation.

Results of multiple regression stepwise analysis performed for each species and the environmental variables tested, revealed statistical significance only for number of C. hollensis larvae with elevation and phosphorus content of the soil.

Larval Morphometrics

Data from larval head capsule measurements (HL, HW, HR) for C. furens, C. hollensis, and C. melleus are presented in Table 8. Dyar's Law (1890) was used with head capsule measurements of a series of different-sized larvae of the same species. This allowed for determination of the instar. Larvae of C. furens increased in headlength by a geometric progression factor of 1.34. Larvae of C.

hollensis increased in headlength by a factor of 1.49, and C. melleus larvae by a factor of 1.25. The minimum, maximum and mean values for head measurements were recorded for the four instars of each species. Analysis of variance of instar data for each species showed that instars varied significantly in head dimensions at the 0.05 level of probability using Duncan's multiple range test (Table 8).

Seasonal Distribution of Larval Instars

Larvae recovered over the period 28 April 1984 to 31 May 1985, were identified to species and instar for seasons of the year. Larval instars of C. furens plotted by season are presented in Figure 9. Not all 146 plots were sampled for a full season in the spring of 1984, but data obtained did reveal second-instar larvae to be the most abundant life stage. No fourth-instar larvae of C. furens were recovered. In the following season (summer 1984), larvae of every instar had increased in number with third-instar larvae most abundant. The number of each larval instar recovered during the fall of 1984 decreased as compared to the previous summer season with exception of the fourth-instar. Winter of 1985 showed increases in number of each instar with exception of the fourth-instar which decreased. A near threefold increase of third-instar larvae from that of the previous fall was indicated. Larvae recovered in the spring of 1985, though not indicative of a full season, revealed the following trends: increases of first and second-instar larvae and a decrease in number of third and fourth-instars.

Larval instars of C. hollensis plotted for seasons are presented in Figure 11. Larvae recovered in the spring of 1984 indicate second-instar larvae to be most prevalent. In the summer season of 1984, larvae of all instars increased with third-instars as the most abundant life stage. Larvae recovered during the fall of 1984 decreased in number for all instars. Winter of 1985 showed an increase in all instars with that of the fourth-instar showing the largest increase. The subsequent spring of 1985 showed the following trends: increases in both first and second-instars, and decreases of third and fourth-instar larvae of C. hollensis (Fig. 10).

Larval instars of C. melleus plotted for seasons are presented in Figure 11. Larvae recovered in the spring of 1984 indicate third-instar larvae to be most abundant. The summer season indicated larvae of C. melleus to increase for all instars. During the fall season of 1984 larval instars decreased with no first-instars collected. The winter of 1985 indicated the number of each instar increased over the previous fall with fourth-instar larvae being most abundant. The spring of 1985 showed decreasing trends for third and fourth-instar larvae with second-instar larvae most prevalent.

Adult Emergence

A total of 3759 adult ceratopogonids of the genera Culicoides, Dasyhelea and Leptoconops emerged from salt marsh soil samples retained in the laboratory (Table 9). Samples representing all elevation levels yielded adults of the three dominant species of Culicoides: C. furens (40%), C. hollensis (45%) and C. melleus (15%). The numbers of emerged adult ceratopogonids obtained from plot soil samples by the environmental variables of elevation, soil pH, and soil mineral composition are presented in Table 10. The dominant vegetation and the adults emerging from sampled plots is presented in Table 11.

Adults of C. furens emerged from soil samples collected throughout the marsh, and were found most abundant (greatest mean number/ plot/ sample) in habitat characterized by: pH of 5.6, vegetation dominated by J. roemerianus (Table 11), and an elevation (0.002 m) located in the intermediate elevation zone (Table 10).

Adults of C. hollensis emerged from soil samples collected throughout the marsh, but were most abundant (greatest mean number/ plot/ sample) in habitat characterized by: pH of 5.6, vegetation dominated by an intermediate height (0.3-1.2 m) of S. alterniflora, and an elevation (-0.021 m) located in the low elevation zone.

Adults of C. melleus also emerged from soil samples collected throughout the marsh, but were found most abundant (greatest mean number/ plot/ sample) in habitat characterized by: pH of 5.6, vegetation dominated by D. spicata, and an elevation (0.044 m) located in the intermediate elevation zone.

Adults of Dasyhelea mutabilis (Coquillett) emerged most (greatest mean number/ plot/ sample) from soil samples collected on the marsh having the following characteritics: pH of 5.5, a dominant vegetation of marsh shrubs (Table 11), and an elevation (0.071 m) located in the high elevation zone.

Adults of Leptoconops linleyi Wirth and Atchley emerged most (greatest mean number/ plot/ sample) from soil samples collected on the marsh having the following characteristics: pH of 5.2, a dominant vegetation of J. roemerianus, and an elevation (0.220 m) located in the high elevation zone.

Mean number of emerging adult Culicoides/ plot at each elevation zone is depicted in Figure 9. Mean number of emerging C. furens adults/ plot (10.5) was greatest in the intermediate elevation zone. Mean number of emerging C. hollensis adults/ plot (15.9) was greatest in the low elevation zone. Mean number of emerging C. melleus adults/ plot (5.5) was greatest in the intermediate elevation zone.

Results of the multiple regression stepwise analysis for emerging ceratopogonids and the environmental variables tested, reveal correlation of C. furens for calcium and potassium at the 0.05 level of significance. Number of C.melleus collected was significantly correlated with phosphorus content at the 0.05 level. Number of C. hollensis collected was significantly correlated for elevation at the 0.05 level. Number of L. linleyi collected was significantly correlated with elevation at the 0.05 level.

Sex ratios of emerging adult C. furens, C. hollensis, D. mutabilis, and L. linleyi revealed statistically significant deviations from an expected 1:1 sex ratio (Table 9). Number of C. furens females exceeded that of the males with the reverse true of

C. hollensis. Data obtained for *C. melleus* indicates normal sex distribution of a population.

DISCUSSION

Species Present

Species present on Sea Island, Georgia (Table 1) were similar to findings of other studies along the Atlantic and Gulf coasts of the United States (Beck 1958, Jamnback 1958, Ah 1968, Khalaf 1969, Henry 1973). In all of these works, *C. furens*, *C. hollensis* and *C. melleus* were the dominant salt marsh species. The distribution and breeding habitat of the species collected on Sea Island are discussed in alphabetical sequence. The occurrence and method of collection are also noted.

Culicoides arboricola Root and Hoffman is an ornithophilic, tree hole breeding species found in the eastern U.S. from Minnesota and Texas to Connecticut and Florida (Blanton and Wirth 1979). Messersmith (1965) trapped large numbers of engorged females in poultry houses in Virginia, suspecting it to be a vector of avian infectious synovitis. *Culicoides arboricola* has been found associated with wet wood debris in tree cavities in Virginia (Hair et al. 1966), and in tree or stump holes of oak, maple and yellow poplars in Georgia (Henry 1973). In the present study, a few (19) individuals of this species were collected by LT and SCT from four of the six collection sites during spring and fall of 1984 and 1985 (Table 2). Presence of this species is expected due to the availability of suitable larval habitat and appropriate climate.

Culicoides baueri Hoffman is distributed in the southeastern U.S. from Tennessee and Louisiana to Maryland and Florida (Blanton and Wirth 1979), and prefers inland freshwater habitats (Battle and Turner 1970). Williams (1955a) collected and reared C. baueri from stream and spring margins in Baker County, Georgia. In the present study, C. baueri was collected by LT and LTP from all locations, except the horse stables (Site 6), during spring and fall of 1984 and 1985. The margins of few freshwater ponds located on the island may have provided the primary habitat for this species.

Culicoides bermudensis Williams, a coastal marsh species, has been reported from Bermuda and along the coastline of the United States from New York to Florida and to Texas (Blanton and Wirth 1979). This species was the first in the family Ceratopogonidae found to demonstrate complete obligate thelytoky in conjunction with autogeny in nature and the second from a group of primarily biting Diptera (Williams 1961). In the present study, two females were collected by LT from the north end (Site 5) on 18 and 27 April 1984 and one female from Site 3 on 3 May 1984.

Culicoides biguttatus (Coquillett), found throughout eastern North America from Wisconsin to Nova Scotia and south to Louisiana and Florida (Blanton and Wirth 1979), is commonly associated with freshwater stream and pool margins (Hair et al. 1966). Ah (1968) in Georgia, collected females by LT in poultry houses from April through August. In the present study, C. biguttatus was collected by LT and SCT in April and May of 1984 and 1985 from all locations except Site 1.

Culicoides crepuscularis Malloch, one of the most common and widespread species in North America, is found from southern Alaska and Canada to northern Mexico, Florida and Bermuda and is abundant in grassy sunlit habitats adjacent to forests (Blanton and Wirth 1979). The frequent presence of parasitic mermithid nematodes in the abdominal cavity of this species (Beck 1958) could suggest why this gnat has not built up large populations despite its widespread range. Primarily an ornithophilic species (Fallis and Bennett 1961), C. crepuscularis was collected in Georgia by Ah (1968) from open fields in Clarke County from April through October 1966. In the present study, two females were collected by LT from the island's north end (Site 5) on 5 April and 4 May of 1984.

Culicoides debilipalpus Lutz is distributed in southeastern U.S. from Maryland and Kentucky to Florida and Louisiana, in Central America from Honduras to Panama, and in South America to Brazil and Argentina (Blanton and Wirth 1979). Messersmith (1964) found larvae in the decaying contents of a white oak stump. In Trinidad, Williams (1964) reared this species from rotting cocoa pods and bamboo stumps. In Georgia, Ah (1968) collected only two females by LT in August of 1967. Varnell (1967) noted this gnat's preference for dry tree holes in his study of Culicoides of Alachua County, Florida. In the present study, a female was collected from Site 3 on an SCT positioned in trees in early July of 1984. A male was collected from the maritime forest (Site 4) on an SCT in early May of 1985.

Culicoides furens is a widely distributed coastal species found on both the Atlantic and Gulf coasts from Massachusetts to Florida and Texas, Central and South America to Brazil, and in the West Indies. On the Pacific coast, it occurs from Mexico to Ecuador (Blanton and Wirth 1979). This species is a general feeder but with a preference for mammals, particularly man. The bite of C. furens can cause serious lesions and inflammation in someone sensitive. Ah (1968) reported C. furens as the second most abundant biting midge collected, finding it most prevalent during summer in coastal Georgia. In the present study, C. furens was collected by LT, LTP and SCT from all locations throughout the study period with exception of the coldest months of the year (Table 2) and was the second most abundant gnat species collected.

Culicoides guttipennis (Coquillett) is distributed throughout eastern U.S. from Minnesota to Vermont, and Oklahoma to Florida (Blanton and Wirth 1979), and is common in water-filled tree holes in Tennessee (Snow et al. 1957) and stump holes in Georgia (Ah 1968). Humphreys and Turner (1971) found this species to be a general feeder, having a variety of hosts. Ah (1968) collected adults by LT from mid-April through mid-October with a peak in July. In the present study, a single female was collected by LT from Site 3 on 19 October 1984. Its preference for tree locations with tree canopy cover (Snow 1955) might explain why more of this species were not collected on Sea Island.

Culicoides haematopotus Malloch is widespread throughout the U.S., southern Canada, and northern Mexico (Blanton and Wirth 1979). Jones (1961) reported that this species can be found breeding in most freshwater soil habitats. This species has been recovered from soils with a wide range of nutritional and chemical properties (Battle and Turner 1972). Williams (1955a) collected C. haematopotus commonly by LT's operated at 1.8 m and 12 m heights from August 1952 through January 1953 in Baker County, Georgia. Ah (1968) found this species relatively common year round and most prevalent in the vicinity of the University of Georgia, Poultry Disease Research Laboratory, Athens, GA. In the present study, C. haematopotus was collected by LT and SCT from all locations during spring and fall of 1984 and spring of 1985.

Culicoides hinmani Khalaf is found in the U.S. from Wyoming to Maryland, south to Colorado, Texas and Florida (Blanton and Wirth 1979), and has been reared from tree holes in oak in Texas (Wirth and Bottimer 1956) and in dry tree holes in Virginia (Hair et al. 1966). Ah (1968) found C. hinmani was ornithophilic and most abundant in collections from July through September. In the present study, a single female was collected by SCT from the maritime forest (Site 4) in early October of 1983.

Culicoides hollensis is widely distributed along the Atlantic coast of the U.S. from Maine to northern Florida (Blanton and Wirth 1979) and the Florida Gulf coast (Beck 1958), Louisiana and Mississippi (Khalaf 1967, 1969). Koch and Axtell (1979) found that C. hollensis fed on varied hosts, with a preference for larger animals. In coastal Georgia, Ah (1968) collected few individuals of this species in LT's during the summer of 1967. In the present study, C. hollensis was collected by LT, LTP and SCT from all locations on Sea Island every month of the 20-month period, except August 1984. Peaks of abundance occurred in spring and fall. Culicoides hollensis was the most abundant species, comprising 50 percent of the total collection for LT, LTP and SCT.

Culicoides loughnani Edwards distributed in the Bahamas, Cuba, Jamaica, Florida, Texas and Australia (Blanton and Wirth 1979), is cactiphilic and has been reared by Jones (1962) from rotting stems of prickly pear Opuntia sp. cacti in Texas. Beck (1958) collected C. loughnani in Lee County, Florida between March and July. Dyce (1969) traced the presence of this species in Australia to an accidental introduction in cactus rot organisms to be used in biocontrol of that country's prickly pear plant. C. loughnani has not been previously reported in Georgia (Blanton and Wirth 1979). The northernmost report of this species on the Atlantic coast was from Duval County, FL by Beck (1952). In the present study, two females (verified by W.L. Grogan) were collected by LT from the north end (Site 5) on 15 June 1984. Possible larval host plants were two species of cactus present at that site.

Culicoides melleus is found along the Atlantic and Gulf coasts of the U.S. from Maine to Louisiana, and in the Bahamas (Blanton and Wirth 1979). Foote and Pratt (1954) reported that this primarily anthropophilic species bites during the hottest part of the day in Mississippi, while Kline and Axtell (1975) indicated C. melleus was crepuscular in its biting activity in North Carolina. Ah (1968) collected C. melleus from Chatham County, GA in July 1967. In the present study, C.melleus was collected by LT, LTP and SCT from all locations on Sea Island throughout most of the 20-month period with exception of the coldest months (January and February) of the year. This species was the third most abundant from LT, LTP, and SCT.

Culicoides niger Root and Hoffman is distributed in the coastal plain of eastern U.S. from Massachusetts to Florida and Louisiana (Blanton and Wirth 1979). Root and Hoffman (1937) reared pupae collected in cattail marsh in Maryland. In Georgia, Ah (1968) collected low numbers of females by LT in poultry houses in June, 1967. In the present study, only females were collected by LT and LTP from all locations March through May and August through September 1984 with a peak of abundance in early May. This species was the fourth most abundant collected.

Culicoides paraensis is widely distributed in the southeastern U.S. from Pennsylvania to Louisiana, Mexico, West Indies, Central America and South America to Argentina and Bolivia (Blanton and Wirth 1979). Smith (1965) reported this species from northern Florida to be diurnal, man-biting, and breeding in tree hole debris. In Georgia, Ah (1968) collected this gnat from May through September in Clarke County, and noted it to be the most common man-biting species in inland Georgia. In the present study, two males and three females were collected by LT, LTP and SCT from the maritime forest (Site 3) from late August to mid-September 1984.

Culicoides piliferus Root and Hoffman is distributed in eastern North America from Wisconsin to Nova Scotia, south to Florida and Louisiana (Blanton and Wirth 1979), and is associated with soft mud along shaded stream margins (Hair et al. 1966). Ah (1968) found this species prevalent near poultry houses in Clarke County, Georgia from April through September, with a peak of abundance in May. In the present study, ten females were collected by LT from the maritime forest location (Site 4) on 28 March 1985.

Culicoides spinosus Root and Hoffman has a distribution identical to C. piliferus, and has been reared from substrate collected along the edges of freshwater streams, creeks and ponds in North Carolina (Battle and Turner 1970). Henry (1973) collected this species in coastal South Carolina from March through December. Ah (1968) collected only a few adults by LT near poultry houses in Clarke County, Georgia from April through August. In the present study, only females were collected by LT and LTP during late March through early May and again in early October and early December 1984 from all locations except Sites 1 and 2.

Culicoides stellifer (Coquillett) is distributed in North America from Montana and Nova Scotia, south to California and Florida (Blanton and Wirth 1979), and is commonly associated with sunny, flowing freshwater habitats with muddy bottoms and grassy margins (Kardatzke and Rowley 1971). In Georgia, Ah (1968) reported this species to be relatively common in LT collections from May to October. In the present study, only females were collected by LT and SCT at all locations from April to July 1984.

Culicoides venustus Hoffman is widely distributed east of the Mississippi River in eastern North America; it occurs from Wisconsin to Nova Scotia, south to Louisiana and Florida (Blanton and Wirth 1979). Jones (1961) found this species present as larvae in sand

and mud along stream margins. Williams (1955a) collected adults in October and November 1952 in Baker County, Georgia. Ah (1968) found C. venustus present from mid-April to late October 1966. In the present study, a single female was collected by LTP at the maritime forest location (Site 4) on 12 August 1984. C. venustus has not previously been reported as diurnal (Blanton and Wirth 1979).

Culicoides spp. A (near hollensis) and B (near mississippiensis) were both collected by LT from Site 3 on 19 October 1984. These specimens are being held for further taxonomic study by W.W. Wirth.

Seasonal Incidence of Dominant Species

Results from collections over the 20-month period indicate that C. furens adults were present from March through December. C. furens were more abundant in mid-to late spring (April and May) and early fall (September and October) than in the summer months (Fig. 5). Ah (1968) only made collections in coastal Georgia on four collection nights in July, thus he could not deduce accurate seasonal patterns. In South Carolina, Henry (1973) found C. furens present March through December, and observed a spring peak in late May. Kline (1975) in his study of salt marsh Culicoides in North Carolina termed C. furens a summer species, present April to October with peaks in late May and in early fall.

Beck (1958) sampled populations of C. furens from both the Atlantic and Gulf coasts of Florida. On the northwest Gulf coast this species was present April through September; while on the southeastern Atlantic coast, C. furens was present each month December through June and numbers peaked in April. Khalaf (1969) found C. furens to be aestival on the Gulf coast, and noted a higher incidence in winter from regions on the Atlantic and Caribbean coasts. These regions include Panama (Banton et al. 1955), Vero Beach, FL (Linley et al. 1970), Puerto Rico (Fox and Garcia-Moll 1961) and Grand Cayman (Davies and Giglioli 1977a). Linley and Davies (1971) considered this species to be one of the most important economic pests of the Caribbean.

The periods of seasonal incidence of C. furens become more limited at northern latitudes as indicated by Jamnback et al. (1958). In his Long Island study, C. furens was found active only from late June to late July and in low numbers. Lewis (1959) in Connecticut collected C. furens during summer months, with two major peaks during this period.

In general, C. hollensis adults were present throughout most of the year, but diminished considerably during the coldest and warmest months (Fig. 6). The relative number and specific dates of population peaks varied slightly from year to year. Overall, C. hollensis were more abundant in early spring and again in early fall. Henry (1973) in South Carolina, collected this species by LT from March through June and again in August and she noted the larger spring peak. Kline (1975) reported C. hollensis abundant in spring and fall in coastal North Carolina. Unlike Kline's findings, the period of incidence of C. hollensis on Sea Island was longer, appeared earlier in spring and disappeared later in fall. Beck

(1958) found this species more abundant on the Gulf coast of Florida than on the Atlantic. She reported a peak of abundance in spring, but present year round. Khalaf (1967, 1969) found this species to have a bimodal seasonal pattern in Louisiana, with fewer during winter months.

In northern states seasonal incidence of C. hollensis, like that of C. furens, was reduced. Jamnback et al. (1958) reported a bimodal pattern for C. hollensis in New York, in early and late summer. A single peak of abundance for this species in mid-July was reported by Lewis (1959) in Connecticut.

In general, C. melleus adults were present from early March through December with fewer present in the summer months (Fig. 7). C. melleus were more abundant in the mid-spring (April) and early fall (September and October). Beck (1958) in Florida found this species to be most abundant in LT from March through May on both coasts, and least abundant on the northwest coast. Khalaf (1969) found C. melleus rare along the Mississippi Gulf coast, appearing in small numbers between 8 April and 14 June. In South Carolina, Henry (1973) reported C. melleus was present from early March to late October. Kline and Axtell (1975) found C. melleus continuously present from early April through mid-October, but most abundant from late spring through early summer. Mid-summer peaks were reported for this species in New York (Jamnback 1958), Connecticut (Lewis 1959), and Massachusetts (Wall and Doane 1960).

Results of the present investigation, when compared to data collected in other regions, clearly indicate that seasonal incidence of adult C. furens, C. hollensis and C. melleus on the Atlantic coast of the United States varies with latitude: shorter in the more northern latitudes and longer in the more southern latitudes.

Vertical Distribution on Sticky Cylinder Traps

Vertical distribution of salt marsh Culicoides has been examined by Snow et al. (1958), Bidlingmayer (1961), Breeland and Smith (1962), and Henry and Adkins (1976). In the open marsh, Henry and Adkins (1976) found biting midges most frequent at heights of 7.6 m and 13.7 m. In wooded areas, Bidlingmayer (1961) found male C. furens most abundant in arboreal resting sites and females most abundant near ground level. Snow et al. (1958) observed C. furens to be most active at ground level at all times of day. Results of the present study revealed no significant trends for height preference at 0.6 m, 1.2 m, or 1.8 m for either of the three species. Kline and Axtell (1977) found these same heights to affect significantly collections of C. hollensis but not C. furens. Factors which determine appropriate prefered elevation for a particular species have not been fully investigated. Service (1971) suggested flight patterns near the ground in certain Culicoides could be caused by host-seeking and/or oviposition. Henry and Adkins (1976) felt vertical distribution of Culicoides could vary due to temperature, evaporation, migration, or illumination levels.

Influence of Environmental Variables

Meteorological effects on seasonal incidence of biting midges have been investigated in several studies. In his early work on sand flies, Myers (1935) identified low temperature, strong light and high wind as inhibitory factors on adult Culicoides activity.

The effect of wind on Culicoides activity has been regarded as an important environmental factor by many authors. Travis (1949) noted flight of Alaskan species of Culicoides to be impaired by winds >3.5 mph. Kettle (1957) and Rueben (1963) both found biting rates and suction-trap catches of C. impunctatus Goethebuer to be inversely related to wind speed. Bidlingmayer (1961) recorded his largest LT catches of C. furens at winds <4 mph, with some collected with winds up to 9 mph. Walker (1977) demonstrated the inhibitory effects of winds >3 mph for Culicoides in Kenya. In the present study, the mean wind velocity is the average of hourly readings (for 10-14 hour collection period) and not the mean value for continuous wind recording or more frequently measured wind speeds as in many previously mentioned works.

Effects of air temperature is proposed to provide upper and lower limits for Culicoides activity. Travis (1949) noted that activity of Alaskan Culicoides declined at temperatures below 12.7^{o}C. Parker (1949) found no apparent correlation between temperature and numbers of Culicoides captured by netting method in Scotland, but noted largest catches occurred at temperatures from 10^{o}C-20^{o}C. At Vero Beach, Florida, Bidlingmayer (1961) reported temperatures of C. furens activity at sunset and sunrise to be 25^{o}C -30^{o}C, and 19^{o}C-25^{o}C respectively. Kline and Axtell (1976) in North

Carolina found LT catches of C. furens to be significantly correlated with temperature, but not for C. hollensis.

Mean air temperatures at which the greatest number of biting midges were collected at Sea Island was from 9.1°C to 28.8°C, with each species having a range within these values. The activity of only C. hollensis was found to be statistically significant for mean air temperature. One explanation could be that an environmental factor not measured may have influenced the other species. It should be noted that Kline and Axtell (1976), who found significance for temperature and activity of the three species, made collections only April through October thus bypassing effects of colder winter temperatures upon collections. Some biting midge activity was evident during these colder months in the present study.

No effects were evident for rainfall (as measured for 7, 14, and 28 days before LT collections) on Culicoides spp. population dynamics. Walker (1977) determined from monthly LT and suction trap collections of adult Culicoides that populations of all species remained present throughout the year regardless of the amount of rainfall. Prolonged periods without rain would reduce population size of some species, while others increased during rainless periods. Fox and Garcia-Moll (1961) in Puerto Rico, did not find a relationship between LT collections of C. furens and rainfall. Parker (1949) reported light rain had no effect on collections of Culicoides in Scotland. Davies and Giglioli (1977b) determined in Grand Cayman that peaks of emergence and of LT catches for C. furens occurred during drier months, before and after the rainy season.

Heavy rainfall which occurred at Sea Island during a few collection nights was observed to reduce gnat collections. Overall the rainfall did not significantly influence the seasonal activity of the biting midges. This absence of rainfall effects might be expected since the three abundant species are all salt marsh species, whose life cycle is probably more closely synchronized with tides and temperature.

Light trap collections were not found to be significantly correlated with moon phase. Kline (1975) found no significant correlation between collections of salt marsh Culicoides and moon phase in North Carolina, but noted greater numbers caught during a new moon. A reduction in catch at full moon is generally thought to be caused by moonlight competing with the trap light. Results of the present study revealed more C. furens and C. hollensis collected during full moon than at any other time (Table 5). Collections of C. melleus were largest during first and last quarters, with new moon a close second and full moon a distant third. The influence of various factors such as temperature, cloudcover, and altitude of the moon from the horizon, etc., probably modify the effects of moonlight upon gnat activity (Williams et al. 1956).

Larval Habitats of Dominant Species

The first detailed study of the larval habitat of C. furens was by Hull et al. (1934) who found larvae of C. furens in greatest numbers near the edge of grassy salt marshes and along wet banks of ditches that were reached by high tides for only a few days each month. Myers (1935) in the Bahamas found preferred larval habitat of C. furens to be sand, mixed with humus and shaded and not flooded, but permanently waterlogged with salt or brackish water. Larval studies by Carpenter (1951), Woke (1954), Blanton et al. (1955) and Breeland (1960) found C. furens larvae in the Panama Canal Zone in tidal marshes, in low areas during the rainy season and along margins of muddy streams and ditches in the dry season. In the four studies, larvae were most abundant in areas exposed to sunlight and rarely flooded by high tides. In contrast, Goulding et al. (1953) and Bidlingmayer (1957) in Florida found larvae of C. furens more abundant in shady locations along drainage ditches at a level between high and low tide marks where the soil remained soft and wet. The degree of shade seems to affect larval distribution, with larvae most abundant in shaded locations in summer months and unshaded areas in the winter.

Linley and Davies (1971) reported the coastal range of C. furens larval habitat to be extensive in brackish water, though larvae can be found in damp saline soil, not permanently inundated. The most frequently reported habitats for this species are mangrove swamps, salt marshes and banks of ditches (Rogers 1962, Linley et al. 1970), yet Williams (1964) found C. furens in freshwater habitats. Kline and Axtell (1975) found larvae of C. furens in sandy intertidal areas, but most abundant in salt marsh vegetation of short S. alterniflora and D. spicata.

The preference of an acidic media for salt marsh sand flies was first indicated by Dove et al. (1932). Battle and Turner (1972) in

Virginia found the larval habitat of C. furens characterized by a mean pH of 5.6 and high mean mineral content (compared to habitats of inland species) for calcium, magnesium, phosphates, and potash.

Larvae of C. hollensis have been found in salt marshes near Charleston, SC associated with grassy, shaded areas (Dove et al. 1932). Jamnback and Wall (1958) on Long Island, NY found larvae in marsh areas covered by high tides with S. alterniflora ($\geq$2 feet) and a thin covering of mud over the sod. Wall and Doane (1960) on Cape Cod, Massachusetts and Hair et al. (1966) in Virginia found larvae most abundant along the edges of bays and drainage ditches where tall S. alterniflora dominated. The same habitat was described in Virginia by Hair et al. (1966). Kline and Axtell (1977) reported C. hollensis widely distributed through the grassy marsh, but most abundant in tall S. alterniflora nearest the low water mark.

Larvae of C. melleus are reported from intertidal sand on beaches, bays and inlets in Florida (Goulding et al. 1953), Virginia Beach (Hair et al. 1966), New York (Jamnback and Wall 1958, Jamnback 1965) and on Cape Cod, Massachusetts (Wall and Doane 1960, Wall 1973). Linley and Adams (1972) reported that C. melleus larvae in Florida were associated with sandy areas where wave action was minimal (such as coves and inlets). In coastal North Carolina, Kline and Axtell (1975) found C. melleus larvae together with larvae of C. furens in sandy intertidal habitats. They noted that C. melleus larvae preferred unvegetated areas. Jamnback and Wall (1958) found C. melleus larvae most abundant in a band about equidistant between high and low tide. Width of this band varied for each site depending on the slope and tidal range. More gradual slopes were associated with higher tides and thus a wider band of larval occurrence.

Larval distribution for Culicoides furens, C. hollensis, and C. melleus from the coastal Georgia salt marsh is in general agreement with that of previous findings. Attempts to demonstrate the larval preferences for the variables tested did not show significance when examined statistically. While not significant at 0.05 level, C. hollensis distribution may be related to soil phosphorus content and elevation of plots as indicated by multiple linear regression analysis.

Kline and Axtell (1977) found the number of larvae recovered from soil was significantly correlated (0.05 level) with amounts of calcium, magnesium, and soluble salts in the soil and with percentage of time of marsh flooding. Other factors they tested, such as content of potassium, magnesium, sodium, organic matter and nitrate-nitrogen in soil, were not significant. Though trends in the distribution of larval species by elevation and vegetation are indicated in data from the present study, a more intensive study such as that suggested by Kline and Axtell (1977) examining physical properties of substrate or food content in soil is needed.

The adaptability, survivability and tolerance of salt marsh Culicoides immatures have not been fully investigated. Linley (1966) demonstrated the ability of C. furens pupae to emerge as adults after several days completely submerged in water. In the present study, the author has observed that the three species of

Culicoides larvae (C. furens, C. hollensis and C. melleus) can survive in vials of tap water for up to 14 days.

Larval Morphometrics

The first general description of Culicoides larval morphology was that of Carter, Ingram and Macfie (1920) which described certain West African species. Painter (1926) described the biology of C. furens in British Honduras, but included only a limited description of its immature stages. Comprehensive works by Lawson (1951) followed by Kettle and Lawson (1952) presented detailed descriptions of immature stages of British biting midges. Wirth (1952) was first to describe the larval stages of C. furens and C. melleus. A second detailed description of C. furens larvae was made by Linley and Kettle (1964). A limited description of C. hollensis is found in Jamnback et al. (1958).

Larvae of Culicoides like other Nematocerous flies, possess a sclerotized head capsule followed by a short collar (pseudosegment), three thoracic and nine abdominal segments. The terminal segment has a pair of four-lobed anal processes resembling bloodgills which may be extruded or retracted into the anus. The pigmentation pattern varies with the species and is best defined in thoracic segments.

Number of instars or stages which an insect assumes between molts varies in types of insects with the more primitive such as Ephemeroptera having 30-45 and the more advanced such as Nematocera, only four. Number of larval instars may vary among closely related groups of insects and even between sexes of the same species (Chapman 1971). Dyar's Law may be applied to head capsule measurements of larval instars. This geometric progression factor that is characteristic of a species for each instar has been reported for many species of Culicoides (Hill 1947, Kettle and Lawson 1952, Linley and Kettle 1964, Kettle and Elson 1976).

Head indices of Sea Island C. furens instars were compared to instars of C. furens from Jamaica (Linley and Kettle 1964). A progression factor based on mean values of head measurements plotted by the number of instars, was determined in C. furens larvae of the present study to be 1.34. This value compared well with that of Jamaican C. furens. Values for headlengths and headwidths for each instar were larger for Sea Island C. furens except for minimum headwidths which were slightly smaller (Table 8). It should be noted that Linley and Kettle's determinations were based on measurements of a total of 61 larvae compared to measurements of 1497 larvae in the present study.

The fourth-instar of C. hollensis was described by Jamnback (1958, 1965), based on less than ten specimens and HL was measured by a slightly different method. Head measurements for C. hollensis larvae in the present study were found to be larger on the average than those of C. furens (Table 8). Mean head indices of C. melleus larvae were generally found to be smaller than the other species.

Seasonal Distribution of Larval Instars

Larval populations of C. furens, C. hollensis and C. melleus showed differences in relative numbers of instars with seasonal changes. For a given species, a higher proportion of young larvae might be expected during periods of adult abundance caused by increased oviposition. Recovery of early-stage larvae from soil is probably less effective, considering their small size and short duration in that stage of development. Predictions of Culicoides larval development might not be accurate if based entirely upon numbers of first-instar larvae recovered.

The observation that third-instar larvae of C. furens constituted a greater proportion of the total recovered for that species during each season, offers several possible explanations. Arrested growth or a prolonged period at this stage during larval development might be one interpretation. Larval diapause is more commonly restricted to the last instar for most insects (Chapman 1971), yet diapause may occur in every individual of each generation resulting in a unimodal or univoltine cycle.

Linley (1969b) found third-instar larvae of Leptoconops becquaerti (Kieffer) to be the most abundant instar in soil samples from breeding habitats in Jamaica. These third-instar larvae were later found to be an autogenous form of the species, induced by a lack of moisture. The occurrence of autogeny has been documented in many species of Culicoides, including the three dominant species in the present study (Linley et al. 1970, Kettle 1977, Koch and Axtell 1978). The role of autogeny in maintaining a population of C. furens was suggested by Linley et al. (1970) at Vero Beach, FL. Autogenous females have the potential to produce viable eggs, emerge in response to warmer temperatures and may contribute to a rapid population build-up.

The possibility exists of both autogenous and anautogenous C. furens forms in the Sea Island population. Linley, (1969b) in examining development in both forms of L. becquaerti, found eggs reared from blood-fed anautogenous females resulted in emergence of a single large peak of adults. He found the fourth-instar to be the longest larval stage. In contrast, progeny reared from eggs of autogenous females (Linley 1968) resulted in a prolonged third-instar stage and a pattern of intermittent adult emergence. Rapid development to last-stage larvae and adult emergence is probably most dependent on soil moisture and temperature (Linley 1969b, Linley et al. 1970, Linley and Adams 1972). Anautogenous forms might occur only during periods of optimum conditions, whereas autogenous females might emerge during less stable environmental conditions and allow more time for emergence and oviposition.

Females which emerged during cooler temperatures were larger and produced more viable eggs autogenously than smaller females emerging in warmer months (Linley 1968). The role of autogeny in the geographical distribution of Culicoides is unknown, as is the extent of autogeny among natural populations. Linley et al. (1970) found vast differences in percentages (0% to 91%) of autogenous C. furens females from five breeding sites only a few miles apart in Jamaica.

Low larval densities of C. hollensis were found on Sea Island in spring and fall, coinciding with its periods of adult emergence.

No indications were evident as to which larval stage, if any, might diapause. Facultative diapause in which alternate generations are free of diapause could result in a multivoltine cycle. Two generations or a bimodal cycle has been previously indicated for C. hollensis. A larger percentage of larvae recovered prior to periods of adult emergence was last-stage larvae, unlike that found for C. furens. Though a bimodal incidence is indicated by patterns of adult and larval occurrence of C. hollensis, the possibility of autogeny in the natural Sea Island population cannot be overlooked.

Recording seasonal fluctuations in adult size (wing length), which is inversely related to temperature (Linley et al. 1970, Linley and Hinds 1976) may offer some indication of interpretation. Culicoides hollensis, unlike C. furens and C. melleus was present during the colder part of the year. Finding large females with increased quantities of stored reserves to be used in egg production might support the evidence of autogeny among the population. The large percentage of fourth-instar larvae found during the winter of 1985, also supports the case for autogeny. The factors of increased size and storage of reserves in adults have the effect of further prolonging the larval stage, since such larvae would presumably take longer to mature.

Evidence for C. hollensis having two generations a year, though not conclusive, is further suggested by the presence of a high larval density during peak adult activity (spring 1985). Sufficient larvae present during this spring period in the soil could indicate a slowly developing larva preparing for fall emergence.

Larval density during the spring of 1985 was not as high for C. melleus as for C. hollensis. It should be noted that C. melleus was not as widely distributed on the marsh as C. furens and C. hollensis. Extensive sampling of areas positive for larvae of C. melleus over an extended period of time might reveal clearer trends. Larvae of C. melleus, as for the other two species, were found in all stages of development during any given season. The large percentage of fourth-instar larvae recovered during winter (prior to spring emergence) follows Linley's model for the anautogenous population of L. becquaerti mentioned earlier. Periods of adult activity were mirrored by periods of low larval density.

The bimodal seasonal cycle indicated by larval and adult populations of C. melleus suggests the existance of alternate diapausing generations. No indications were evident as to which larval stage might undergo diapause. Investigations of seasonal changes in size and female fecundity may offer more evidence for the presence of autogeny and its role in the seasonal incidence of C. melleus. Another possibility accounting for a bimodal seasonal distribution will be discussed at this point, but may apply to either populations of C. hollensis or C. melleus. Climatic factors while capable of considerably modifying a bimodal distribution, probably do not entirely account for it (Kettle 1950). The existence of two biological races was suggested by Kettle (1950) for the bimodal seasonal distribution of C. impunctatus in Scotland. This hypothesis was based on a statistically significant difference between sex ratios of the two populations, statistically different vertical and horizontal distributions, and the belief that a bivoltine distribution in Scotland would be unlikely because of the presence of a univoltine population 200 miles to the south. Rearing of larvae recovered prior to both periods of adult emergence would lend support to the hypothesis of a bivoltine population of either C. hollensis or C. melleus on Sea Island. A detailed vertical and horizontal distribution study conducted during and between periods of adult peak activity could identify any behavioral or biological differences of these two possible races.

The environmental factors affecting larval development have not been fully determined. The spatial separation of larval species at different elevations on the marsh (all within 0.065 m) could indicate partitioning of available resources. Patterns of adult seasonal abundance are probably influenced by many interacting environmental variables. The varied seasonal incidences of the three salt marsh Culicoides may have evolved to reduce competitive interactions (for larval habitat, host availability, etc.). The complex biological mechanism(s) influencing seasonality of larval development remain unknown.

Adult Emergence

Characteristics of the larval habitat for the three species of Culicoides was found to coincide well with characteristics of soil samples positive for emerging adult species. Mean elevations for larvae ranged from 0.041 m to -0.066 m compared with 0.044 m to -0.021 m for emerging adults. Mean values for elevation were higher for samples yielding adults than samples from which larvae were recovered. This may be attributed to failure of larvae collected from plots in lower elevation zones to pupate because of a less than optimum degree of moisture. Contact with air is essential for pupation to be successful. In nature, late instar larvae of C. melleus were observed (Linley and Adams 1972) to migrate to a higher elevation in drier soil prior to pupation. Linley (1966) described the mechanism of adult emergence in C. furens. Mature larvae, ready to pupate, must attach to a solid object such as a plant stem to maintain contact with air and ensure emergence. Biting midges can pupate despite marsh tidal flooding as long as contact is made with air.

The presence of L. linleyi is of interest since this is the first report from the state of Georgia. Females of this genus are vicious day-biters which attack man (Kettle and Linley 1967, Laurence and Mathias 1972). Knowledge of Leptoconops as a disease vector is limited, with L. bequaerti the only member known to support development of parasitic microfilariae (Linley et al. 1983). Larval habitats are associated with damp, sandy soil on sloping, protected beaches between the high tide mark and the vegetation fringing the beach (Wirth and Atchley 1973). Leptoconops linleyi has been reported on seacoasts of Massachusetts, North Carolina and Florida (Wirth and Atchley 1973). Habitat on Sea Island would appear to be well suited for L. linleyi, yet this species emerged from only a few soil plots collected in April and July 1984. No collections by LT, LTP, or SCT included this species.

The significant deviations from the expected 1:1 sex ratio for emerging ceratopogonids, with exception of C. melleus, could be caused by differences in mortality or different behavioral activity of the sexes (Kettle 1952). Parker (1949) found highly significant deviations from a 1:1 sex ratio in all species collected by sweep net in Scotland. An inherited factor has been found in Aedes aegypti which causes a predominance of males (Clements 1963). This factor is transmitted only in males and its frequency can be increased by selection. Craig, Hickey and VandeHey (1960) found that this excess of males was not due to differential mortality; Craig, VandeHey and Hickey (1961) found in 19 strains analyzed, that the proportion of females ranged from 18.6 to 51.5 percent although sex ratio within strains was constant over several generations. Ford (1961) emphasized that sex is a case of balanced ploymorphism subject to selective forces that influence departure from the 1:1 ratio. Knowledge of emergence periods, genetic crosses and subsequent activity peaks of both sexes for a species are essential to understand the life cycle of any insect.

In conclusion, data from the present investigation revealed three dominant man-biting species of sand gnats from Sea Island: C. furens, C. hollensis, and C. melleus. Larval and adult collections were utilized to predict peaks of incidence in coastal Georgia and environmental factors which might influence these periods. C. loughnani, a cactiphilic species, was reported for the first time from Georgia.

Larval habitats and adult emergence sites of the dominant species were identified for coastal Georgia and included data on vegetation, elevation, pH, and soil mineral characteristics. The morphometrics of larval instars of the three dominant salt marsh Culicoides were also described.

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Table 1. Species of _Culicoides_ obtained by scotophase light traps (LT), photophase light traps (LTP), and sticky cylinder traps (SCT) on Sea Island, GA, from September 1983 through May 1985.

Species	Collection Methods: LT Male	LT Female	LTP Male	LTP Female	SCT Male	SCT Female	Total no./ species
C. arboricola	1	17	0	0	0	1	19
C. baueri	1	78	0	3	0	0	82
C. bermudensis	0	3	0	0	0	0	3
C. biguttatus	0	217	0	0	0	3	220
C. crepuscularis	0	2	0	0	0	0	2
C. debilipalpus	0	0	0	0	1	1	2
C. furens	147	61,801	0	2359	5999	15,599	85,905
C. guttipennis	0	1	0	0	0	0	1
C. haematopotus	3	32	0	0	2	23	60
C. hinmani	0	0	0	0	0	1	1
C. hollensis	163	39,998	0	2174	31,481	35,660	109,476
C. loughnani	0	2	0	0	0	0	1
C. melleus	10	13,223	0	859	1033	8993	24,118
C. niger	0	560	0	3	0	0	563
C. paraensis	2	1	0	1	1	0	5
C. piliferus	0	10	0	0	0	0	10
C. spinosus	0	42	0	3	0	0	45
C. stellifer	0	154	0	0	0	1	155
C. venustus	0	0	0	1	0	0	1
_C._ species A*	0	1	0	0	0	0	1
_C._ species B**	0	1	0	0	0	0	1
					Total collected		220,670

*Possible new species (near _hollensis_) (Wirth 1985, personal communication)
**Possible new species (near _mississippiensis_)

Table 2. Seasonal distribution by months of Culicoides species captured in light traps and sticky cylinder traps from Sea Island, GA (1983-85).

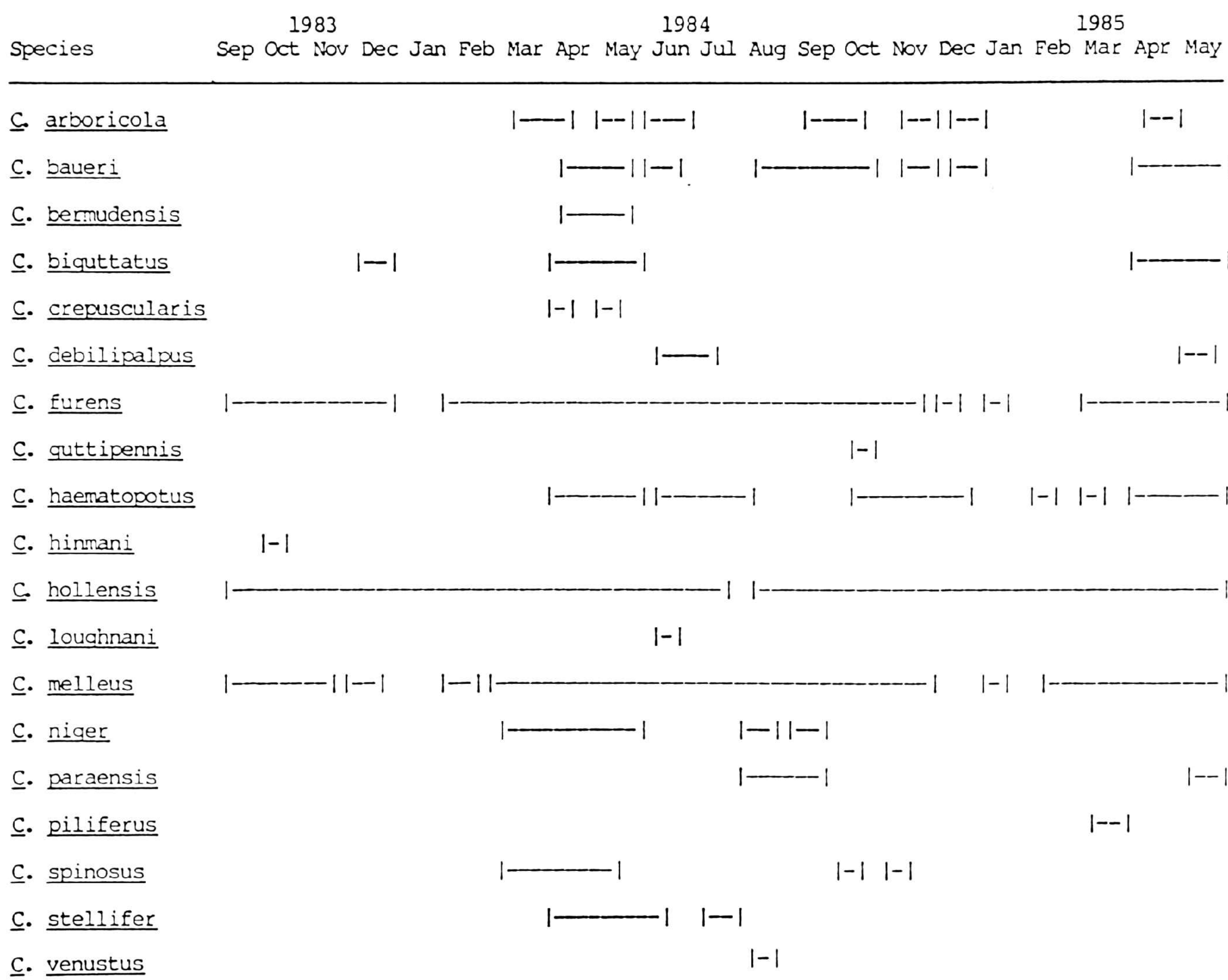


Table 3. Collections of _Culicoides furens_, _C. hollensis_, and _C. melleus_ on Sea Island at three heights of sticky cylinder traps. Values not significant with Chi square analysis at 0.05 level.

Height (m)	Mean no. adults/ trap/ collection period								
	C. furens			_C. hollensis_			_C. melleus_		
	Males	Females	Total	Males	Females	Total	Males	Females	Total
0.6	3.5	10.2	13.7	18.8	23.5	42.3	0.8	7.5	8.3
1.2	4.7	13.1	17.8	25.6	28.3	53.9	0.9	7.2	8.1
1.8	5.2	12.0	17.2	27.0	29.0	56.0	0.6	5.5	6.1

Table 4. Photophase light trap collection of _Culicoides_ from six sites on St. Simons and Sea Islands, GA for the period January through December 1984.

Species	Monthly Photophase Collections Mean number/ trap day												Total/ species
	J (2)*	F (2)	M (3)	A (2)	M (2)	J (3)	J (2)	A (2)	S (2)	O (2)	N (2)	D (2)	
C. furens	0.1	0.2	8	19	0.1	0.1	0	0	0.1	3.5	0.4	3.2	34.7
C. hollensis	0	0	0	5	4	12	3	6	7	2	0.3	0.1	29.4
C. melleus	0	0	0.2	15	0.2	0.2	0.1	0	0.2	0.2	0.2	0.2	18.3
												Total	82.4

* Number of Collections/ month

Table 5. Summary of environmental factors affecting light trap (LT) collections (scotophase).

Species	Min. air temp.*	Max. mean air temp.**	Mean wind speed (kts)***	Moonphase Full moon	Last or first qtr.	New moon	Min. air temp.****	Max. air temp.*****
C. furens	16.4	28.8	11.3	4456 (41.6%)	3156 (29.5%)	3049 (28.5%)	14.4	30.5
C. hollensis	9.1	24.6	11.3	2812 (39.1%)	2624 (36.5%)	1835 (25.5%)	7.2	28.3
C. melleus	13.4	27.2	9.3	345 (14.8%)	1068 (46.0%)	939 (40.4%)	7.7	28.3
Minimum	-1.6	-1.6	0.0				-1.1	6.1
Maximum	31.1	28.8	20.2				26.6	31.1

* Mean nightly temp. above which ≥99% of the mean number/ trap night by species were collected.
** Mean nightly temp. below which ≥ 99% of the mean number/ trap night by species were collected.
*** Nightly wind speed below which ≥99% of mean number/ trap night were collected at or below this wind speed.
**** The lowest temp. recorded temp. above which ≥ 99% gnats/ trap night were collected.
***** Highest temp. below which ≥99% of gnats were collected.

Table 6. Environmental characteristics of the soil habitat from which *Culicoides* spp. larvae were extracted.

Species	Elevation(m)	pH	Minerals (ppm)			
			Calcium	Phosphorus	Potassium	Magnesium
C. furens n = 1497	-0.060±0.207	5.68±0.36	2003±1017	143±114	800±270	928±173
C. hollensis n = 3021	-0.066±0.226	5.69±0.35	2060±1141	129±101	803±273	923±178
C. melleus n = 1199	0.041±0.250	5.60±0.42	1646±888	210±146	627±320	826±253
Minimum	-0.777	4.2	286	19	63	214
Maximum	0.783	6.6	5855	999	999	999

Table 7. Mean number of *Culicoides furens*, *C. hollensis* and *C. melleus* larvae from soil in various vegetative zones in a salt marsh.

Vegetation Type	Mean No. Larvae/ plot/ sample		
	C. furens	*C. hollensis*	*C. melleus*
Tall *Spartina alterniflora*, near creek edge and river bank	2.99	5.43	2.65
Intermediate *S. alterniflora*, marsh flat	3.81	8.24	1.11
Short *S. alterniflora*, near salt pan	1.19	4.75	2.29
Distichlis spicata	1.88	0.88	5.31
Juncus roemerianus	2.64	0.75	3.53
Marsh shrubs	1.11	1.85	0.82

Table 8. Minimum, maximum and mean head length (HL), head width (HW), and head ratio (HR), for first to fourth instar larvae of _Culicoides_ _furens_, _C._ _hollensis_, and _C._ _melleus_ and the standard error from the mean.

Species	Instar	No. of Larvae	Head Length (um) Min.	Max.	Mean	Head Width (um) Min.	Max.	Mean	Head Ratio Min.	Max.	Mean
_C._ _furens_											
	1	92	61	100	90±0.9a*	29	98	67±1.3a	0.92	2.68	1.37±0.03a
	2	487	102	132	116±0.4a	49	127	84±0.5a	0.92	2.09	1.38±0.00a
	3	812	135	181	151±0.3a	85	170	104±0.2a	1.00	1.84	1.45±0.00a
	4	106	182	270	217±1.5a	96	185	152±1.3a	1.25	2.08	1.43±0.01a
_C._ _hollensis_											
	1	28	56	85	75±1.4b	45	76	63±1.6b	0.86	1.56	1.18±0.03b
	2	611	86	127	110±0.5b	49	127	82±0.6b	0.84	2.08	1.34±0.00b
	3	964	130	188	152±0.4b	67	168	108±0.4b	0.83	2.23	1.41±0.00b
	4	1418	190	295	230±0.4b	104	204	162±0.3b	1.05	2.25	1.41±0.00b
_C._ _melleus_											
	1	77	61	85	78±0.6c	40	122	55±1.3c	0.68	1.77	1.42±0.02c
	2	217	86	107	100±0.4c	49	102	73±0.7c	1.04	2.00	1.38±0.01c
	3	324	109	132	121±0.4c	70	156	89±0.7c	0.76	1.67	1.37±0.00c
	4	581	135	229	156±0.6c	80	188	113±0.5c	1.07	2.06	1.38±0.00c

* Figures followed by the same letter in the same column for the same instar are not significantly different at the 0.05 level of probability using Duncan's multiple range test.

Table 9. Species of ceratopogonids (Culicoides, Dasyhelea, Leptoconops) obtained by emergence from soil collected on a salt marsh study site at the north end of Sea Island, GA.

Species	Male	Female	Sex ratio (% female)	Totals/ species
C. furens (Poey)	542	709	56.7**	1251
C. hollensis (Melander and Brues)	813	626	43.5**	1439
C. melleus (Coquillett)	230	253	52.4	483
D. atlantis Wirth and Williams	0	1	--	1
D. mutabilis (Coquillett)	228	315	58.0**	543
L. linleyi Wirth and Atchley	30	12	28.6*	42
			Total emerged adults	3759

* Exceeds .01 level of significance
** Exceeds .001 level of significance

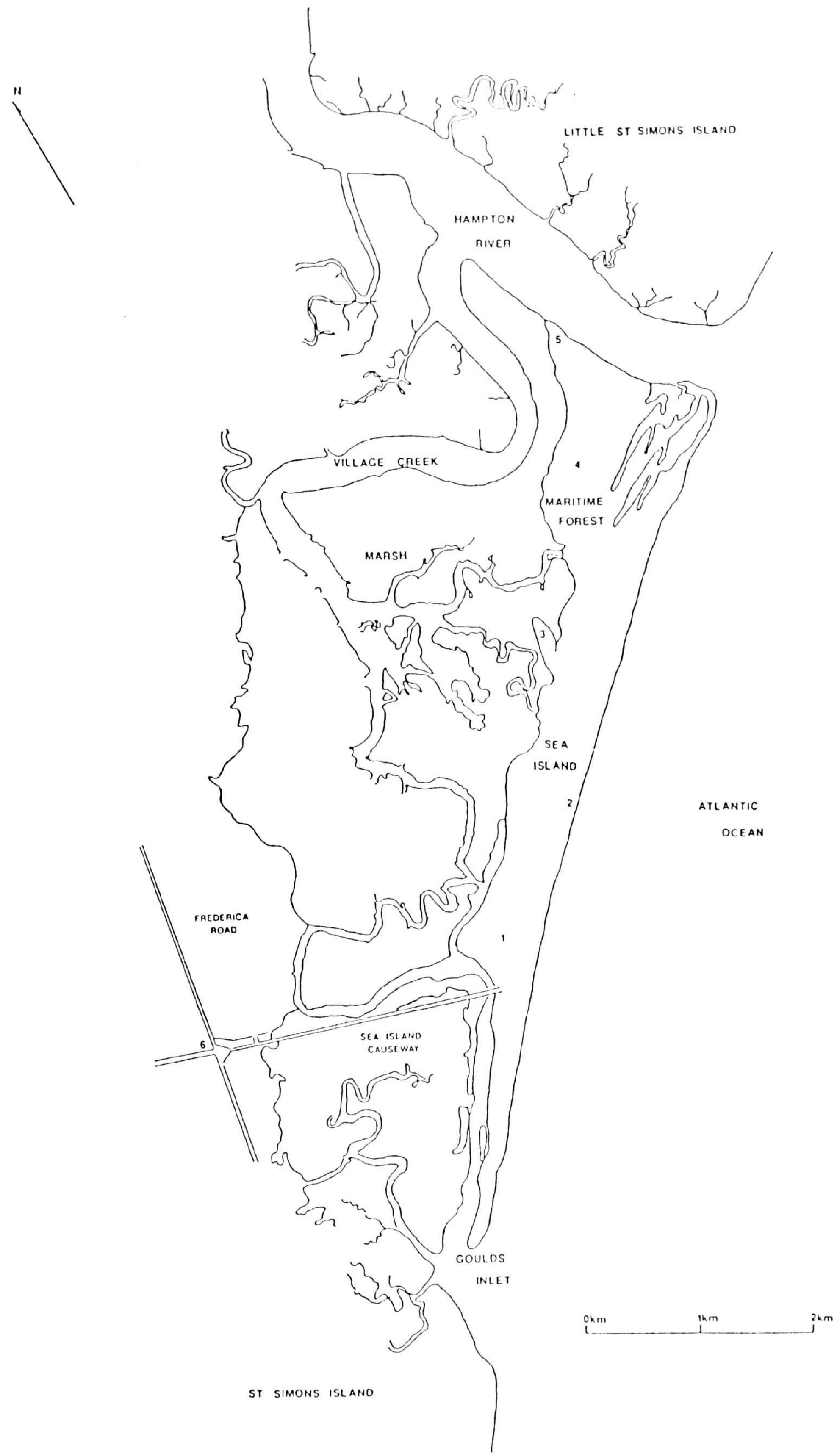
Table 10. Environmental characteristics of the soil habitat from which have emerged adults of the genera (*Culicoides*, *Dasyhelea*, and *Leptoconops*).

Species	Elevation(m)	pH	Minerals(ppm) Calcium	Phosphorus	Potassium	Magnesium
C. furens n=1251	0.002±0.284	5.66±0.40	1945±1150	143±120	733±321	883±213
C. hollensis n=1439	-0.021±0.260	5.66±0.39	2045±1130	144±120	776±300	905±203
C. melleus n=483	0.044±0.248	5.65±0.40	1917±1059	184±146	706±323	881±218
L. linleyi n=42	0.220±0.305	5.29±0.57	1252±649	116±81	513±396	740±265
D. mutabilis n=543	0.071±0.307	5.55±0.45	1670±990	148±135	646±370	808±267
Minimum	-0.777	4.2	286	19	63	214
Maximum	0.783	6.6	5855	999	999	999

Table 11. Emergence of ceratopogonid adults (Culicoides, Dasyhelea, and Leptoconops) from soil collected from a salt marsh research site on the north end of Sea Island, GA.

Vegetation Type	No. Emerging Adults/ plot/ sample				
	C. furens	C. hollensis	C. melleus	L. linleyi	D. mutabilis
Tall Spartina alterniflora (>1.2m) near creek edge and river bank	1.65	1.76	0.14	0.05	1.1
Intermediate S. alterniflora (0.3-1.2m) marsh flat	3.43	7.09	0.53	0.02	1.14
Short S. alterniflora (<0.3m), near salt pan	1.88	3.38	0.92	-	0.53
Distichlis spicata	6.80	0.50	1.36	0.39	0.89
Juncus roemerianus	1.68	2.00	6.60	0.06	-
Marsh shrubs	1.24	0.45	0.76	0.05	1.18

Figure 1. Map of ceratopogonid research area on Sea Island and Sea Island, GA The six sampling sites were: Site 1, lightly wooded area near tennis courts at Cloister hotel/ restaurant; Site 2, beach site near W.A. Jones' residence; Site 3, marsh site near G.A. Deeds' residence; Site 4, maritime forest; Site 5, marsh site at north end; Site 6, Sea Island horse stables. See materials and methods for description of six sites.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VILLAGE CREEK
4
MARITIME
FOREST
MARSH
3
SEA
ISLAND
2
ATLANTIC
OCEAN
FREDERICA
ROAD
1
6
SEA ISLAND
CAUSEWAY
GOULDS
INLET
0km
1km
2km
ST SIMONS ISLAND

Fig. 2. Diagram of elevation and vegetation zones in the salt marsh study site at the north end of Sea Island, GA. MHW, mean high water; MSL, mean sea level; MLW, mean low water.

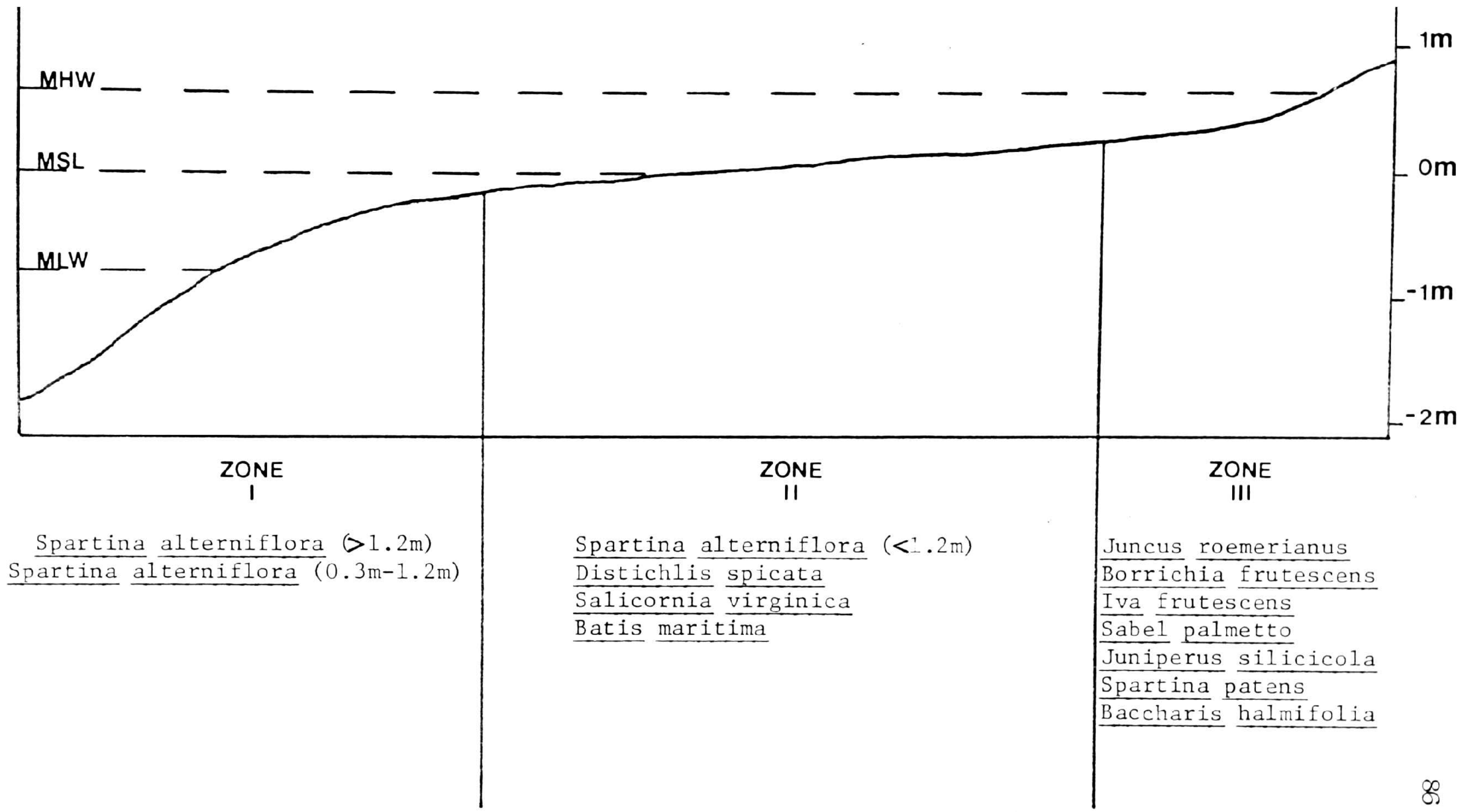

MHW
MSL
MLW
1m
0m
-1m
-2m
ZONE I
ZONE II
ZONE III
Spartina alterniflora (>1.2m)
Spartina alterniflora (0.3m-1.2m)
Spartina alterniflora (<1.2m)
Distichlis spicata
Salicornia virginica
Batis maritima
Juncus roemerianus
Borrichia frutescens
Iva frutescens
Sabel palmetto
Juniperus silicicola
Spartina patens
Baccharis halmifolia

Fig. 3. Diagram of ceratopogonid salt marsh study site at the north end of Sea Island, GA, showing the 146 (10 m X 10 m) research plots. Solid lines indicate isoclinal elevation in meters above or below mean sea level.

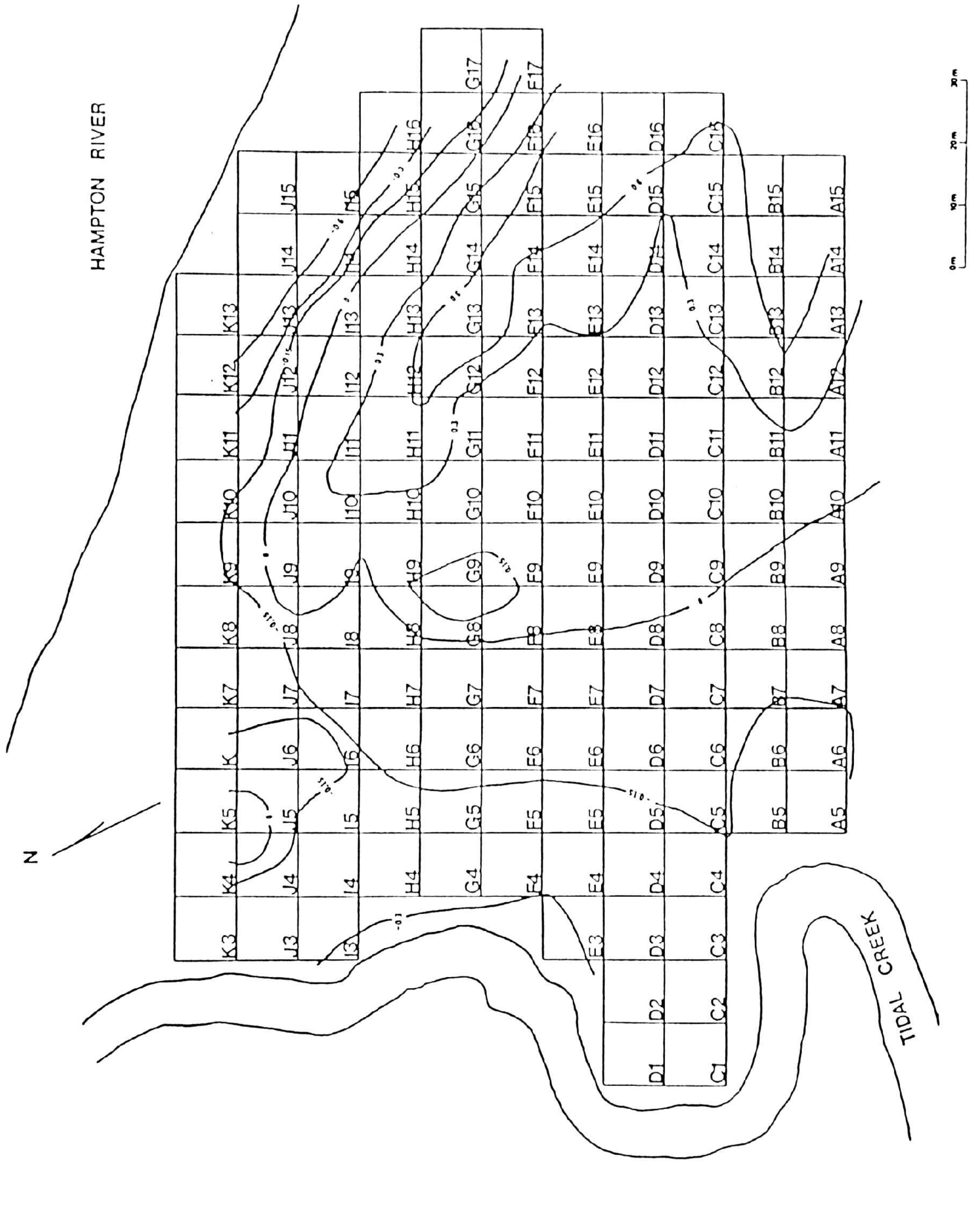

HAMPTON RIVER
TIDAL CREEK
N

Fig. 4. Number of Culicoides species captured per month in scotophase light traps, photophase light traps and sticky cylinder traps from Sea Island and St. Simons Island, GA, for the period of September 1983 through May 1985.

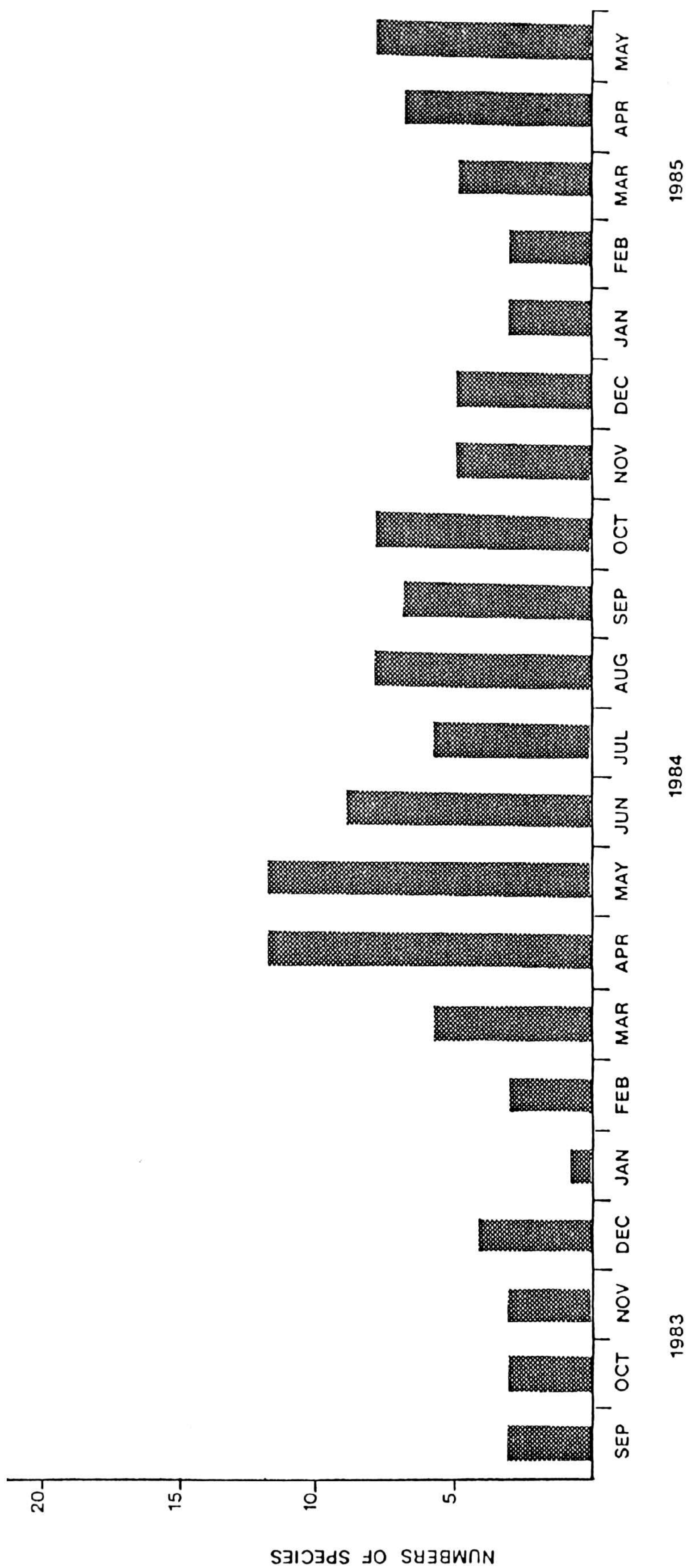
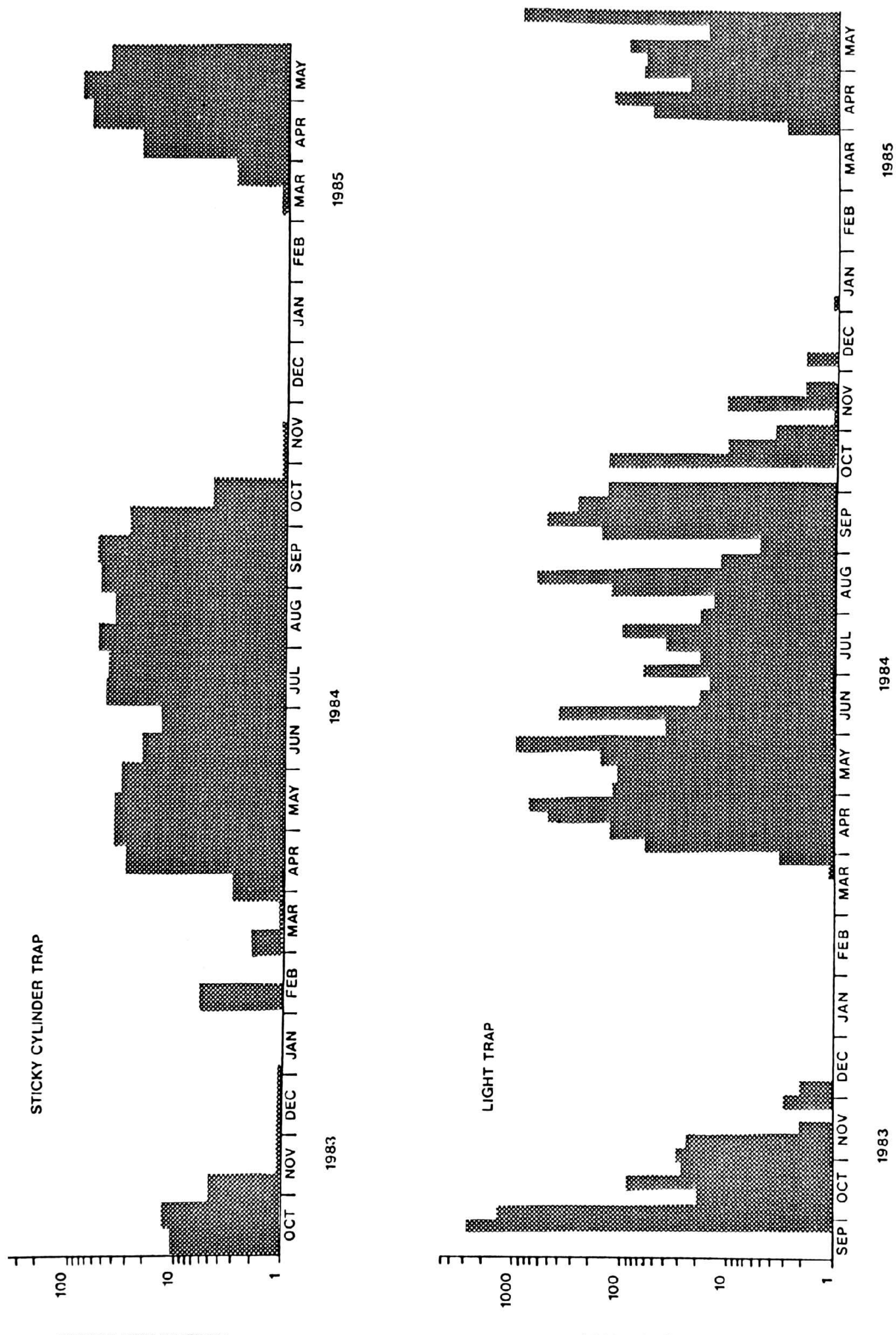

NUMBERS OF SPECIES
20
15
10
5
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
1983
1984
1985

Fig. 5. Seasonal incidence of <u>Culicoides</u> <u>furens</u> as monitored by sticky cylinder traps and scotophase light traps at Sea Island and St. Simons Island, GA, for the period September 1983 through May 1985.



STICKY CYLINDER TRAP
NUMBER/TRAP PERIOD
100
10
1
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
1983
1984
1985
LIGHT TRAP
NUMBER/TRAP NIGHT
1000
100
10
1
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
1983
1984
1985

Fig. 6. Seasonal incidence of Culicoides hollensis as monitored by sticky cylinder traps and scotophase light traps at Sea Island and St. Simons Island, GA, for the period September 1983 through May 1985.

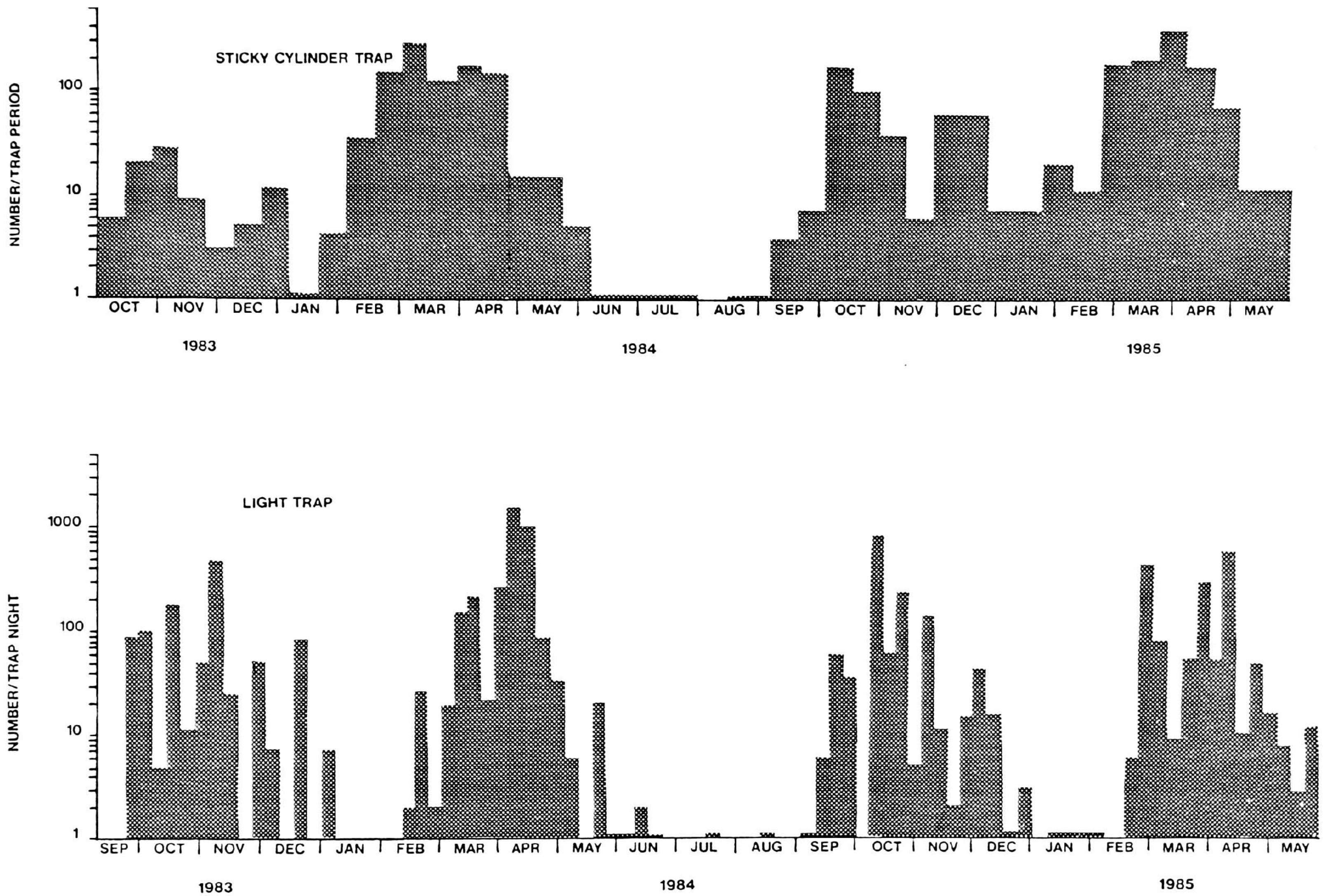
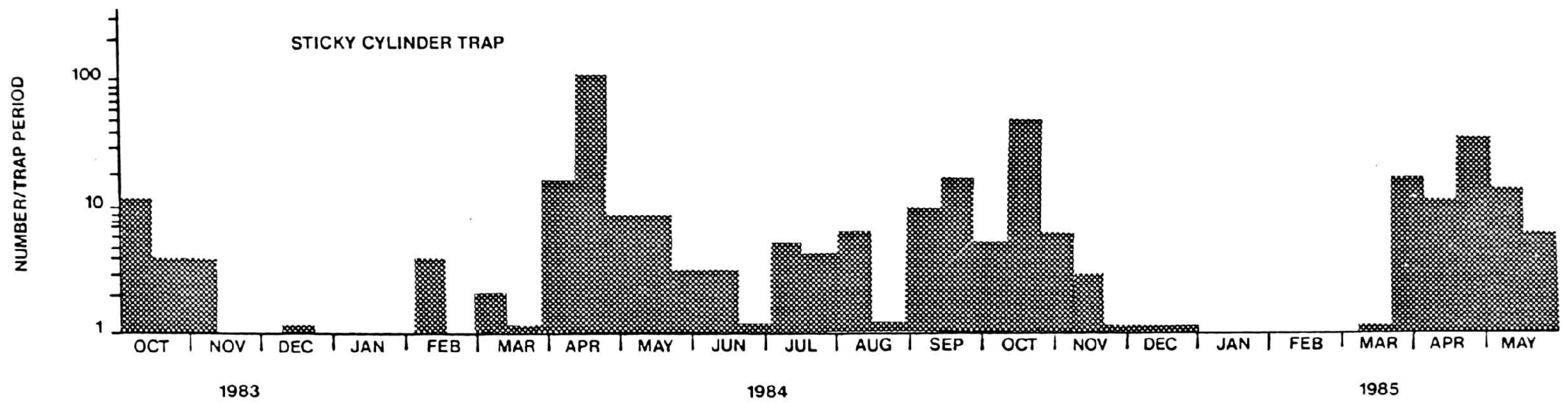
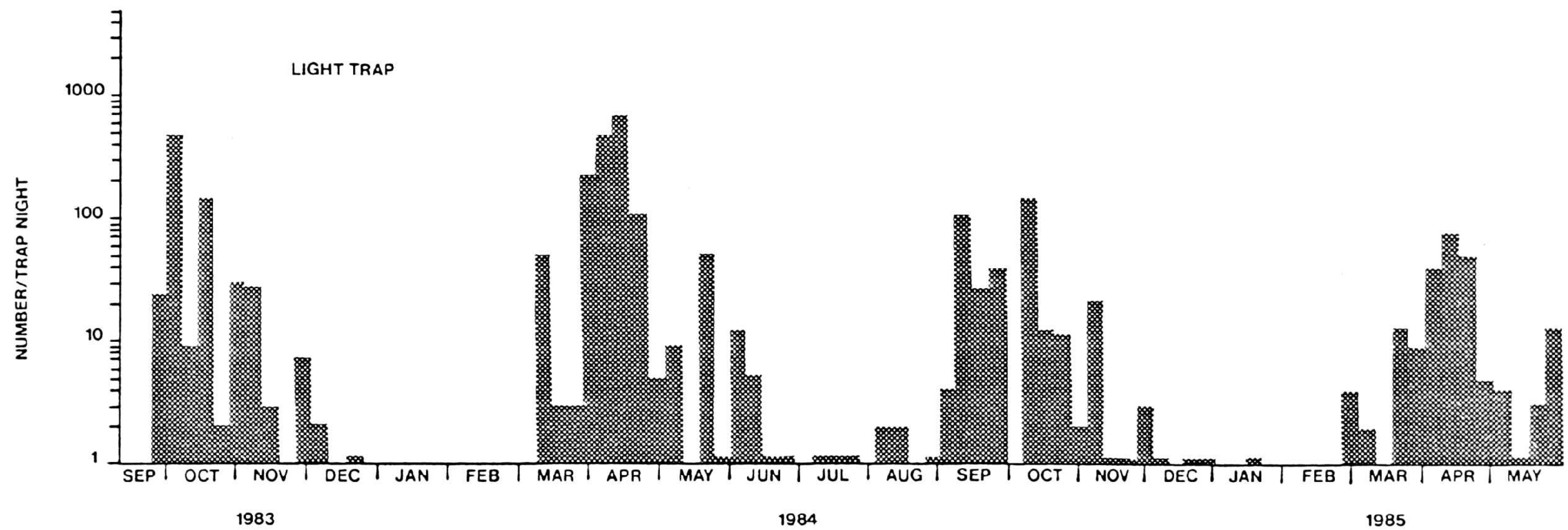

STICKY CYLINDER TRAP
NUMBER/TRAP PERIOD
100
10
1
OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY
1983
1984
1985
LIGHT TRAP
NUMBER/TRAP NIGHT
1000
100
10
1
SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY
1983
1984
1985

Fig. 7. Seasonal incidence of <u>Culicoides</u> <u>melleus</u> as monitored by sticky cylinder traps and scotophase light traps at Sea Island and St. Simons Island, GA, for the period September 1983 through May 1985.



STICKY CYLINDER TRAP
NUMBER/TRAP PERIOD
100
10
1
OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY
1983
1984
1985



LIGHT TRAP
NUMBER/TRAP NIGHT
1000
100
10
1
SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY
1983
1984
1985

Fig. 8. Distribution of *Culicoides* larvae (*C. furens*, *C. hollensis* and *C. melleus*) in three elevation zones on the salt marsh at the north end of Sea Island, GA.

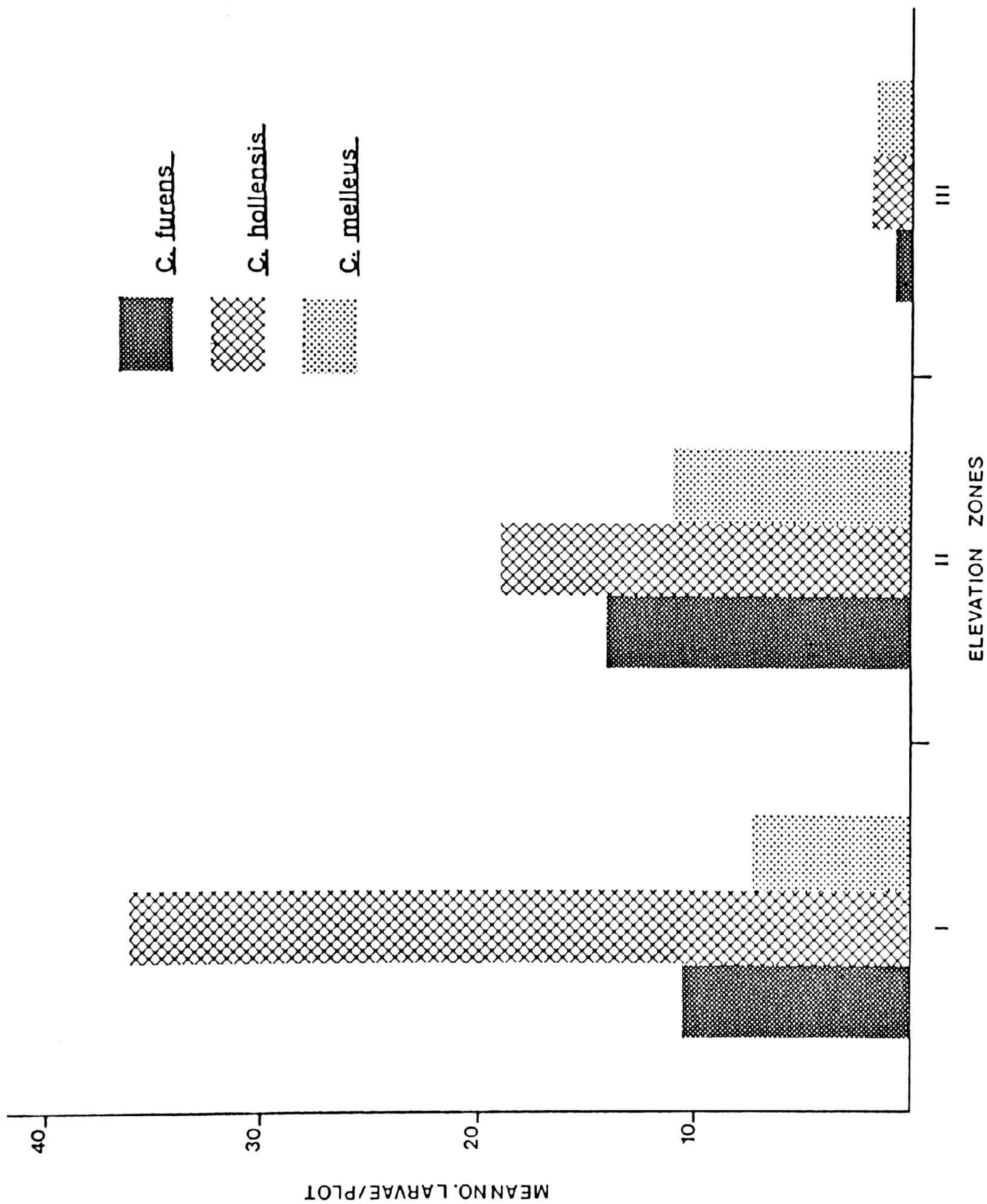

C. furens
C. hollensis
C. melleus
I
II
III
ELEVATION ZONES
MEAN NO. LARVAE/PLOT
10
20
30
40

Fig. 9. Seasonal distribution by instar of *Culicoides furens* larvae recovered from a salt marsh at the north end of Sea Island, GA.

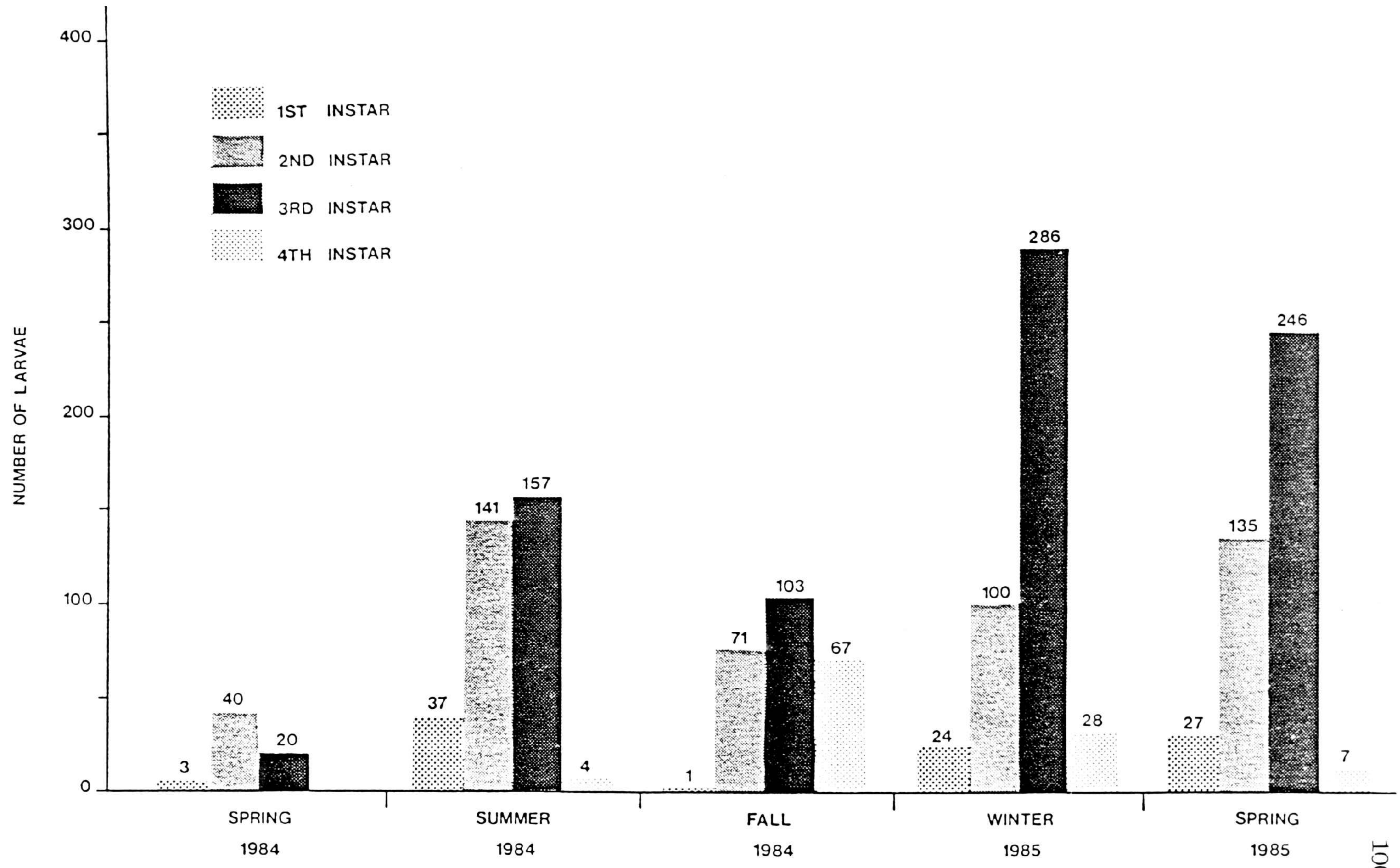

NUMBER OF LARVAE
0
100
200
300
400
1ST INSTAR
2ND INSTAR
3RD INSTAR
4TH INSTAR
3
40
20
37
141
157
4
1
71
103
67
24
100
286
28
27
135
246
7
SPRING
1984
SUMMER
1984
FALL
1984
WINTER
1985
SPRING
1985

Fig. 10. Seasonal distribution by instar of Culicoides hollensis larvae recovered from a salt marsh at the north end of Sea Island, GA.

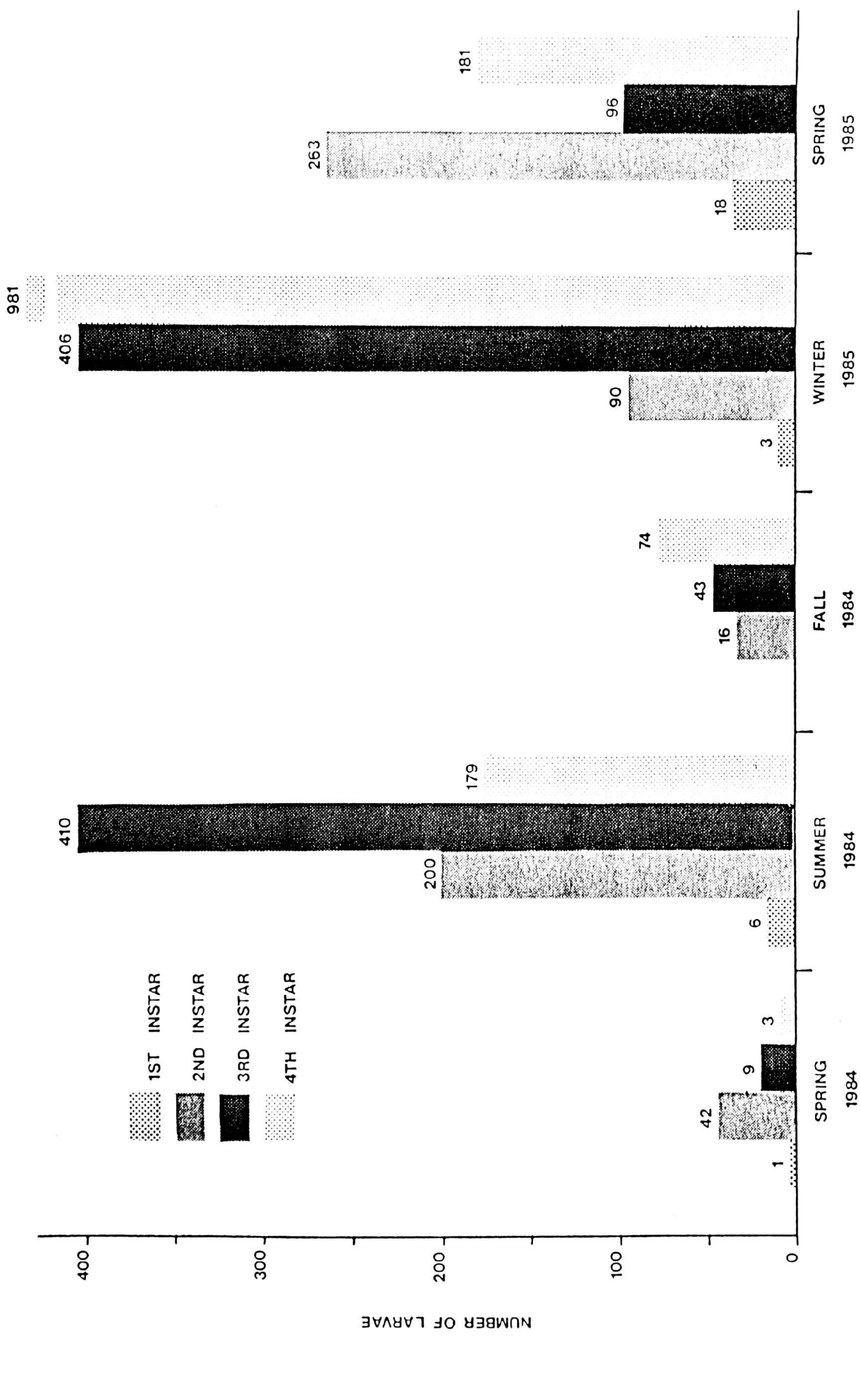

1ST INSTAR
2ND INSTAR
3RD INSTAR
4TH INSTAR
NUMBER OF LARVAE
0
100
200
300
400
SPRING 1984
SUMMER 1984
FALL 1984
WINTER 1985
SPRING 1985
1
42
9
3
6
200
410
179
16
43
74
3
90
406
981
18
263
96
181

Fig. 11. Seasonal distribution by instar of _Culicoides melleus_ larvae recovered from a salt marsh at the north end of Sea Island, GA.

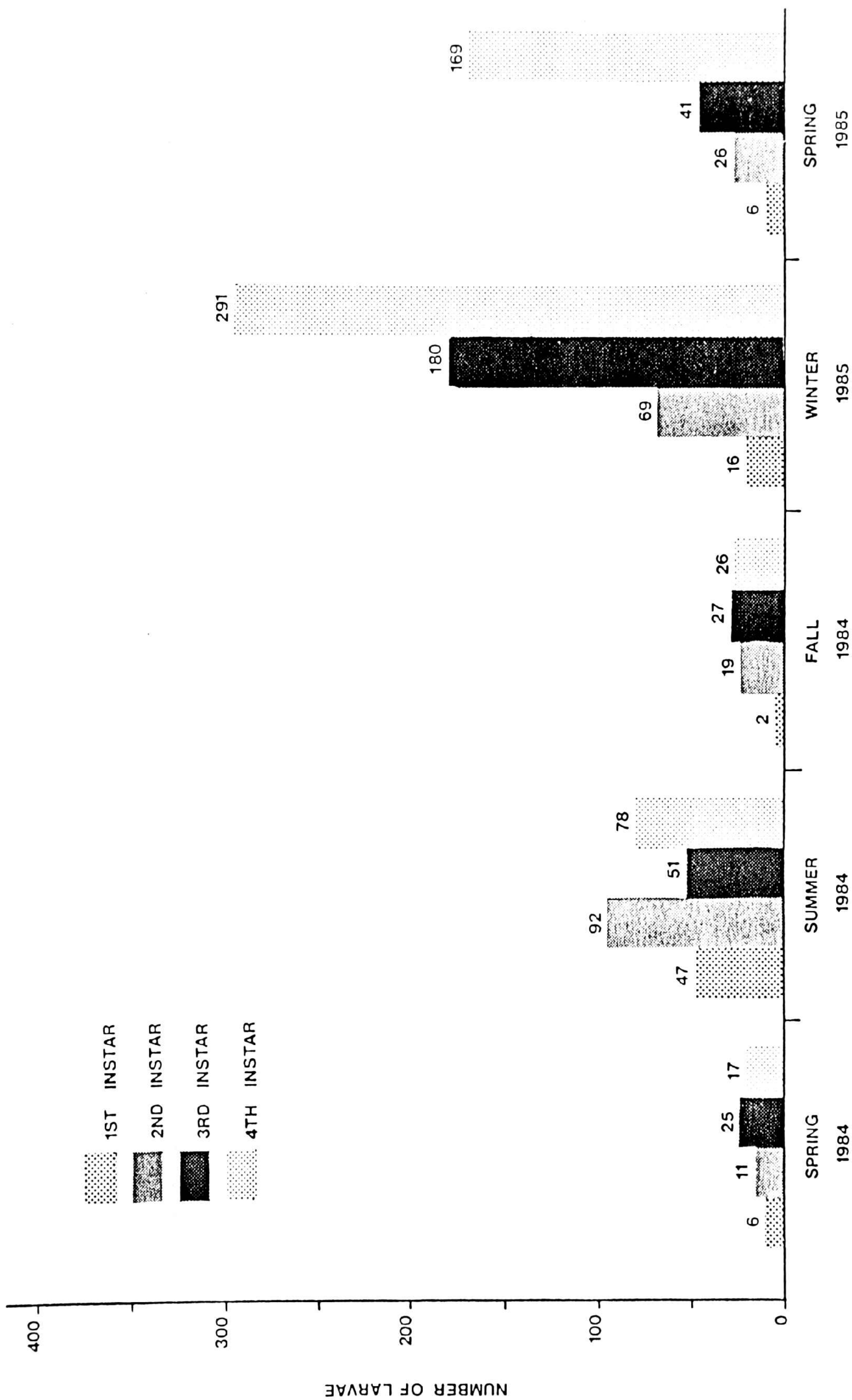
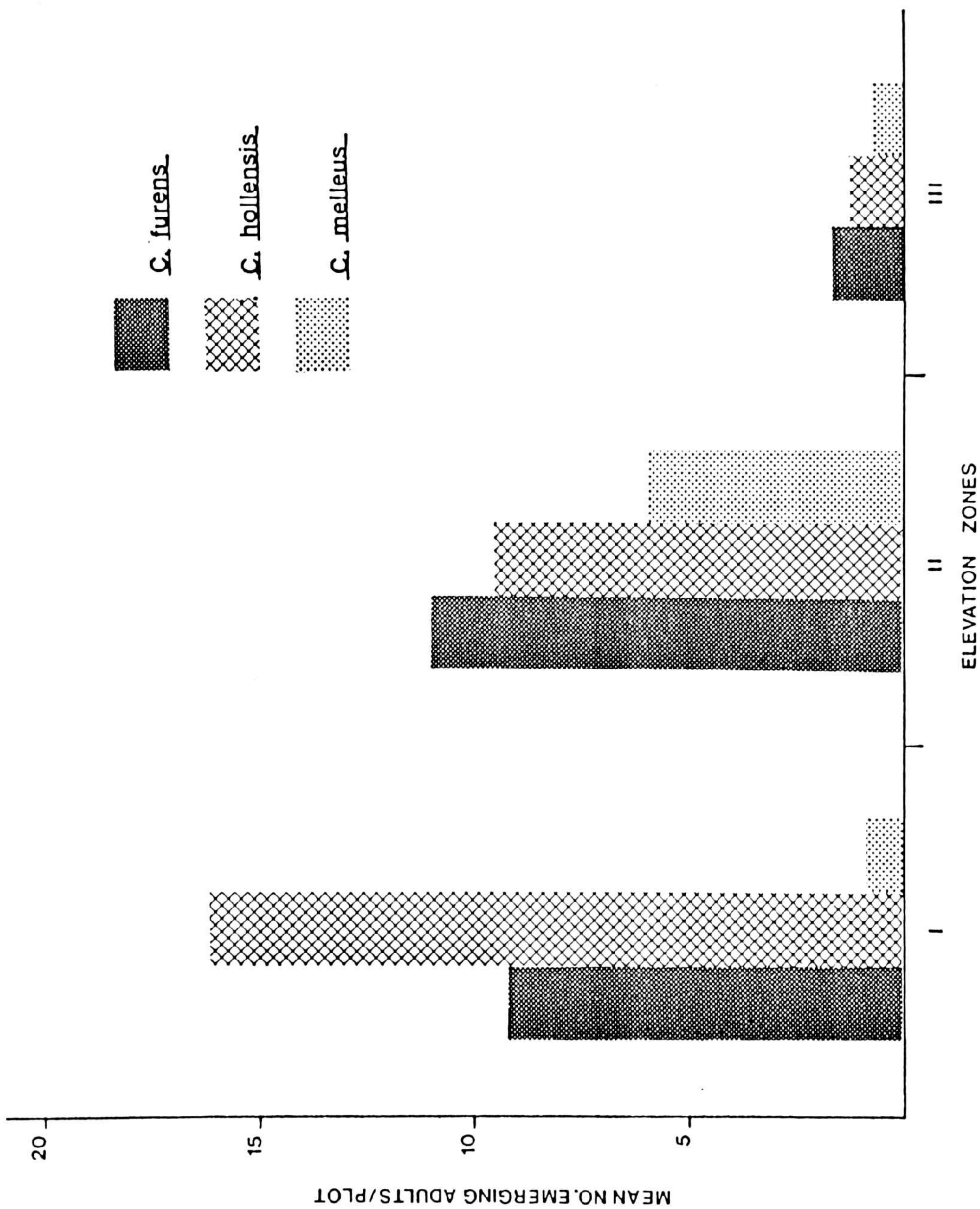

1ST INSTAR
2ND INSTAR
3RD INSTAR
4TH INSTAR
NUMBER OF LARVAE
0
100
200
300
400
SPRING 1984
6
11
25
17
SUMMER 1984
47
92
51
78
FALL 1984
2
19
27
26
WINTER 1985
16
69
180
291
SPRING 1985
6
26
41
169

Fig. 12. Distribution of emerging adult Culicoides (C. furens, C. hollensis and C. melleus) recovered from soil samples collected in three elevation zones on the salt marsh at the north end of Sea Island, GA.


C. furens
C. hollensis
C. melleus
MEAN NO. EMERGING ADULTS/PLOT
20
15
10
5
ELEVATION ZONES
I
II
III