Spring 1983

A Quantitative Study of the Aquatic Macroinvertebrates in an Irregularly Flooded Salt Marsh, Smith Island, Virginia

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A QUANTITATIVE STUDY OF THE AQUATIC MACROINVERTEBRATES IN AN IRREGULARLY FLOODED SALT MARSH, SMITH ISLAND, VIRGINIA

by

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A Thesis Submitted to the Faculty of

Old Dominion University in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

Biology

Old Dominion University

May, 1983

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Abstract

Little is known about the aquatic macroinvertebrate community structure in coastal salt marshes. This study investigated the aquatic macroinvertebrate community structure in a coastal Virginia salt marsh. Sixteen samples were taken weekly from two different sites on Smith Island, Virginia, from April to mid-October 1982. Bimonthly samples were taken during the months of March and November due to low density of organisms and reduced growth rates at these times.

A total of 46 taxa were collected with 17 occurring regularly, indicating a relatively diverse fauna. Wide fluctuations in the physical parameters were observed; however, temporal changes in the macroinvertebrate community cannot be attributed to these fluctuations in the physical environment except during extremes. Seasonal changes in the community were attributed to seasonal cycling of the community due to the individual life cycles of the resident organisms.

Species diversity remained quite high throughout the growing season and was only drastically reduced during drought periods. Fast recolonization of the prey species made the sites with the most severe conditions (highest frequency of drying) the most productive. This was thought to be due to predator elimination caused by drying.

ACKNOWLEDGEMENTS

The author wishes to express his sincere appreciation to Dr. James F. Matta whose expertise and endless patience enabled this work to be conceived and completed. Most important is the friendship and guidance I received from Dr. Matta that enabled my program to be both enlightening and enjoyable. I also extend thanks to Drs. Raymond W. Alden III and Daniel M. Dauer for their critical review of the manuscript.

In addition, I extend my sincere thanks to Susan W. Alexander, Annabel C. Blanco, Michael P. Crosby, and all the others who gave their unselfish help on the collecting trips to make this research possible. I also thank all the personnel in the Marine Benthic Ecology Laboratory, Old Dominion University, for their cooperation in the identification of many of the specimens.

Special thanks to Nancy L. Wade for an excellent education in general biology and two years of professional growth as an educator.

Finally, I would like to thank the Barrier Islands Program at Old Dominion University, the Virginia Coast Reserve chapter of the Nature Conservancy and the Office of Academic Affairs, ODU, for their support in this project.

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INTRODUCTION

The Atlantic and Gulf coasts of the United States possess extensive expanses of salt marshes which are among the most productive in the world and a vital habitat necessary for the completion of the life cycle of many organisms (de la Cruz 1980). There have been a number of studies dealing with these marsh ecosystems and ecological energy flow in salt marshes (Teal 1962, Day et al. 1973, Howarth and Teal 1980, and Cammen et al. 1982). Estimates of invertebrate populations, especially the insects, reported in these studies were obtained either from very few samples or published data from previous studies.

The macroinvertebrate community has been shown to be an important part of the food web in coastal marshes (Nixon and Oviatt 1973, Cammen et al. 1982). Teal and Teal (1969) pointed out that coastal marshes provide habitats for a number of different animals, and the macroinvertebrate community is an important food source for a number of these animals. To better understand these relationships, the macroinvertebrates of salt marshes must be studied at the community level.

In recent years, there have been several studies done on the terrestrial insects of salt marshes that involved the association of insect faunas with various types of salt marsh grasses (Davis and Gray

1966, Denno 1977, 1980, and Raupp and Denno 1979).

In the early seventies, two studies were done on the east coast involving the macroinvertebrate faunas of two different salt marshes (McMahan et al. 1972, and Wall 1973). However, even though these studies provided important preliminary information, they were by no means totally comprehensive surveys. McMahan and his coworkers used a vacuum method of sampling which the authors admitted usually missed the grasshoppers, dragonflies, large spiders, and arthropods larger than a few millimeters in length and active enough to escape suction. The study reported by Wall (1973) was not a quantitative investigation but merely a taxonomic listing of organisms found in interitdal sand and salt marshes of Cape Cod.

The coastal salt marshes have long been recognized as extensive breeding sites for many species of blood-sucking Diptera such as mosquitoes, horse flies, deer flies, and sand flies. Because of their importance to man, these organisms have been the most extensively studied (Jamnback and Wall 1959, Rockel and Hansens 1970a, 1970b, Pechumen 1972, Hansens and Robinson 1973, Dukes et al. 1974, and Wirth and Blanton 1979). Due to the potential threat that these organisms pose to man, they have been subjected to many water level management and pesticide control programs (Connell 1940, Chapman and Ferrigno 1956, Ludwig et al. 1968, Wall and Marganian 1973, and Campbell and Denno 1976).

The non-biting aquatic macroinvertebrates of salt marshes have been virtually ignored until recently. In the past few years, a number of studies have been done on these formerly obscure organisms (Campbell and Denno 1978, Kelts 1979, Campbell 1979, and Thiery 1979). Documentation on the great abundance of insects and other macroinvertebrates in salt marshes has only come recently and is scattered throughout the literature. Teal (1962) listed about 40 insect and arachnid species that he collected from a Georgia Spartina marsh. Marples (1966), while studying trophic levels of marshes near the same area, identified only the more prominent marsh species. Davis and Gray (1966) reported over 350 different species of aquatic and terrestrial insects from Spartina, Juncus, and other salt marshes near Beaufort, North Carolina. Bickley and Seek (1975) contributed to the knowledge of the insects around the Chesapeake Bay by sampling in brackish and salt marshes in Maryland. They listed 491 terrestrial and aquatic insects from the marshes. Matta (1980) lists some 43 aquatic insects from Parramore Island, Virginia. This collection included specimens from a wide variety of habitats ranging from salt marshes to freshwater woodland pools.

Campbell and Denno (1978) contributed

substantially to the knowledge of salt marsh aquatic insect community structure by quantitatively studying *Spartina patens* salt marsh pools along the New Jersey coast. The importance of this study is demonstrated by the authors' integrated approach to quantifying the aquatic insect community. In the past, only certain segments of the salt marsh aquatic insect communities were studied, leaving the total community relationships obscure. However, by excluding all non-insect macroinvertebrates, important groups such as the annelids and crustaceans were eliminated from their study.

The purpose of this study was threefold: (1) to quantify species abundance and diversity of macroinvertebrates in an irregularly flooded salt marsh over the course of one growing season; (2) to compare the macroinvertebrate communities of two different sampling sites in two different locations; and (3) to determine how fluctuations in water temperature, depth, salinity, and dissolved oxygen affect the species diversity and abundance of macroinvertebrates in the salt marsh.

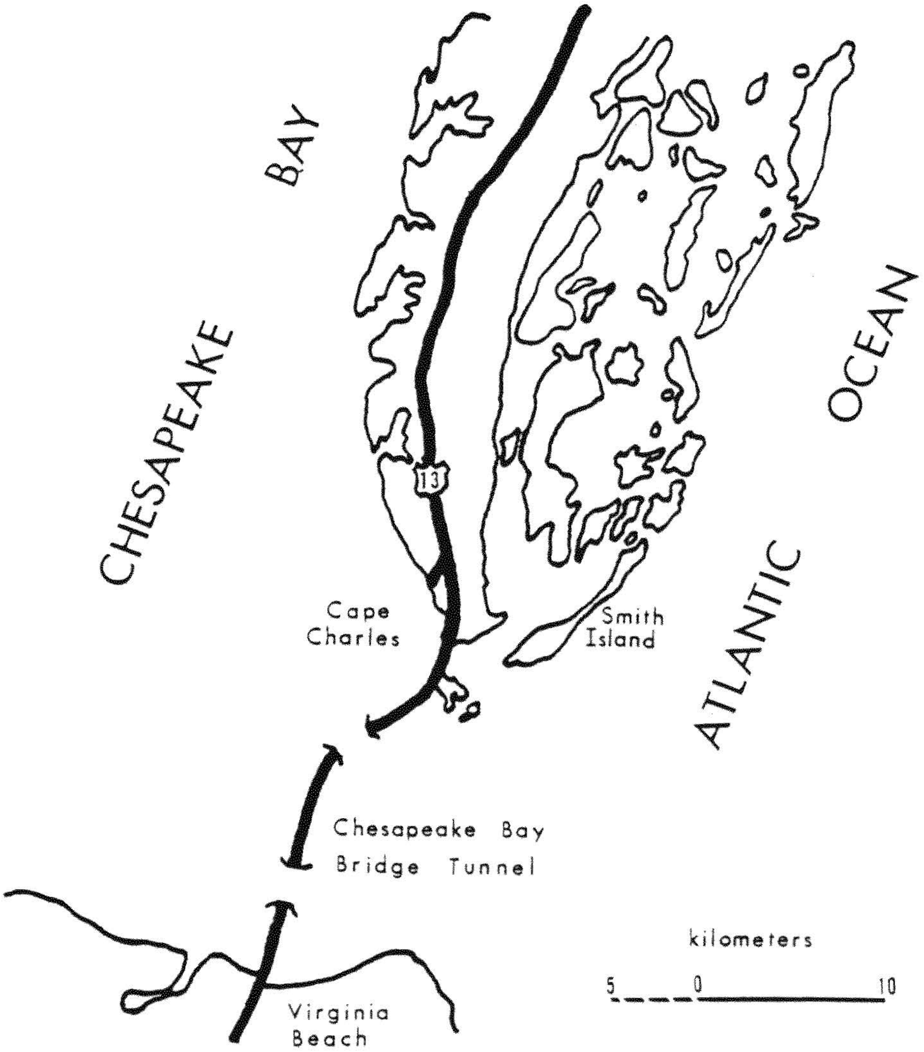
DESCRIPTION OF STUDY AREA

The study area was located on Smith Island, Virginia, the twelfth island from the north end of the Virginia Barrier Island Group. It is also the second island from the south end of the group at Chesapeake Bay, approximately 2 km east of Cape Charles, Virginia (Fig. 1). Smith Island is one of the longer Barrier Islands; its length is 11.4 km and it ranges in width from 150 m to 1500 m with an average width of 1000 m. The island is divided into two distinct sections: a low lying, northern section which is frequently overwashed and characterized by homogeneous stands of *Spartina alterniflora*; and a main, southern section of alternating wooded dune ridges and salt marshes.

Sampling was done on the southern portion of the Island which is nearly 1.5 km wide and almost 3 km long. McCaffrey (1976) described this portion of the island as having the most diverse vegetation. East-west oriented dune ridges are numerous; these are densely vegetated by hardwood forests and tall *Myrica cerifera* (Wax Myrtle) thickets. Between these wooded ridges lie the salt marshes where the samples were taken. The relief of this part of the Island is relatively low, ranging from 1.5-2.0 m in the beach ridge areas to 0.0-1.0 m over the rest of the island.

Clovis (1968) provides an extensive review of

Fig 1. Map of the southern tip of the Eastern Shore of Virginia showing the location of Smith Island, Virginia.

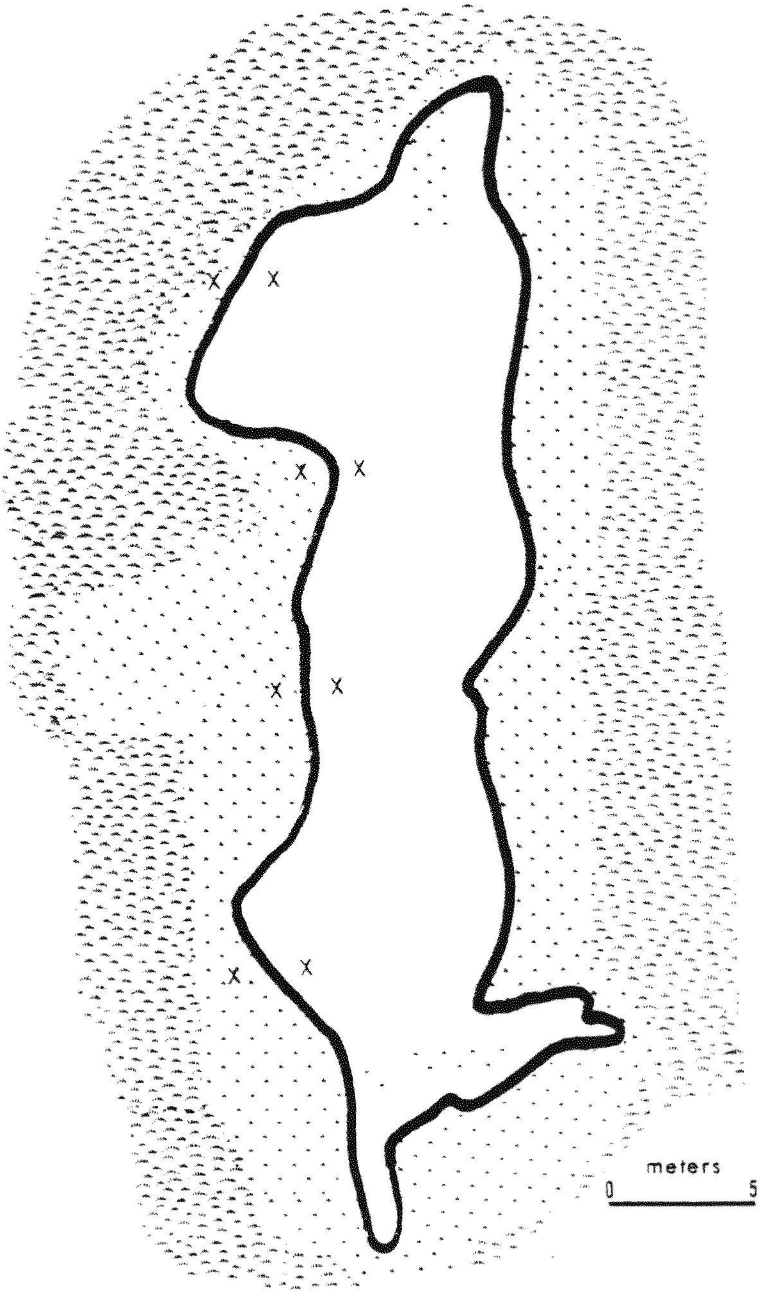

BAY
CHESAPEAKE
OCEAN
ATLANTIC
13
Cape
Charles
Smith
Island
Chesapeake Bay
Bridge Tunnel
Virginia
Beach
kilometers
5
0
10

the vegetation of the southern part of the Island, and lists many of the dominant plant species found there. The interior salt marshes are characterized by two dominant grasses: Spartina patens and Distichlis spicata. These plants are dominant components of salt marshes along most of the Atlantic and Gulf coasts of North America. S. patens occupies a narrow elevational zone of partially-drained soil above high water level where it can grow in extensive pure stands that are occasionally inundated by tides, as in near upland areas (Blum 1968, and Redfield 1972). D. spicata grows in lower parts of the marshes, covering large areas as monotypic vegetation and intermixed with S. patens (Eleuterius 1980).

The criteria used in the selection of the sampling sites were: (1) degree of accessibility; (2) whether or not the plant stands appeared to be representative; and (3) distance from the beach. The two sampling sites used in this study were characterized by landlocked, shallow pools surrounded by Distichlis spicata, with Spartina patens growing farther from the ponds at slightly higher elevations near the wooded ridges. During the study, the depth of the water in the pools varied from a minimum of 0 cm when the pools were dry in the summer to a maximum of approximately 45 cm after periods of heavy rain. Sampling site 1 was near the narrow southern tip of the island and within 200 m of both Magothy Bay and the Atlantic Ocean. This site was surrounded by a narrow strip of marsh grass and encircled by higher, upland areas vegetated by woody thickets (Fig. 2). Sampling site 2 was farther north on the wider part of the southern half of the island. This site was not surrounded by upland ridges, but was encompassed by extensive homogeneous expanses of *D. spicata* and *Juncus roemerianus* (Fig. 3). The elevation of this site is lower than that of site 1; being less than 0.5 m above mean high water and occasionally flooded by high spring tides.

Fig. 2. Vegetational map of study site 1 near the southern tip of Smith Island, Virginia. Each sample location is indicated by an "X".

Distichlis spicata   Woody shrubs




Distichlis spicata
Woody shrubs
Juncus roemerianus
meters
0
5

METHODS AND MATERIALS

Eight samples were taken weekly from each sampling site from April to mid-October 1982. Bimonthly samples were taken during the months of March and November due to the low density of organisms and to relatively slow growth of organisms during those periods. At each sampling site, 4 samples were taken from the flooded marsh at the edge of each pool, and 4 samples were taken from the open pool approximately 1 m from the edge of the marsh. Samples were not taken if there was no standing water present. Water temperature, salinity, and dissolved oxygen were measured before each sample was taken. An open-ended cylinder (22.9 cm diameter x 61.0 cm high) was plunged at random into the substrate at each pre-selected site. The cylinder was securely pushed into the mud , and water depth was measured. The contents of the cylinder (water, organisms, mud, and plant material) were stirred and then scooped out of the cylinder to a depth of 5 cm below the substrate surface. The contents of the cylinder were then placed into a 0.5 mm sieve, with water used to remove the fine particles of mud and detritus from each sample. Pieces of plant material too large for the collecting bottles were removed from the sieve and inspected for any clinging organisms before they were discarded. The remaining detritus and organisms were then emptied into plastic collecting bottles containing 10% formalin and Rose Bengal stain, and returned to the laboratory.

In the laboratory, each sample was again sieved through 0.5 mm mesh and the remaining material was placed into a 2 l cylinder. A saturated saline solution was added, and the contents were stirred and then allowed to stand. The macroinvertebrates floated to the top, and were then placed into a white enamel pan and removed with forceps. This procedure was repeated for each sample a minimum of 3 times or until no more organisms floated to the top. Campbell and Denno (1978) reported that this method of removing organisms from detritus is 95% effective, and this has been confirmed in our laboratory. The organisms were then placed into vials containing 70% alcohol and stored for identification.

After identifying and counting the macroinvertebrates, the following parameters were calculated to characterize community structure for each collection:

(1) species richness= the number of species in the community

(2) species evenness=the distribution of individuals among the species

(3) species diversity=

$$H' = - \sum_{i=1}^{n} (P_i)(\ln P_i)$$

where P_i was the decimal proportion of individuals out of the total which belonged to the ith species (Shannon and Weaver 1949).

Before further analyses were done, the rare species were eliminated by a 5% inclusion criterion; only those species that occurred in at least 5% of the total samples were considered in subsequent analyses. This procedure was used because rare species only occur sporadically, tending to inordinately increase the total variation in the data and thus, confuses the subsequent analyses. Also, the rare species do not significantly contribute to the information about the communities. In order to normalize the data, a log base 10 transformation was used (Log_{10} X+1).

Statistical analyses were performed on a DEC-10 computer using the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975) and Biomedical Computer Programs (BMDP) (Dixon and Brown 1979). These two statistical packages offer a variety of both univariate and multivariate statistical techniques which are relatively easy to perform and interpret.

Analysis of variance (ANOVA) was performed to determine how the measured physical parameters varied between and within the two sampling sites. This was accomplished by first separating the marsh and pond locations at each site then pooling the locations to observe differences between the two sites.

Principal components analysis (PCA) was performed using the SPSS Factor procedure. PCA is a multivariate statistical technique that assesses the variation and its sources in the data. Daultrey (1976) provides complete and well-detailed documentation for this statistical procedure. Before the factor scores were produced, varimax rotation was performed. The factor scores that were produced were used in subsequent analyses.

Discriminant analysis was performed to determine how well the sites and the locations within and between the sites could be separated on the basis of the occurrence of the selected species. Due to the failure of SPSS to extract the eigenvalues in the discriminant analysis, BMDP was used. A stepwise selection method based on minimizing Mahalonobis distance was used which selects variables (species) for entry into the analysis on the basis of their discriminating power. This enables the researcher to subsequently select the "next best" discriminator at each step, which tends to reduce the number of variables (Klecka 1975). Klecka (1980) provides an excellent explanation of the uses and the assumptions of this statistical test. Additional details of the analyses are presented in the Results section.

RESULTS

Macroinvertebrate Analysis

A total of 47,369 individuals representing 46 taxa were collected during the sampling period. Only 17 species were present in at least 5% of the samples, and these species were considered the dominant species in the two communities. The numbers of individuals collected at sites 1 and 2 varied dramatically; 39,555 and 7,814 individuals, respectively. Four phyla were represented in the samples, with the majority of species being arthropods (Table 1).

The larval chironomid, Dicrotendipes leucoscelis (Townes), was clearly the dominant species in terms of numbers (27,811 individuals), accounting for 59% of the total number of individuals collected. The oligochaete, Paranais litoralis (Muller), was the second most abundant species (7,236 individuals). Immatures of the mosquito, Aedes sollicitans (Walker), the ceratopogonid, Culicoides furens Poey, the dolicopodid, Hydrophorus sp., the corixid, Trichocorixa verticalis (Fieber) and the polychaete, Capitella capitata (Fabricius), were also relatively abundant; each species was represented by more than 600 individuals. All the tabanids, Chrysops atlanticus Pechuman, C. fuliginosus Wiedemann, C. vittatus Wiedemann, Tabanus nigrovittatus Macquart, and

Table 1. Taxonomic composition of the macroinvertebrates collected in the samples.

PHYLUM PLATYHELMINTHES

Class Turbellaria
Bdelloura sp.

PHYLUM ANNELIDA

Class Polychaeta
Streblospio benedicti Webster
Lycastopsis pontica (Bobretsky)
Capitella capitata (Fabricius)
Capitomastus aciculatus Hartman

Class Oligochaeta
Lumbriculidae sp.
Peloscolex sp.
Paranais litoralis (Muller)
Chaetogaster sp.
Marionina spicula (Leuckart)

PHYLUM MOLLUSCA

Class Gastropoda
Hydrobia totteni Morrison

PHYLUM ARTHROPODA

Class Cirripedia
Chthamalus fragilis Darwin

Class Malacostraca
Palaemonetes pugio Holtuis
Orchestia grillus Bosc
Gammarus palustris Bousfield
Philoscia vittata Say

Class Insecta

Order Collembola
Family Isotomidae
Isotomurus palustris (Muller)

Order Hemiptera
Family Corixidae
Trichocorixa verticalis (Fieber)
Family Mesoveliidae
Mesovelia mulsanti bisignata Uhler

Table 1 (cont'd)

Order Odonata
  Family Coenagriidae
    Ischnura verticalis (Say)
  Family Libellulidae
    Erythrodiplax berenice Drury
  Family Aeshnidae
    Anax junius (Drury)

Order Coleoptera
  Family Helodidae
    Helodidae sp.
  Family Dytiscidae
    Liodessus affinis (Say)
    Hygrotus impressopunctatus (Schaller)
    Thermonectus basillaris (Harris)
  Family Hydrophilidae
    Berosus striatus (Say)
    Tropisternus quadristriatus (Horn)
    Enochrus hamiltoni (Horn)

Order Diptera
  Family Ceratopogonidae
    Culicoides furens Poey
    Dasyhelea sp.
  Family Chironomidae
    Dicrotendipes leucoscelis (Townes)
  Family Culicidae
    Aedes sollicitans (Walker)
  Family Dolichopodidae
    Hydrophorus sp.
  Family Empididae
    Empididae spp.
  Family Ephydridae
    Ephydra subopaca Loew
    Paralimna sp.
    Helaeomyia sp.
    Brachydeutera argentata (Walker)
  Family Muscidae
    Muscidae spp.
  Family Stratiomyidae
    Odontomyia sp.
  Family Tabanidae
    Chrysops atlanticus Pechumen
    Chrysops fuliginosa Wiedemann
    Chrysops vittatus Wiedemann
    Tabanus atratus Fabricius
    Tabanus nigrovittatus Macquart

T. atratus Fabricius, rarely occurred in the samples (<10 individuals). Other taxa rarely collected are listed in Table 1.

Each of the 17 species that met the 5% inclusion criterion and subsequently entered into the analyses were collected from both sites (Table 2). Almost 5 fold more organisms were collected at site 1 than at site 2. The number of individuals from the marsh and pond within each site were relatively even, although more samples were taken from the ponds. Plots of these 17 dominant species with each of the physical parameters (water temperature, depth, salinity, and dissolved oxygen) revealed no significant linear regression relationships. Due to the failure of the physical variables to explain a substantial amount of the variation observed in the species, principal components analysis was performed to determine the major sources of the variation.

The first principal components analysis, dealing with the variation observed in the species in marsh 1, revealed the first 4 principal components explained 51.8% of the observed variation (Table 3). Three taxa loaded heavily on prinicipal component I; *Enochrus hamiltoni*, *Aedes sollicitans*, and Muscidae spp. These taxa were all early season colonizers and became less abundant as the growing season progressed. In addition, these species also showed high reproductive potentials in the late

Table 2. Taxa that occurred in at least 5% of the samples and their average number for each location (/.05 m^2) over the sampling period.

TAXON	MARSH 1	POND 1	MARSH 2	POND 2	TOTAL
Dicrotendipes leucoscelis	210	86	27	3	67
Paranais litoralis	31	45	2	<1	18
Aedes sollicitans	4	10	<1	19	9
Trichocorixa verticalis	2	12	2	5	5
Capitella capitata	<1	12	<1	<1	3
Culicoides furens	3	8	<1	<1	3
Hydrophorus sp.	<1	6	<1	<1	2
Enochrus hamiltoni	2	<1	3	<1	1
Berosus striatus	3	1	<1	<1	1
Ephydra subopaca	<1	2	<1	<1	<1
Helodidae sp.	<1	<1	2	<1	<1
Orchestia grillus	3	<1	<1	0	<1
Erythrodiplax berenice	1	<1	<1	<1	<1
Tropisternus quadristriatus	<1	<1	1	<1	<1
Muscidae spp.	<1	<1	<1	<1	<1
Palaemonetes pugio	<1	<1	<1	<1	<1
Mesovelia mulsanti	<1	<1	<1	<1	<1

Table 3. The first 4 principal components for each location at site 1 and the associated eigenvalues and % of variation explained by each component.

MARSH 1

Component	Eigenvalue	% of variation	Cumulative %
1	3.03772	17.9	17.9
2	2.37030	13.9	31.8
3	1.83898	10.8	42.6
4	1.56671	9.2	51.8

POND 1

Component	Eigenvalue	% of variation	Cumulative %
1	2.78219	16.4	16.4
2	2.29964	13.5	29.9
3	1.63564	9.6	39.5
4	1.33788	7.9	47.4

spring and early summer as indicated by their abundances at these times. Thus, this component can be viewed as the "early season bloom" as demonstrated by the abundance of these 3 species. Palaemonetes pugio, Trichocorixa verticalis, and Berosus striatus all loaded heavily on component II. These species were only collected in substantial numbers late in the growing season. This component revealed the "late season bloom" of these organisms which were not found at earlier times in the marsh. T. verticalis loaded on component III along with the odonate, Erythrodiplax berenice. These species were moderately abundant in the fall and were slow to recolonize after a drought period. This component was influenced by those species that were slow colonizers in the late fall, particularly after a dry period. Helodidae sp., Culicoides furens, and Hydrophorus sp. loaded on component IV. These species all showed weak mid-summer peaks, and they were fast to recolonize after drought periods. This component is viewed as "rapid recolonization" as demonstrated by the above species.

The first 4 principal components of the principal components analysis of pond 1 explained 47.4% of the variation observed in the species (Table 3). Capitella capitata, Berosus striatus, and Ephydra subopaca loaded onto component I. These species were most abundant during the fall months and thus represented the "late season bloom" of organisms in the pond. *Trichocorixa verticalis*, *Dicrotendipes leucoscelis*, and *Hydrophorus* sp. loaded onto component II; these species showed high abundances before the mid-season drought and low numbers thereafter. This pattern of low numbers continued into the fall, never showing substantial recovery to previous mid-season levels. This component was strongly influenced by species that were unable to substantially recover following summer drought, and thus represents the "early season bloom" of these species. Component III was influenced by those species that showed mid-season abundances, with a general decline through the fall: *Erythrodiplax berenice*, *B. striatus*, and Muscidae spp. This component represents the pattern of mid-season abundances of organisms which gradually tapered off throughout the fall. Two species loaded on component IV: *Culicoides furens* and *Aedes sollicitans*. These species showed very rapid recolonization after rehydration of the pond following a drought. These species showed dramatic abundances shortly after rehydration of the pond and were not found under other conditions. This factor represents that part of the variation in the data caused by rapidly recolonizing species.

Due to the extremely low numbers of macroinvertebrates collected from both locations in site

2, principal components analysis was unable to provide any useful information in determining the major sources of variation at this site. A larger sample size was indicated for this site since a greater number of specimens was needed to determine the major sources of variation.

Physical Environment Analysis

There were wide fluctuations in water temperature, depth, salinity, and dissolved oxygen at the sites over the sampling period (Table 4). As drying occurred in the 4 locations, water depth and dissolved oxygen decreased, in contrast to increasing water temperature and salinity. During drying periods, both ponds showed a tendency to become hypersaline. Pond 1 reached a maximum salinity value of 50 ppt while the corresponding high value for pond 2 was 38 ppt. These extremely high salinities were lowered when the ponds rehydrated after rain.

Dissolved oxygen demonstrated radical fluctuations throughout the sampling period. At both sites, conditions ranged from highly aerobic (<15.0 ppm) to extremely hypoxic (<1.0 ppm). Generally, site 2 tended to be relatively hypoxic most of the time, with dissolved oxygen levels of less than 5.0 ppm. Pond 2 was characterized by a thick layer of organic ooze. Frequently during sampling, a characteristic sulfur odor

Table 4. The mean, minimum and maximum values for the physical parameters measured at the 4 locations.

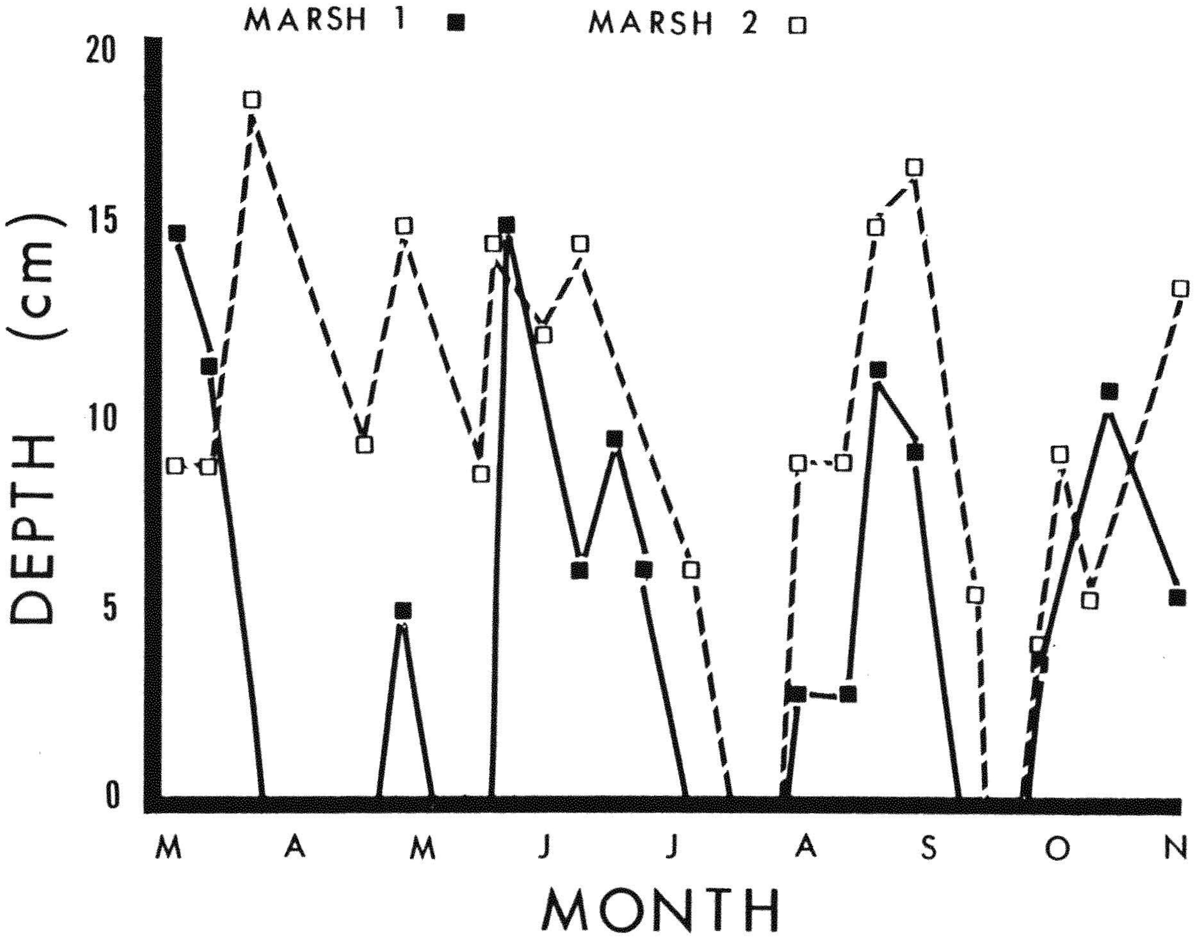
LOCATION	TEMPERATURE (°C)			DEPTH (cm)			SALINITY (ppt)			DISS. O2 (ppm)		
	X	MIN	MAX	X	MIN	MAX	X	MIN	MAX	X	MIN	MAX
MARSH 1	22.1	12.2	31.5	7.9	0.0	17.0	18.8	5.0	31.0	8.2	1.7	17.5
POND 1	23.4	11.5	33.8	22.2	0.0	44.0	20.4	5.5	50.0	7.0	0.3	13.6
MARSH 2	21.7	8.5	33.0	10.4	0.0	21.0	13.9	0.0	32.0	6.6	0.1	19.8
POND 2	22.6	7.0	35.5	24.3	0.0	45.0	16.6	0.5	38.0	4.5	0.1	18.6

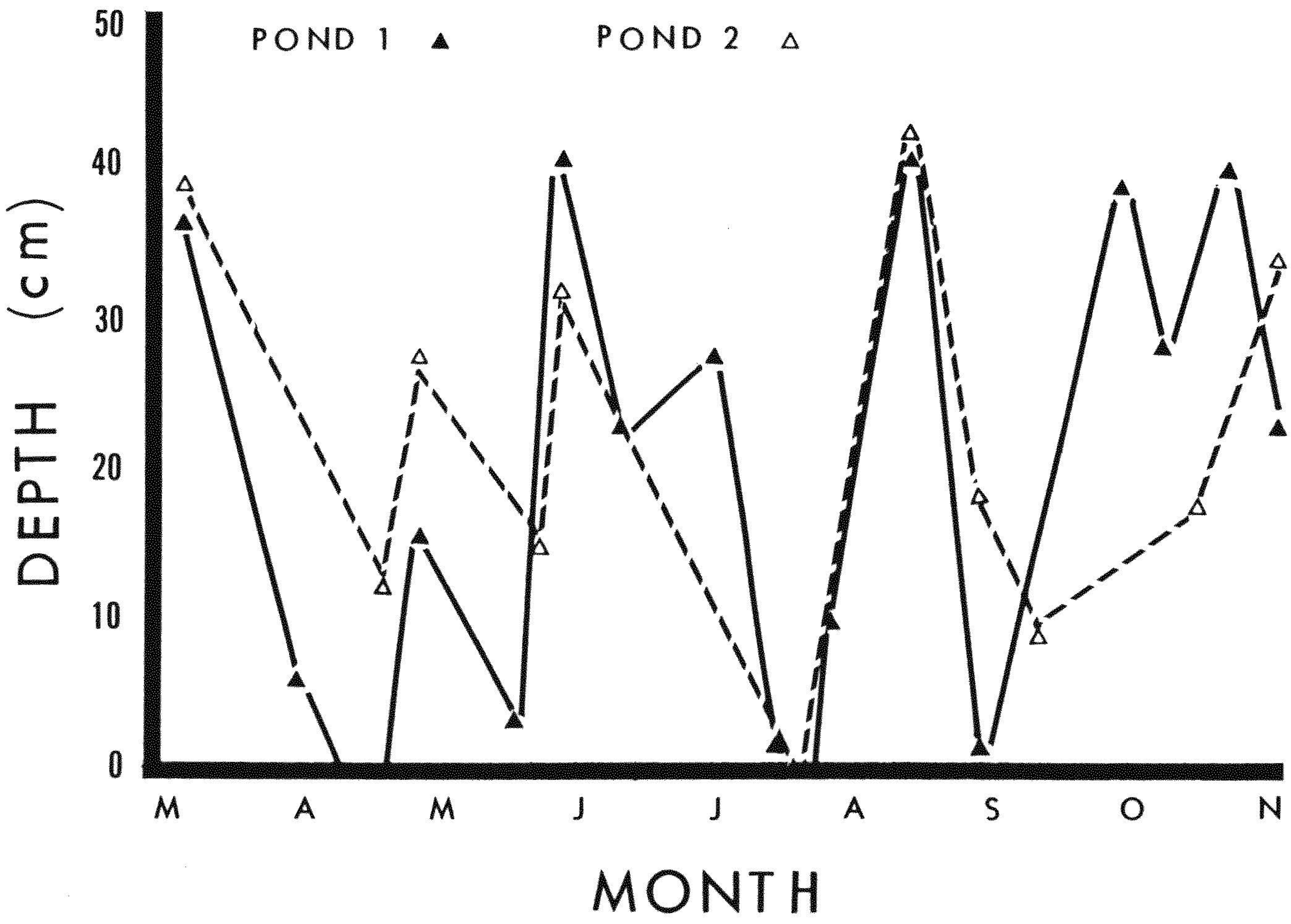
caused by anaerobic bacteria could be detected. Highest levels of dissolved oxygen were recorded at both sites during or shortly after periods of heavy rain.

The marshes at both sites went dry more often and for longer periods than the ponds at the respective sites (Figs. 4 and 5). Marsh 1 went dry a total of 4 times during the sampling period while marsh 2 only went dry twice. Pond 1 had three dry periods in contrast to pond 2 which only went dry once. The major fluctuations in the physical parameters were mainly due to the cyclic drying and flooding of the sites. Flooding was primarily due to rainfall or occasionally from high spring or storm tides. The range in the physical parameters demonstrated that both sites had a wide range of environmental conditions over the course of the growing season.

Analysis of variance was used to test the significance of the differences observed in these physical parameters. There were no significant differences in depth or temperature between the two sites; however, the differences in salinity and dissolved oxygen were highly significant ($p<.001$). Subsequent analyses revealed significant differences ($p<.001$) in depth, salinity, and dissolved oxygen between the marshes (marsh 1 and marsh 2) at both sites, as well as significant differences ($p<.01$) in salinity and dissolved

Fig. 4. Water depth in the marsh locations surrounding the ponds at both sites over the sampling period.


MARSH 1
MARSH 2
DEPTH (cm)
20
15
10
5
0
M
A
M
J
J
A
S
O
N
MONTH


POND 1
POND 2
DEPTH (cm)
0
10
20
30
40
50
M
A
M
J
J
A
S
O
N
MONTH

oxygen between the ponds (pond 1 and pond 2) at the sites. The ANOVA between the marsh and pond at each site revealed significant differences ($p<.05$) in depth and dissolved oxygen between the two locations at site 1 and also significant differences ($p<.05$) in depth, dissolved oxygen, and salinity between the locations at site 2.

Differences in Faunal Assemblages

The discriminant analysis showed that only the 2 pond locations could not be distinctly separated by the species collected. Nine of the 17 dominant species that were entered into the analysis had highly significant ($p<.001$) discriminating abilities (Table 5). These were the species that were most abundantly collected during the sampling period. These species are listed in descending order of their ability to discriminate between the locations, as indicated by their respective F values.

Table 6 shows how the cases were classified into the 4 locations. The 2 locations (marsh 2 and pond 2) at site 2 had the greatest percentage of correctly classified cases, 84.8% and 91.2%, respectively. These high percentages of correctly classified cases indicates that these two locations were relatively different based on the species used in the analysis. The percentage of correctly classified cases for marsh 1 and pond 1 were relatively lower than those for site 2, 73.7% and 54.6%,

Table 5. Species that were able to significantly discriminate between the locations.

STEP NUMBER	SPECIES	F VALUE	SIGNIF.
1	Dicrotendipes leucoscelis	379.345	<.001
2	Capitella capitata	276.692	<.001
3	Paranais litoralis	262.188	<.001
4	Berosus striatus	222.226	<.001
5	Helodidae sp.	193.571	<.001
6	Orchestia grillus	174.868	<.001
7	Enochrus hamiltoni	154.205	<.001
8	Ephydra subopaca	137.674	<.001
9	Aedes sollicitans	125.100	<.001

Table 6. Classification of cases into the locations.

GROUP	% CORRECT	GROUP CLASSIFICATION			
		MARSH 1	POND 1	MARSH 2	POND 2
MARSH 1	73.7	56	7	11	2
POND 1	54.6	5	59	1	43
MARSH 2	84.8	10	1	89	5
POND 2	91.2	1	10	0	114
TOTAL	76.8	72	77	101	164

respectively. The misclassified cases for marsh 1 were generally split between pond 1 and marsh 2. Contrastingly, about 40% of the cases for pond 1 were misclassified into pond 2. The reason for this high percentage of misclassified cases for pond 1 was due to the relative similarity of the two ponds and the high number of cases (samples) for pond 2 which was not dry as often as pond 1. Overall, 76.8% of the cases were correctly classified, demonstrating relatively good separation of the locations by the species entered into the analysis.

The spatial relationship of the "distance" (Mahalonobis distance) between the 4 locations is easily seen when the group centroids are plotted on the first 2 canonical variables ($p<.001$, Fig. 6). The graph shows wide separation of the two marsh locations and also the marshes from the ponds. Due to similarity of the faunal assemblages of the two ponds a high percentage of cases were misclassified in pond 1. For this reason, the ponds as well as the sites do not show wide separation.

The canonical coefficients for the discriminating species (Table 7) indicate how each species discriminated between the locations. Capitella capitata, Paranais litoralis, and Aedes sollicitans all had positive values for both canonical coefficients. This indicates that these species shift the cases toward the marshes on axis

Fig. 6. Group centroids for the 4 loocations plotted against the first two discriminant functiions representing the separation of the locations.

M1= marsh 1 M2= marsh 2

P1= pond 1 P2= pond 2

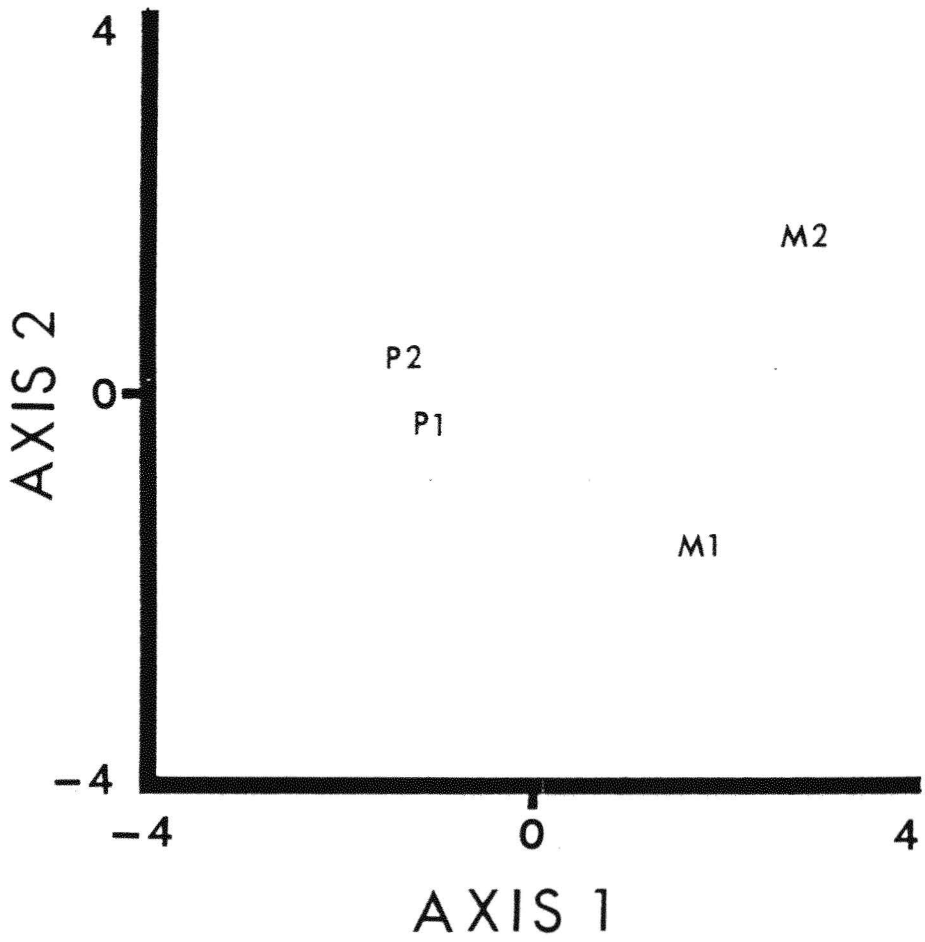

4
0
-4
AXIS 2
M2
P2
P1
M1
-4
0
4
AXIS 1

Table 7. Coefficients for the canonical correlations and the associated eigenvalues for the first two canonical variables.

SPECIES	C.V. 1	C.V. 2
Capitella capitata	2.66506	1.47981
Paranais litoralis	1.42292	0.38601
Orchestia grillus	0.85216	-2.28291
Helodidae sp.	-1.06714	0.51110
Berosus striatus	1.35073	-1.50123
Enochrus hamiltoni	-0.92195	-1.66457
Dicrotendipes leucoscelis	0.79454	-0.80160
Aedes sollicitans	0.40637	0.17623
Ephydra subopaca	-0.47446	1.15382
EIGENVALUE	3.11594	0.95832

1 and towards site 2 on axis 2. *Orchestia grillus*, *Berosus striatus*, and *Dicrotendipes leucoscelis* all had positive values for the first canonical coefficient and negative values for the second canonical coefficient. The positive values for canonical coefficient 1 shifted the cases towards the marshes and the negative values 33 for the second canonical coefficient shifted the cases towards site 1. *Ephydra subopaca* and Helodidae sp. had negative values for the first canonical and positive values for the second canonical coefficient. These species shifted the cases in the direction of the ponds on axis 1 and in the direction of site 2 on the second axis. *Enochrus hamiltoni* is the only species that had negative values for both the canonical coefficients. These negative values shifted the cases in the direction of the ponds on axis 1 and in the direction of site 1 on axis 2.

Macroinvertebrate Diversity and Community Structure

Species diversity (H'), species richness, and species evenness were calculated for each sample taken during the sampling period (Appendices I-III). There were no significant linear regression relationships between species diversity or species richness and any of the measured physical parameters. This was not surprising since none of the species showed significant linear relationships with any of the physical parameters. For the two locations at site 1, species diversity was plotted for each sampling trip over the course of the sampling period (Figs. 7 and 8). Due to the low numbers of macroinvertebrates collected at site 2, species diversity was not plotted for this site.

There were 4 drought periods in marsh 1, two each in spring and mid-summer. After each drought period in the marsh, species diversity rebounded rapidly due to reinvasion from the pond. Before the mid-summer drought in July, species diversity showed a general decline over several weeks. This reflects the decline of the early season colonizers of the marsh during the hot summer months sychronized with the gradual drying of the marsh. The decline in species diversity after the last drought in early fall reflected the seasonal disappearance of many organisms with the onset of the fall season. The species assemblages before and after the third and fourth dry periods were essentally the same except for two species (Table 8). Aedes sollictans and Orchestia grillus were never collected before the dry periods but were relatively abundant after the marsh reflooded. These species were most abundant following rehydration of the marsh after a drought and declined in abundance shortly afterwards. Drying and reflooding did not seem

Fig. 7. Plot of the species diversity (Shannon-Wiener Index) for each sample taken in the marsh at site 1 over the sampling period. Boxed in areas represent periods when no water was present.

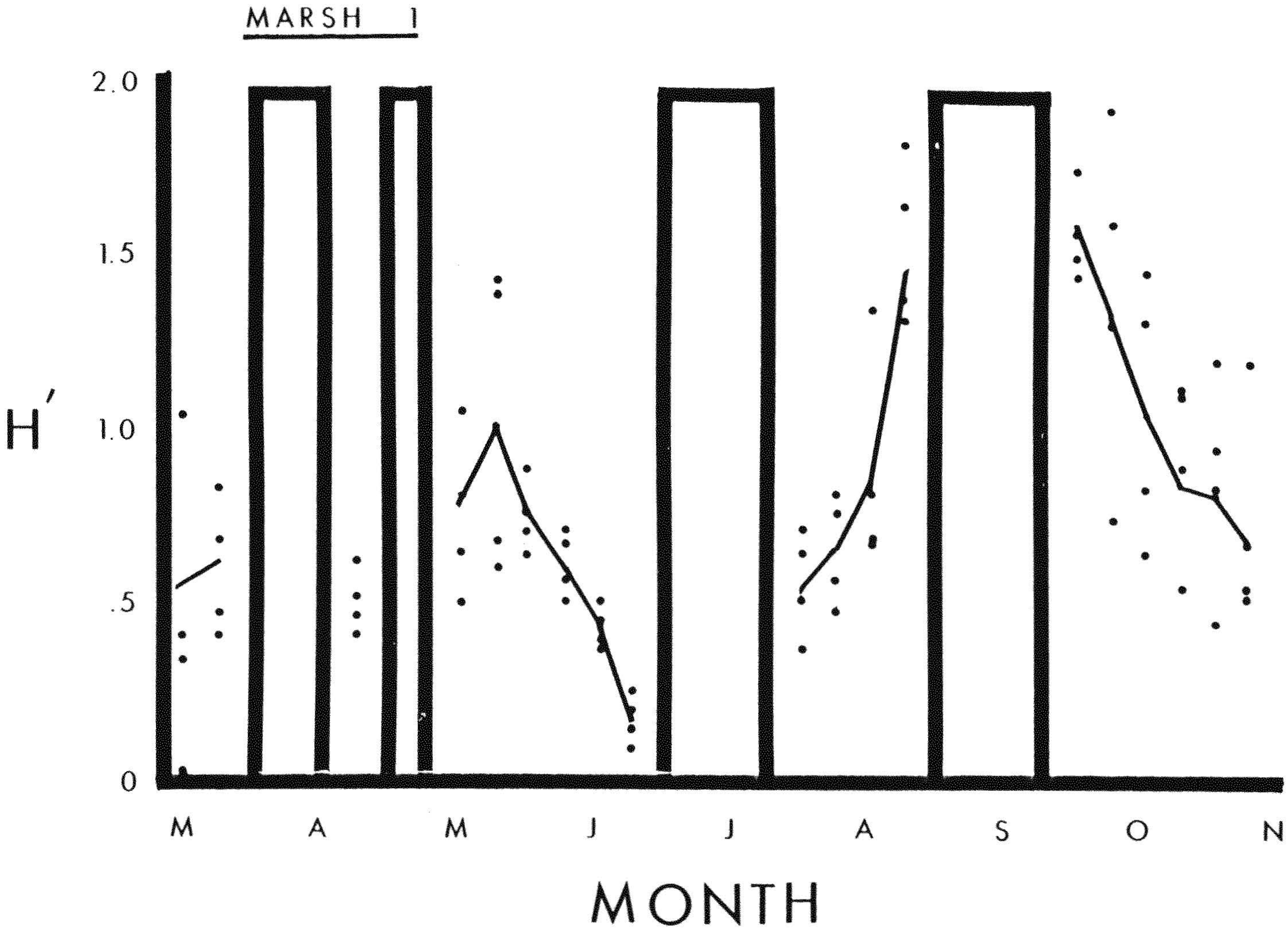

MARSH 1
H′
2.0
1.5
1.0
.5
0
M
A
M
J
J
A
S
O
N
MONTH

Fig. 8. Plot of species diversity (Shannon-Wiener Index) for each sample taken in the pond at site 1 over the sampling period. Boxed in areas represent periods when the pond was dry.

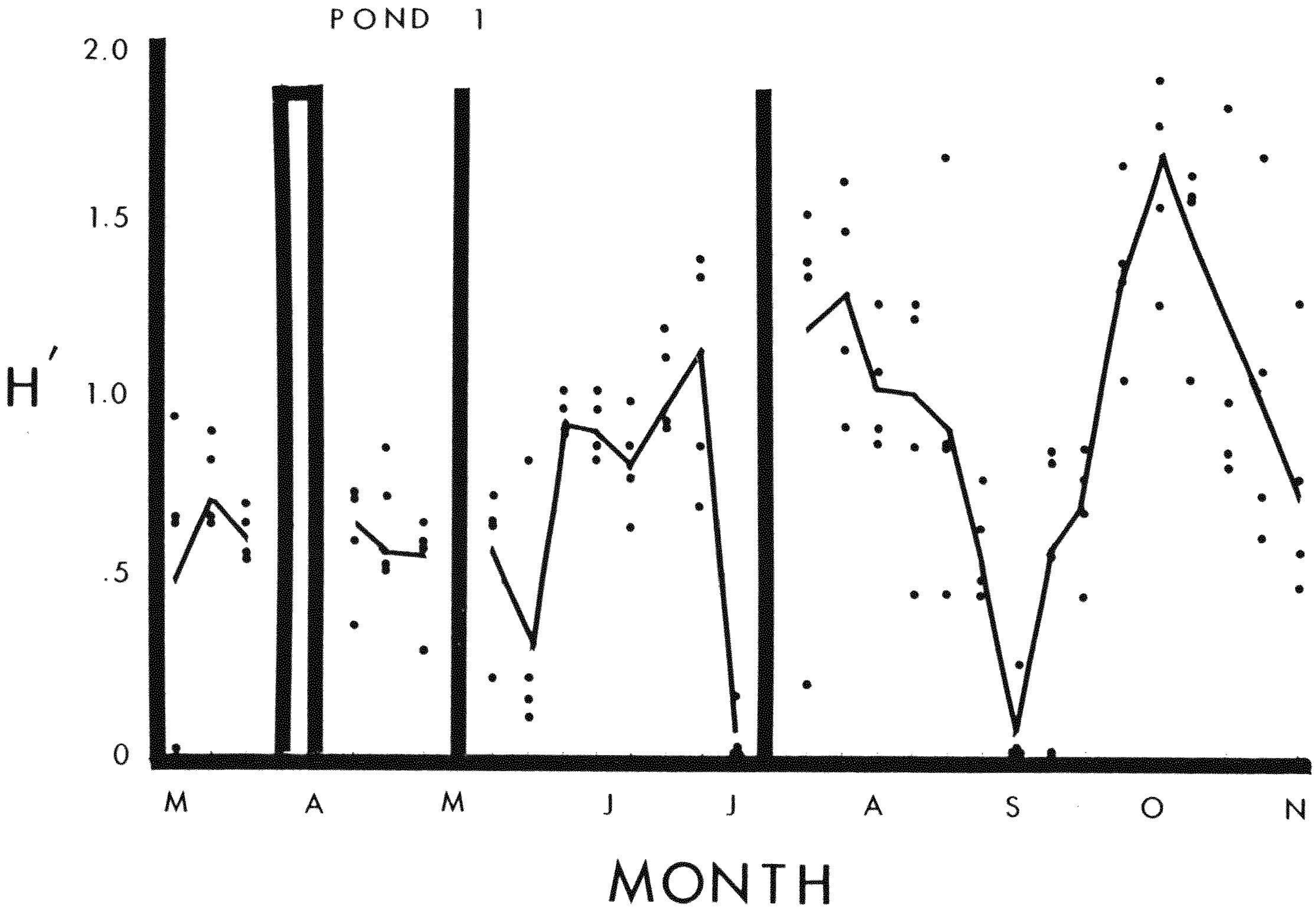

POND 1
H′
2.0
1.5
1.0
.5
0
M
A
M
J
J
A
S
O
N
MONTH

Table 8. Species composition and abundance (/m^2) in marsh 1 before and after the 3rd and 4th drought periods.

3RD DROUGHT			4TH DROUGHT	
BEFORE	AFTER	SPECIES	BEFORE	AFTER
0	1,627	*Aedes sollicitans*	0	1,748
0	3,132	*Orchestia grillus*	0	1,093
0	73	Muscidae spp.	97	194
66,139	23,892	*Dicrotendipes leucoscelis*	3,739	6,628
121	48	*Hydrophorus* sp.	48	291
267	0	*Culicoides furens*	364	364
0	0	*Ephydra subopaca*	242	48
24	0	*Berosus striatus*	1,044	1,044
631	0	*Enochrus hamiltoni*	194	242
0	0	*Tropisternus quadristriatus*	48	242
0	24	*Liodessus affinis*	48	0
0	97	*Mesovelia mulsanti*	0	24
437	24	*Trichocorixa verticalis*	947	0
48	0	*Erythrodiplax berenice*	437	97
0	0	*Hydrobia totteni*	73	0
4,273	0	Oligochaeta	48	97
24	48	Polychaeta	388	0

to affect the other species in the marsh in a similar manner.

In pond 1, species diversity did not show significant changes until after the second drought. This rise in diversity was influenced by the seasonal "summer bloom" of macroinvertebrates in the pond. The species diversity was dramatically affected during the two times the pond went hypersaline during July and September. At these times, salinity went above 40 ppt and most of the organisms either left the pond or perished due to high salinity. As soon as the pond reflooded after a rain, the species diversity quickly rebounded to relatively high levels. Again, the decline in diversity during October and November was due to the autumn decline in the abundance of organisms, particularly the insects.

The fluctuations in the abundances of the predators and prey throughout the sampling period demonstrated "classic" predator-prey relationshsips (Figs. 9-12). Both predators and prey were most abundant during the summer months with a seasonal tapering off in their numbers in the fall. Except for rare occasions, the abundances of the predator populations were always significantly less than that of the prey populations at the 4 locations. As the graphs of the predators and prey indicate, the numbers of prey were as much as 1,000 times greater than the predators. The drought periods had an

Fig. 9. Plot of the abundance of the predator and prey species at marsh 1 during the sampling period. Blank portions of the graph represent dry periods when no samples were taken.

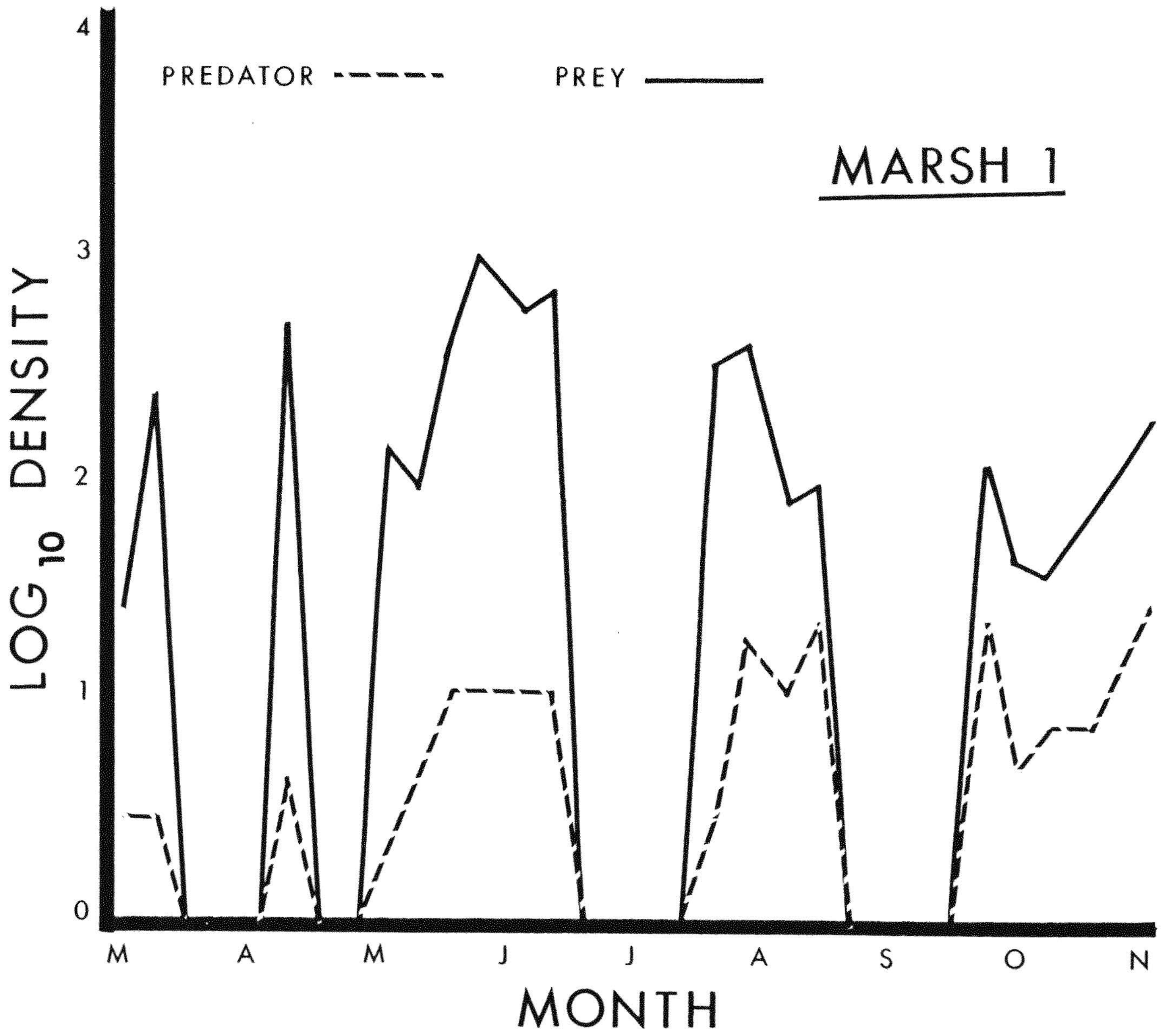

PREDATOR
PREY
MARSH 1
LOG10 DENSITY
4
3
2
1
0
M A M J J A S O N
MONTH

Fig. 10. Plot of the abundance of the predator and prey species at pond 1 during the sampling period. Blank portions of the graph represents dry periods when no samples were taken.

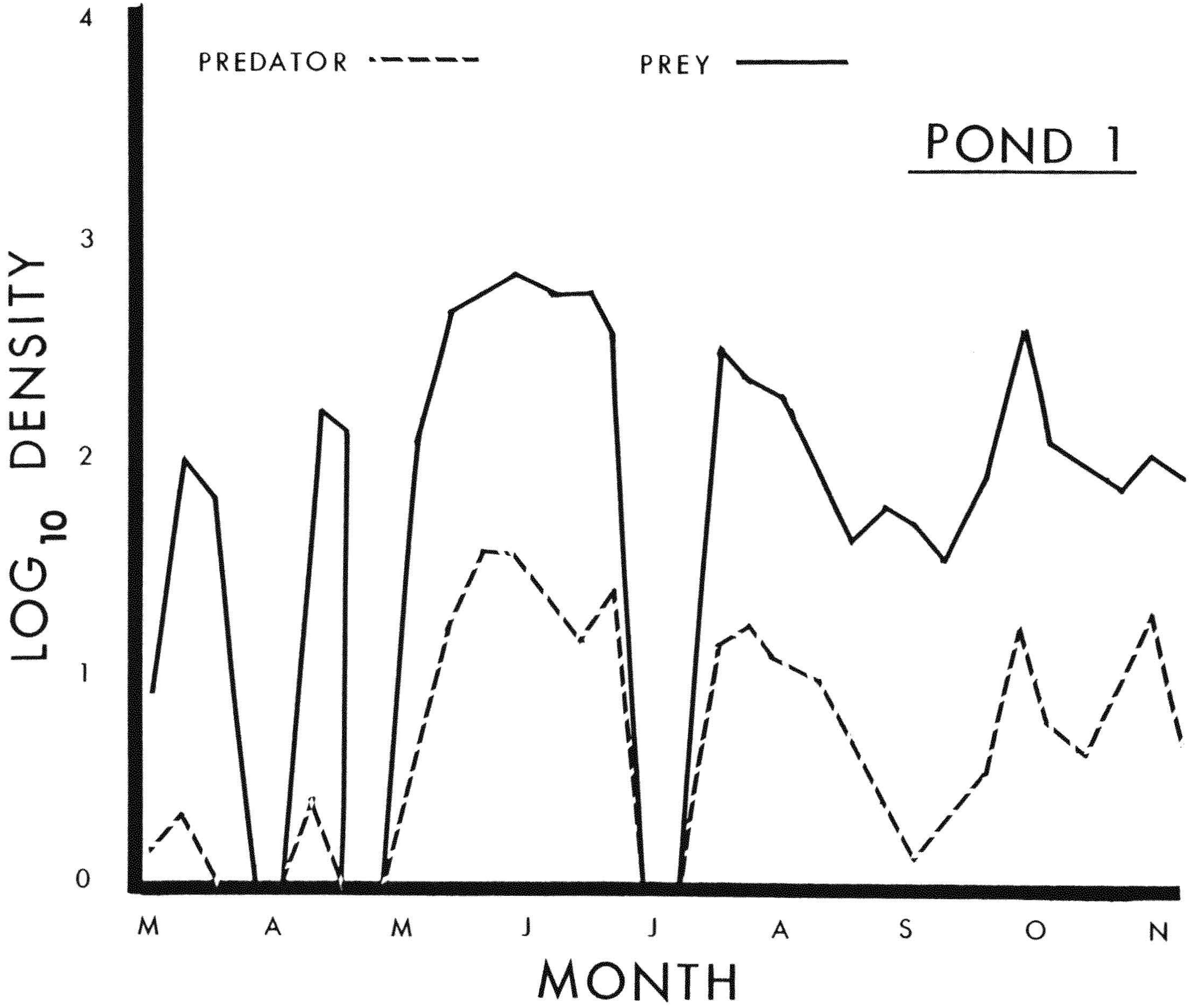
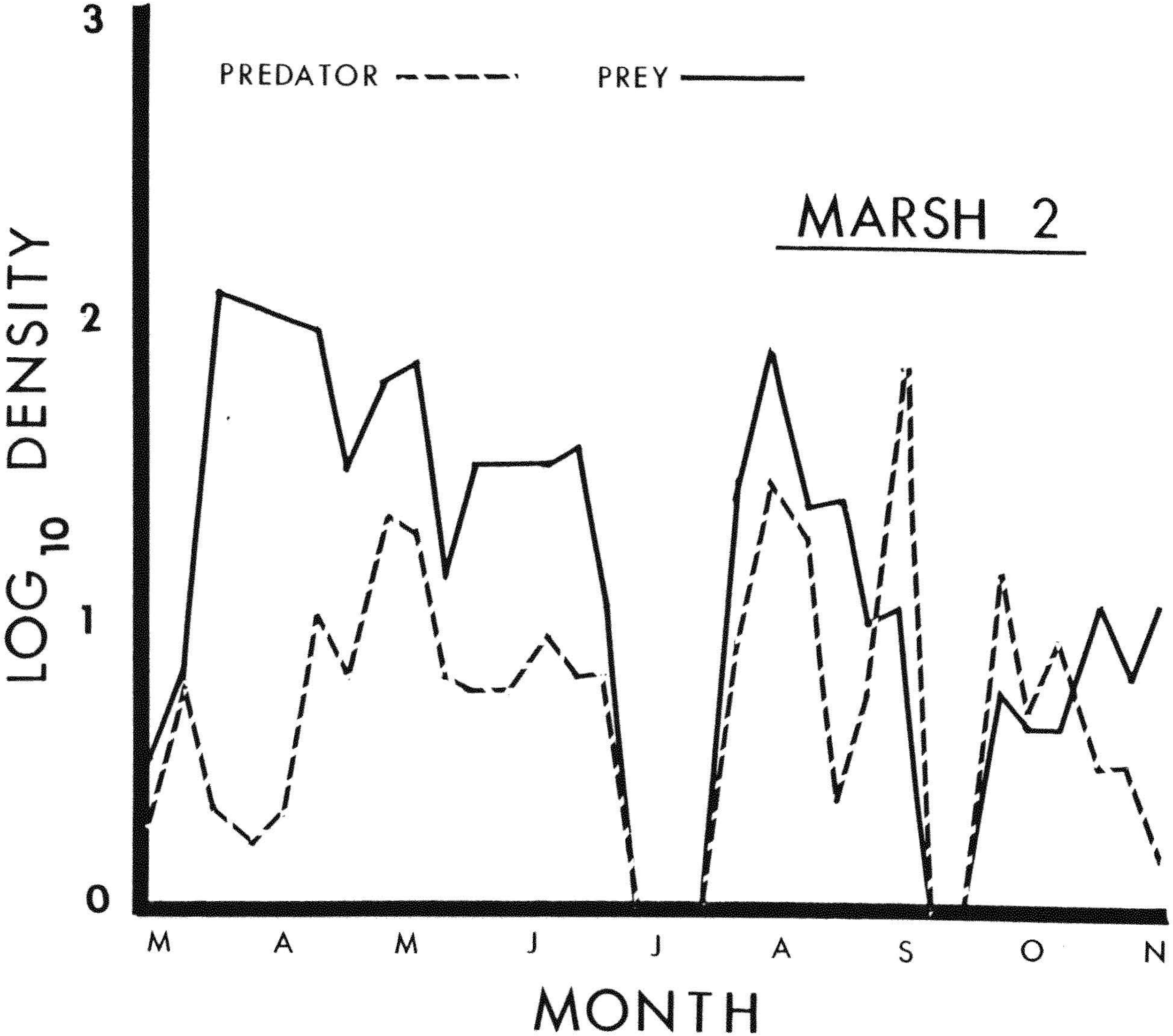
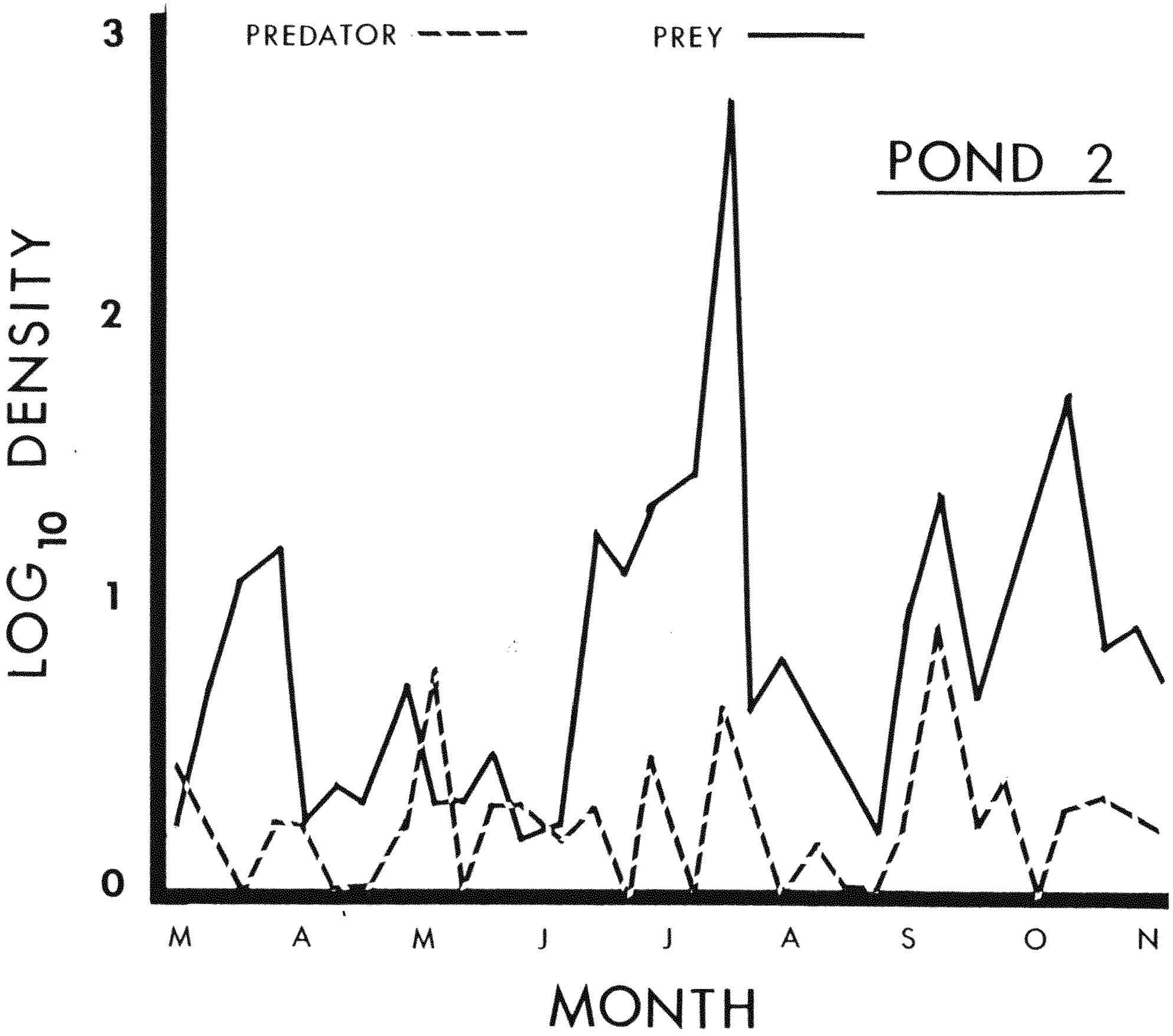

PREDATOR
PREY
POND 1
LOG$_{10}$ DENSITY
4
3
2
1
0
M
A
M
J
J
A
S
O
N
MONTH

Fig. 11. Plot of the abundance of the predator and prey species at marsh 2 during the sampling period. Blank portions of the graph present dry periods when no samples were taken.



3
2
1
0
PREDATOR
PREY
MARSH 2
LOG10 DENSITY
M
A
M
J
J
A
S
O
N
MONTH

Fig. 12. Plot of the abundance of the predator and prey species at pond 2 during the sampling period.


PREDATOR
PREY
POND 2
LOG10 DENSITY
3
2
1
0
M
A
M
J
J
A
S
O
N
MONTH

obvious effect on the numbers of predators and prey; as the locations dried up the numbers in these two groups showed a sharp decline. As drying of the locations continued, the aquatic organisms either moved to more favorable habitats, burrowed into the moist substrate, or perished. After reflooding of the locations occurred the prey species recovered rapidly in contrast to the predators which recolonized at a much slower rate. The fluctuations of both populations were generally synchronous, a change in the prey abundances were reflected by a similar yet smaller change in the predators. The times when the predator populations were more abundant than the prey could be a result of two factors; either the predators experienced a sudden burst in numbers or sampling error could account for these extreme fluctuations.

DISCUSSION

Species Composition and Adaptations

The 17 species considered as the dominant organisms in the communities do not indicate a depauperate fauna as reported by a previous study on a coastal salt marsh in New Jersey (Campbell and Denno 1978). This previous study only lists 8 species as "occurring regularly". Although the species richness is somewhat less (<10 per sample) than those reported for highly productive aquatic systems such as montane streams, it is larger than the maximum of 6 reported by Campbell and Denno (1978). The faunal assemblage of the marsh is relatively diverse and demonstrates great abundance at certain times during the year. This correlates well with the findings of Gerlach (1965) who reported a rich and varied microfauna from a Spitzbergen salt marsh.

Many of the organisms rarely collected are believed to have been imported from other areas, seemingly by passive means. This point is clearly demonstrated by the sporadic collection of the tabanid species. It is hypothesized that the few individuals that were collected were passively transported into the marsh by flooding caused by either rain or extreme high tides. Early work by Gerry (1950) indicated that larval tabanid migrations occurred from open creek banks to thatch piles in higher marsh areas. However, subsequent studies, (Rockel and Hansens 1970a, 1970b) reported no evidence of such larval migrations. This is supported by observations made during this study and the fact that tabanids have been shown to be primarily associated with marsh sod in stands of _Spartina alterniflora_ frequently inundated by tides (Jamnback and Wall 1959, Dukes et al. 1974, Dale and Axtell 1976, Meany et al. 1976). The tabanid larvae that were collected cannot be considered resident species but rather imports from other habitats. This "passive transport" hypothesis is further supported by the rare appearance of other organisms typically found in surrounding habitats. The marine barnacle, _Chthamalus fragilis_ was only collected once after a violent summer storm which left evidence of wash-over from the ocean. The semi-terrestrial isopod, _Philoscia vittata_, was only collected on one occasion after a heavy rainfall; this organism probably washed in from the surrounding drier areas of the marsh. From this evidence, it is felt that the rarely occurring species are indeed not regular inhabitants of the flooded marsh but rather end up there by chance as a result of some external natural force.

The dominant species (present in greatest numbers) that occur in the marsh have specialized mechanisms for dealing with the extreme conditions such as high salinities and low oxygen levels found during drought periods. The numerically dominant species, Dicrotendipes leucoscelis, survives during these harsh periods by having an extremely low oxygen demand commensurate with its tube-dwelling mode of existence. Chironomids have long been recognized for their ability to live in extremely hypoxic environments to which their small body size and relative inactivity are especially well suited.

The ecology of the corixid, Trichocorixa verticalis, has been studied extensively (Kelts 1979). This organism has well developed powers of osmoregulation and can hyporegulate in saline waters (Tones and Hammer 1975). Kelts (1979) reported that T. verticalis responds to low oxygen by leg-pumping behavior or "fanning". This behavior first reported by Comstock in 1887 suggests that the exposed surface of the bubble might act as a physical gill to assist in the removal of oxygen from the water. Wigglesworth (1972) suggests that this activity supplements oxygen bubble uptake without increasing the surfacing activity, thereby conserving energy and avoiding surface predation. The eggs of T. verticalis have been shown to be extremely resistant to drying and radical fluctuations in both water temperature and salinity (Kelts 1979). Delayed egg development followed by remarkable recovery following reflooding is also an adaptation for population maintenance in frequently drying environments (Macan 1974).

Aedes mosquitoes respire by means of a respiratory siphon at the air-water interface and thus, are not affected by low oxygen levels in the water. Many beetles have a physical gill whereby a bubble of oxygen is carried in the space between the dorsum of the abdomen and the wings, consequently eliminating the need for extracting oxygen directly from the water. Less adapted organisms such as some littoral beetles and intertidal aphids are unable to withstand prolonged submergence with depleted oxygen levels thus limiting their distributions (Evans et al. 1971, Foster and Treherne 1975), respectively.

Physical Environment

The wide range of physical parameters in the marsh were consistent with those reported by Campbell and Denno (1978) for a New Jersey salt marsh and Balling and Resh (1982) for a California salt marsh. This study supports the long established idea that salt marsh environments are rigorous and unpredictable.

Water depth was most frequently influenced by drying and rainfall. In addition, I have observed that marsh flooding can also occur when high spring tides flood from the bay and when storm tides overwash the dune ridges on the ocean beach. Water depth and salinity are closely related. The major water input (rainfall) causes drastic reductions in salinity in a matter of hours during times of heavy precipitation. Besides the simple diluting effect of the rainfall, another mechanism which serves to dilute the saline water is proposed. During heavy rainfall, the ponds become stratified into a relatively "fresh" top layer and a more saline bottom layer. This is caused by the fresher rain water floating on top of the more dense saline waters below. The weight of this fresh water tends to push the more saline water out of the pond system and into the surrounding water table resulting in lowered salinities. Due to this process, the repeated heavy winter rains result in some ponds becoming essentially "fresh" during this season.

The anaerobic conditions found in some salt marsh ponds are supposedly due to the lack of vegetation in the pools. Respiratory activities of the roots of plants and the decay of old roots produce gas in the soil of the marsh. This tends to make the soil in these areas more aerobic (Chapman 1960). During the summer months when there is little rain, the ponds tend to become stagnant and the bottom detrital layer typically becomes anaerobic. These anaerobic ponds are characterized by sulfur bacteria and a substratum of black ooze. Rainfall and wind increase the dissolved oxygen in these ponds by a physical mixing process.

The differential drying of the two sites undoubtedly plays a major role in contributing to the physical differences observed between the two sites. The elevational differences between the sites and the relationship to both ground water level and flooding frequency play major roles in determining site characteristics such as the detrital content of the soil and soil moisture content.

Macroinvertebrate Community Structure

Species richness shows a significant decrease during periods of high salinity preceding total drying of the sites. Both Foster and Treherne (1976) and Heydemann (1979) report that high salinities and frequent tidal inundations which typify salt marshes restrict arthropod species richness. Matta (1980) reported that the extreme fluctuations in the physical environment on Parramore Island, Virginia, which resulted in lowered insect species richness, was linked to the cyclic drying and reflooding of the marsh. Just prior to total drying of the marsh, only a few of the most highly adapted macroinvertebrates are able to withstand the extreme conditions. With the event of reflooding of the marsh and less extreme conditions, species richness increases dramatically. Balling and Resh (1982) cite research by Foster and Treherne (1976) which suggests that when these harsh conditions subside there is an invasion of less tolerant species due to decreased energetic cost of survival. Increased plant structural diversity in salt marshes can be a correlate of arthropod diversity (Murdoch et al. 1972, Hatley and MacMahan 1980). Although no quantitative data is available to test this hypothesis for the marshes on Smith Island, this same relationship should hold true for most salt marshes. Increased arthropod diversity due to an increase in plant structural diversity can be attributed to a number of factors: (1) increased food resources; (2) increased availability of shelter (van Emden and Williams 1974); and (3) increased variation in microclimate (Tallamy and Denno 1979).

The two factors that have the greatest effect on species diversity in the Smith Island salt marshes are drying and the seasonal changes in species composition due to intrinsic factors related to organismic life cycles. This latter idea is supported by other research on marsh invertebrates. Cameron (1972) noted that the seasonal changes in herbivore and saprovore diversities were not due to changes in abundance of individuals per species but to an addition or subtraction of species in response to resource availability. The seasonal changes in macroinvertebrate composition observed in the marsh is undoubtedly closely linked to resource availability and the ecologies of the species present. However, drought has the greatest influence on diversity. Since these organisms are aquatic, drying of the environment has a catastrophic effect on the community. This effect is quickly reversed after flooding as evidenced by rapid increases in species diversity to pre-drought levels.

As a result of more frequent drying of site 1, this site is considered to be harsher and should therefore, have lower numbers of organisms. Actually, just the opposite is true; this site showed a much greater macroinvertebrate abundance than site 2 which went dry less often. The plots of the predator and prey abundances at each location (Figs. 9-12) indicate that after reflooding the prey species show a great burst in numbers while the predator abundance characteristically lags behind. If a marsh goes dry often as site 1 does, the predators do not have the long periods necessary to increase their numbers to keep the prey population at low levels. In marshes that go dry infrequently, as does site 2, the predators have the time necessary to substantially build in numbers to decrease the prey species. The ponds act as "reservoirs" for the predators; this prevents dramatic increases in the prey abundances as seen when predators are not present.

The drying of the marsh also tends to synchronize the cohorts of the many species. The species that do not burrow into the substrate or move to other environments rely on their eggs to survive the dry periods. These eggs hatch soon after reflooding occurs. Since most of the eggs of a species will hatch within a few days of each other, this causes the offspring to all be approximately the same age. As time progresses in the flooded areas, the cohorts become increasingly unsynchronized until individuals of all ages are present.

CONCLUSION

Few studies dealing with aquatic macroinvertebrate community structure in salt marshes have been done in the past. This is probably due to the great abundance of biting insects during the warmer months and the problems associated with quantitatively sampling the resident invertebrate faunas. This study has shown that relatively simple sampling methods are quite useful in community studies and as a result, useful information can be gained about salt marshes.

It has been a long established idea that salt marshes are extremely harsh environments and for this reason the associated invertebrate faunas are depauperate. This idea is perhaps a result of observations made from poorly sampled areas or areas that were not sampled over a long period of time. This premise is not supported by the findings of this research. Relatively diverse communities were found at the two sites studied. At certain times of the growing season, great abundances of organisms can be observed in the aquatic marsh habitats. Species diversity is relatively high in the marsh throughout most of the growing season and only shows significant reductions during drought conditions. It is true that the numbers of the organisms greatly fluctuate over time and thus if one was to sample only during drought periods, unrealistic conclusions could be made about the marsh fauna.

No relationship is observed between the measured physical parameters and the abundance of organisms as reported by previous studies. The only time the physical environment has a negative effect on the resident organisms is when the physical conditions near the extremes. These extremes are characterized by salinities above 35 ppt and water depths near zero. It is evident that the resident species of the salt marshes are well adapted to the variable physical conditions. Although these conditions exclude many organisms from invading this habitat, the ones that have adapted do quite well. These residents have evolved a variety of mechanisms to deal with even the most severe conditions.

The results suggest that fast recolonization makes the sites with the most severe conditions (greatest frequency of drying) the most productive. This phenomenon is thought to be due to predator elimination. Rapid recolonization after reflooding is accomplished by the prey species. Because the predators colonize at a much slower rate, the numbers of the prey species are not controlled by predation. This results in great "blooms" of the prey species at these times.

Due to the highly variable nature of the macroinvertebrate communities in salt marshes, the data base needs to be expanded. Sampling over short periods of time (less than 1 growing season) are ineffective in attempting to characterize salt marsh communities. One study will certainly not provide all the information needed about aquatic macroinvertebrate community structure in salt marshes. Many studies investigating numerous avenues of research are needed in this area.

In recent years, there has been renewed interest in the preservation of coastal salt marshes. The age of dredging and filling these marshes has come to a close in response to public outcry. The present concern is in managing the marshes in order that they be preserved to provide needed habitat for the unique flora and fauna. The final consideration is the aesthetic value of these wetlands and in recent years this has been an extremely important argument in support of saving these valuable resources.

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APPENDIX I

Species Diversity

Trip	Marsh 1		Pond 1		Marsh 2		Pond 2	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
1	0.38	0.48	0.58	0.40	0.48	0.71	0.26	0.52
2	0.49	0.27	0.78	0.12	1.23	0.35	0.65	0.49
3	----	----	0.65	0.06	0.34	0.26	0.73	0.16
4	----	----	----	----	0.20	0.19	0.21	0.24
5	----	----	----	----	0.86	0.72	0.17	0.35
6	0.31	0.07	0.64	0.12	0.58	0.40	0.00	0.00
7	----	----	0.66	0.12	1.00	0.35	0.00	0.00
8	----	----	----	----	1.34	0.15	0.67	0.54
9	0.73	0.31	0.56	0.14	1.45	0.14	0.82	0.63
10	1.07	0.45	0.37	0.28	1.35	0.21	0.00	0.00
11	0.77	0.11	0.90	0.07	0.91	0.27	0.56	0.74
12	0.64	0.09	0.86	0.10	1.02	0.32	0.17	0.35
13	0.46	0.06	0.77	0.16	1.22	0.33	0.00	0.00
14	0.16	0.09	0.98	0.08	0.48	0.46	0.78	0.27
15	----	----	1.00	0.34	1.23	0.28	0.17	0.33
16	----	----	0.04	0.07	----	----	0.53	0.42
17	----	----	----	----	----	----	0.00	0.00
18	----	----	1.09	0.54	----	----	0.49	0.58
19	0.55	0.22	1.26	0.22	1.21	0.46	0.73	0.15
20	0.68	0.19	1.07	0.15	0.94	0.07	0.16	0.32
21	0.90	0.25	0.96	0.37	1.30	0.33	0.64	0.10
22	1.41	0.22	0.97	0.44	0.69	0.27	0.00	0.00
23	----	----	0.66	0.21	0.94	0.66	0.00	0.00
24	----	----	0.06	0.12	1.14	0.53	0.43	0.21
25	----	----	0.62	0.44	----	----	0.78	0.81
26	----	----	0.79	0.18	----	----	0.37	0.43
27	1.43	0.12	1.25	0.21	1.15	0.22	1.18	0.18
28	1.29	0.40	1.55	0.33	1.07	0.77	1.06	0.34
29	1.01	0.28	1.37	0.22	1.27	0.63	1.02	0.44
30	0.89	0.26	1.09	0.45	1.39	0.28	0.77	0.63
31	0.84	0.30	0.97	0.46	1.00	0.27	0.90	0.37
32	0.71	0.29	0.73	0.34	0.74	0.26	0.59	0.71

APPENDIX II

Species Richness

Trip	Marsh 1		Pond 1		Marsh 2		Pond 2	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
1	2.50	1.73	1.75	1.26	2.25	1.89	1.25	1.26
2	4.00	0.82	3.50	0.58	4.75	2.22	2.25	0.96
3	----	----	2.50	0.58	3.00	0.82	2.25	0.50
4	----	----	----	----	1.75	0.50	1.75	0.96
5	----	----	----	----	3.00	2.16	0.75	0.96
6	5.00	1.41	3.25	0.96	5.50	1.73	0.75	0.50
7	----	----	3.25	0.96	4.75	1.26	0.50	0.58
8	----	----	----	----	7.00	0.82	2.50	1.29
9	6.00	0.82	4.00	1.83	8.75	1.71	3.00	1.63
10	6.25	2.75	4.75	2.06	5.00	0.82	0.50	0.58
11	6.25	1.71	5.25	0.96	4.75	0.96	1.75	2.36
12	8.00	1.83	6.75	0.96	5.50	1.73	1.00	0.82
13	7.75	1.26	5.00	0.00	6.00	0.82	0.75	0.50
14	7.75	2.75	6.00	0.82	2.75	1.26	3.00	0.82
15	----	----	7.50	1.00	4.25	0.50	1.25	0.50
16	----	----	1.50	3.00	----	----	2.00	0.82
17	----	----	----	----	----	----	0.25	0.50
18	----	----	7.00	1.15	----	----	4.00	0.00
19	5.00	1.83	9.00	0.82	5.75	2.22	2.25	0.50
20	7.00	1.41	7.25	1.50	6.50	3.42	1.25	0.50
21	6.50	2.38	5.25	0.50	6.00	2.16	2.00	0.00
22	8.75	1.71	5.00	1.15	4.00	2.00	0.75	0.50
23	----	----	3.50	1.91	3.50	1.91	0.50	0.58
24	----	----	1.00	2.00	6.75	2.75	2.00	0.00
25	----	----	3.00	2.00	----	----	5.25	4.57
26	----	----	4.75	0.96	----	----	1.75	1.71
27	10.00	0.82	8.00	1.41	4.75	1.50	4.50	1.73
28	7.50	2.38	8.00	1.41	4.25	2.87	4.00	1.15
29	7.00	1.41	7.50	1.29	5.25	2.63	4.75	0.96
30	5.75	0.50	6.75	2.06	4.75	1.71	3.00	2.16
31	6.75	1.50	6.50	1.00	3.25	0.96	3.00	1.15
32	7.00	2.16	5.25	0.96	2.50	0.58	2.50	1.91

APPENDIX III

Species Evenness

Trip	Marsh 1		Pond 1		Marsh 2		Pond 2	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
1	0.10	0.12	0.15	0.11	0.12	0.18	0.07	0.14
2	0.13	0.07	0.20	0.03	0.32	0.09	0.17	0.13
3	----	----	0.17	0.02	0.09	0.07	0.19	0.04
4	----	----	----	----	0.05	0.05	0.05	0.06
5	----	----	----	----	0.22	0.19	0.05	0.09
6	0.08	0.02	0.17	0.03	0.15	0.10	0.00	0.00
7	----	----	0.17	0.03	0.26	0.09	0.00	0.00
8	----	----	----	----	0.35	0.04	0.18	0.14
9	0.19	0.08	0.15	0.04	0.38	0.04	0.21	0.17
10	0.28	0.12	0.10	0.07	0.35	0.06	0.00	0.00
11	0.20	0.03	0.23	0.02	0.24	0.07	0.15	0.19
12	0.17	0.02	0.22	0.03	0.27	0.08	0.05	0.09
13	0.12	0.02	0.20	0.04	0.32	0.09	0.00	0.00
14	0.04	0.02	0.26	0.02	0.13	0.12	0.20	0.07
15	----	----	0.26	0.09	0.32	0.07	0.04	0.09
16	----	----	0.01	0.02	----	----	0.14	0.11
17	----	----	----	----	----	----	0.00	0.00
18	----	----	0.29	0.14	----	----	0.13	0.15
19	0.14	0.06	0.33	0.06	0.32	0.12	0.19	0.04
20	0.18	0.05	0.28	0.04	0.25	0.02	0.04	0.08
21	0.24	0.06	0.25	0.10	0.34	0.09	0.17	0.03
22	0.37	0.06	0.25	0.12	0.18	0.07	0.00	0.00
23	----	----	0.17	0.05	0.25	0.17	0.00	0.00
24	----	----	0.02	0.03	0.30	0.14	0.11	0.06
25	----	----	0.16	0.11	----	----	0.20	0.21
26	----	----	0.21	0.05	----	----	0.10	0.11
27	0.37	0.03	0.33	0.06	0.30	0.06	0.31	0.05
28	0.34	0.11	0.40	0.09	0.28	0.20	0.28	0.09
29	0.26	0.07	0.36	0.06	0.33	0.17	0.27	0.11
30	0.23	0.07	0.28	0.12	0.36	0.07	0.20	0.17
31	0.22	0.08	0.25	0.12	0.26	0.07	0.23	0.10
32	0.19	0.07	0.19	0.09	0.19	0.07	0.16	0.19