

Fall 1977

ECOLOGY OF TWO TIDAL MARSH  
INSECTS, TRICHOCORIXA VERTICALIS  
(HEMIPTERA) AND ERYTHRODIPLAX  
BERENICE (ODONATA), IN NEW  
HAMPSHIRE

LARRY JIM KELTS

Follow this and additional works at: <https://scholars.unh.edu/dissertation>

---

**Recommended Citation**

KELTS, LARRY JIM, "ECOLOGY OF TWO TIDAL MARSH INSECTS, TRICHOCORIXA VERTICALIS (HEMIPTERA) AND ERYTHRODIPLAX BERENICE (ODONATA), IN NEW HAMPSHIRE" (1977). *Doctoral Dissertations*. 1168.  
<https://scholars.unh.edu/dissertation/1168>

This Dissertation is brought to you for free and open access by the Student Scholarship at University of New Hampshire Scholars' Repository. It has been accepted for inclusion in Doctoral Dissertations by an authorized administrator of University of New Hampshire Scholars' Repository. For more information, please contact [nicole.hentz@unh.edu](mailto:nicole.hentz@unh.edu).

## INFORMATION TO USERS

This material was produced from a microfilm copy of the original document. While the most advanced technological means to photograph and reproduce this document have been used, the quality is heavily dependent upon the quality of the original submitted.

The following explanation of techniques is provided to help you understand markings or patterns which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting thru an image and duplicating adjacent pages to insure you complete continuity.
2. When an image on the film is obliterated with a large round black mark, it is an indication that the photographer suspected that the copy may have moved during exposure and thus cause a blurred image. You will find a good image of the page in the adjacent frame.
3. When a map, drawing or chart, etc., was part of the material being photographed the photographer followed a definite method in "sectioning" the material. It is customary to begin photoing at the upper left hand corner of a large sheet and to continue photoing from left to right in equal sections with a small overlap. If necessary, sectioning is continued again - beginning below the first row and continuing on until complete.
4. The majority of users indicate that the textual content is of greatest value, however, a somewhat higher quality reproduction could be made from "photographs" if essential to the understanding of the dissertation. Silver prints of "photographs" may be ordered at additional charge by writing the Order Department, giving the catalog number, title, author and specific pages you wish reproduced.
5. PLEASE NOTE: Some pages may have indistinct print. Filmed as received.

**University Microfilms International**  
300 North Zeeb Road  
Ann Arbor, Michigan 48106 USA  
St. John's Road, Tyler's Green  
High Wycombe, Bucks, England HP10 8HR

---

7813002

KELTS, LARRY JIM

ECOLOGY OF TWO TIDAL MARSH INSECTS,  
TRICHOCORIKA VERTICALIS (HEMIPTERA) AND  
ERYTHRODIPLAX BERENICE (ODONATA), IN NEW  
HAMPSHIRE.

UNIVERSITY OF NEW HAMPSHIRE, PH.D., 1977

University  
Microfilms  
International

300 N. ZEEB ROAD, ANN ARBOR, MI 48106

---

© 1977

LARRY JIM KELTS

ALL RIGHTS RESERVED

ECOLOGY OF TWO TIDAL MARSH INSECTS, TRICHOCORIXA  
VERTICALIS (HEMIPTERA) AND ERYTHRODIPLAX  
BERENICE (ODONATA), IN NEW HAMPSHIRE

by

LARRY J. KELTS

B.S., Cornell University, 1959

M.S., Southeastern Massachusetts University, 1971

A THESIS

Submitted to the University of New Hampshire  
In Partial Fulfillment of  
The Requirements for the Degree of

Doctor of Philosophy  
Graduate School  
Department of Zoology  
September, 1977

This thesis has been examined and approved.

*Philip J. Sawyer*

Thesis director, Philip J. Sawyer,  
Prof. of Zoology

*R. L. Blickle*

Robert L. Blickle, Prof. of Entomology

*A. C. Borrer*

Arthur C. Borrer, Prof. of Zoology

*Larry G. Harris*

Larry G. Harris, Assoc. Prof. of Zoology

*Michael Mazurkiewicz*

Michael Mazurkiewicz, Assoc. Prof. of  
Biology

*8/19/77*

Date

TO MY MOTHER AND FATHER  
IN MEMORY OF THEIR LOVE AND  
DEVOTION

## ACKNOWLEDGEMENTS

I extend my sincerest gratitude to my dissertation professor, Dr. Philip J. Sawyer, for his assistance throughout the course of this investigation and for his guidance during my graduate tenure at the University of New Hampshire. Special appreciation is extended to Dr. Robert L. Blickle for his advice and assistance in Entomology, and to Dr. Arthur C. Borror for his invaluable assistance in the revision of this thesis and for numerous enlightening discussions during my graduate studies. My appreciation also to the other members of my doctoral committee, Drs. Larry G. Harris and Michael Mazurkiewicz, for their advice during the course of this research. A very special thanks are due to my family, and in particular to my wife, Kaori, for the encouragement, patience and understanding that I received during the past several years while I pursued my graduate studies.

I am indebted to the following for their assistance in species confirmation: Dr. R. I. Sailer, University of Florida; Dr. John F. Burger and Mr. Wallace J. Morse, University of New Hampshire. Support provided by the research facilities at the Jackson Estuarine Laboratory, University of New Hampshire, is gratefully acknowledged.

## TABLE OF CONTENTS

LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
ABSTRACT.....	x
I. INTRODUCTION.....	1
Description of Marsh.....	3
Study Area.....	6
Salicornia Bed (SB; site 1).....	12
Shallow Panne Left (SPL; site 2).....	12
Isolated Panne Left (IPL; site 3).....	13
Far Edge Main Panne (FEMP; site 4).....	14
Platform Pool (Pl P; site 5).....	14
Rotten Panne (RP; site 6).....	20
II. <u>TRICHOCORIYA VERTICALIS VAR. SELLARIS: ITS</u> <u>LIFE HISTORY AND SOME ENVIRONMENTAL FACTORS</u> <u>AFFECTING IT</u> .....	23
Introduction.....	23
Methods and Materials.....	27
Field.....	27
Qualitative Sampling.....	28
Quantitative Sampling.....	30
Birds: Food Item Analysis.....	31
Laboratory.....	31
Cultures.....	33
Salinity and Variable Temperature Tolerance.....	34
Salinity and Constant Temperature Tolerance.....	36
Egg Hatching: Salinity and Temperature Tolerance.....	37
Diurnal Activity: Aquarium Observations.....	37
Results.....	38
Field.....	38
Seasonal Occurrence by Size Class and Stage.....	51



Observations on <u>T. Verticalis</u>	
Invertebrate Predators.....	60
Predation on <u>T. Verticalis</u> by Fish.....	64
Birds: Food Item Analysis.....	65
Associated Biota-Community Composition..	68
Laboratory.....	79
Egg Hatching: Salinity and Temperature	
Tolerance.....	79
Nymphal and Adult Instars.....	82
First Instar.....	82
Second Instar.....	84
Third Instar.....	84
Fourth Instar.....	84
Fifth Instar.....	85
Sixth Instar (Adult).....	85
Aquarium Observations.....	86
Salinity and Variable Temperature	
Tolerance.....	88
Salinity and Constant Temperature	
Tolerance.....	93
III. <u>ERYTHRODIPLAX BERENICE DRURY</u> (ODONATA):	
<u>OBSERVATIONS OF LARVAL AND ADULT ABUNDANCE AND</u>	
<u>SOME ENVIRONMENTAL FACTORS AFFECTING IT.....</u>	96
Introduction.....	96
Methods and Materials.....	99
Field.....	99
Laboratory.....	99
Results.....	100
Field.....	100
Observations and Abundance: 1974	
and 1975.....	100
Laboratory.....	104
Culture: Salinity and Variable	
Temperature.....	104
Culture: Feeding and Food Source.....	105
IV. DISCUSSION.....	108
LITERATURE CITED.....	132

## LIST OF TABLES

1.	Seasonal occurrence of birds in the high marsh.....	32
2.	Spring tidal flooding depth/salinity sequence effect on previously dry site 3 (IPL), 8/16/74.....	46
3.	Number of <u>Trichocorixa verticalis</u> from bottom (open water) samples, site 3 (1975).....	56
4.	<u>T. verticalis</u> embryonic development in the field in relation to season, salinity and temperature at site 3.....	57
5.	<u>T. verticalis</u> embryonic development in the laboratory: eggs collected at site 3, and held at different salinities and temperatures.....	59
6.	Seasonal occurrence of insects in the Adam's Point marsh.....	61
7.	Invertebrates recovered (% of total recognizable prey) from shorebird gut analysis of summer and fall 1974, 1975.....	67
8.	Number of fauna from bottom (open water) samples, site 4 (8/13/74).....	68
9.	Number of fauna and high density dates in the algal mat at sites 4 and 5.....	69
10.	Comparison of 5 naiads of <u>Erythrodiplax berenice</u> collected and cultured to adult emergence at various salinities and temperatures.....	106

## LIST OF FIGURES

1.	Great Bay and Adam's Point, New Hampshire.....	4
2.	Tidal marsh and study area.....	5
3.	High marsh at Adam's Point.....	7
4.	Flood tide at Adam's Point Marsh.....	7
5.	Diagrammatic transect of marsh.....	8
6.	Exposed high marsh during neap tidal drought.....	9
7.	Site 5 (Pl P): Water retention and partial exposure during neap tidal drought (algal mat substrate).....	9
8.	Site 6 (RP): Water retention and partial exposure during neap tidal drought.....	10
9.	Site 3 (IPL): Complete exposure during neap tidal drought (dry, algal crusts and cracked surface silts).....	15
10.	Salinity changes at sites 3, 4, 5 and Little Bay from 7/8 to 10/28/74, showing tidal and rain effects.....	16
11.	Site 4 (FEMP): Water retained during dry neap tidal drought.....	18
12.	Site 6 (RP): Ice covered and surface water.....	22
13.	Site 6 spring (RPS): Area of open ice.....	22
14.	Activity measurements during aquarium observations of <u>T. verticalis</u> var. <u>sellaris</u> (mixed stages) at 25 ‰ salinity.....	39
15.	Relationships between seasonal salinities, water temperatures and air temperatures measured on each sample date.....	42
16.	Relationships between seasonal salinities and water temperatures measured on each sample date.....	43
17.	Spring salinity distribution on 5/12/75 during a dry neap tidal period.....	45
18.	Rainfall (cm/day) during period Aug. 20 - Sept. 13, 1974.....	48

19.	Vertical halocline at site 4, days A - D.....	48
20.	Halocline, site 5 (6/5/75), in floating algae.....	50
21.	Length-frequency distribution of 5 size class categories of <u>T. verticalis</u> var. <u>sellaris</u> collected from Adam's Point site 3 between 4/24 and 8/10/75 showing nymph/adult ratios.....	52
22.	Length-frequency distribution of 5 size class categories of <u>T. verticalis</u> var. <u>sellaris</u> collected from Adam's Point site 3 between 8/14 and 10/22/75 showing nymph/adult ratios.....	54
23.	Diagrammatic salt marsh panne system including floating algal subsystem and bottom subsystem, some major associated biota and a corresponding list of organisms illustrated.....	72
24.	Egg hatching in <u>T. verticalis</u> var. <u>sellaris</u> : effects of salinity and temperature.....	83
25.	Mortality of <u>T. verticalis</u> var. <u>sellaris</u> (mixed immatures) at different salinities and uncontrolled variable temperatures (21-32 $\pm$ 1 C)...	89
26.	Mortality of <u>T. verticalis</u> var. <u>sellaris</u> (Adults) at different salinities and uncontrolled variable temperatures (21-35 $\pm$ 1 C).....	91
27.	Mortality of <u>T. verticalis</u> var. <u>sellaris</u> (mixed stages at different salinities and constant temperatures.....	94
28.	Observed summer occurrence and abundance of adult <u>E. berenice</u> in 1975 in the upper intertidal marsh at Adam's Point, N. H. including sample dates for naiads (X), adults in tandem (♂/♀) and relative abundance of <u>Aedes sollicitans</u> .....	102
29.	Diagrammatic representation of some major food web components in a high salt marsh panne system, Adam's Point, N. H.....	110

ABSTRACT

ECOLOGY OF TWO TIDAL MARSH INSECTS, TRICHOCORIXA  
VERTICALIS (HEMIPTERA) AND ERYTHRODIPLAX  
BERENICE (ODONATA), IN NEW HAMPSHIRE

by

LARRY J. KELTS

This thesis deals with the ecology of the high tidal marshes with emphasis on certain aquatic insects, and constitutes a holistic, yet autecological approach to understanding the natural history of a corixid, Trichocorixa verticalis var. sellaris and an odonate, Erythrodiplax berenice. The high marsh panne ecosystem has been described in relation to temperature and salinity factors, and laboratory experiments were correlated with observations of seasonal occurrence and abundance of the two insects. In addition, behavioral and life history observations were made of other important organisms found in the pannes.

Within the upper intertidal marsh at Adam's Point, N. H., pannes were monitored for salinity and temperature between 1972 - 1975. The high marsh was dominated by physical and chemical factors associated with highly variable salinities and temperatures caused by irregular tidal flooding. Neap-tidal dry periods produced exposure gradients from the highest regions of the marsh to the lowest high marsh region which was subjected to more regular and prolonged tidal coverage.

T. verticalis was the only corixid found living and completing its life cycle in the high marsh pannes. These boatmen reached average densities of  $591.8/m^2$  in the floating algal mat with a high of  $26,914.2/m^2$  in open shallow pannes, where salinities from 0 to 60 o/oo and temperatures from 0 to 40 C were recorded. They deposit large numbers of eggs throughout the summer and fall. Through a staggered hatching mechanism, T. verticalis populations survived long neap tide drought periods. Numbers were replenished soon after reflooding. Winter eggs developed and hatched between salinities of 0 to 30 o/oo at 20 C and between 0 to 20 o/oo at 10 C. Summer eggs hatched between salinities of 0 to 55 o/oo when held at variable, uncontrolled temperatures (20 - 36 C). Embryonic development and eclosion are described, and body and molt measurements with descriptions of the 5 nymphal and the adult instars are given in this report.

Aside from being herbivores and detritivores, T. verticalis are predatory, feeding on chironomid larvae and oligochaetes. These boatmen are in turn, a food item for both invertebrates and vertebrates of the marsh, and they provide a substantial food source for migratory shorebirds.

Erythrodiplax berenice was the only dragonfly found completing its life cycle in the salt marsh. Two adult population peaks (June and August) were recorded at Adam's Point, and oviposition by tandem pairs was observed. Naiads were found in the pannes throughout the year.

In the laboratory, naiads were fed Artemia and held in culture at salinities between 0 and 90 o/oo. Feeding

activity ceased and mortality occurred at 91 to 92 o/oo. Emergence took place from culture salinities between 0 and 48.5 o/oo at uncontrolled variable temperatures.

The data in this thesis indicate a highly successful adaptation to the intertidal marsh by these two insects, and suggest that food and salinity/temperature tolerances would not be limiting factors for the successful invasion and habitation of open coastal and oceanic environments. Since these insects are dependent on surface contact for air and adult emergence, it would seem probable that an unavailable surface substratum, unstable surface conditions and depth could likely be important limiting factors.

## CHAPTER I

### INTRODUCTION

Insects are a most successful group of animals, comprised of about 3 million described species, and though adapted to a variety of habitats, they are typically terrestrial. Only 10 orders of insects have aquatic representatives, and of these, only 8 (Diptera, Coleoptera, Hemiptera, Collembola, Trichoptera, Lepidoptera, Ephemeroptera and Odonata) have been found in salt water (Gosner, 1971; Usinger, 1957).

Insects listed in estuarine or salt marsh surveys usually are recorded as simply "insects" or "dipteran larvae (unidentified)". A few lists are general invertebrate records and tend to ignore the occurrence of insects (Teal, 1962; Wells, 1961). Other citations record only those insects most conspicuous (Barnes, Dorey and Little, 1971; Dexter, 1947). Recently, a survey by Wall (1973) provided a relatively substantial listing of sand and marsh inhabiting insects of Cape Cod, Massachusetts. Although insects may form an important part of the tidal marsh fauna, our knowledge of them is limited, and seldom has been reviewed (Cheng, 1976; Gustafson and Lane, 1968; Usinger, 1957). Recent papers do report specific semiaquatic and aquatic insects of tidal marshes (Brown, 1948; Davis, 1966; Dukes, Edwards and Axtell, 1974; Johnson and Hays, 1973; Sutcliffe, 1960).

The present research was undertaken to provide information on larval and adult aquatic insect ecology in a salt marsh



at Adam's Point, New Hampshire. I discovered appreciable numbers of insects, including one species of water boatman and one dragonfly, that survive in tidal habitats, despite high salinities and temperatures. The combined ecological and physiological importance of temperature and salinity has been emphasized by numerous authors. Concentration, magnitude, and rate of change of these factors are ecologically significant. They could act to control activities and survival of tidal marsh insects.

The necessity of a fuller understanding of the biological complexity of the estuaries of the northeastern coast of the United States is becoming greater with increasing stress put on these systems by our increasing population and its technology (Borrer, 1975; Lauff, 1967). Considering our chosen standard of living and the population density, the coastal ecosystem cannot remain unutilized and undisturbed (Barbour et al., 1973). Perhaps information gained from this research will be significant in future considerations of salt marsh manipulations. The effects of physical factors on the occurrence and distribution of T. verticalis may be considered significant when spatial differences can be related to environmental factors associated with pollution. In this respect, consideration of this boatman as an indicator organism might be possible.

Animals and plants are the important features of the environment, and the desirability or otherwise of any changes proposed by man cannot be assessed without a sound knowledge of what species occur and why (Macan, 1974). In this study an attempt was made to identify other organisms associated with

the boatman in the high marsh ecosystem. As stated by Sailer (1948), "Until man has available all knowledge concerning the vastly complex structure of life in such areas and understands all its causations and manifestations, an exact statement of the importance of any organism or group of organisms to man's economy must necessarily be relative if not ambiguous."

By combining a 3-year field investigation (1972-1975) with laboratory rearing and testing, this thesis constitutes a holistic, yet autecological approach to understanding the natural history of two little known, but abundant salt marsh insects, a corixid, Trichocorixa verticalis var. sellaris (Abbott) and an odonate, Erythrodiplax berenice Drury. As stated by Teal and Teal (1969), the animals are there to study, but the way they fit into the marsh system is almost unknown. Possibly this study will help rectify some of that lack of knowledge.

#### Description of the Marsh

Investigations were carried out in a tidal marsh on Adam's Point, Durham, New Hampshire ( $43^{\circ} 5' 22''$  North Latitude;  $70^{\circ} 5' 15''$  West Longitude). It is a nearly rectangular, semi-enclosed area ( $300 \text{ m}^2$ ) bounded by upland field and forests to the north and south, and a road to the east. The marsh is at the north end of Great Bay and is open to mud flats to the west, the direction from which the area is flooded by high tide (Figs. 1, 2). The mean tidal amplitude is approximately 2.5 m but varies considerably from predicted values due to the extensive tidal flats and the shallowness of the estuary

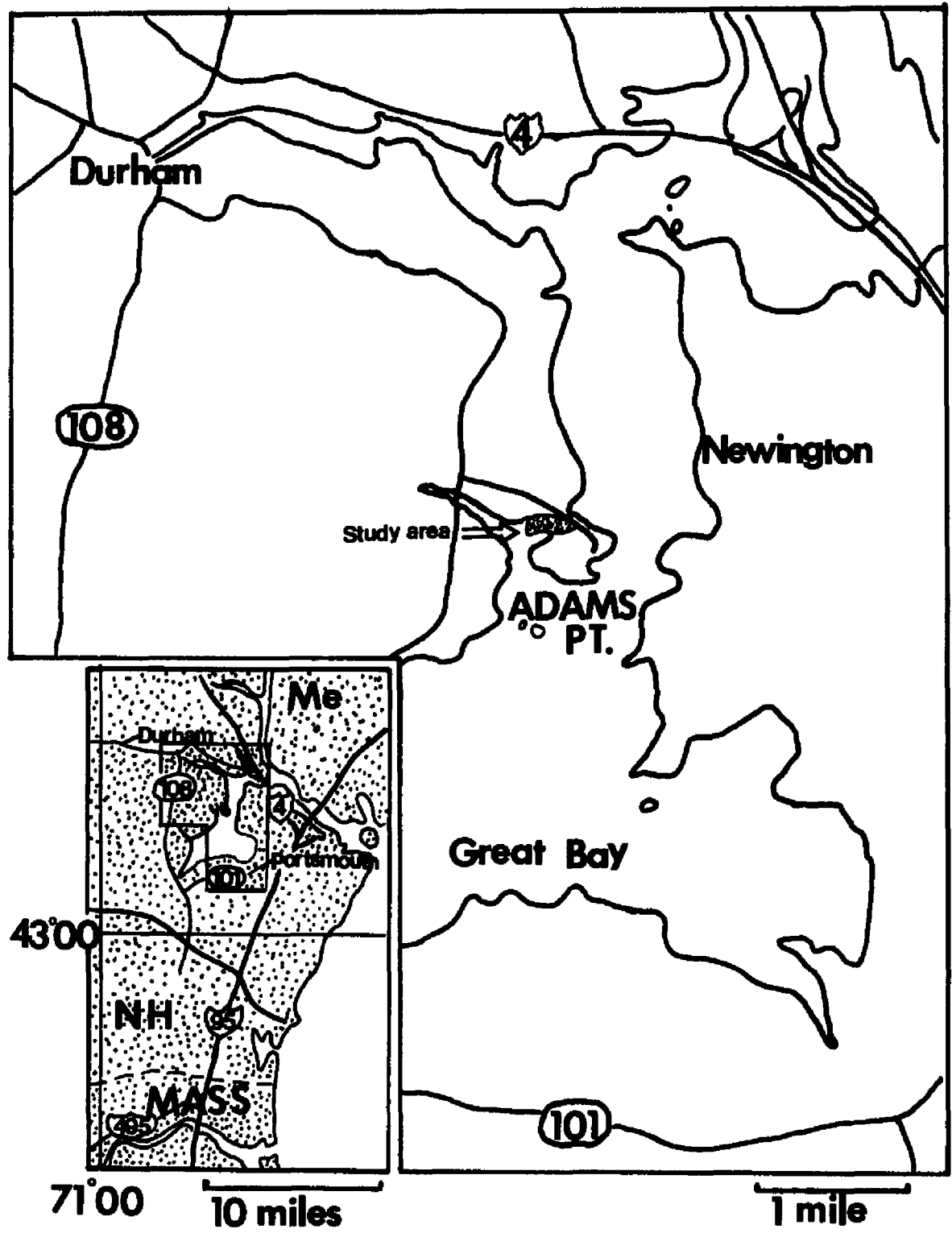


Figure 1. Great Bay and Adam's Point, New Hampshire.

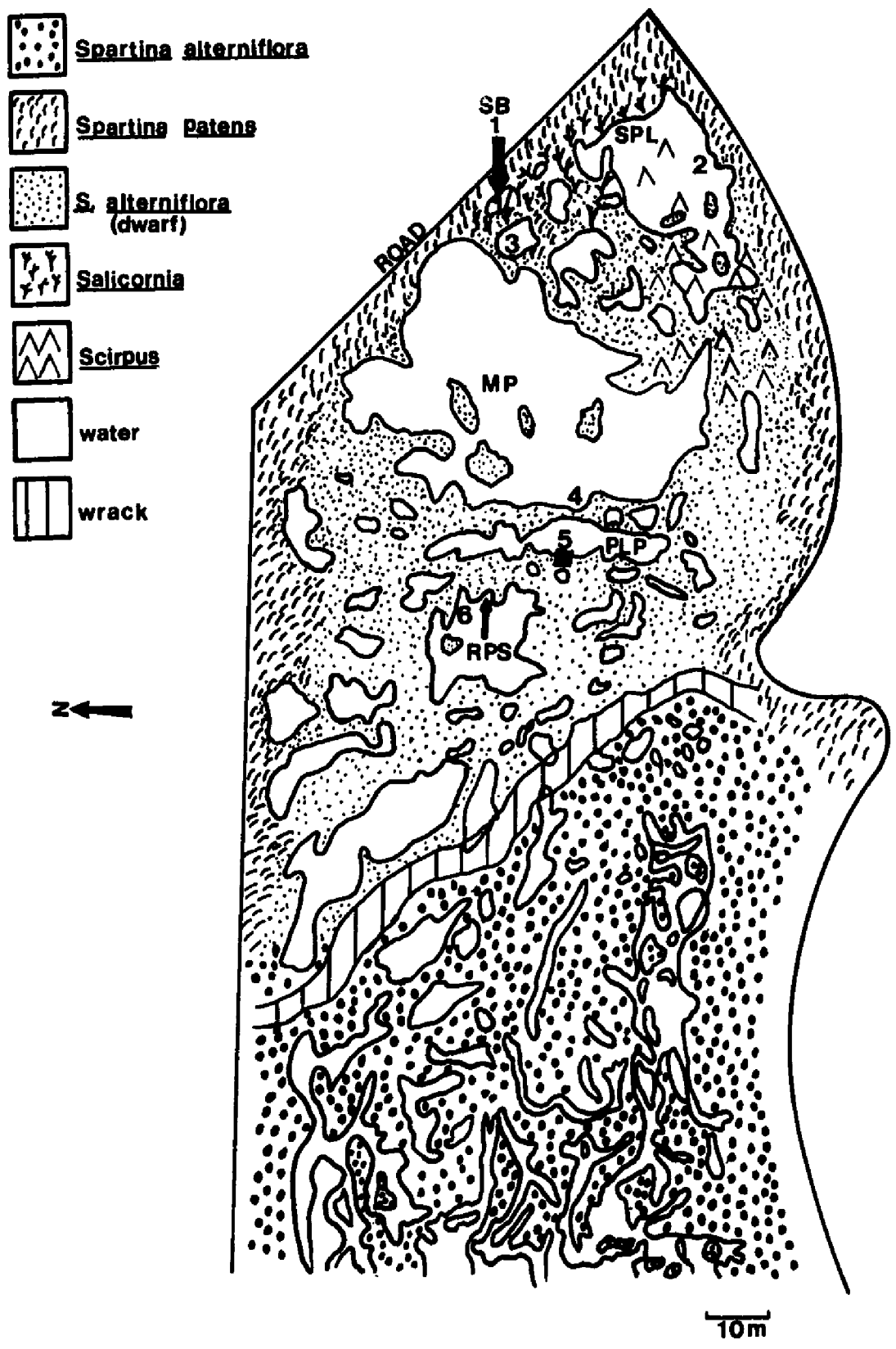


Figure 2. Tidal marsh and study sites.

(Borrer, 1975). Spring high tide water level reaches the road edge at the top of Fig. 2 (Figs. 3, 4).

The high marsh study area lies within that portion comprised of the northeastern-most 100 m<sup>2</sup> area and contrasts sharply with the "lower marsh", indicated by a dominant vegetation of tall Spartina alterniflora (Figs. 2, 5). A small number of extensive pannes, elongated in an east-west direction, are confined to the high marsh area.

The marsh peat overlies terrestrial silts, bedrock and glacial deposits. The fibrous peat is thickest near the center of the marsh and becomes thinner toward the landward and bayward sides (Breeding et al., 1974).

The area in Fig. 2 is covered by 15-45 cm of ice by mid-February, and in the coldest winters, ice extends to the bottom of the deeper pannes in the upper marsh (Borrer, 1975). During spring ice-out the lower marsh is scoured free of vegetative cover, but the upper marsh remains relatively free of such disturbance. Late winter and early spring storm tides can push much of the scoured debris up into the high marsh area.

During summer dry periods the water in the shallow depressions and pannes at the top of Fig. 2, may evaporate (Fig. 6), but the deeper pools in the outer high marsh show varying degrees of water retention (Figs. 7 and 8). There are extensive seasonal developments of filamentous green and blue-green algae in deeper pannes.

#### Study Area

The plants of the marsh at Adam's Point are similar to that of other salt marshes of the North Atlantic coast reported

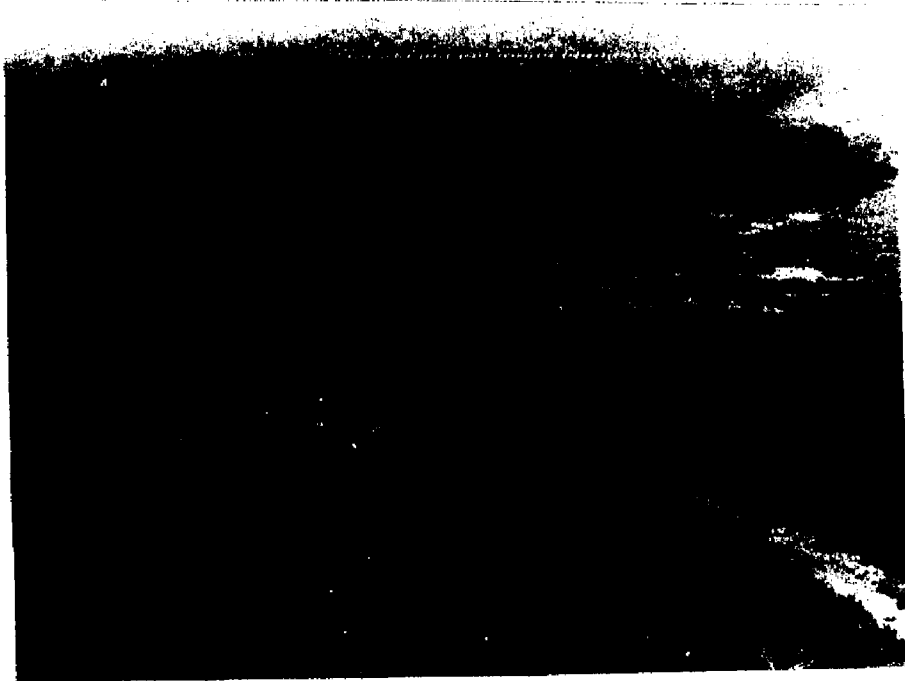


Figure 3. High marsh at Adam's Point.



Figure 4. Flood tide at Adam's Point Marsh.

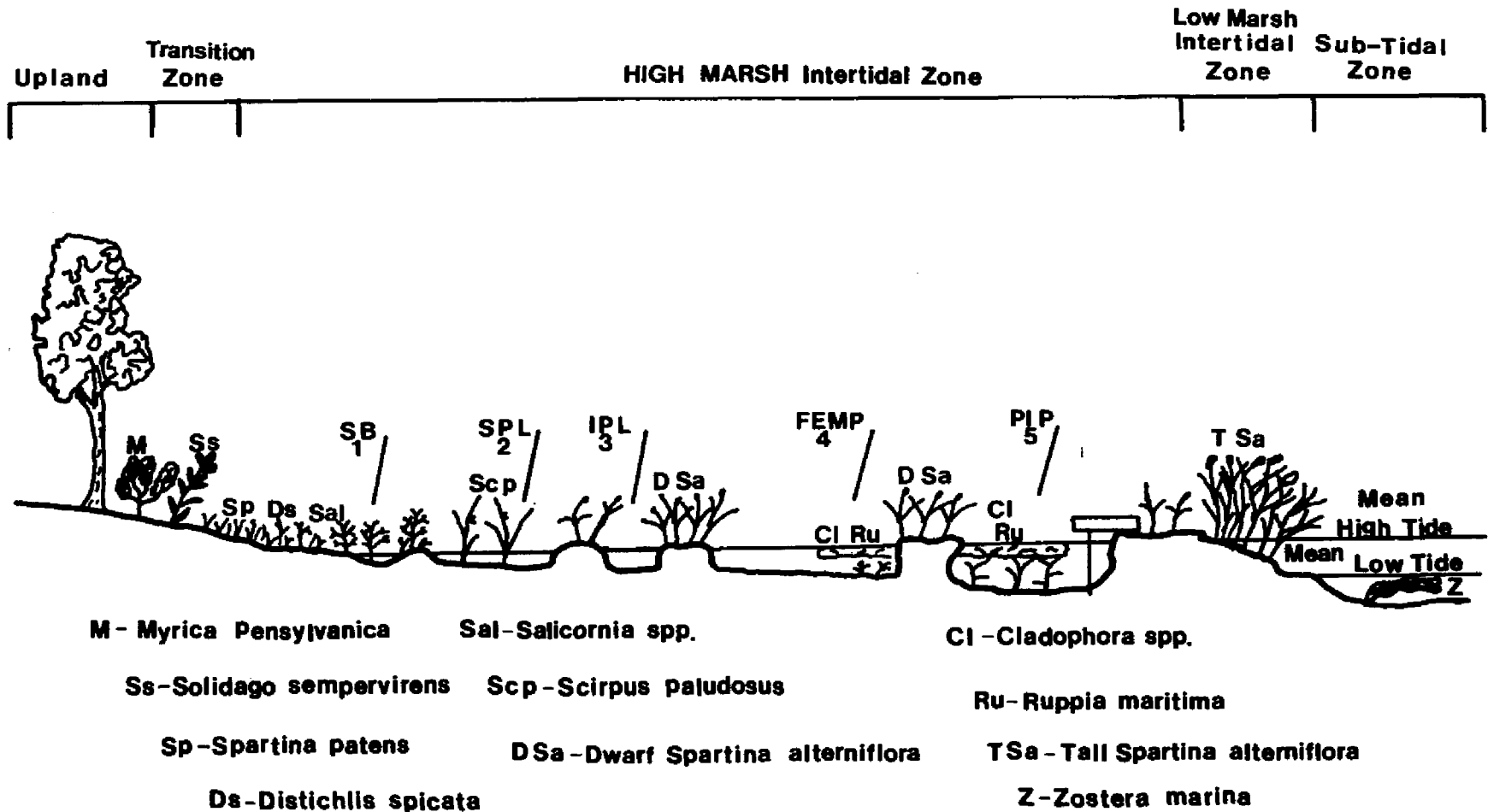


Figure 5. Diagrammatic transect of marsh.

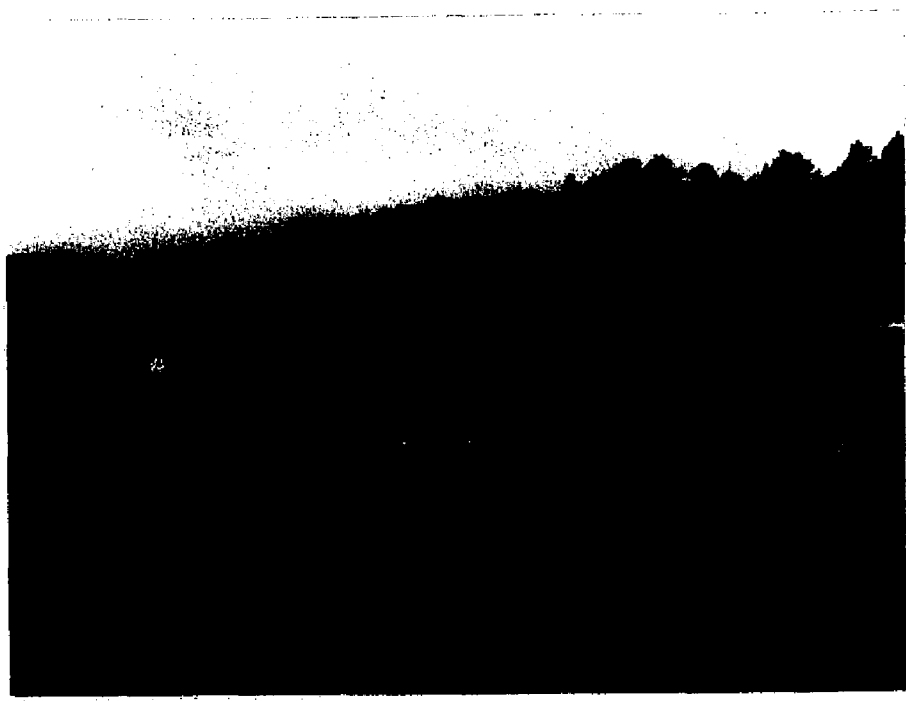


Figure 6. Exposed high marsh during neap tidal drought.

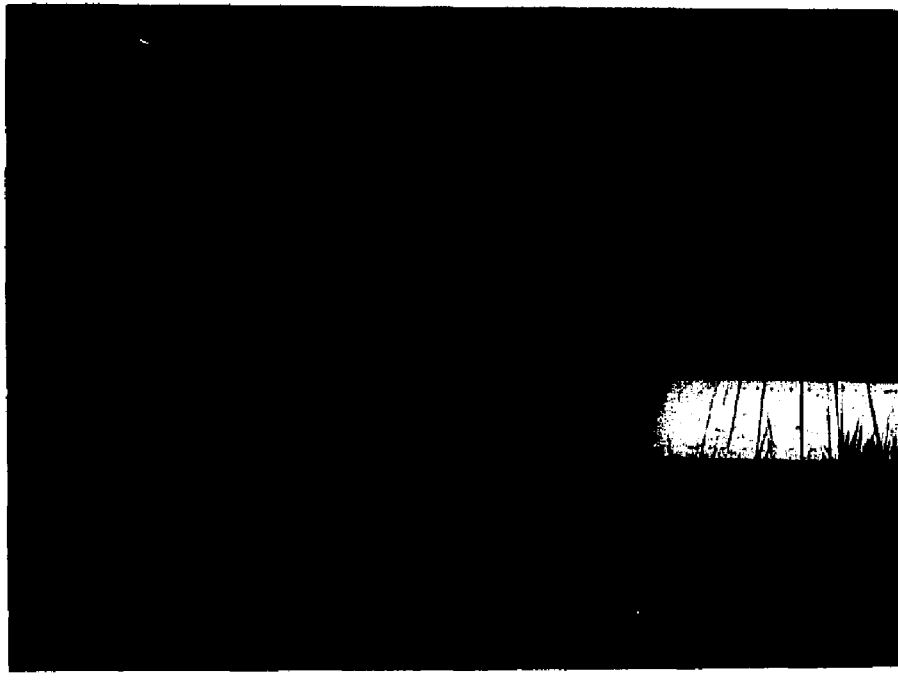


Figure 7. Site 5 (Pl P): Water retention and partial exposure during neap tidal drought (algal mat substrate).



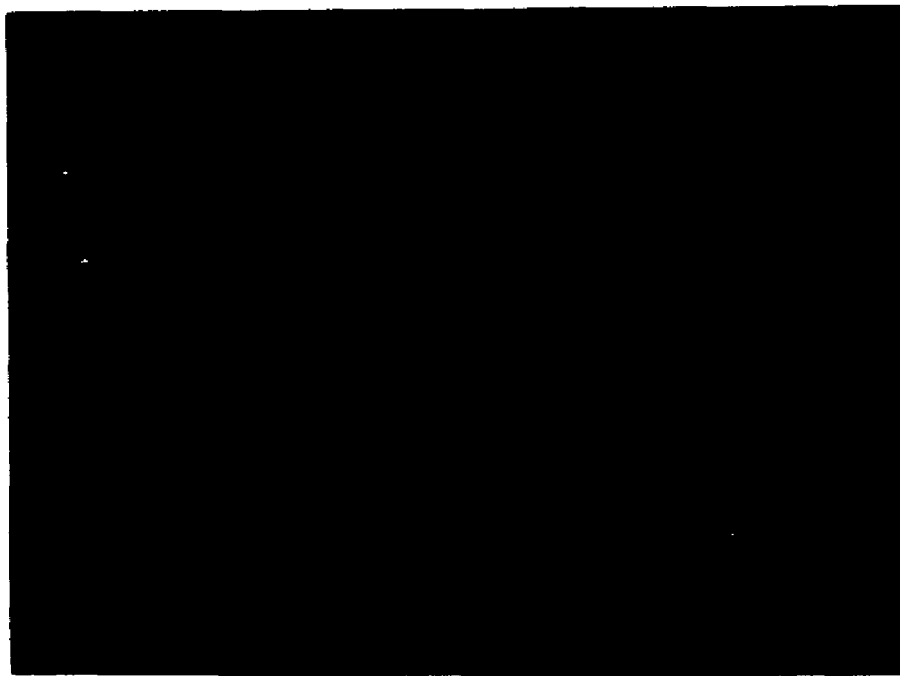


Figure 8. Site 6 (RP): Water retention and partial exposure during neap tidal drought.

by Miller and Egler (1950), Vagenas (1969) and Breeding et al. (1974). The two species of Spartina are zoned as in Fig. 2. Spartina alterniflora reaches heights of 1-2 m in the lowest intertidal emergent marsh, and generally is flooded at high tide.

The adjacent higher intertidal emergence marsh is dominated by dwarf Spartina alterniflora, 15-35 cm high, bordered by a narrow band dominated by Spartina patens and Distichlis spicata. Its lower edge is clearly marked by an open area of Wrack (Fig. 2). This relatively flat area includes the pannes selected for this study.

The shallow edges of the high pannes are occupied by pure stands of Salicornia europaea. Scirpus paludosus is found throughout the shallow pannes at the southern edge of the high marsh near the forested upland border (Figs. 2, 5). Other herbs present include Juncus gerardi, Triglochin maritima, Solidago sempervirens, Potentilla anserina, Plantago oliganthos, Lythrum salicaria, Limonium nashii, Panicum virgatum, Atriplex patula and Aster subulatis.

Five pannes and 1 depression were monitored regularly, and a location within each panne was marked with a yellow stake to indicate a constant area for measurement of depth, salinity and temperature. A representative sequence of pannes and pools of different types classified by Miller and Egler (1950) were selected for regular monitoring in this study. Six sites were included in 6 panne types representing areas from the highest emergence marsh, flooded only by spring high tides, to the lower (outer) zone of dwarf S. alterniflora (Fig. 2). These

panne types include a shallow Salicornia depression (4.3 cm d), a Forb Panne (6 cm d), a Salt Panne (10.8 cm d), a Pond Hole (20 cm d), a Ruppia Panne (27.5 cm d) and a Pothole (14.3 cm d). The following names were used in this study for each of the 6 sites within the panne types referred to above.

Salicornia Bed (SB; site 1). A shallow, flat-bottomed depression included in a narrow zone of dense Salicornia europaea containing an occasional concavity that retained water for short periods following spring tides, or substantial precipitation (Figs. 2, 5). This zone could be described best as one of sporadically occurring concentrations of salts, which accumulated during periodic exposure to progressive evaporation and dessication, ice formation and salt crystalization. It is also an area of extreme temperature range (-1 to 40 C). The substratum of this depression was hard and firm.

Shallow Panne Left (SPL; site 2). The second site consists of an area of Forb Panne that was shallow and highly susceptible to exposure during drying. This panne could be readily identified by the scattered stands of bright green Scirpus paludosus (Fig. 2). The range of salinities and temperatures produced by upland drainage, evaporation, and solar heating were extensive.

This panne had a fairly firm, hard substratum covered with a thin layer of detritus. It is bounded on the southern edge by a dense sward of S. patens and a few scattered forbs. The eastern edge was lined by stands of S. europaea replaced progressively landward by S. patens and D. spicata bordering the road at the top of Fig. 2.

This is the area of the most variable and colorful of tidal marsh plant association (Miller and Egler, 1950). It is in this zone that the majority of competition-affected forbs flower and fruit to best advantage. Even the northern and western border of dominant dwarf S. alterniflora assumes a conspicuous diversity here that is lacking in the pure stands of yellow and depauperate plants extending bayward.

Isolated Panne Left (IPL; site 3). This site was in a smaller, nearly round, salt panne about 2 m in diameter and is located near site 1, and north of site 2 (Fig. 2). It has an average depth of 10-12.5 cm, when not under spring tidal waters, and maintained an insignificant growth of Ruppia maritima, submergent ditch grass, and a Cladophora sp. floating mat, briefly during late spring. These plants would die-off following the first drying exposure. The bottom contained 10 to 15 cm of soft, silty ooze.

Site 3 became interconnected with surrounding pannes only during the highest spring tides. It was affected by hypersaline conditions produced during drying and freezing periods, but retained water for longer periods than site 1 and 2. In winter, ice extended to the bottom of site 3, as it did at sites 1 and 2. During spring high water flood the entire panne was covered to depths of 45 to 50 cm for a short time, but such depths decreased rapidly with tidal ebbing.

Following spring plant growth and the first seasonal drying exposure of site 3, a filamentous algal mat mixed with Ruppia covered the substratum. This blanket of plants retarded evaporation, leaving variable amounts of hypersaline moisture

beneath. With an extended dry period, the substratum would eventually become dry and brittle (Fig. 9). Hummocks of S. patens at the panne edge provided similar moisture laden mats of over-hanging stems and leaves.

Far Edge Main Panne (FEMP; site 4). This panne, classified as a Pond Hole by Redfield (1972), is labeled FEMP due to its outer location in the largest of the pannes included in this study (Figs. 2, 5). This pool was devoid of substantial Ruppia growth but maintained a thin algal mat, of approximately 1 meter width, near the outer edge. This panne increased in depth gradually from the uppermost, eastern edge to the lower, western edge, within the deeper section (15-25 cm d) of the panne (Fig. 2).

When compared to sites 1-3, this location was more affected by spring tides, and it was drastically altered only by extreme conditions. Because of increased volume and depth of water at site 4, (Fig. 5), the ranges of temperature and salinities were less extensive than in the first three panne sites, as seen in Fig. 10.

An extended drought (summer, 1974) left the substratum at the sampling marker partially exposed, but interrupted pockets of hypersaline water were retained until tidal reflooding (Fig. 11). Water 7.5 - 10 cm deep was present at site 4 when sites 1-3 were completely exposed. Some water remained beneath winter ice at this site.

Platform Pool (Pl P; site 5). This sample site is located in a Ruppia panne found in the middle zone of the dwarf S. alterniflora marsh about 10 m out in the marsh from site 4



Figure 9. Site 3 (IPL): Complete exposure during tidal drought (dry, algal crusts and cracked surface silts).

Figure 10. Salinity changes at sites 3, 4, 5 and Little Bay from 7/8 to 10/28/74, showing tidal and rain effects. Vertical lines indicate the periods during which tidal flooding effects were noted.

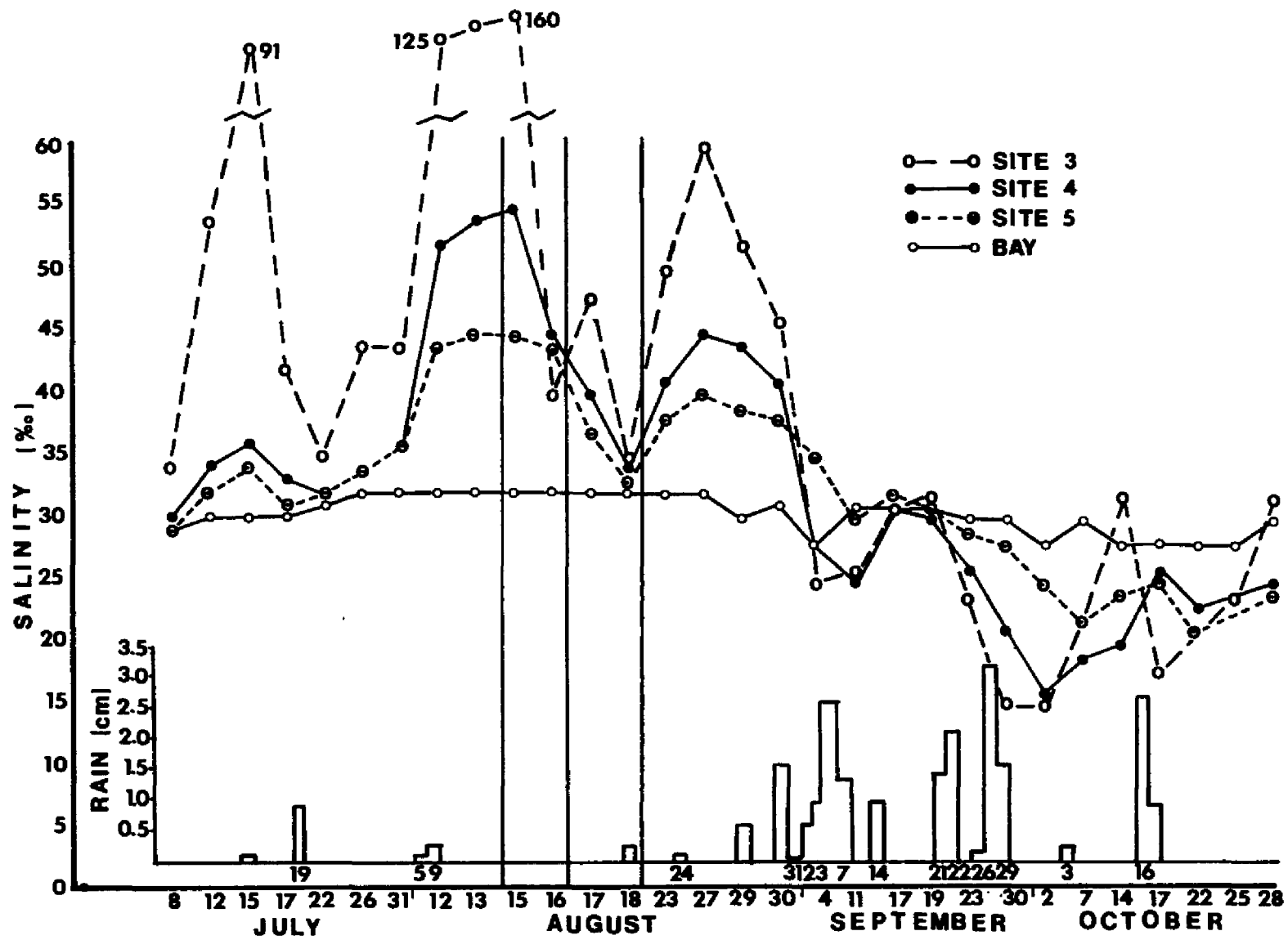






Figure 11. Site 4 (FEMP): Water retained during dry neap tidal drought.

(Fig. 2). Site 5 has a mean depth of 27.5 cm, a dense growth of submergent ditch grass, R. maritima, and a floating mat of entangled Cladophora sp. filaments (Fig. 5). This mat sometimes covered 80 - 90 % of the panne surface. It formed a dense stratum of algal filaments from late spring to early winter. Ditch Grass occupied 50 - 70 % of the bottom area of this panne during the summer, and its terminal portions became entangled with the algal filaments. The mat formed a floating stratum that reduced solar heating of waters below. This factor combined with increased depth, more constant water level and more frequent tidal flooding, produced less variation of salinity and temperature during periods of climatic extremes (Fig. 10).

The bottom of Pl. P. was relatively firm, but was covered by a surface layer of submerged plant material and silt. Following high spring flood tides and storm winds, floating plant material formed wrack beds that were deposited on the panne surface and eventually sunk to the bottom. This material, combined with submerged algal mat and Ruppia, contributed to a blanket of soft, silty debris several centimeters thick overlying a firm peat layer beneath.

A 12 C isotherm causes cessation of growth in Ruppia in the fall, and below 6 C, there is die-back, and standing crop decreases markedly (Fish, 1964). This die-back of Ruppia associated with low temperature was noted here in autumn. New growth reappeared during late spring. Much of the Cladophora mat was maintained within and beneath the ice during winter freezing at Adam's Point, and Fish (1964) suggested a cessation

of additive growth but maintenance of green, living filaments at this time.

The bottom and algal mat showed pink areas in large and intensely pigmented masses during late summer and fall. This color is produced by purple sulfur bacterial growth (Jones, personal communication).

Rotten Panne (RP; site 6). The bottom of this pothole contained anaerobically decomposing debris. There was a nearly constant condition of milky-colored turbidity in the water composed of suspended sulfur (Jones, personal communication). A strong odor of  $H_2S$  was present at this panne. Site 6 is located lowest intertidally in the study area (Fig. 2). During the majority of sample periods, this pothole retained a milky-white appearance, in strong contrast to the clear water condition in nearby pannes.

Redfield (1972) referred to these ponds, formed by decay of surface turf, as "rotten spots" or pannes which appear to represent successive stages in development of the large pond holes. Following storm and tidal flooding, this panne contained large accumulations of wrack debris pushed back from the intertidal tall Spartina marsh and Great Bay. This organic accumulation was noted also in nearby pannes.

A very limited, brownish-green crop of floating algal mat occasionally appeared at the edges of R.P. No significant growths of Ruppia were noted here, and the substratum consisted of a thick, black, oozy silt, often coated with a thin layer of white sulfur.

During winter through summer, 1975, a localized area of relative constant temperature and salinity was discovered at approximately 2 m east and south of the marked sample site 6, in R.P. When the entire sampling area was covered by 15-45 cm of ice (Fig. 12), this particular area of approximately 0.5 to 2 m x 0.5 to 1 m was open and ice free, with clear water exposing a white and green encrusted substrate (Fig. 13). Beneath the sulfur and bacterial surface, a soft, black silt nearly one meter deep occurred upon a semifirm peat layer. The odor of  $H_2S$  was often detected without prior disturbance of the substrate here. This area was entitled "Rotten Panne Spring" and is indicated by an arrow in Fig. 2.

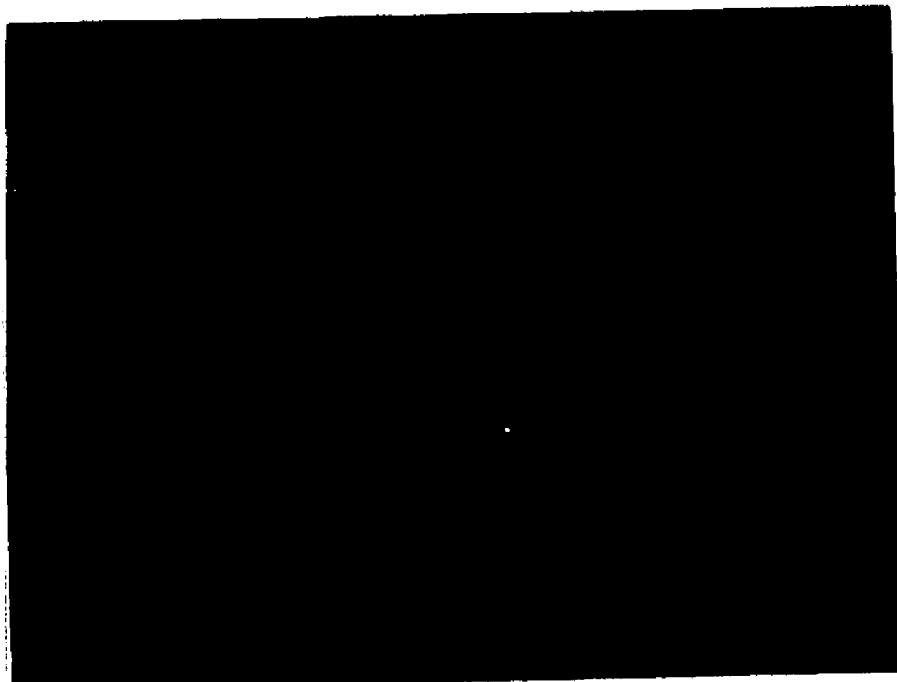


Figure 12. Site 6 (RP): Ice covered and surface water.

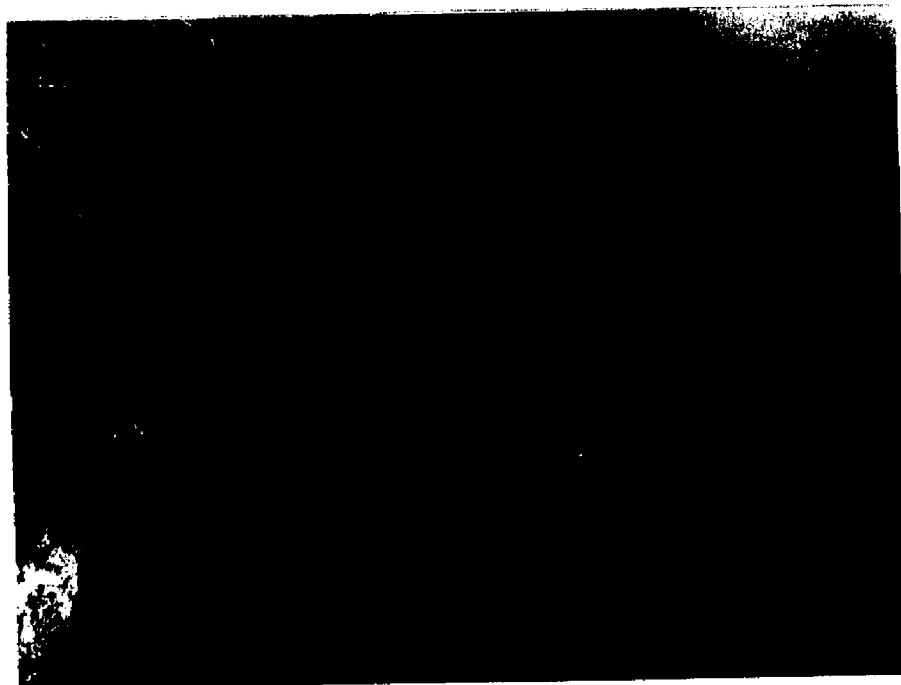


Figure 13. Site 6 spring (RPS): Area of open ice.

## CHAPTER II

TRICHCORIXA VERTICALIS VAR. SELLARIS: ITS LIFE

## HISTORY AND SOME ENVIRONMENTAL FACTORS

## AFFECTING IT

INTRODUCTION

Trichocorixa verticalis var. sellaris, a form of the subspecies T. v. verticalis according to Sailer (1948), is a member of a large and widely distributed order of insects (Hemiptera: Heteroptera), composed of 52 families (Borror and Delong, 1971). In an order containing 25,000 known species, members of 16 families of Hemiptera occur in, on or near water (Miller, 1956; Usinger, 1956). This boatman is one of approximately 300 species in the family Corixidae (water boatmen), and belongs to a genus of small, generally elongate corixids common throughout the Western Hemisphere. Little has been published concerning the biology, morphology or distribution of the species in this genus, for most of the attention has been by systematic workers (Davis, 1966; Sailer, 1948; Tones and Hammer, 1975).

Several corixids have been recorded from marine thalassic, athalassic, and hypersaline waters, and some references to saline waterboatmen have been published (Barnes et al., 1971; Bayly, 1972; Beadle, 1943; Butler and Popham, 1958; Davis, 1966; Hutchinson, 1931; Sailer, 1948; Scudder, 1969, 1976; Thorpe, 1932; Tones and Hammer, 1975; Usinger, 1957). One account of Corixa selecta from waters at 45 o/oo in Sussex, England, was

reported by Thorpe (1932), and examples of C. selecta, C. stagnalis and C. falleni are listed most frequently in 50 % sea water or more. Six other corixids have been found in 20 to 25 % sea water at Spurn, Yorkshire, where it was reported also that C. stagnalis lived in 65 to 85 % sea water (Butler and Popham, 1958).

At least three species of Trichocorixa, T. reticulata, T. verticalis and T. louisianae, usually live in coastal zones, but T. v. interiores is common only in high plains and intermountain regions where alkali and salt water are common (Sailer, 1948). T. verticalis was reported by Hutchinson (1931), in plankton tows from Delaware Bay. Except for the study of ecology and reproduction of T. reticulata by Davis (1966) and the osmotic regulation and salinity tolerance of T. v. interiores by Tones and Hammer (1975), little information is available concerning the biology of this group of saline-tolerant corixids.

T. reticulata was recorded surviving in salinities of 43 o/oo in the egg, immature and adult stages (Davis, 1966). Eggs hatched equally well in water of 43 o/oo and 4.3 o/oo salinity, but the process was more rapid in dilute media. Hatching did not occur above 43 o/oo salinity (Davis, 1966). In reference to this species, Bayly (1972) suggested the capability of hypo-osmotic regulation, since it could occur in athalassic saline or marine hypersaline environments.

From the results of freezing point depression determinations of hemolymph of first and third instars and adults, Tones and Hammer (1975), demonstrated that T. v. interiores

has well-developed powers of osmoregulation and can hyporegulate in saline water. These findings agreed with the prediction of Bayly (1972), that T. v. interiores is a "halobiont regulator", capable of both hypo- and hyper-osmotic regulation (Tones and Hammer, 1975). A summary of freezing point depressions of the hemolymph for Corixidae from saline waters is presented and the graph of Sigara stagnalis is similar in shape to that of T. v. interiores (Tones and Hammer, 1975). Sigara stagnalis and T. v. interiores are the only corixids presently shown capable of hypo-osmoregulation at this time.

In order to determine which factors were the most limiting to the distribution of T. v. var. sellaris and to understand further the possibility that this coastal subspecies may be a halobiont regulator inhabiting thalassic rather than athalassic waters, experiments were carried out to determine survival at various salinities and temperatures. These factors were investigated to understand the degree of euryhaline and eurythermal characteristics of this species and to establish possible optimum salinities at controlled and uncontrolled temperatures. Beadle (1959) (in Tones and Hammer, 1975) said that species which prefer inland saline waters between 15 o/oo and 50 o/oo may also inhabit saline water below 15 o/oo and some may even occur in fresh water. In this study an attempt was made to ascertain if T. v. var. sellaris fits Beadle's classification in this respect. Future studies of osmoregulation of T. v. var. sellaris might verify this fact as predicted from ecological observations and experimental data presented here.



Corixids are important ecologically as primary herbivores, and serve also as an early link in the animal food chain, by scooping up and ingesting small benthic organisms (Usinger, 1956). Further, they must assume importance when present in abundance as food for fish and birds. They are the most numerous of all aquatic Hemiptera, are found in a wide variety of aquatic habitats, and are known for their great abundance where optimal environmental conditions exist (Davis, 1966; Sailer, 1948; Tones and Hammer, 1975; Usinger, 1957).

In a Jamaican salt-water pool, T. reticulata was the most numerous and conspicuous animal inhabitant (Davis, 1966), where they consumed gelatinous and flocculent bottom deposits. Usinger (1957) referred to numerous brackish pools where coastal trichocorixids were the most characteristic inhabitants. From a quantitative sampling of T. verticalis interiores in 6 lakes in central Saskatchewan, Tones and Hammer (1975) found a maximum density of 1978 adult T. v. interiores/m<sup>2</sup> from Big Qwill Lake (mean summer conductivity = 35,500  $\mu$ mhos/cm at 25 C). T. verticalis var. sellaris is a numerous and conspicuous macrofaunal inhabitant of the pannes at Adam's Point.

During fall and spring, shorebirds form dense multi-specific aggregations in marine littoral pools, where local concentrations of food, including large numbers of trichocorixids, may help to attract and hold these birds. Migratory birds utilize this rich food source only temporarily and yet they are vitally dependent on it (Barbour et al., 1973; Recher, 1966). I made shorebird food item analysis to understand further the importance of T. verticalis in this respect.

My selection of T. verticalis for study resulted from a supposition of its ecological importance based on preliminary observations in salt marsh pannes. Thus, I have described the high marsh panne ecosystem in relation to temperature and salinity, and correlated laboratory tests with observations of seasonal occurrence and abundance of the boatman. This study involved also laboratory investigations to determine possible factors causing various behavioral phenomena observed in the field. In addition to data on T. verticalis, habitat, behavioral and life history observations were made of other important organisms found in the pannes.

#### METHODS AND MATERIALS

##### Field

At a permanent station in each of the 6 sample pannes, surface and bottom salinity and temperature, ice thickness, water depth, and substrate color and structure were monitored at intervals of 1 to 2 weeks during the period from August, 1972, to August, 1975. Other variables observed sometimes included precipitation, wind velocity, air temperature, plant abundance, H<sub>2</sub>S odor, sulfur deposits, purple sulfur bacteria, tidal inundation and bottom exposure. Simultaneous measurements of salinity and water temperature were made from the adjacent open bay.

Salinity measurements were made with an American Optical Refractometer with a special salinity scale (accuracy = 1 o/oo), which was checked periodically by hydrometer and silver nitrate

titration. Water samples (vol = 15 ml) were collected with a rubber-bulbed, plastic-tubed, pipette. Occasionally water was collected at depth intervals of 2.5 cm, to determine the presence or absence of a halocline. Air temperatures were measured at 0.5 to 1.0 m above the marsh surface in open areas. During winter, ice holes 20 to 30 cm in diameter were cut at the markers to facilitate sampling.

In addition to my recordings of weather conditions, climatological data charts (NOAA) for the Durham area were used to verify and supplement my data. Notations of tidal levels on the Little Bay mud flats and within the marsh were recorded and compared with published tide tables.

#### Qualitative Sampling

Samples were taken at 6 sites at irregular periods throughout the year. Macrofaunal sampling and observations during all seasons were recorded within each of 140 sample periods, from 31 August, 1972, to 22 October, 1975. All insects and other aquatic macrofauna were collected and recorded.

Bottom and floating algal mat strata were taken by long-handled dip net and apron net (Needham Net) as illustrated in Pennak (1953) and Usinger (1956). Large samples of aquatic insects were collected with a long-handled (1.5 m) dip net (mesh size = 1.0 mm). Animals were placed in large plastic buckets and glass jars with panne water and carried to the laboratory, where they were sorted and set up in acclimation cultures. Small amounts of filamentous algae were added for substratum, food and oxygen source. Adult terrestrial insects

were included if necessary in order to help associate taxonomic and ecological information.

For floating algae sampling, the long-handled dip net was pushed beneath the floating algae and lifted straight up from below the mat area to be sampled. All net contents were rinsed and sieved by agitating the net in open panne water, holding the rim above the water surface, and keeping the contents submerged. Each sample was then placed in a bucket, and transferred to the laboratory where the contents were sorted. Anoxic conditions often existed in such samples, so immediate sorting was necessary.

For bottom qualitative collecting, sweeps 30 - 60 cm long were made with dipnets (rim diameter = 25 cm). These collections included the upper 5 - 10 cm of surface substrate. The apron net was used on bottoms heavily laden with Spartina stems to facilitate sampling.

Masses of attached trichocorixid eggs collected from submerged Spartina and Ruppia stems, leaves, and water-soaked driftwood were divided into separate samples for further experimentation. Observations of egg development in the field were compared with coinciding laboratory cultures.

A standard insect sweep-net was used to collect terrestrial insects. Most specimens were killed immediately in cyanide jars, and later pinned and labeled.

During each field sample period, observational notes were recorded on a "Sony, TC-45," Cassette-corder. Separate tapes could be retained for later transcribing and rechecking of sample data.

### Quantitative Sampling

Before sampling quantitatively, a pilot survey was carried out during 1973 and 1974 to gain information on population structure of the boatmen in both open pannes and in the floating algal mat. This survey included major hydrological features and crude estimates of abundance of developmental and adult stages, and observations of behavior. Both physical measurements and biota checks (occasional counts) were incorporated into a number of environmental determinations considered in the final sampling program. The information gained by the pilot survey served as a guide to the application of sampling methods. Stratified random sampling was used for quantitative collecting, based on pilot survey information (Edmondson and Winberg, 1971).

Adult and immature boatmen were collected with fine-mesh (mesh size = 0.5 x 0.7 mm) aquarium nets (Pennak, 1953). Six nets (10 x 13 cm rim; 25.5 cm handles) were partially buried by silt on the bottom of the sample panne. After a period of 20 - 30 min, the nets were raised rapidly with minimal disturbance. Net contents were put into separate containers with clear bay water, sorted and counted within 30 - 40 min after collection. Depth and location of each sample was recorded. Nets were situated randomly throughout the sample panne. Successive samples were taken to coincide with the life-history stage development and environmental stress periods, as determined during earlier pilot survey investigations.

For quantitative sampling of floating algal mat, the above described aquarium nets were inserted beneath the algae, held off the bottom and raised rapidly to the surface. Any algal mat overhanging the net rim was cut away immediately leaving a 10 x 13 cm section of algae within the net. Net contents were then placed in empty labelled jars, and either sorted in a living state, or, when a delay was necessary, preserved in 70 to 85 % ethanol. To avoid excessive dilution, from the moisture laden algae, the weakened alcohol was decanted to about 1 cm from the bottom after a day or two, and the jar was refilled with 70 % ethanol.

#### Birds: Food Item Analysis

During the periods August - September, 1974, and July - August, 1975, 12 specimens of 6 species of shore birds were collected for gut analysis to determine their role as predators on these insects and their developing stages. Specimens were collected by use of a 16 guage shot gun with special load # 20 shot and by a 22 guage smooth-bore rifle using # 12 shot. Birds were collected during active feeding; gut analyses were performed within 30 minutes after collection. Additionally, I made notes of any birds frequenting the area, including seasonal residents, transients, and those using the marsh for nesting and, or feeding (Table 1).

#### Laboratory

All samples were maintained at 12 - 15 C until sorted and counted. In some cases, red dye stain (phyloxin-B) was

Table 1. Seasonal occurrence of birds in the high marsh

SPECIES	MONTH											
	2	3	4	5	6	7	8	9	10	11	12	
<u>Ardea herodias</u> Great Blue Heron			X	X	X	X	X	X	X	X		
<u>Butorides virescens</u> Green Heron				X	X	X	X	X				
<u>Egretta thula</u> Snowy Egret				X	X	X	X					
<u>Nycticorax nycticorax</u> Black-crowned Night Heron				X			X					
<u>Botaurus lentiginosus</u> American Bittern							X	X	X			
<u>Anas discors</u> Blue-winged Teal							X					
<u>Rallus limicola</u> Virginia Rail						X	X					
<u>Charadrius vociferus</u> Killdeer		X	X	X	X	X	X	X				
<u>Squatarola squatarola</u> Black-bellied Plover								X				
<u>Tringa solitaria</u> Solitary Sandpiper				X		X	X	X	X			
<u>Tringa melanoleuca</u> Greater Yellowlegs			X	X	X	X	X	X	X	X		
<u>Tringa flavipes</u> Lesser Yellowlegs						X	X	X	X			
<u>Calidris minutilla</u> Least Sandpiper						X	X	X				
<u>Calidris pusilla</u> Semipalmated Sandpiper				X		X	X	X	X			
<u>Erolia alpina</u> Dunlin								X				
<u>Sterna hirundo</u> Common Tern				X	X		X					
<u>Megaceryle alcyon</u> Belted Kingfisher	X	X	X	X	X			X	X	X	X	

added to preserved samples to facilitate sorting. Samples of representative species were preserved in 70 % ethanol. To corroborate identification, living larvae were isolated for further development and metamorphosis.

Insects and other organisms in quantitative samples were identified, counted directly and later preserved and labeled. Age of individuals of insects was determined from measurements.

### Cultures

Eggs, nymphs and adults of T. verticalis were maintained in containers such as petri dishes, assorted jars, finger bowls (2" - 8"), compartmented plastic boxes (vol = 100 ml) and a 38 liter aquarium. All were satisfactory for holding and rearing boatmen. The eggs, attached to Ruppia and Spartina patens, were kept in petri dishes and jars containing clean panne water that had been filtered through aquarium nets (mesh size = 0.5 x 0.7 mm). On hatching, the 1st instars (1.0 mm long) were transferred to larger containers with clean panne water, net filtered panne detritus (0.5 - 1 cm depth), and washed sections of algal mat material (5 - 15 cm). Four boatmen were reared successfully in containers of 100 ml to 1 liter size. Mass cultures of 20 to 80 boatmen were maintained in 3 liter jars, and aquaria containing 70 - 80 % surface cover algal mat (Cladophora sp.) and 4 - 5 cm bottom detritus.

Cultures were maintained at  $25 \pm 5$  C and  $25 \pm 3$  o/oo, similar to the natural situation in summer in the pannes.



Boatmen tolerated extensive temperature fluctuations through continued generations in the laboratory, remaining viable when daily temperatures ranged from 20 to  $35 \pm 5$  C. Culture temperatures were raised gradually to  $41 \pm 2$  C and lowered to  $0 \pm 2$  C during separate experimental observations to determine the temperature extremes tolerated by the boatmen. Behavior and mortality were recorded during these experiments.

#### Salinity and Variable Temperature Tolerance

During a 10-day period, adult boatmen were maintained at 15 salinities, and an uncontrolled variable temperature range between 21 -  $35 \pm 1$  C. Salinity and temperature ranges were selected to resemble possible ambient variations, based on field measurements. All test animals were collected from the Adam's Point study area and were acclimated at 15 C and 30 o/oo for 5 days previous to experimentation. This acclimation period was found to be sufficient for elimination of boatmen affected by initial temperature shock and to establish a viable population for testing. Experimental animals were acclimated in covered plastic buckets (vol = 5 - 6 l) half-filled with net-filtered 30 o/oo panne water containing approximately 100 ml of filamentous algae. Water temperatures were raised gradually from 15 C to  $23 \pm 2$  C over a period of 12 hours just prior to initial experimentation, to lessen effects of temperature shock only to a mortality of 0 to 2 %.

Test containers were two clear plastic "Trans-boxes", (33.8 x 22.5 x 5.8 cm) series # P 824 of Vlochek Plastics Co., with twenty-four 5.5 x 5.5 x 5.8 cm compartments each. Each

box had a hinged, tight top preventing evaporative salinity change. In preliminary tests, Trichocorixa survived several months and had developed, in fact, from egg to adult in the compartments. Boxes were pre-soaked in distilled water for 3 days before experimental use, and filled to 4 cm with selected media 12 to 18 hrs before this experiment.

After acclimation, healthy adult boatmen (length 4 - 5 mm), including at least one pair, were placed in each of 4 boxes (two controls and 2 test boxes). Twelve boatmen were exposed to each of 15 different salinities (4 insects for each of 3 compartments). Two control boxes were maintained at 30 o/oo salinity and 15 C. They were tested in two replicates.

Salinities between 0.0 and 70 o/oo at intervals of 5 o/oo were established, based on extremes recorded in the field and laboratory observations. A 4 cm depth of test media was maintained in each compartment, in addition to selected sections of pre-soaked and pre-examined green filamentous algae, free of macrofaunal and observable purple bacterial components. Fresh, filtered, pond water from the study area drainage system was used for the 0.0 o/oo media. Salinity in each compartment was maintained at  $\pm 3$  o/oo.

For a period of 4 days, the time of any death (failure to respond to prodding stimulus) or unusual behavior was recorded, and % mortalities were determined. Additionally, compartments were monitored 6 additional days at 12 hr intervals to determine longterm tolerance. Extended observations over 65 days allowed recording of egg laying, hatching and nymph development.

Similar groupings of nymphs (second stage = 1.5 mm to fifth stage = 3.5 mm) at a variable temperature range ( $21 - 32 \pm 1$  C) were subjected to salinities of 0, 15, 25, 30, 35, 45, 55, 65 and 70 o/oo and monitored as above for 10 days.

#### Salinity and Constant Temperature Tolerance

During autumn, 1974, 1044 boatmen obtained from Adam's Point during October and November were acclimated at 15 C and  $19 \pm 2$  o/oo for 1 month. They were tested in 3 replicates at 3 different constant temperatures (4, 10, 20 C) and at 6 different salinities (0, 10, 20, 30, 40, 50 o/oo). Recently hatched nymphs were tested in separate compartments, while older immatures were mixed. Containers and procedures for testing and acclimation cultures were similar to those of variable temperature experiments described above.

Boxes were set up with selected media in the controlled temperature rooms 12 to 18 hrs before initial experimentation. After the animals were added, observations were recorded at hours 1 - 6, 12, 24 - 30, 36, 48, 60, 72, 84, and 96. All insects were measured and sorted according to size range. Recently hatched trichocorixids were selected from laboratory egg cultures and held at 15 C and  $19 \pm$  o/oo salinity in glass Petri dishes. Size range classification by total length for this experiment was just hatched, 1.0 mm (JH), early instar, 1.5 to 2.5 mm (E), advanced instar, 3.0 to 3.5 mm (A), and adult, 4.0 to 5.0 mm (M). All stages except the (JH) were mixed in test compartments to simulate field populations, prevent injury to smaller 1st. instars and facilitate observations. No cannibalism was noted.

### Egg Hatching: Salinity and Temperature Tolerance

During late autumn 1974, non-eyespot trichocorixid eggs of early stage (cream color) were collected from site 3 (IPL) and held at 4 C and  $20 \pm 3$  o/oo salinity for 2 weeks. Lots of 100 eggs still attached to stems of Spartina patens were placed in 18 plastic Petri dishes (vol = 50 ml, diameter = 9.3 cm). One group of 6 dishes, with a series of 0.0, 10, 20, 30, 40, and 50 o/oo, was cultured for 105 days at each of three temperatures (4, 10 and 20 C).

Experimental media were prepared as described above for immature and adult tests. In addition to the Spartina included with the eggs, 1 - 2 cm sections of clean filamentous algae were added for substrate and food source. For each salinity and temperature combination, I recorded hatching success, stage of development and abnormalities of all eggs.

### Diurnal Activity: Aquarium Observations

In the field, I had noted varying intensities of certain behavior including rates of swimming, surfacing, flight and pairing that might be related to changing conditions of solar light exposure, temperature, salinity and H<sub>2</sub>S production.

To study these activities under artificial conditions simulating the natural environment and allowing closer observation, I established a 38 liter, 90 x 47 x 62 cm, glass covered aquarium in a semi-exposed, outside area. Two to three cm of net-filtered detritus and a few straws and water-logged sticks were added to provide egg attachment sites. Net-filtered panne water of  $25 \pm 3$  o/oo was used, and it was

maintained at a depth of 23 cm. Cladophora sp. was provided in an amount covering 60 - 70 % of the water's surface. Then 60 to 70 trichocorixids of mixed instars and adults were added. This sample number was suitable for the space and food conditions provided and resembled field concentrations observed.

The aquarium received mid to late daily solar exposure, but was protected from rain. It could be viewed without vibration disturbance. Detritus and algae provided substratum and food, with an assumed diurnal oxygenation cycle as reported for panne systems with floating algal mats (Nicol, 1935; Richardson, personal communication).

After 4 - 5 days acclimation, corixid activities, water and air temperatures, light conditions, and salinity were recorded hourly between 0600 and 2400 hrs daily. These data included one 5 min observation period per hr, and a total per minute activity count was established with periodic successive replicate counts. These data were combined and expressed into nine 2-hr time periods (Fig. 14). Dead animals were recorded, removed and preserved in 70 % ethanol. Momentary illumination of the aquarium with indirect light allowed for nocturnal examination, without altering activities of the animals.

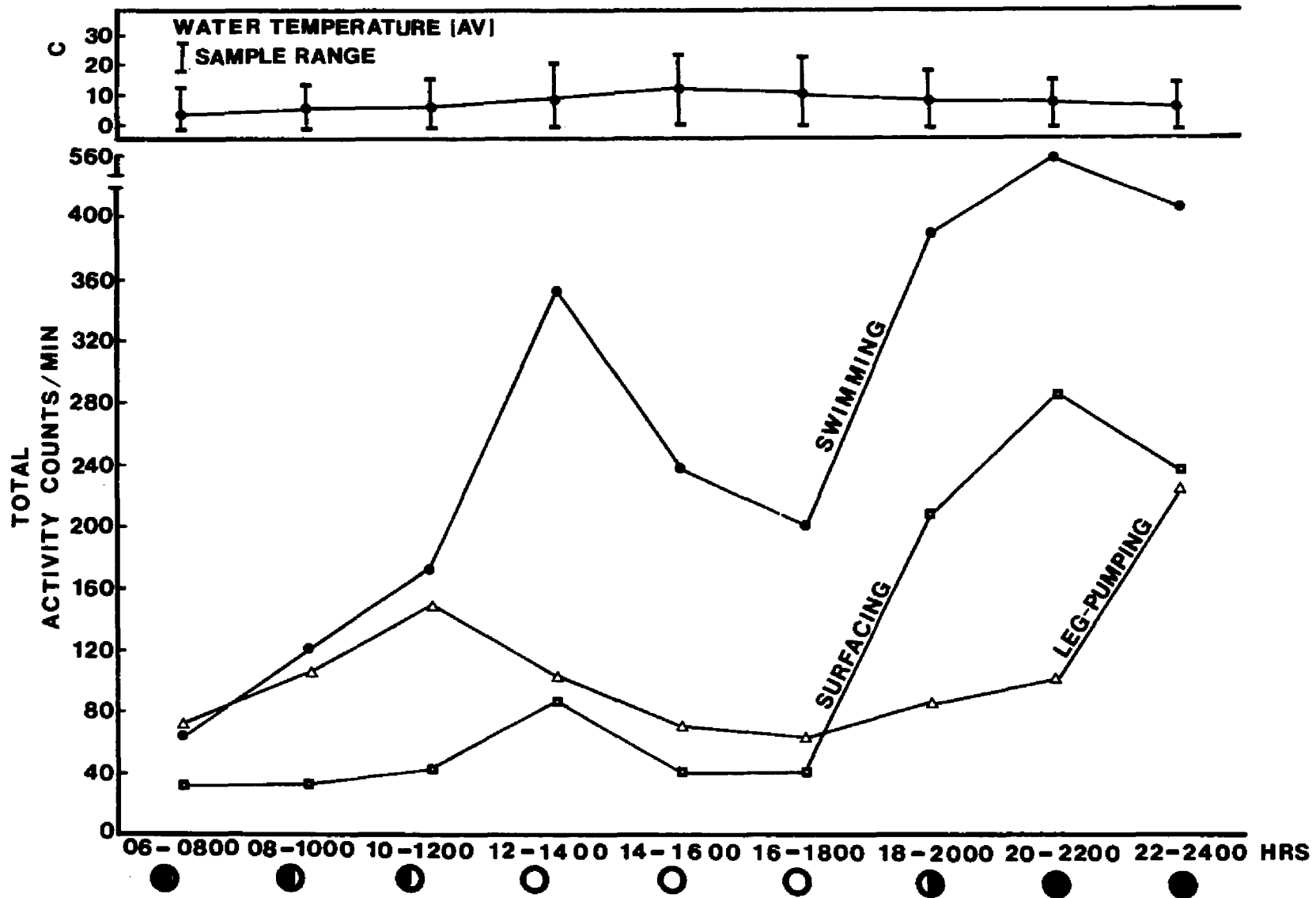
## RESULTS

### Field

The upper, shallow pannes, sites 1 - 3, showed wide diurnal and seasonal variations in salinity and temperature.

Figure 14. Activity measurements during aquarium observations of T. verticalis var. sellaris (mixed stages) at 25 o/oo salinity. Solar exposure and water temperatures recorded hourly and all measurements in bi-hourly periods between 10/3 and 11/26/75.

- = Darkness
- ◐ = Partial Sun (AM)
- ◑ = Partial Sun (PM)
- = Full Sun



Variations were less extreme in lower, deeper pannes, sites 4 - 6. Over 3 years (1972 - 1975) water temperature ranged between -1.0 C and 40 C with salinities between 1 o/oo and 160 o/oo (Figs. 15 and 16).

Diurnal variations were least during winter when ice and shorter periods of solar exposure reduced daily changes in light and temperature. However, winter salinities were variable during intermittent freezing and warming trends, and they ranged between 1 o/oo and 50 o/oo. Temperatures measured between -1.0 C and 4 C, with exception of RPS near site 6, where temperature was recorded between 4 - 6 C (Figs. 15 and 16).

During spring, increasing solar exposure, snow melt, precipitation, and spring tides produce higher and more variable diurnal water temperature ranges and wide ranging salinities. At ice-out in March, vegetative cover of tall Spartina (Fig. 2) was scoured free, and rafts of debris were washed into the upper marsh. Scouring by ice altered the entire marsh.

Salinity distribution was measured on 5/12/75 (Fig. 17). A range between 10 and 50 o/oo salinity and from 20 - 30 C were recorded in the upper marsh (50 % exposed). Seasonal drainage caused lowest salinities near site 2.

On dry, hot summer days and cool nights, a 24-hr range of  $15 \pm 5$  C was measured (sites 1 - 3) where salinities reached 40 - 68 o/oo. Following an extended period of drought conditions at site 3 changed from hypersaline (100 + o/oo) to euhaline (36 - 40 o/oo in less than 1 hr, during a spring tidal flood (Table 2). During long droughts, the substrate



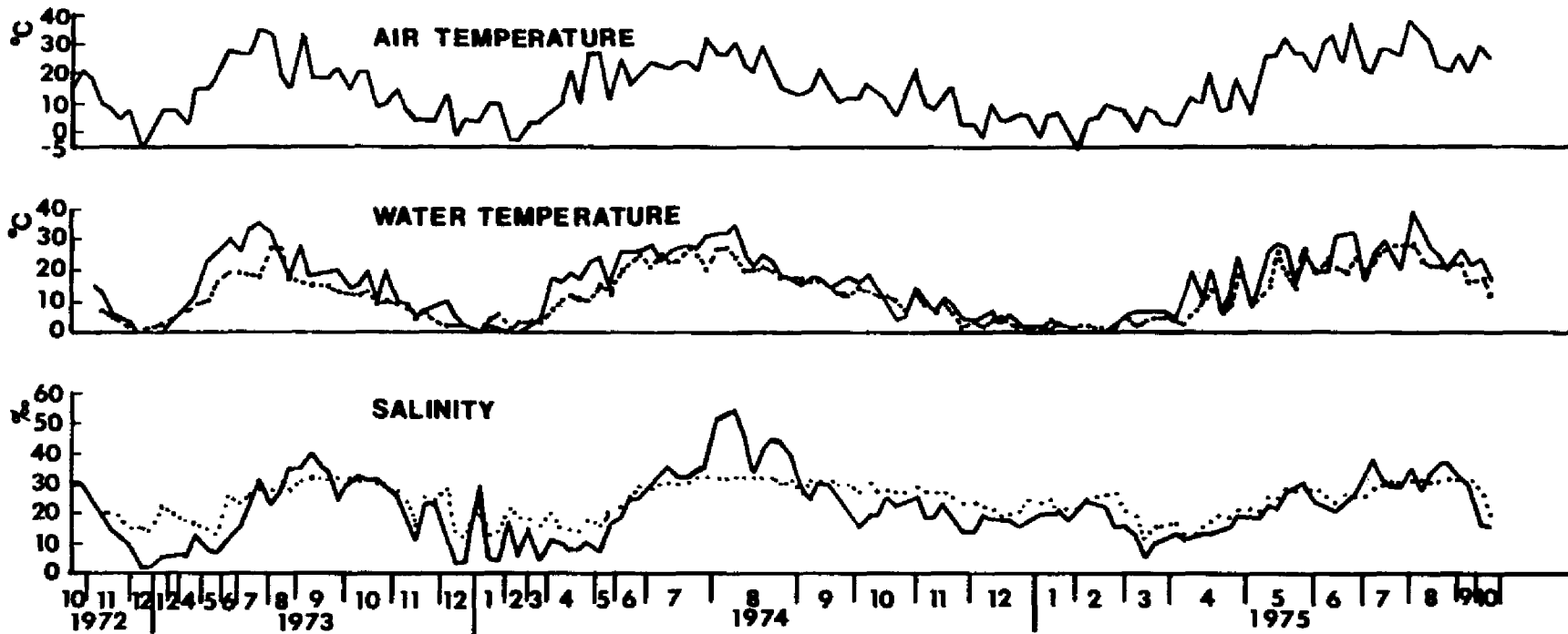
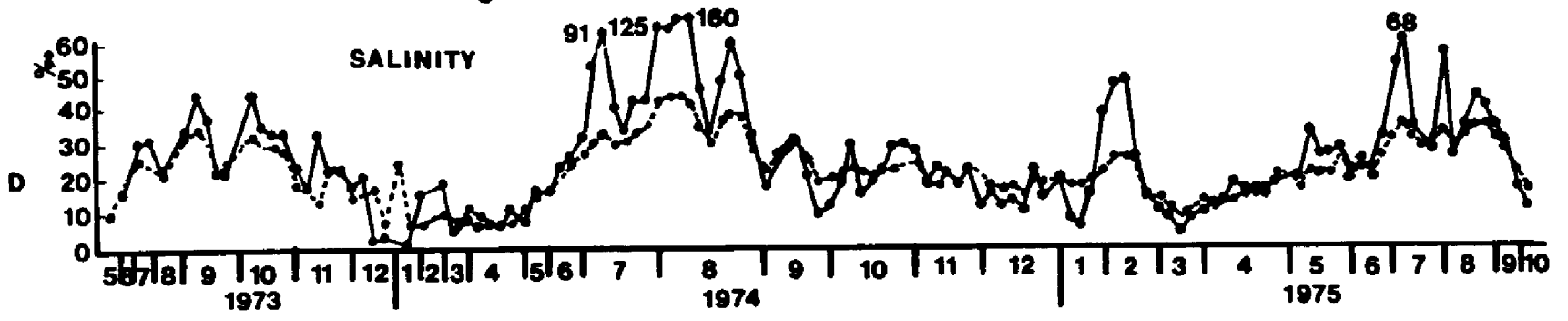
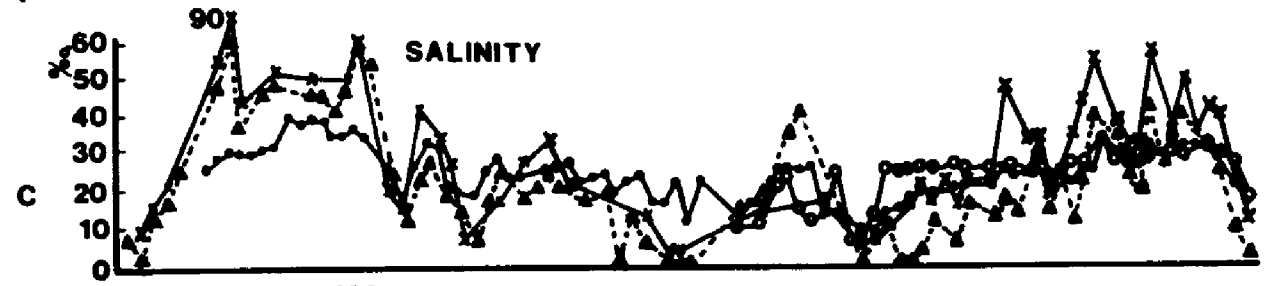
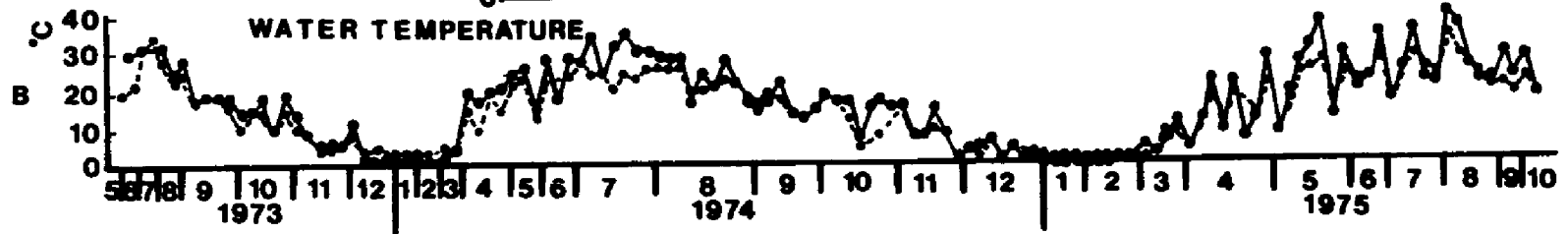
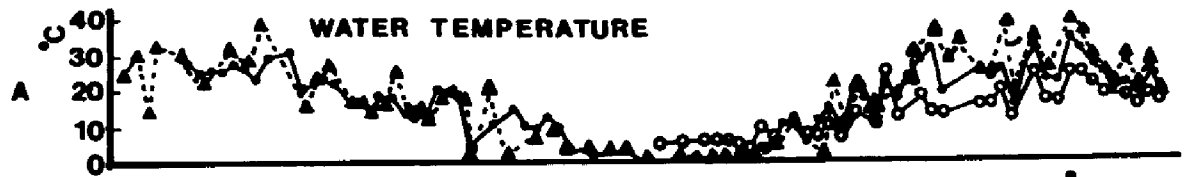


Figure 15. Relationships between seasonal salinities, water temperatures and air temperatures measured on each sample date.

— Site 4  
 ..... Little Bay

Figure 16. Relationships between seasonal salinities and water temperatures measured on each sample date.

	x————x	Site 1
Graph A & C	▲-----▲	Site 2
	•————•	Site 6
	○————○	RPS
Graph B & D	•————•	Site 3
	•-----•	Site 5



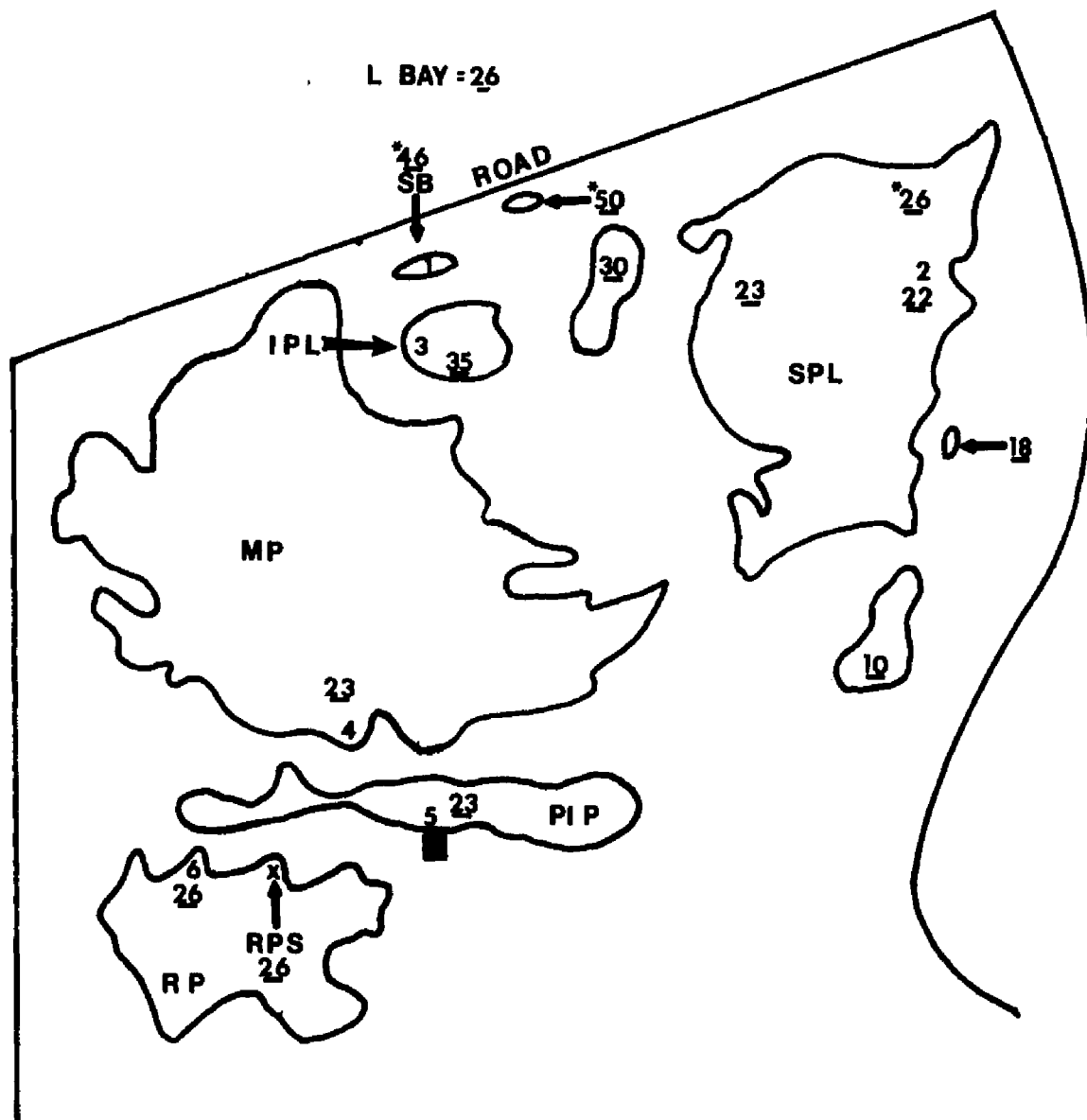


Figure 17. Spring salinity distribution on 5/12/75 during a dry neap tidal period.

Numbers underlined = Salinity (o/oo)

\* = Pressed H<sub>2</sub>O from surface peat

Table 2. Spring tidal flooding depth/salinity sequence effect on previously dry site 3 (IPL), (8/16/74)

TIME (HRS)	WATER DEPTH AT MARKER (CM)	BOTTOM SALINITY AT MARKER (o/oo)	REMARKS
0028	1.0	160.0	Preflooding period with water pressed from exposed substrate (17 C)
0035	2.5	36.0	Initial flooding (16 C)
0045	5.0	37.0	Increasing salinity due to early substrate salt diffusion effect
0050	7.5	40.0	Panne depression covered with H <sub>2</sub> O
		42.0	In deepest hole
0105	8.8	40.0	Slack tide IPL 100 % flooded

became dry, with caked mud, brittle algal crusts and cracked, silty layers (Fig. 9), and subsurface water had to be pressed to the surface for salinity measurements. Drooping Spartina leaves sheltered bottom areas that retained some hypersaline surface moisture during drought.

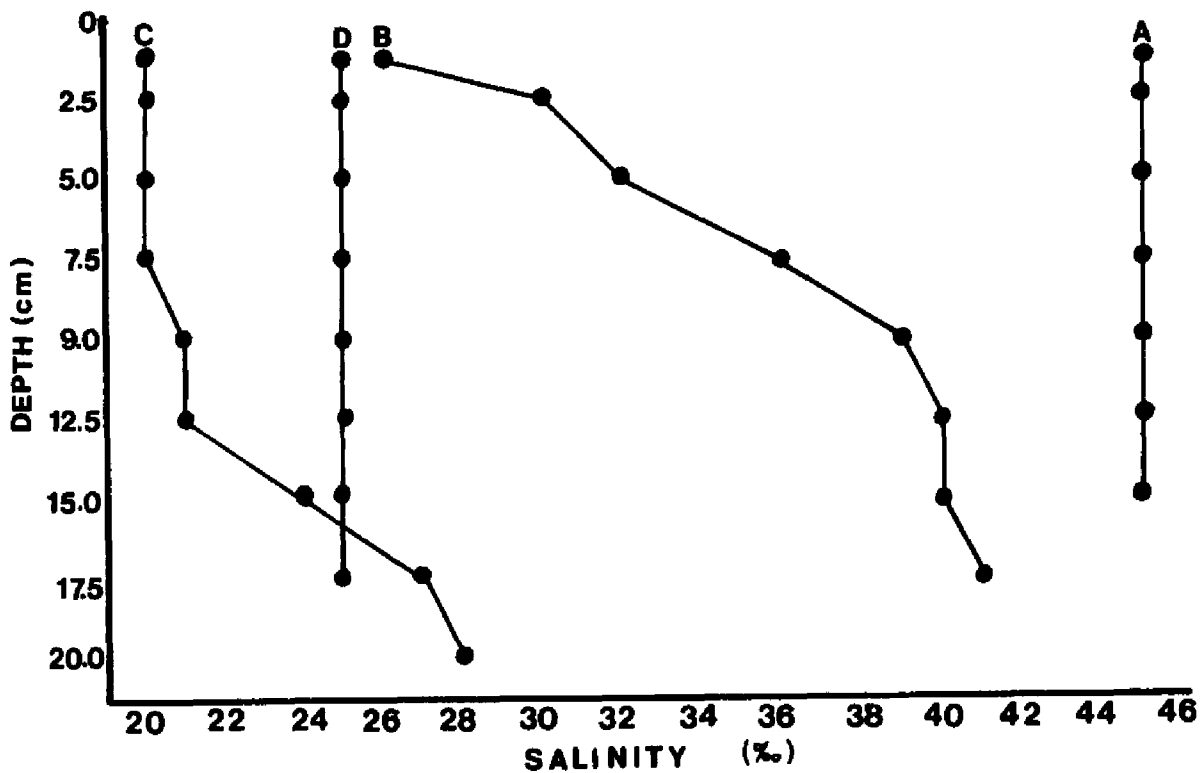
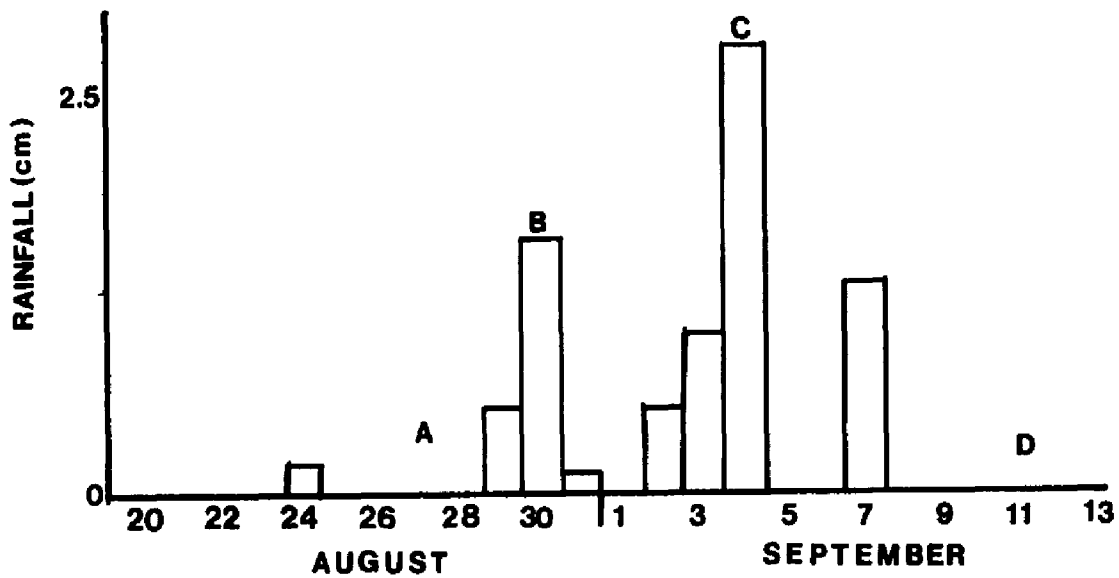
Upper sites 1, 2 and 3 were more shallow and least affected by flooding than sites 4, 5 and 6 (Fig. 5). Salinity and temperature variations were greater at the higher sites (Figs. 10 and 16). A dry period produced high salinities that were sharply reduced twice (July and August) under spring tidal influence (Fig. 10). A 1.0 cm (0.4") rainfall followed by neap tidal drought (substrate salt diffusion and evaporation) partially influenced the July/August salinity fluctuation, and increased fall precipitation reduced salinities further (Fig. 10).

The effects of evaporation and rainfall on salinity stratification of the pannes at Adam's Point were recorded at sites 4 and 5 (Figs. 18, 19 and 20). At site 4, salinity/depth variations were measured during a neap tidal period which coincided with rain that terminated summer dry conditions (Figs. 18 and 19). Surface (2.5 cm depth) water showed a greater range and more rapid salinity changes with a 19 o/oo decrease in 3 days (Days A and B), following heavy rains and calm weather (Fig. 19). Rainfall greatly exceeded evaporation so that surface waters became less saline, but because the pools were not mixed vertically by wind, bottom salinities showed only a 4 o/oo change (45 - 41 o/oo).

The range of surface/bottom salinities (26 - 41 o/oo) on August 30th (Fig. 19, day B) was changed by continued

Figure 18. Rainfall (cm/day) during period Aug. 20 - Sept. 13, 1974. (Letters denote days vertical halocline measured; see next fig.)

Figure 19. Vertical Halocline at site 4, days A - D (see Fig. 18).





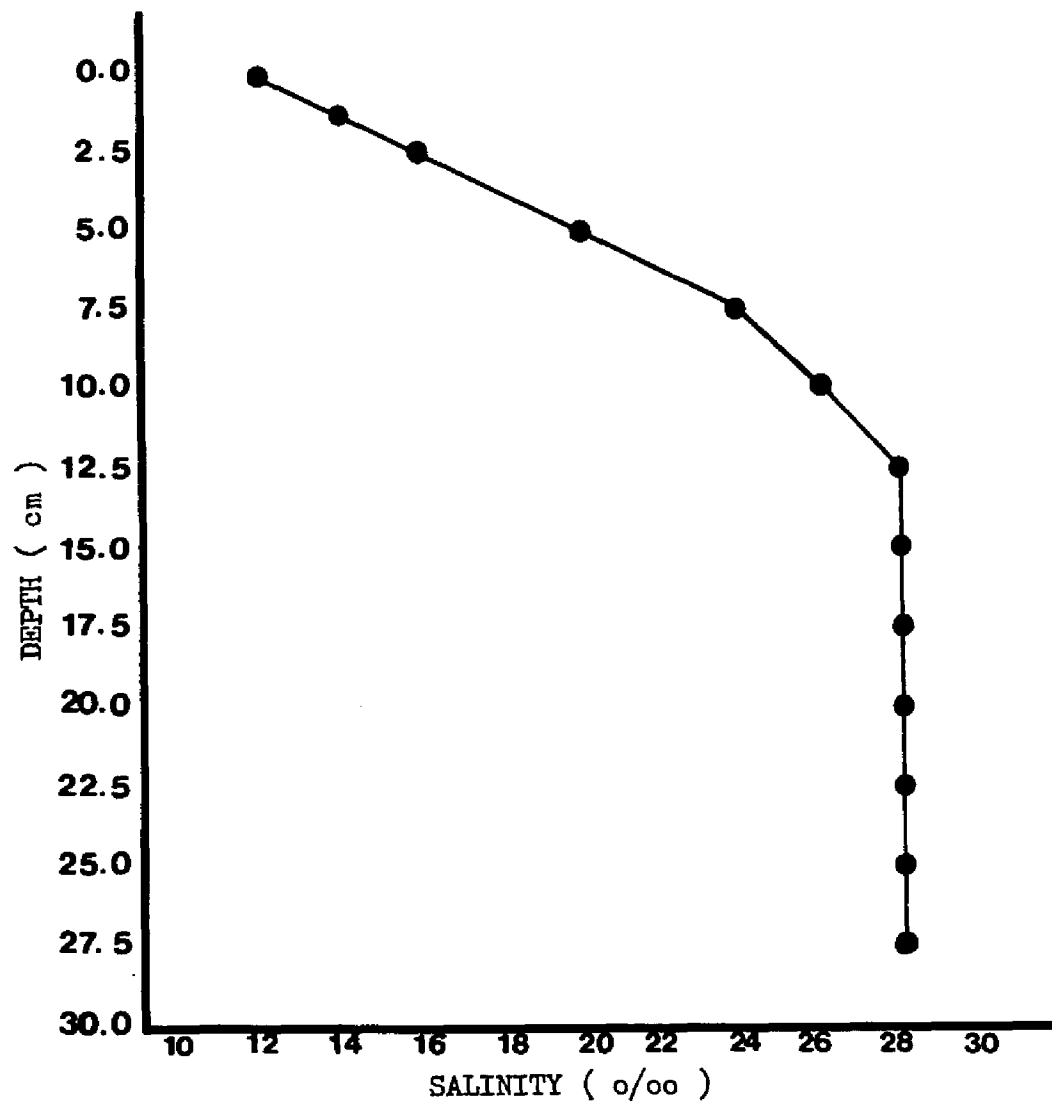


Figure 20. Halocline, site 5 (6/5/75), in floating algae.

rainfall accompanied by wind, as shown by measurements made on September 4th and 11th. On September 4th (day C), salinities from 20 to 28 o/oo existed from surface to bottom. From the 12.5 cm depth to the bottom, mixing was reduced, and less uniform conditions were found (Fig. 19). On September 11th (day D), a uniform salinity curve (25 o/oo) was measured from surface to bottom, resulting from reduced rainfall, evaporation and continued vertical mixing (Figs. 18 and 19).

A salinity curve similar to day B (Fig. 19) was measured at site 5 on 6/5/75 following a period of rainfall and limited mixing (Fig. 20).

#### Seasonal Occurrence by Size Class and Stage

Between April and October, 1975, a quantitative study of the Trichocorixa verticalis population in site 3 (IPL) was undertaken to determine the time of winter (dormant) egg development, first hatching, instar development to adult, and corixid densities in situ (Figs. 21 and 22) (Table 3). An abundance of dormant winter eggs had been found at site 3 during preliminary surveys (1974 - 1975), and 2 years of winter sampling indicated a total mortality of adult corixids by January. This situation presented an excellent opportunity to study development from egg to adult.

During earlier studies, I discovered initial hatching of winter eggs of T. verticalis on 4/22/74. In spring, 1975, the initial hatching dates were within 1 - 2 days of the preceding year, but physical conditions for both periods were different. There was a warm, moist spring in 1974 and a dry, cool spring in 1975 (Table 4). Seasonal salinity and

Figure 21. Length-frequency distribution of 5 size class categories of T. verticalis var. sellaris collected from Adam's Point site 3 between 4/24 and 8/10/75 showing nymph/adult ratios.

\*  
DP = Dry Period

Body Length

A = 1.0 mm

B = 1.5 mm

C = 2.0 - 2.5 mm

D = 3.0 - 3.5 mm

E = 4.0 - 5.0 mm (Adults)

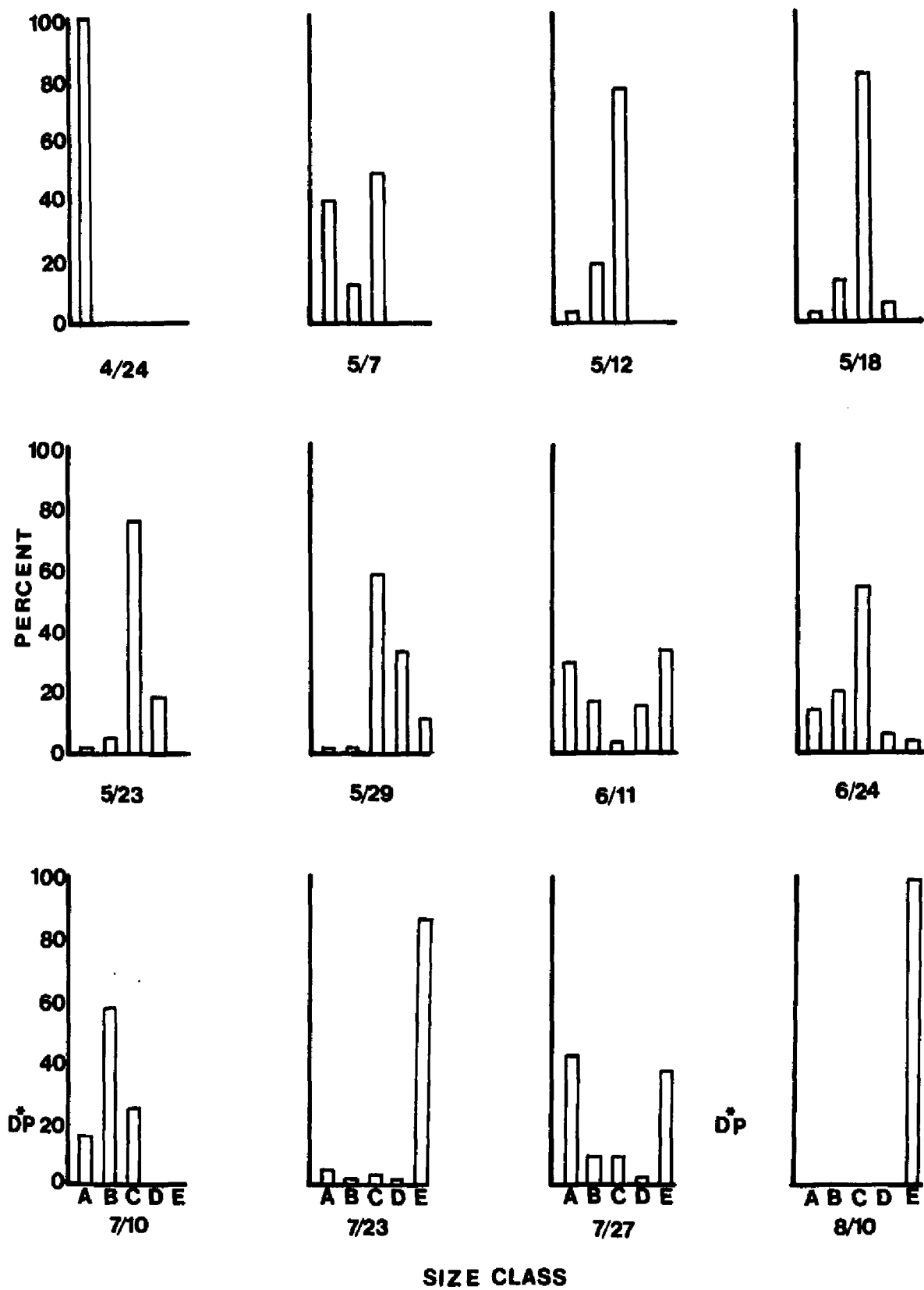


Figure 22. Length-frequency distribution of 5 size class categories of T. verticalis var. sellaris collected from Adam's Point site 3 between 8/14 and 10/22/75 showing nymph/adult ratios.

Body Length

A = 1.0 mm

B = 1.5 mm

C = 2.0 - 2.5 mm

D = 3.0 - 3.5 mm

E = 4.0 - 5.0 mm (Adults)

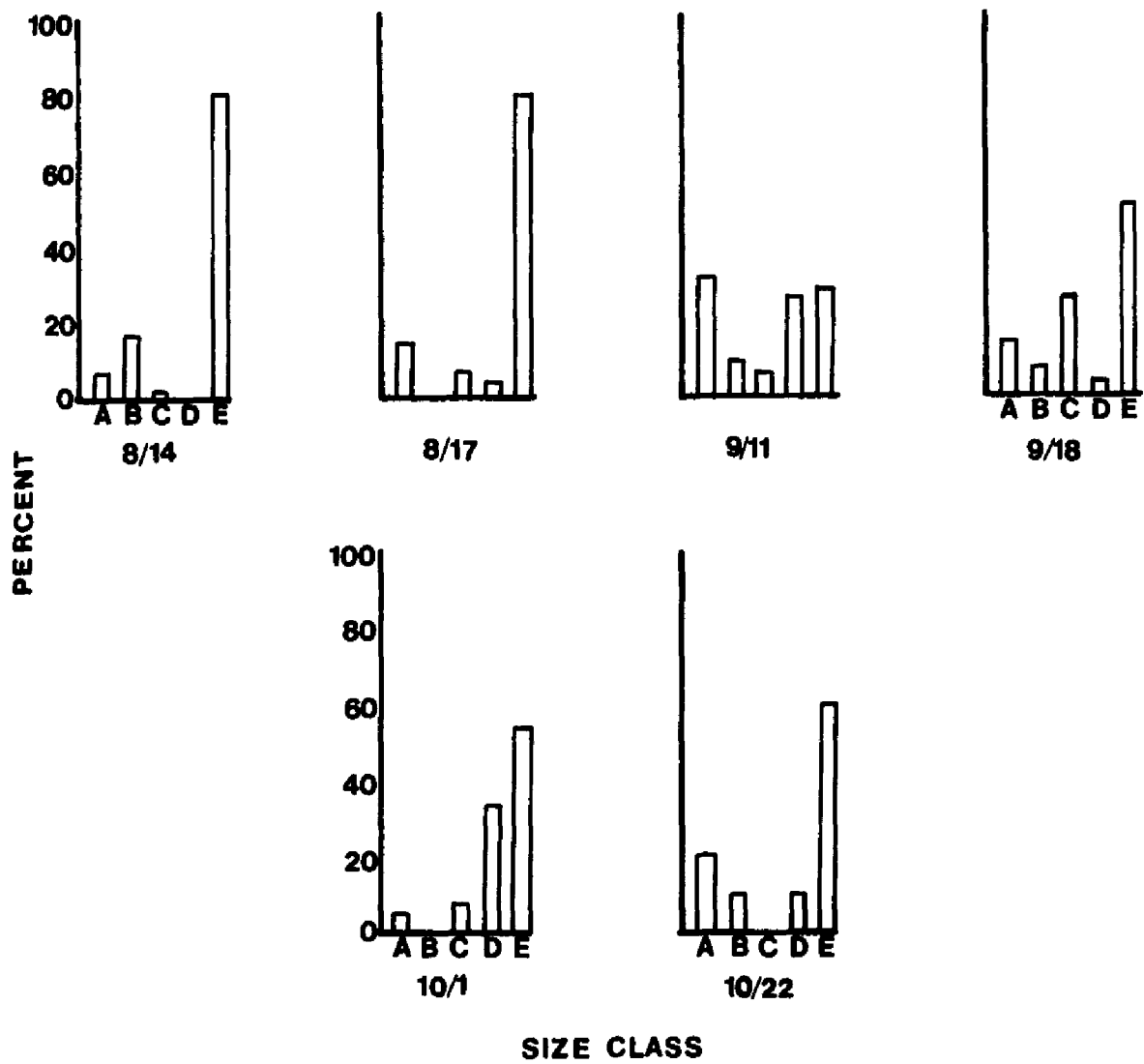


Table 3. Number of *Trichocorixa verticalis* from bottom (open water) samples, site 3 (1975).

SAMPLE DATE	NUMBER (m <sup>2</sup> )	BOTTOM	
		SAL. (o/oo)	W.T. (C)
4/24 <sup>a</sup>	75.4	20	12
5/7	1,960.1	22	20
5/12	26,914.2	35	30
5/18	5,428.1	28	32
5/23	1,492.7	29	38
5/29	3,392.6	33	14
6/11	2,299.4	24	18
6/24 <sup>b</sup>	12,567.5	33	23
7/10 <sup>b</sup>	180.9	38	36
7/23	776.5	31	22
7/27 <sup>b</sup>	851.9	30	17
8/10 <sup>b</sup>	75.4	28	37
8/14	663.4	36	26
8/17	904.7	45	23
9/11	399.6	36	29
9/18	1,281.6	32	23
10/1	980.1	18	28
10/22	128.2	12	18
Range	75.4 - 26,914.2	12 - 45	12 - 38
Mean	3,909.6	29.4	24.8

<sup>a</sup>First hatched winter eggs

<sup>b</sup>Change in number of animals following re-flooding of dessicated pools (See also Fig. 21)

N = 108

Table 4. T. verticalis embryonic development in the field  
in relation to season, salinity and temperature  
at site 3

Sample Date	Salinity (o/oo)	Water Temperature (C)	Egg Stage
4/7/74	10	20	No eyespots, Cream-yellow
4/12/74	8	18	Pin-point red eyespots
4/18/74	8	20	Distinct red eyespots and dorsal glands
4/19/74	8	21	
4/22/74	13	25	First Hatch, 1st instars
-----			
4/4/75	12	5	No eyespots, Cream-yellow
4/10/75	14	12	No eyespots, Cream-yellow
4/11/75	15	23	No eyespots, Cream-yellow
4/16/75	20	10	Pin-point red eyespots No dorsal glands
4/18/75	18	22	Distinct red eyespots Few dorsal glands
4/21/75	18	7	Distinct red eyespots Many dark dorsal glands
4/24/75	20	12	First Hatch, 1st instars All egg stages present



temperature differences for the 2 years did not seem to alter corixid egg hatching dates at site 3.

Egg development was duplicated in the laboratory at variable temperatures including a constant 15 C and an uncontrolled range of 20 - 25 C (M 22.5 C), and at separate salinities of 14 and 20 o/oo (Table 5). Field salinities and temperatures at site 3 during this same period (4/75) are indicated in Table 4. Laboratory egg development followed a similar pattern as did the eggs at site 3 (Tables 4 and 5). Development proceeded to hatching on 4/23, which was within 12 hours of observed field hatching.

Masses of eggs at all developmental stages were present on 4/24/75 at first egg hatching. Further, within any mass, eggs were in different stages of development, including creamy, cream-yellow early eyespot and dorsal gland formation.

Following appearance of adult T. verticalis, sampling was continued through spring and summer. Breeding produced pulses of size classes hence successive variation in per cent size class ratios and continual population replenishment. The importance of this staggered egg hatching became clear during two periods of drought between 6/24 - 7/10 and 7/29 - 8/10 (Figs. 21 and 22), when juvenile - adult stages died, and only the eggs survived. Undeveloped eggs survived under mats of Spartina stems, and when reflooded (in the field or in culture), they developed and hatched.

A natural cycle of development from egg to third size class (2.0 - 2.5 mm) juveniles followed the drought between

Table 5. T. verticalis embryonic development in the laboratory: eggs collected at site 3, and held at different salinities and temperatures

Collection Date Egg Stage	Holding Conditions Salinity      Water Temp. (o/oo)          (C)		Observation Date Egg State
4/11/75 No eyespots Cream-yellow	14	21 - 24	4/15/75 Pin-point red eyespot
4/21/75 Distinct red eyespot and dorsal glands	20	15	4/28/75 First Hatch 1st instars (7 days)
4/21/75 Distinct red eyespot and dorsal glands	20	20 - 25	4/23/75 First Hatch 1st instars (2 days)

sampling dates 6/24 and 7/10. Fourth size class (3.0 - 3.5 mm) juvenile and adults (4.0 - 5.0 mm) were missing (Figs. 21 and 22), as expected.

#### Observations on T. verticalis Invertebrate Predators

The adult Hygrotus nubilis (Coleoptera: Dytiscidae), with characteristic dytiscid swimming proficiency, were in open water, bottom silts, or under drift deposits. In winter, adults were inactive beneath debris, encased in ice. Hygrotid larvae remain within floating algae, can swim or crawl rapidly on the bottom, and fed on nymphal T. verticalis.

Enochrus hamiltoni (Coleoptera: Dytiscidae) was the most common beetle in the pannes. It is a slow swimmer and crawls to the bottom on submerged vegetation and debris, from which it can rapidly float to the surface. Adults were in the pannes throughout the year, while larval occurrence was from May through September (Table 6). During dry periods, Enochrus larvae and adults crawl across the moist, exposed algae and Ruppia mats, and brief flights by adults were observed in late April and early May. Leech and Chandler (1956), refer to hydrophilid spring dispersal flights. I observed this means of dispersal used also during dry periods.

Enochrus form a copulatory amplexus, head to head, male dorsal to female, but several instances of tail to tail, abdominal tip attachment were noted also. The male rocks forward and backward, and wobbles side to side above the female. The males abdominal tip is bent forward and beneath the female while eggs are laid into a hardened, preconstructed,

Table 6. Seasonal occurrence of insects in the Adam's Point marsh

Species	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
Odonata, Libellulidae	I	I	I	I	I	I	I	I	I	I	I	I
<u>Erythrodiplax berenice</u>					A	A	A	A	A			
<u>Sympetrum vicinum</u> <sup>a</sup> (MS)									A	A	A	
Hemiptera, Corixidae				I	I	I	I	I	I	I	I	I
<u>Trichocorixa verticalis</u>				A	A	A	A	A	A	A	A	A
Mesoveliidae					I	I	I					
<u>Mesovelia mulsanti</u>					A	A	A	A	A	A		
Trichoptera, Limniphilidae			I	I	I							
<u>Limniphilus submonilifer</u> (MS)												
Lepidoptera, Pyralidae							I					
<u>Nymphula</u> sp. (MS)												
Coleoptera, Dytiscidae				I	I							
<u>Hygrotus nubilus</u>	A	A	A	A	A	A	A	A	A	A	A	A
Hydrophilidae					I	I	I	I	I			
<u>Enochrus</u> spp. ( <u>E. hamiltoni hamiltoni</u> )	A	A	A	A	A	A	A	A	A	A	A	A
<u>Tropisternus quadristriatus</u>						I	I	I	I			
Diptera, Culicidae			I	I	I	I	I	I	I	I		
<u>Aedes sollicitans</u>					A	A	A	A	A	A		
Chironomidae	I	I	I	I	I	I	I	I	I	I	I	I
<u>Chironomus</u> sp.					A	A						
Ceratopogonidae	I	I	I	I	I	I	I	I	I	I	I	I
					A	A	A	A	A			
Stratiomyidae			I	I	I	I	I	I	I	I	I	I
<u>Odontomyia cincta</u>					A	A	A					
Tabanidae				I	I	I	I	I	I	I	I	I
<u>Tabanus atratus</u> (MS)												
Dolichopodidae		I	I	I			I	I	I		I	I
					A	A		A	A	A	A	A
Syrphidae, Eristalinae (sp. ?)				I			I	I	I	I	I	I
<u>Polydontomyia curvipes</u> <sup>a</sup>					A	A	A	A	A			
Ephydriidae		I	I	I	I	I	I	I	I	I	I	I
<u>Ephydra subopaca</u>	A	A	A	A	A	A	A	A	A	A	A	A

A = Adult

I = Immature

a = Adults only

(MS) = Migratory Subsystem Species

silk-like cocoon. These white egg cocoons (4.0 - 5.0 mm long) are numerous in late spring and early summer and are attached to Ruppia stems and algal filaments. Fifteen to 20 bright orange eggs were enclosed in the cocoon by the female, which sex, according to Pennak (1953), is equipped with a pair of spinnerets at the apex of the abdomen. Developing larvae were removed from each of several E. hamiltoni cocoons.

In laboratory cultures, Enochrus larvae fed on T. verticalis nymphs of the 2nd instar (1.5 mm). Beetle larvae hold captured trichocorixids in their mandibles, as they progress forward and backward, until located above the water surface. This leaves the anterior 1/3 of the larval body free of the Spartina stem. With mandibular flexing the beetle forces its head into the body cavity of the trichocorixid, and appeared to wear it like a hat. About 10 to 15 minutes passed before the empty corixid carcass was discarded. These beetles feed on other invertebrates as well.

Tropisternis quadristriatus (Coleoptera: Hydrophilidae) is the largest (10 - 13 mm long) aquatic beetle in the pannes. The larvae and adults swim more proficiently than Enochrus hamiltoni. Adult Tropisternis surface and dive rapidly from both algal mat and open water bottom silts. This beetle was not observed in flight during this study..

From late May through July, T. quadristriatus adults stridulate beneath Cladophora mat near the base of Spartina stems. In aquaria they often stridulate after dark, as individual adults produce a cricket-like succession of clicks of 4 to 5 seconds duration. In July at site 5, several beetles

were stridulating in unison and they reminded me of a miniature chorus of frog mating calls.

Tropisternis show similar copulatory amplexus as that described for Enochrus. During late May through June, large white egg cocoons (8 - 10 mm long) of T. quadristriatus were in dense masses on drooping, submerged S. alterniflora leaves at the edge of site 5. The cocoons, unlike Enochrus, were not attached underneath partially submerged driftwood.

T. quadristriatus larvae were more abundant in algal samples, though in exposed areas they were on the bottom. Like Enochrus larvae, they were observed moving across the moist, exposed substrates during dry periods, and fed on immature T. verticalis and other invertebrates.

Several semiaquatic Hemiptera are permanent inhabitants of the Adam's Point salt marsh, where their eggs, developing nymphs and adults were seen. The species observed form part of the Families Mesoveliidae, Lygaeidae, and Saldidae. Mesovelgia mulsanti and many saldids, including Pentacora sphacelata, frequented the pannes throughout late spring and summer (Table 6). Britton (1923), mentions both Pentacora and Saldula pallipes (Saldidae), and Mesovelgia sp. on sea beaches, salt marshes and tidal flats in Connecticut. I collected both Pentacora and one species of Lygaeidae at Adam's Point.

Both winged and wingless adult Mesovelgia were commonly on the surface of sites 4 and 5, usually near areas of heavy Cladophora and Ruppia mat. Parts of Ruppia with their eggs embedded were unintentionally collected and later discovered in laboratory culture, where they were held until hatching.

First and second stage nymphs (1.0 - 2.0 mm) remained submerged for long periods and fed on first stage Trichocorixa by holding and piercing this bug beneath the abdominal edge. Later stage Mesovelgia (2 - 3 mm) were also held in culture with T. verticalis eggs of pre-eyespot stage, and the "water treaders" pierced the egg chorion near the attached end. Several empty egg cases resulted from this egg predation. Adult M. mulsanti feed on struggling immature and adult T. verticalis on the water surface during extreme stress effects of summer drought. Apterous adults were found more often than macropterous specimens, as reported by Usinger (1956).

Saldids were more common on exposed mud and shallow pannes (sites 1 - 3). According to Brown (1948), the nymphs are more aquatic than the adults, a fact I verified in the marsh. Developing nymphs were submerged in pannes during May and June, whereas adults were on exposed muds. Usinger (1956) referred to their predation on small insects while submerged and on the surface, and I suspect their prey includes nymphal and adult T. verticalis.

#### Predation on T. verticalis by fish

Gut analysis of 10 Fundulus heteroclitus (2 - 4 cm long) collected in the marsh showed that 67 % of the food consisted of immature trichocorixids. Larval Ephydra subopaca, Enochrus hamiltoni, Aedes sollicitans and some algal filaments made up the remaining stomach contents of the fish. In aquaria and in the field, Fundulus were observed holding a near vertical, head-up position, just beneath the floating algal mat, from

which they would obtain juvenile T. verticalis, gammarid amphipods, dipteran larvae and tubificid oligochaetes. Pungitius pungitius and anguilla rostrata fed on T. verticalis in aquaria, but this was not verified in the field.

#### Birds: Food Item Analysis

Of 72 species of birds observed during my study of the Adam's Point Marsh, 4 were nesting species. The Song Sparrow and Red-Winged Blackbird, nest in the Spartina patens and dwarf Spartina alterniflora respectively, while Long-billed Marsh Wrens and Virginia Rails nest in the tall S. alterniflora. An additional 44 species were visitors, but many feed in the marsh. Of the remaining 28 species, one group generally is found in tall Spartina and on flooded and exposed mud flats (including Canada Goose, Black Duck, Herring Gull). The second occurred on high dwarf Spartina marsh and pannes, hence was most likely to be important as insect predators.

Table 1 shows seasonal occurrence of sandpipers, plovers, kingfishers, herons, egrets and some other birds of pannes. Shorebirds usually form multispecies aggregations feeding and resting in pannes and on exposed mud. They were often joined by 1 - 2 Green Herons, and 3 - 4 Snowy Egrets. During late spring and summer, American Bitterns and Black-crowned Night Herons occurred in the high marsh, but more frequently in the tall Spartina. Waders are opportunists, (Recher, 1966), so have different diets at different localities and times (Bent, 1927, 1929; Recher, 1966).

During summer and fall, 1974 - 1975, 12 shorebirds were collected while feeding in the study pannes at Adam's Point



(Table 7). Of these birds, nine gizzards were opened which contained whole bodies or recognizable parts of T. verticalis. For the Least Sandpiper and Greater Yellowlegs sampled, this boatman was a predominant food item (Table 7).

On August 15, 1974, after a period of drought, seven species of shorebirds and waders were together in a small, shallow area of hypersaline water retained in the main panne approximately 2 m into the main depression from site 4, including 19 Least Sandpipers, 10 Semipalmated Sandpipers, 10 Lesser Yellowlegs, 4 Greater Yellowlegs, 4 Killdeer, 1 Green Heron, and 3 immature Snowy Egrets. At that time, many small 8 - 12 cm Anguilla were seen in a belly-up position, incapable of swimming. Some eels were emerging from the water to the mud, but close examination of dying eels revealed no external wounds. Fundulus (4 - 8 cm) were in schools near the surface, but some were dead on the bottom. Dense populations of T. verticalis were constantly surfacing and producing a conspicuous sprinkle effect at the surface (See quantitative data on T. verticalis from this site in Table 8).

Waders and shorebirds find dense and easily acquired fish and insect prey in drying panne areas. The egrets and heron ate Anguilla rostrata (American Eel) and Fundulus heteroclitus (Common Mummichog). Egrets devoured eels immediately after capture, while the heron carried its prey to shore, dropping it and probing with rapid jabs before swallowing it. Both are known, in addition, to be insect feeders (Bent, 1926). Semipalmated Sandpipers appeared to do more actual wading than Least Sandpipers, but both fed near the water/mud

Table 7. Invertebrates recovered (% of total recognizable prey) from shorebird gut analysis of summer and fall 1974, 1975

Invertebrates recovered	Species, Number Analyzed					
	Least Sand-piper (4)	Semi-palmated Sandpiper (1)	Solitary Sandpiper (1)	Lesser Yellow-legs (2)	Greater Yellow-legs (2)	Killdeer (2)
Foreminifera species.....	1.0	—	—	—	—	—
Bryozoa species.....	—	5.0	—	—	—	—
Hydrobia species.....	4.5	—	—	—	1.3	—
Bivalvia 5mm.....	1.0	—	—	—	—	—
Ostracod species.....	3.0	—	—	—	—	—
Harpacticoida Copepoda species....	7.8	—	—	—	—	—
Amphipod species.....	6.1	66.2	—	44.6	1.2	—
Neopanope texana.....	—	—	—	—	12.5	—
Pardosa milivina.....	—	—	—	—	1.3	—
Trichocorixa verticalis.....	23.1	—	5.0	2.6	21.2	—
Mesovelia mulsanti.....	0.9	—	—	—	—	—
Eochrus hamiltoni.....	11.4	27.8	—	—	62.5	39.4
Tropisternus quadristriatus.....	—	—	—	—	—	1.7
Chironomid species.....	0.1	—	—	—	—	—
Ceratopogonid species.....	16.0	—	—	—	—	—
Odontomyia cincta.....	17.2	—	95.0	5.4	—	57.2
Dolichopodid species.....	1.1	—	—	—	—	—
Ephydrid species.....	6.8	—	—	47.4	—	1.7
Fundulus heteroclitus (eggs).....	—	1.0	—	—	—	—

Table 8. Number of fauna from bottom (open water) samples, site 4 (8/13/74)

ORGANISM	AVERAGE DENSITY (m <sup>2</sup> )
<u>Hydrobia</u> sp.	11,195.4
<u>Trichocorixa verticalis</u>	10,976.8
<u>Chironomus</u> sp.	490.0
Ceratopogonidae	75.4
Amphipoda (Gammaridae) <sup>a</sup>	75.4

<sup>a</sup>90 % Juvenile

interface. They picked at the mud surface and beneath the water, but no prey was observed at 4 - 5 m viewing distance. Numerous adult brine flies (Ephydriidae) on the water surface seemed to be ignored by these sandpipers, that have been reported as insectivores (Bent, 1927, 1929). Killdeer and Solitary Sandpipers remained on exposed mud or in very shallow water of sites 1 - 3. Greater and Lesser Yellowlegs waded in the pannes feeding on small eels and picking at smaller organisms stirred up by foot movements.

#### Associated Biota-Community Composition

Floating filamentous algal mats (Cladophora sp.), and bottom surface silt comprise two panne microhabitats. To detect and quantify the macro-fauna of the former, twenty-four samples were collected from sites 3, 4 and 5 from 7/8/74 - 9/18/75.

Algal macrofauna (Table 9), includes 11 species of insects. Trichocorixids and ceratopogonid midges are among

Table 9. Number of fauna and high density dates in the algal mat at sites 4 and 5

ORGANISM	AVERAGE NUMBER (m <sup>2</sup> )	DATE OF PEAK NO.
<u>Hydrobia</u> sp.	6521.3	8/15/74
Turbellaria	1364.6	5/7/75
Oligochaeta	1281.7	5/7/75
Ceratopogonidae (Diptera)	1081.9	8/15/74
<u>Trichocorixa verticalis</u>	591.8	7/27/75
Amphipoda (Gammaridae)	116.9	9/18/75
<u>Enochrus</u> sp. (Coleoptera)	109.3	5/29/75
<u>Odontomyia cincta</u> (Diptera)	98.0	7/26/74
<u>Ephydra subopaca</u> (Diptera)	79.2	8/15/74
Ostracoda	75.4	2/25/75
<u>Mesovelgia mulsanti</u> (Hemiptera)	45.3	8/15/74
<u>Tropisternus quadristriatus</u> (Coleoptera)	22.6	7/27/75
<u>Fundulus heteroclitis</u>	18.9	7/27/75
<u>Nematostella vectensis</u> (Coelenterata)	15.1	9/18/75
Polychaeta	15.1	8/15/74
<u>Erthrodiplax berenice</u>	11.3	3/7/75
<u>Tabanus atratus</u> (Diptera)	11.3	9/18/75
Hydracarina	11.3	5/7/75
<u>Dinophilus gardineri</u>	7.6	5/7/75
<u>Chironomus</u> sp. (Diptera)	7.6	5/29/75
<u>Eristalinae</u> (Diptera)	7.6	9/18/75
Nemertea	3.8	2/25/75
<u>Palaemonetes pugio</u>	3.8	2/25/75
Sciomyzidae (Diptera)	3.8	10/7/74
<u>Pardosa</u> sp.	3.8	5/29/75
<u>Anguilla rostrata</u>	1.5	8/15/74
<u>Pungitius pungitius</u>	1.5	3/7/75

the most abundant species of animals. Table 4 shows seasonal occurrence of the study species and other insects found in the marsh.

The two microhabitats are linked by Ruppia in summer, and by sinking mats of algae under winter ice, and sometimes exchange of organisms can occur. Data in Table 9 are from collections of floating algae, including winter algal sections within and just below the ice.

Some organisms in Table 9 are limited to the algae, but others are bottom inhabitants as well. More permanent bottom invertebrates included tubificid oligochaetes, larval Chironomus, Eristalinae, Adult Hygrotus, tube-dwelling polychaeta, harpacticoid Copepoda, and nematodes. At times, some of the above species and particular stages were in both the algae and bottom substrata. For example, during spring laboratory aquarium observations, tubificids were numerous in bottom silts, but at dusk worms would swim at the surface and crawl through floating algae. Other forms such as free-swimming trichocorixids, amphipods, ostracods, larval and adult Tropisternis quadristriatus and Acarina live in both microhabitats and swim between them.

More surface-oriented larvae are capable of submergence by hydrostatically sinking and are often in bottom silts. They included larval dipterans, Odontomyia cincta (Stratiomyidae), Tabanus atratus (Tabanidae), and Ephydra subopaca (Ephydriidae). Other crawlers like the salt marsh dragonfly naiad, Erythrodiplax berenice, larval Enochrus hamiltoni and Hygrotus nubilis were noted on the bottom.

Some major macrofaunal components of Adam's Point Study Pannes are illustrated in Fig. 23. Some animals are only temporary inhabitants, visiting this system to feed and/or reproduce during periods of high marsh productivity. Obvious examples include bird and fish species exploiting yields in the pannes during seasonal pulses of food supply. Rats, mice, raccoons, fox and deer are probably in this category also. Several invertebrate species including some insects are also temporary inhabitants of the high marsh.

All these animals represent a migrating subsystem (Copeland, Odum and Moseley, 1974), as migrating stocks from one kind of system coupling with the energies of the coastal system. They plug into the energy cycle of the marsh, then unplug and emigrate to other systems.

The most conspicuous migrating non-insects found were the crustaceans such as Carcinus maenas, the Green Crab, and Palaemonetes pugio, the Glass Shrimp, both of which were collected infrequently during the summer, fall and late winter. Other Crustacea belonging to this group were the Amphipoda, Gammarus mucronatus, G. palustris and C. tigrinus; all three were present during winter and spring. On two occasions during early summer, Limulus polyphemus (Merostomata), were observed in the deeper pannes of the lower study zone. The Gastropod, Melampus bidentatus, was found during spring beneath debris that washed into the lower study zone.

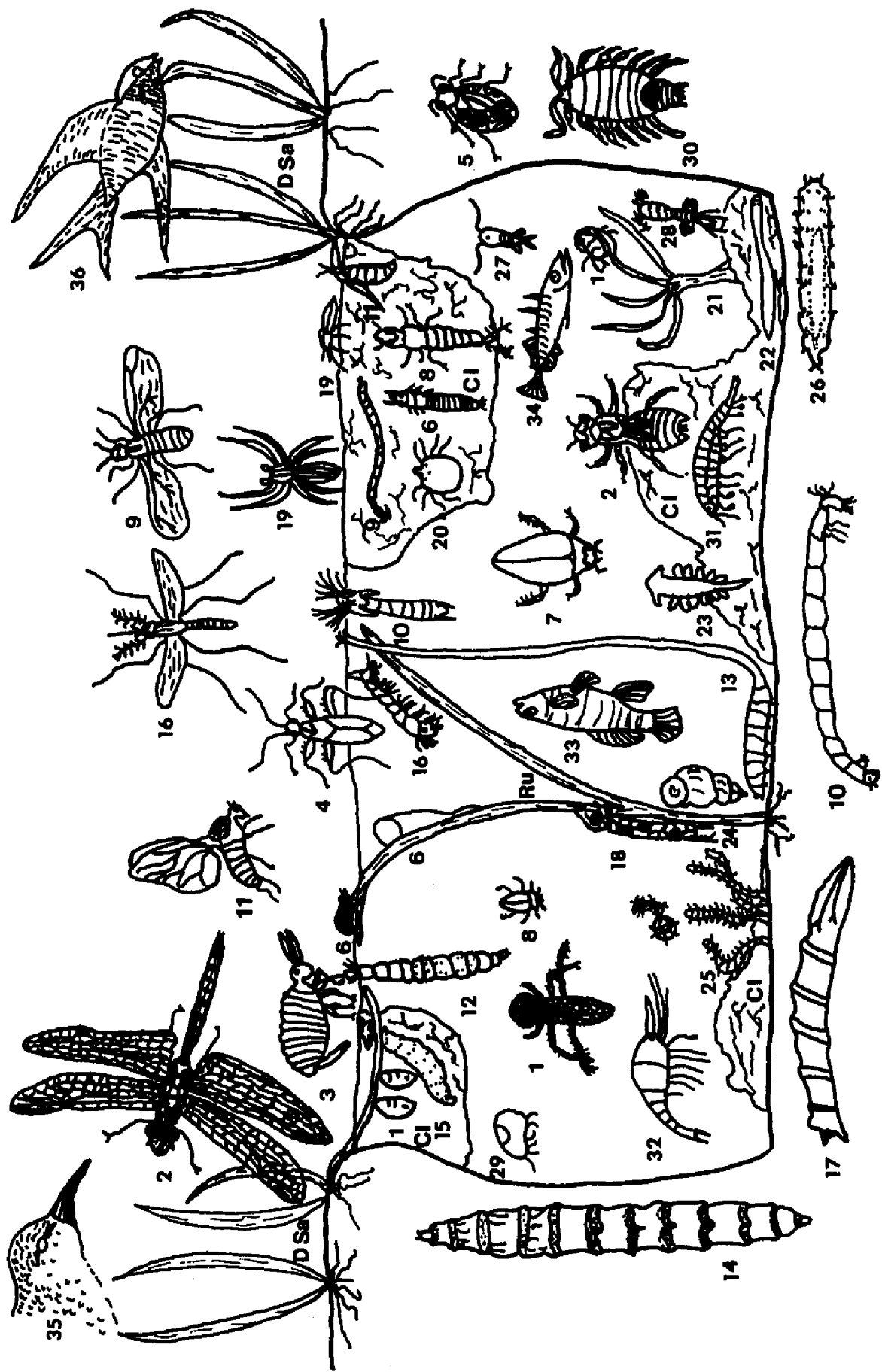
None of the above mentioned organisms are in the high marsh pannes throughout the year, but are generally in the lower intertidal marsh and bay system. Two permanent high

Figure 23. Diagramatic salt marsh panne system including floating algal subsystem and bottom subsystem, some major associated biota and a corresponding list of organisms illustrated.

Ru-Ruppia maritima

Cl-Cladophora sp. (algal  
mat)

D Sa-dwarf Spartina alterniflora





LIST OF ANIMALS ILLUSTRATED IN FIGURE 23 WITH THE  
FOLLOWING DEVELOPING STAGES INDICATED WHEN INCLUDED

(E-eggs, I-immatures, P-pupa and Ad-adults)

1. HEMIPTERA, Corixidae: Trichocorixa verticalis var. sellaris (water boatmen) (E,I,Ad)
2. ODONATA, Libellulidae: Erythrodiplax berenice (dragonfly) (I,Ad)
3. COLLEMBOLA, Poduridae: Annurida maritima (springtail) (Ad)
4. HEMIPTERA, Mesoveliidae: Mesovelia mulsanti (water treader) (Ad)
5. HEMIPTERA, Saldidae: Pentacora sphacelata (shore bug) (Ad)
6. COLEOPTERA, Hydrophilidae: Enochrus hamiltoni hamiltoni (scavenger beetle) (E-cocoon, I, Ad) (Ad)
7. COLEOPTERA, Hydrophilidae: Tropisternus quadristriatus (Ad)
8. COLEOPTERA, Dytiscidae: Hygrotus nubilis (diving beetle) (I,Ad)
9. DIPTERA, Ceratopogonidae: Dasyhelia sp. & Culicoides sp. (biting midge) (I, Ad)
10. DIPTERA, Chironomidae: Chironomus sp. (nonbiting midge) (I,P)
11. DIPTERA, Ephydriidae: Ephydra subopaca & Cirrula gigantea (P,Ad)
12. DIPTERA, Stratiomyidae: Odontomyia cincta (soldier fly) (I)
13. DIPTERA, Syrphidae: Eristalinae (flower fly) (I)
14. DIPTERA, Tabanidae: Tabanus atratus (horse-fly) (I)
15. DIPTERA, Sciomyzidae: species ? (marsh fly) (I)
16. DIPTERA, Culicidae: Aedes sollicitans (salt marsh mosquito) (I,Ad)
17. DIPTERA, Dolichopodidae: species ? (long-legged fly) (I)
18. TRICHOPTERA, Limniphilidae: Limniphilus submonilifer (I)
19. ARACHNIDA, Lycosidae: Pardosa milivina (wolf spider) (Ad)
20. ARACHNIDA, Acari, Prostigmata: species ? (Ad)

21. ANTHOZOA, Nematostella vectensis
22. TURBELLARIA, species ?
23. GASTROPODA, Opisthobranchia: Elysia chlorotica & Stiliger fuscatus
24. GASTROPODA, Prosobranchia: Hydrobia salsa
25. OLIGOCHAETA, Tubificidae: tubificid species ?
26. ARCHIANNELIDA, Dinophilus gairdneri
27. CRUSTACEA, Copepoda, Calanoida: Eurytemora affinis
28. CRUSTACEA, Copepoda, Harpacticoida: species ?
29. CRUSTACEA, Ostracoda, species ?
30. CRUSTACEA, Malacostraca, Isopoda: Oniscus sp.
31. CRUSTACEA, Malacostraca, Amphipoda: Gammarus palustris
32. CRUSTACEA, Malacostraca, Decapoda: Paleomonetes pugio
33. CYPRINODONTIFORMES, Cyprinodontidae: Fundulus heteroclitus
34. GASTEROSTEIFORMES, Gasterosteidae: Gasterosteus aculeatus
35. CHARADRIIFORMES, Scolopacidae: Calidris minutilla (Least Sandpiper)
36. PASSERIFORMES, Hirundinidae: Hirundo rustica (Barn Swallow)

marsh crustaceans, Orchestia grillus and Orchestia uhleri (Amphipoda: Talitridae) were under debris and swimming in the pannes. One isopod of the maritime terrestrial Family, Oniscidae, was found also as a permanent high marsh crustacean, but only under drift debris at the highest marsh level (shrub/grass interface).

Based on resource use, developmental stage, and duration of the marsh utilization period, there are two groups of insects of the migrating subsystem. Group one consists of adults that visit the marsh for feeding only, having completed oviposition and larval development in outside systems. Species of Hemiptera, Odonata and Coleoptera were major components of group one.

Group two is more limited, and consisted of species utilizing the high marsh panne for feeding and larval rearing by "plugging into" the marsh system only during the egg and immature stages. In this group, Trichoptera and Lepidoptera were in the study area pannes, and each order was limited to 1 species.

Only during spring and early summer were the adult hemipterans (group 1), Notonecta undulata (Notonectidae), Gerris sp. (Gerridae) and Ranatra fusca (Nepidae) present. They were present during periods of reduced salinities and high production.

A few adult dragonflies and damselflies (Anisoptera and Zygoptera respectively) of group one were foraging over the Spartina and pannes during summer and fall. Although frequent tandem flight and occasional oviposition by a few

species was observed, no hatching and developing naiads were encountered from any of the Odonata of this group (Enallagma sp., Ischnura sp., Leucorrhinia intacta, Sympetrum vicinum and Sympetrum rubicundulum).

The 2 zygopteran species frequently foraged over the area throughout late spring and summer. Both Enallagma and Ischnura fly in tandem and oviposit on algal mats, but no nymphs were observed.

Unlike the zygopterans, the 3 anisopterans were separated chronologically as adults; the 2 Sympetrum species were in large numbers, resting and flying with short, erratic flights over the dwarf Spartina alterniflora and S. patens zones during late August through October (Table 6). Many tandem flights were observed with some touching of the panne surface with the abdominal tip (possible oviposition). No eggs or naiads of Sympetrum were found. Individual Leucorrhinia intacta were observed flying repeatedly back and forth over Ruppia pannes in May and June, but no tandem flight or oviposition was seen.

Adults of the neustonic beetle, Gyrinus sp. (Coleoptera: Gyrinidae) were noted on 8 occasions during brief periods of reduced salinity in April and October. Only adult Gyrinus were found.

During late March, April and early May, 1974 and 1975, the larvae of Limnephilus submonilifer (Trichoptera: Limnephilidae) (group 2) were at sites 2 and 3 at Adam's Point. Early stage (2 - 3 mm) and late stage (10 - 14 mm) larvae were living and developing in the run-off freshened, shallow pannes of the

upper high marsh. Adults emerged in the laboratory at 5 o/oo salinity from larvae collected at ambient salinities of 5 to 15 o/oo. Benthic diatoms layer the substrate of these pannes and early stage L. submonilifer build cases of a silty, diatomaceous material. Later stages were in cases of Spartina and on one occasion, a section of trichocorixid hemelytra was included. This caddisfly has one generation per year, but adults live in the forest system for periods of up to 6 months, from emergence in late spring to oviposition in late summer (Wiggins, 1973). Thus, I would consider L. submonilifer in group two.

During June, 1974, I saw 8 moth larvae (Lepidoptera: Pyralidae) of the genus Nymphula on the surface of 2 pannes near site 6 (RP). Their abdomens were enclosed in 10 - 12 mm long cases composed of a double length of Spartina stems and leaves, from which the larvae extended the anterior one-half of their bodies. A bubble of air covered the abdomen. Since adult pyralids probably feed in other habitats, I include Nymphula sp. in group two.

Some of the salt marsh dipterans might be included in the group two category. Aedes sollicitans (Diptera: Culicidae) and the Tabanidae (horse flies) will venture out into other habitats in search for a blood-meal. As most salt marsh dipterans seldom breed in freshwater habitats, they must return to the tidal marsh for a suitable breeding site (O'Meara, 1976; Axtell, 1976).

## Laboratory

Egg Hatching: Salinity and Temperature Tolerance

Oviposition by T. verticalis took place during and immediately following amplexus. Many eggs of T. verticalis were observed hatching. Eclosion condition was determined when two circular, red to brown-pigmented spots showed toward the apex (distal end) of the yellow eggs. Eggs are ovoid, about 0.5 mm long with a cream-colored chorion. The red to brown-pigmented distal spots indicate developing eyes of late stage eggs, and similarly pigmented kidney-shaped spots on the mid-section (dorsally) indicate developing dorsal glands. Occasionally eyespots developed at the basal disk (proximal), but in all such cases hatching failed to occur.

Eclosion was an explosive rupture of the chorion, which, according to Cobben (1968), bursts open under the pressure of the serosal cuticle, which suddenly bulges out at the aperture as a tough bladder. This leaves the egg top broken into six flaps. Just previous to eclosion, abdominal movement was noted near the dorsal glands. After rupture and bubble formation, the prolarva does not move, and the bubble is filled with liquid. This liquid is probably mainly water (Cobben, 1968). The prolarva absorbs this liquid and steadily increases in size. With pulsating wave-like movements, the head moves slowly into the bubble. Normally, within 15 to 20 minutes, the head rises through the chorionic opening and fills the vesicle. According to Cobben (1968), this is through expansion by liquid uptake rather than active movement by the

prolarva, though I observed pulsating movements with T. verticalis.

When the serosal cuticle was entirely filled, 15 to 20 minutes elapsed before movements behind the head region increase, and the prolarva begins to squeeze out. According to my observations and in agreement with Cobben (1968), no reinforcement could be detected on the embryonic cuticle. During the whole hatching maneuver, the front pulsated steadily. Following hatching, the first instar remained near the empty shell, occasionally flexing the hind limbs for 2 to 5 minutes before swimming. The complete hatching process took approximately 40 to 50 minutes.

T. verticalis is a permanent inhabitant of the high marsh (Table 6), but from January to mid-April, only the eggs survived. Adults and immatures died off when water temperatures reach 0.0 to - 2.0 C. This mortality was noted during both laboratory and field observations. At site 3, winter eggs (fall oviposition) survived ice, hypersalinities (40 - 50 o/oo) and high H<sub>2</sub>S production, indicated by black silt and a strong odor. Eggs observed in the laboratory were resistant to freezing conditions, partial desiccation and wide ranging salinity and temperature changes. Initial egg development and hatching took place in the spring (March and April) when temperature increased and salinity decreased (Fig. 16, See site 3).

In 1974 and 1975, T. verticalis eggs were collected from site 3, beneath 12 - 15 cm of ice, in high salinities and H<sub>2</sub>S. These eggs were cream-yellow with no eyespots, but rare

eyespot stages were noted. Eyespot eggs had reached pre-hatching development prior to winter dormancy, and they did not hatch at laboratory temperatures. However, an initial chorionic rupture and serosal cuticle bulge was observed. All other eggs proceeded to develop and hatch at 20 to 25 C and 0.0 to 30 o/oo salinity.

In the spring, staggered hatching was observed in eggs that had wintered in dormant stage. Hatching time required varied for individuals within any one egg mass exposed to higher temperatures. Winter eggs held 3 months at 4 C hatched on a staggered basis when exposed to 20 - 25 C. During initial hatching, other eggs in the same mass were at various developmental stages.

Summer trichocorixid eggs (spring and summer oviposition) hatched in the laboratory at higher salinities and temperatures (0.0 - 55 o/oo and 20 - 36 C). These eggs were laid in ambient field conditions of 30 - 35 o/oo. Summer eggs were held for 2 - 3 months at 4 C and 15 C at salinities of 0.0 - 30 o/oo without continued development, but hatching took place at laboratory temperatures.

In mixohaline culture, eggs hatched that had previously been exposed to hypersaline conditions. The hypersalinities were high enough to withdraw most of the water from the unhatched eggs. All eggs were caved-in and cup-like on one side but filled out to normal shape and hatched in 15 and 20 o/oo media.

In the laboratory, winter eggs hatched at salinities of 0.0 to 30 o/oo at 20 C and 0.0 to 20 o/oo at 10 C (hatching



preference 0 - 10 o/oo and 10 o/oo respectively), (Fig. 24) but not at 40 and 50 o/oo at either temperature. Winter eggs were held also at 4 C for 10 months at 0.0 to 50 o/oo salinities with no development, and eggs remained in the cream color stage throughout the 105 days of experiment. T. verticalis eggs held dormant at 4 C for up to one year at 15 to 30 o/oo salinity showed about 10 % hatching success when exposed to  $25 - 30 \pm 5$  C (room temp.).

At 10 C, up to 40 days were required before initial hatching occurred at 10 and 20 o/oo, but hatching began after 50 days at 0.0 o/oo (Fig. 24). At 10 C and 10 o/oo, the greatest number of eggs hatched in 105 days, however, hatching was best at 0.0 o/oo at 20 C, but similar at 10 o/oo for both 10 C and 20 C (Fig. 24). At 20 C eggs hatched within 6 days at 0.0 and 10 o/oo, and in 7 days at 20 and 30 o/oo. Most eggs at 40 and 50 o/oo salinities were collapsed on one side (cup-shaped) within 10 to 15 days after immersion.

#### Nymphal and Adult Instars

Previous reports indicate that the Corixidae have six instars (Hungerford, 1948; Peters and Ulbrich, 1973), and T. verticalis is no exception. Molt, body measurements and observations of 2 - 3 laboratory generations of T. verticalis were made during this study and contributed to the following life history information.

First Instar. The newly hatched nymph is oval in shape, transparent but depressed, and averages  $1.0 \text{ mm} \pm 0.2 \text{ mm}$  in length and  $0.5 \text{ mm} \pm 0.1 \text{ mm}$  across the widest body region

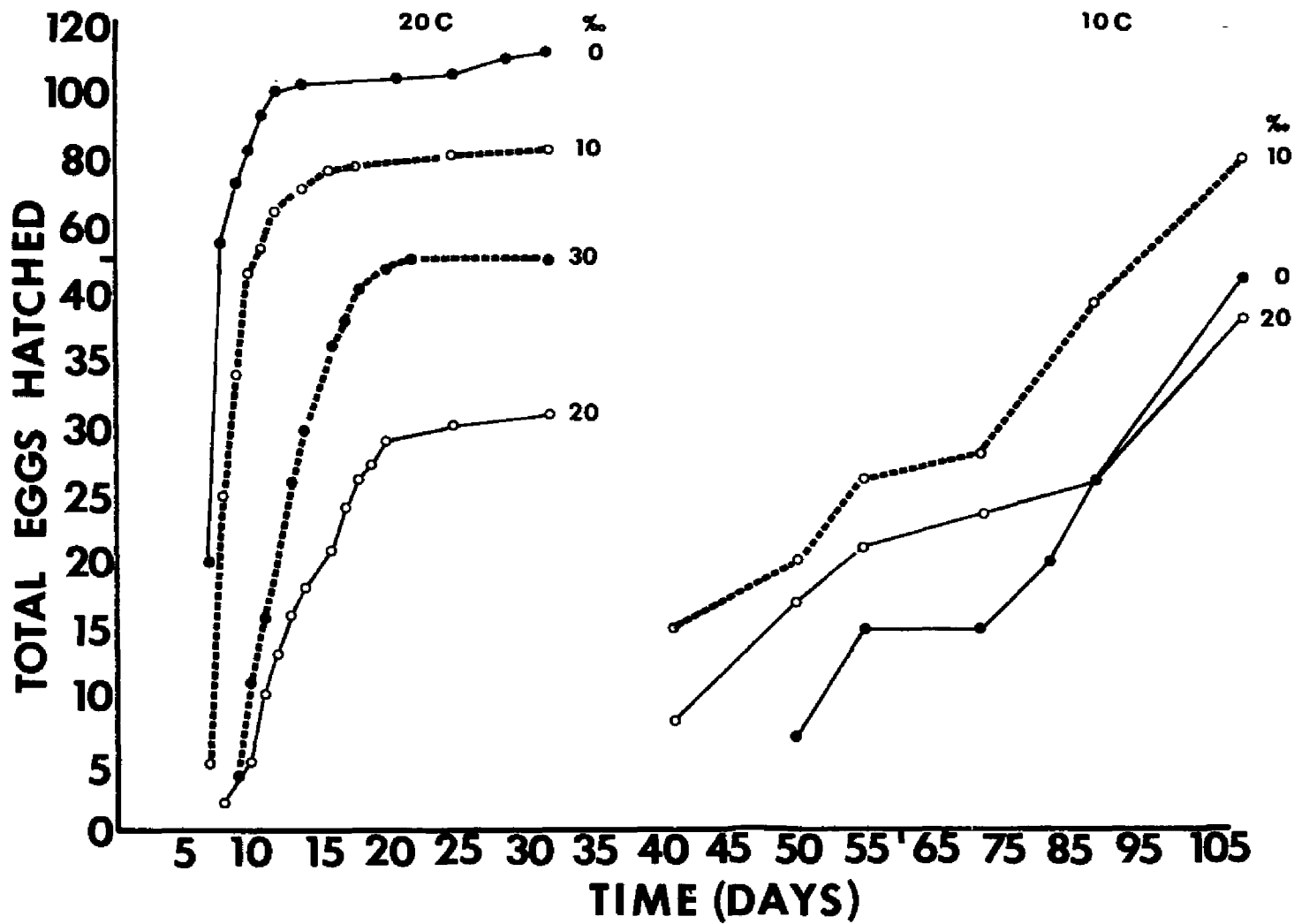


Figure 24. Egg hatching in *T. verticalis* var. *sellaris*: effects of salinity and temperature.

(4th abdominal segment). Head width averages  $0.4 \text{ mm} \pm .02 \text{ mm}$ . The only areas of significant pigmentation are the red, rounded eyespots and the two red abdominal glands on the mid-dorsal surface of the 4th and 5th abdominal segments. There were no wing pads visible at this stage.

Second Instar. The second stage instar is similar in shape and appearance to the 1st. except that it is larger and somewhat more elongate. It averages  $1.5 \text{ mm} \pm 0.1 \text{ mm}$  in length and  $0.8 \text{ mm} \pm .04 \text{ mm}$  in width. The head of this instar is similar to that of the 1st. stage, but it is wider and averages  $0.7 \text{ mm} \pm .05 \text{ mm}$  with somewhat more angular red eyes. No wing pads show on this instar.

Third Instar. The third instar becomes progressively more elongate and begins to show a more adult-like shape. The length increases to  $2.0 \text{ mm} \pm 0.1 \text{ mm}$ , and growth is marked by an expansion in width that averages  $1.1 \text{ mm}$  at the widest abdominal region. The width of the head increases to  $0.9 \text{ mm} \pm .04 \text{ mm}$ . The body is darker, less translucent and more opaque.

The eyes are reddish and have become definitely angular. On the dorsal surface wing pads are noted with distal tips reaching the 1st abdominal segment. The two kidney-shaped abdominal glands become darkened and are still conspicuous on the dorsal abdominal surface. The legs appear much longer in proportion to that in the previous instar, with definite paddle-shaped metathoracic appendages with proportionally thicker setae.

Fourth Instar. In the fourth instar, the nymph continues to elongate and approach adult appearance. It

averages  $2.5 \text{ mm} \pm 0.2 \text{ mm}$  in length and  $1.2 \text{ mm} \pm 0.1 \text{ mm}$  in width. The head measured  $1.0 \text{ mm} \pm .15 \text{ mm}$  and the eyes are darker red and more angular than the 3rd. instar. Both wing pads are conspicuous now and reach the 2nd. abdominal segment. The two abdominal glands are still obvious, and the length of the 3 pairs of legs increased. The tarsus of the third pair of legs is more paddle-shaped and bears denser bristles.

Fifth Instar. The average length of the 5th. stage nymph is  $3.5 \text{ mm} \pm 0.5 \text{ mm}$  and across the fifth abdominal segment it measures  $1.55 \text{ mm} \pm 0.4 \text{ mm}$ . Though it is still more oval-shaped than the adult, the overall appearance is more elongate than the previous instars. The wing pads are very conspicuous, and extend one-half way down on the 3rd. abdominal segment. The head averages  $1.2 \text{ mm} \pm .20 \text{ mm}$  in width and the reddish eyes are more angular. The black kidney-shaped abdominal glands are still rather pronounced and the markings of the thorax dorsally are similar to those in the 4th instar. The legs are similar in structure to those of the previous instar.

Sixth Instar (Adult). The average length of the adult male is  $4.0 \text{ mm} \pm 0.3 \text{ mm}$ , and across the widest abdominal segment it measures  $1.3 \text{ mm} \pm 0.2 \text{ mm}$ . The same measurements for the adult female are  $4.8 \text{ mm} \pm 0.3 \text{ mm}$ , and  $1.5 \text{ mm} \pm 0.2 \text{ mm}$ . The extremely angular eyes are a dark reddish-brown, and the wings are fully developed. The females are easily detected by their larger size, but both sexes are elongate and appear slender compared with late stage nymphal instars. The body is convex above. The head overlaps the prothorax, and the prothorax overlaps the mesothorax. The hemelytra slightly overlaps the

abdominal apex, and they show dark brown lineation on a yellow background. These lines tend toward transverse, sometimes reticulose and undulate. The pronotal disk is almost as long as wide, nearly heart-shaped, and marked with transverse lines similar to those on the hemelytra but wider. Ventrally the adult is cream-yellow with a slight reddish tint.

#### Aquarium Observations

T. verticalis demonstrated both morning and evening activity peaks (Fig. 14). Leg-pumping counts increased sharply during 2200 - 2400 hours. Swimming and surfacing were equal during periods of lowest light intensities before sunrise and after sunset.

Neither activity peak was correlated with highest water temperatures. At the time of maximum temperature (1400 - 1600 hrs), boatmen were relatively quiescent. At this time, they crawl through layers of debris, creating puffs of detritus, or feed in submerged and floating algae.

During 53 days of observation (10/3 to 11/26/75, including a 5-day acclimation period) I recorded all flight attempts, pairing and egg laying. Approximately 96 % of the flights occurred in the first 3 days. The insects surface rapidly, resting dorsal-side-up and floating momentarily with about three-quarters of the body above water. Flight was usually nearly instantaneous on surface contact with minimal floating time (1 - 2 sec). When aquatic re-entry was observed in the field, diving was instantaneous with air/water contact.

Flight occurred over a water temperature range of 19 - 25 C and normally at dusk. At 24 - 25 C, flight counts of 3

per minute were recorded. Floating time was much reduced (1 - 2 sec) at higher temperatures, as compared to 30 - 60 sec floating time at lower temperatures (19 - 20 C). The lower temperature flights were noted during the 1400 to 1600 hr period, corresponding with highest daily water temperature and solar exposure. The insects attempted flight more frequently between 1600 to 1900 hrs. This coincides with summer field observations of flight, and the literature on flight and light trap collections.

While mating, a pair remained coupled during swimming, surfacing and while clinging to the substrate. The smaller male attaches dorsally and somewhat posteriorly to the larger female, and each moving by coordinated rowing-like strokes of the metathoracic legs. According to Hungerford (1948), it seems probable that both the palmar pegs and strigil assist the male in a firm clasp of the female during copulation. I was not sure of this function by the strigil but did observe the palmar legs clasping the female. The male bends the abdomen ventrally to contact the female venter during copulation. Actual copulation appears of short duration (1 - 2 min) with a more extended period (20 - 30 min) of paired amplexus. Pairing of T. verticalis occurred at 6 to 25 C, during cloudy, sunny and nocturnal conditions, but fewer pairs were observed after dark.

Egg masses layed by both unattached and paired females were observed to be attached to straw and sticks, or to previously laid eggs. This behavior was observed in culture and in the field.

During egg laying the female corixid bent the abdominal tip beneath her body directing the venter to the substrate surface. The abdominal tip was then moved back and forth with a scraping-like movement, laying down an adhesive, and then each egg was attached to the substrate by a button-like disk and short stem. It is not uncommon in the field to find egg masses measuring 5 - 10 cm in length on submerged Spartina stems.

#### Salinity and Variable Temperature Tolerance

During laboratory tests of variable uncontrolled temperatures, similar salinity preferences were noted at both the 96-hr and 240-hr period by adult and nymphal T. verticalis (Figs. 25 and 26). Reduced mortality in fresh water (0.0 o/oo) and at 20 to 30 o/oo salinity range occurred in separate experiments at temperatures ranging between 20 to 36 C, M 28 C. Additional tests with a completely independent set of data would be required to determine the statistical significance of the mortality dip at 30 o/oo salinity. The nymphs show a somewhat greater salinity tolerance than do the adults. Salinities from 55 to 70 o/oo were lethal to all trichocorixid stages, with mortality most rapid in the 70 o/oo cultures.

Though more rapid temperature increases and decreases ( $\pm 1.5$  C) were noted in outside test box compartments during exposure to rapidly increasing and decreasing temperatures (solar effect), no significant corresponding mortality was observed.

The high and low experimental temperature extremes and fluctuations were within the summer diurnal (14 - 35 C) and

Figure 25. Mortality of T. verticalis var. sellaris (mixed immatures) at different salinities and uncontrolled variable temperatures (21 - 32  $\pm$  1 C).

┌ Mortality range



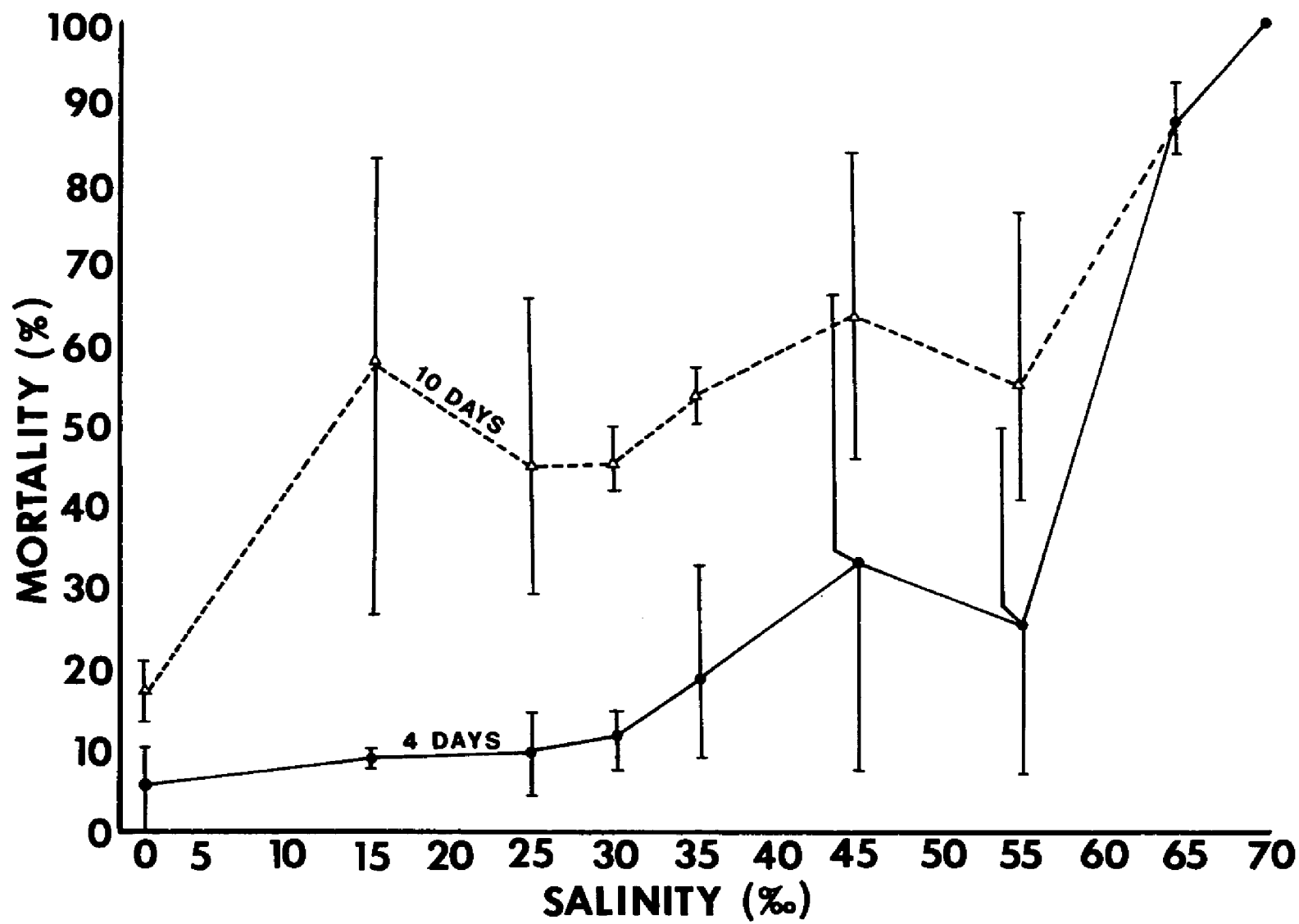
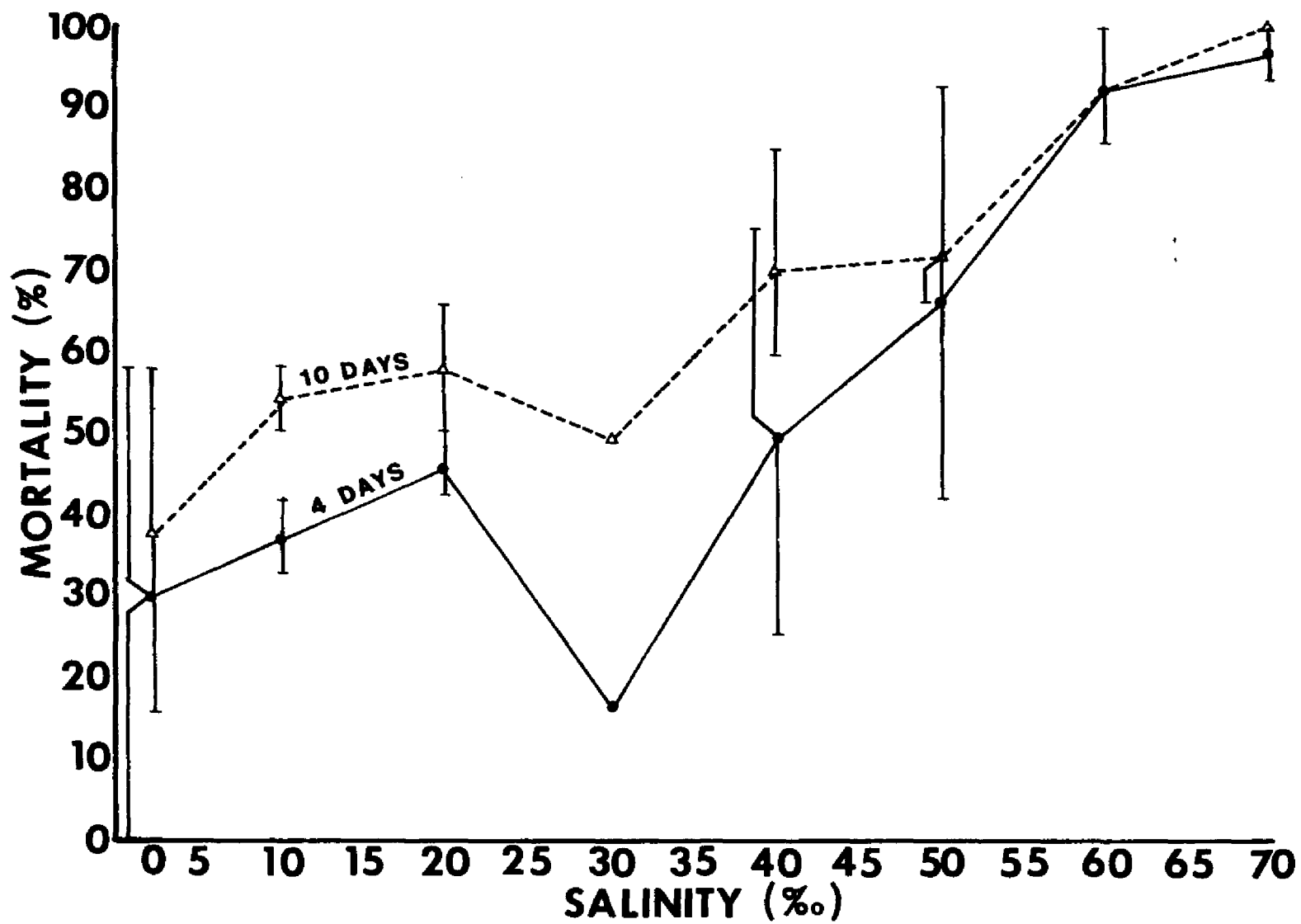


Figure 26. Mortality of T. verticalis var. sellaris (Adults) at different salinities and uncontrolled variable temperatures (21 - 35 ± 1 C).

┌ Mortality range



seasonal (14 - 40 C) ranges recorded in the pannes in which T. verticalis were observed surviving. The mean salinity at site 3 (29.4 o/oo) shown in Table 3, was within the 20 - 30 o/oo salinity range of reduced mortality during experimentation (Figs. 25 and 26).

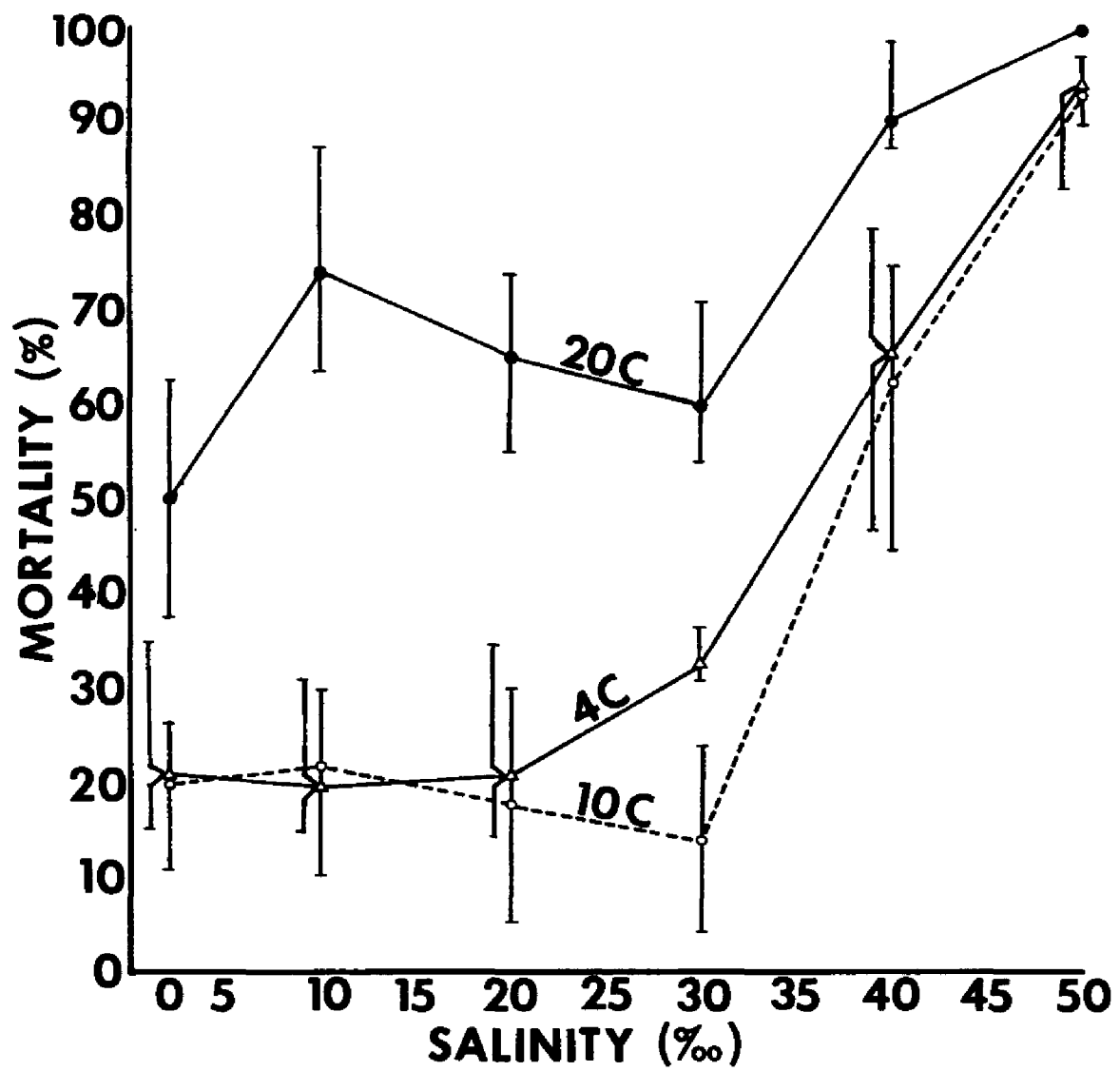
#### Salinity and Constant Temperature Tolerance

Mortality for each of 3 temperature and 6 salinity combinations, recorded during triplicate 96-hr tests are summarized in Fig. 27. Autumn collected T. verticalis were unable to tolerate salinities between 40 and 50 o/oo with less than 50 % mortality at all three temperatures. At 20 C, mortality was highest throughout the experiment. Experimental acclimation conditions (15 C and 19 o/oo) and ambient conditions (4 to 11 C and 17 to 24 o/oo) measured at collecting sites, were nearly similar. Yet, corixids exposed to a temperature 5 degrees higher (20 C) than at acclimation were significantly less tolerant of the experimental salinities. At 5 and 11 degrees below acclimation (10 C and 4 C), mortality was significantly lower than at 20 C but increased rapidly at 40 and 50 o/oo (Fig. 27).

As noted for uncontrolled temperature tests (Figs. 25 and 26), a decrease in mortality of 30 o/oo was measured at 10 C and 20 C. Again, additional tests would be necessary to determine a double preference with statistical significance.

Figure 27. Mortality of T. verticalis var. sellaris (mixed stages) at different salinities and constant temperatures.

[ Mortality range



## CHAPTER III

ERYTHRODIPLAX BERENICE DRURY (ODONATA):  
OBSERVATIONS OF LARVAL AND ADULT ABUNDANCE  
AND SOME ENVIRONMENTAL FACTORS AFFECTING IT

INTRODUCTION

Erythrodiplax berenice (Drury), belongs to the Order Odonata, Sub-order Anisoptera, (dragonflies), and has a completely aquatic immature stage. All stages of insects in this order are predaceous and since they feed on various human pests (examples: Aedes and Ceratopogonidae), they are generally considered beneficial to man.

The non-aquatic adults are conspicuous and easily recognized by their 4 many-veined, membranous wings. The abdomen is long and slender; the cerci have one segment and function as clasping organs in the male; the mouthparts are of the chewing type (Borror and DeLong, 1971). The metamorphosis is simple and incomplete. The wings are of nearly similar size and structure, and there are no wingless species (Comstock, 1950).

Major recent literature referring to North American marine Odonata includes Bayly (1972), Berner and Sloan (1954), Borror (1942), Borror (1951), Gloyd and Wright (1959), Smith and Pritchard (1956), Walker (1953), and Wright (1943). Of the several species of Zygoptera and Anisoptera listed from saline habitats, only Erythrodiplax berenice (referred to as

Micrathyrria berenice in early papers) appears to be confined to brackish waters (Gosner, 1971).

Many normally freshwater species of both Zygoptera and Anisoptera have been found breeding in brackish water, tolerating a salinity up to 14 o/oo (Walker, 1953). In the Mississippi River Delta, Wright (1943) found that E. berenice increased in abundance with increasing salt marsh salinities. According to Gloyd and Wright (1959), at least 2 species, E. berenice and Macrodiplax balteata (Hagen), live in brackish water.

Osburn (1906), collected common odonates from ponds of varying salinities at Woods Hole, Mass. In referring to an upper limit of 20.5 o/oo salinity for 2 zygopteran and 3 anisopteran species tested, he concluded that coastal forms such as Micrathyrria berenice might have a higher limit of salinity tolerance than those species tested, which included Lestes unguiculatus, Ischnura verticalis, Anax junius, Sympetrum rubicundulum and Libellula auripennis. Osburn (1906) goes on to state: "Of the above species, only one, Micrathyrria berenice, is limited in its range to the near coast, and as it also breeds in fresh water in the same region, it can hardly be said to be a typical brackish water species." During this study, E. berenice survived in 0 o/oo culture, although I did not find reference to it or actual individuals breeding in fresh water.

While dragonfly nymphs have been observed in brackish waters by many workers, there are few references to their osmotic behavior and hemolymph composition. Schoffeniels



(1950), Sutcliffe (1962), Moens (1973) and Bedford and Leader (1975) all worked with water balance and hemolymph analysis of odonates, but there have been no salinity tolerance and physiological studies of E. berenice.

Erythrodiplax belongs to the Family Libellulidae (Common Skimmers), most of which are common pond, swamp and marsh species (Borror and Delong, 1971). The adults hover over still water or fly erratically over marsh grasses. Naiads are grouped as sprawlers or climbers in shallow areas (Smith and Pritchard, 1956).

The Genus Erythrodiplax Brauer, is primarily Neotropical and consists of many species with brilliantly colored adults (Borror, 1942). E. berenice is the only species ranging coastally from Ecuador up to Quebec, Canada and has been collected in Maine, Mass., Conn. and R. I. (Borror, 1951; Howe, 1920). It had not been reported from New Hampshire previous to my sample in July, 1974 (White, III and Morse, 1973).

The sexes differ in color and markings, but become obscured by a pruinose coating when fully mature. In teneral females the abdomen is yellowish or yellowish brown, and the wings are usually marked with basal spots, or less likely hyaline. The male shows more black than yellow and the wings are always entirely hyaline.

E. berenice has been listed in systematic papers and general works on the Odonata (Borror, 1942; Borror, 1951; Gardner, 1956; Howe, 1920; Needham and Heywood, 1929; Osburn,

1906; Walker and Corbet, 1975; Wright, 1943). However, publications concerning the biology of E. berenice are lacking.

Because of a lack of biological data for this marine odonate, I have sought to contribute some information on its salinity tolerance, phenology and habits. The significance of E. berenice as predators of highly obnoxious salt marsh Diptera, also favors the acquisition of biological information.

### METHODS AND MATERIALS

#### Field

Adults of E. berenice were collected with a standard insect sweepnet. Live specimens were transported to the laboratory in folded paper as illustrated in Borrer and DeLong (1971). They were counted during separate one-minute periods as they were flushed from Spartina patens and S. alterniflora. Relative abundance of mosquitoes was noted during the dragonfly counts.

Naiads were sorted from floating algal mat samples taken by a long-handled dip net (mesh size = 1.0 mm) and with aquarium nets (mesh size = 0.5 x 0.7 mm). Large 30 to 60 cm diameter algal mat samples were examined under magnification, and naiads were immediately put into culture.

#### Laboratory

E. berenice naiads from 1.0 mm to 14.0 mm length were separated into 10 cm finger bowls at room temperature and various salinities. Sections of Cladophora (2 - 3 cm) were

added to satisfy thigmotactic tendencies of naiads and to provide oxygen. Early to late stage Artemia salina (brine shrimp) nauplii were added systematically to supply the naiads with food. Individual dragonflies were held in salinities ranging from 0 o/oo to 90 o/oo at a wide range of uncontrolled room temperatures. A few late stage naiads (13 - 14 mm length) were transferred to wide-mouth emergence jars (vol = 1250 ml) with a 4 cm water depth, a cheese-cloth top and Spartina stems, so that the naiads could crawl up out of the water to transform to adults.

## RESULTS

### Field

#### Observations and Abundance: 1974 and 1975

A one-year survey of adult and immature stages of Erythrodiplax berenice was taken from late August, 1974, to late September, 1975. From 5/29/75 to 8/25/75, adult male and female dragonflies were collected, and numbers observed during separate one-minute periods were counted as they were flushed out of the Spartina. These data were taken at several locations over the entire study area.

When disturbed, E. berenice fly short distances before alighting and rarely left the marsh area. They stay within the Spartina and do not appear to forage over the open water. When perched, this species was most frequently in a head-up position, holding to a Spartina stem with wings held horizontal

and the abdomen at an approximate 45 degree angle out from the stem.

On each sample date, adult numbers recorded during 3 separate one-minute counts show two distinct peaks in May through August, 1975 (Fig. 28). The greatest number occurred in mid to late June. During adult peaks, numerous dragonflies were flushed from Spartina and easily collected for identification.

A second peak was recorded in mid August, preceded by a month of reduced numbers (Fig. 28). Teneral adults were easily recognized by the brilliant yellow and black markings and newly emerged adults could be readily identified in contrast to the darker, wing-tattered and pruinose older ones. This second adult bloom reached an abrupt one-day count of 12/min on 8/14 that was followed by a sharp decline to total disappearance by 9/11/75. A pilot survey during late August through September and October, 1974, agreed with these results. The most extensive adult bloom was in June, 1975 (Fig. 28).

Observed tandem flights were recorded and are shown by the symbol  $\delta / \text{♀}$ , in Fig. 28. The male grasps the female by the head with the posterior abdominal appendages. Egg laying during tandem flight involved a vertical, circular flight just above the Cladophora mat. The female oviposites on the algal surface intermittently during the forward, down-flight before ascent and looping backward to complete the circle. Ovipositing flights remained within 20 to 30 cm above the panne surface. Mature females were collected and a few eggs were found.

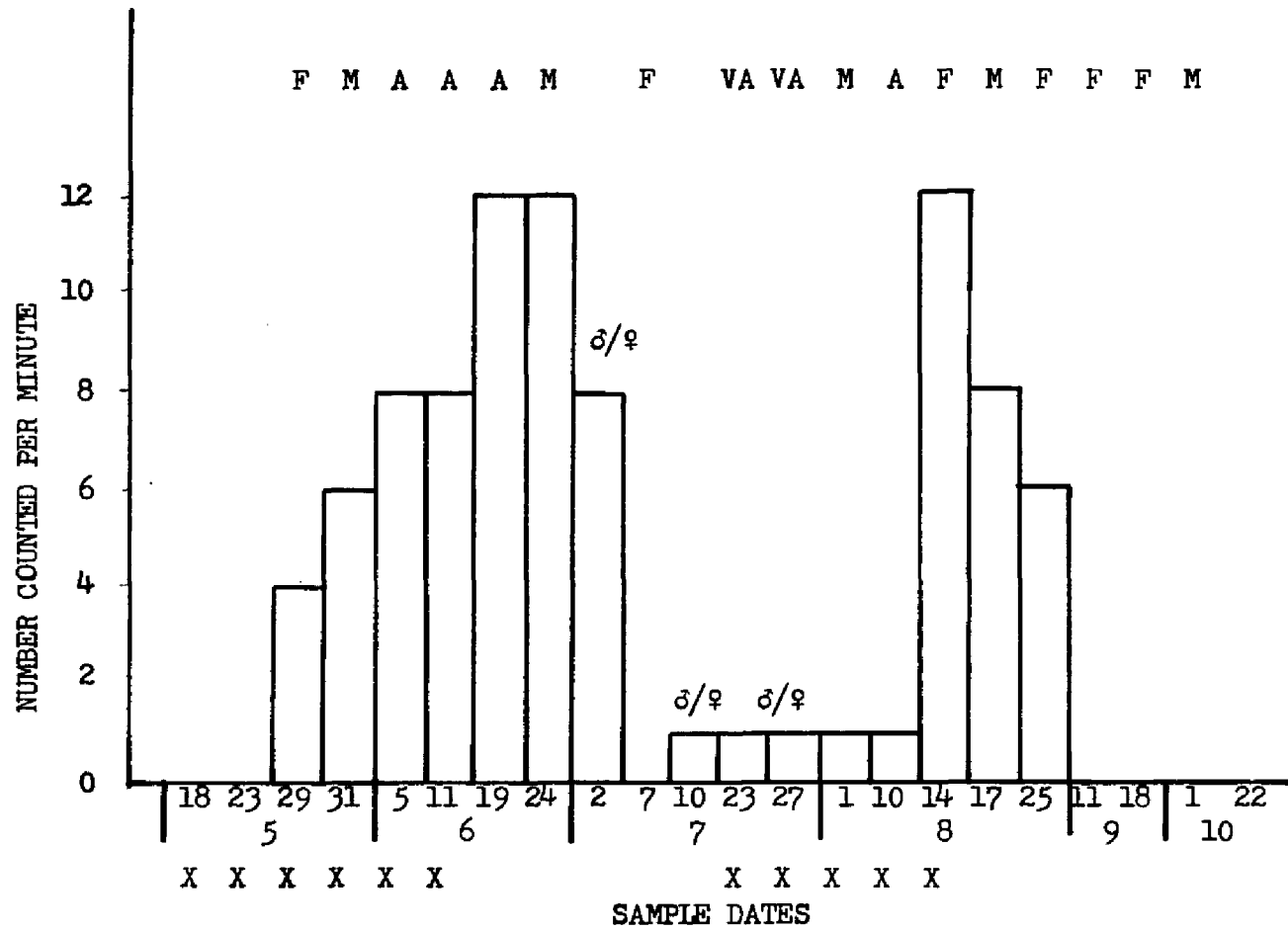
Figure 28. Observed summer occurrence and abundance of adult E. berenice in 1975 in the upper intertidal marsh at Adam's Point, N. H., including sample dates for naiads (X), adults in tandem ( $\sigma/\text{♀}$ ) and relative abundance of Aedes sollicitans indicated as follows:

F = Few

M = Many

A = Abundant

VA= Very Abundant



Large numbers of E. berenice were in the high marsh Spartina in association with intermittent population swarms of adult Aedes (mosquitoes). Fecal pellets from E. berenice often contained 90 to 100 % chitinous mosquito parts. Observations of Aedes were recorded also, with particular emphasis on abundance and location in respect to E. berenice. As indicated by letter symbols in Fig. 28, the relative increase of dragonflies coincides with a decrease in adult mosquitoes.

Naiads of E. berenice were in the high marsh throughout the year from 7/30/74 to 8/14/75 (Table 6), but as indicated by the X marks on Fig. 28, there were intermittent periods in 1975 when they were not collected. Two such periods were during and immediately following the 2 adult population peaks. Mid-size class naiads were collected during July and August, preceding the August adult peak, and indicating a possible polyvoltine life history.

#### Laboratory

##### Culture: Salinity and Variable Temperature

During fall and winter, 1974 - 1975, E. berenice naiads were collected from sites 3 - 6 from Cladophora samples. Dormant naiads 10 to 14 mm length were found beneath thick ice. They resumed active feeding within 10 - 12 hrs at laboratory temperatures.

Five naiads were cultured to emergence in the laboratory. They crawled 4 - 5 cm above the water's surface before ecdysis. Adults were described, papered and refrigerated, and exuviae were labeled and placed in vials. The salinities and

temperatures for the 5 cultures are shown in Table 10. Successful emergence from 0.0 to 48.5 o/oo salinity is indicated at laboratory temperatures.

During naiad culture, a few mortalities were recorded following molts and extended feeding depressions. However, they could survive some starvation. Four mid to late stage naiads survived in culture for 3 months at 8 - 40 o/oo salinities and variable water temperatures from 2 to  $8 \pm 2$  C, without added food. During this period of reduced activity, they did not molt.

In other laboratory temperature cultures, naiads survived between 0.0 and 90 o/oo salinity. Two were held in separate petri dishes in which evaporation and intermittantly added fresh water produced a gradual but fluctuating salinity increase. Naiad I, lived 318 days at an increase of 32 to 71 o/oo salinity. With 5 molts in 276 days, it increased from 2 mm x 0.75 mm to 14 mm x 5 mm (length x width). The last molt was at 65 o/oo, and it died 42 days later during an emergence attempt at 71 o/oo salinity.

Naiad II was collected at site 5 on 8/7/74 at 24 o/oo salinity. It was in culture for 248 days at salinities increasing from 24 to 92 o/oo at 20 to 30 C, and actively fed on Artemia and Aedes at 24 to 90 o/oo. Within a 3-day salinity increase from 90 to 92 o/oo, feeding ceased, activity slowed and mortality occurred.

Culture: Feeding and Food Source

Artemia salina nauplii were a convenient food source for E. berenice naiads. Older naiads of 10 - 14 mm length



Table 10. Comparison of 5 naiads of Erythrodiplax berenice collected and cultured to adult emergence at various salinities and temperatures.

Naiad No.	Mean Salinity of Culture	Mean Temp. and Range of Culture (C)	Days Held Before Emergence	No. Molts In Culture
1	0.0	26 (20-32)	45	1
2	30.0 17.0	26 (22-34)	99 12(111)	0
3	32.0	22 (19-25)	76	1
4	48.5	25 (20-31)	258	3
5	36.0	26 (22-30)	137	1

spent 3 - 5 minutes from capture until final consumption of mature Artemia. The dragonflies remained still until a shrimp came within range of the extended labium. Occasional rapid movement toward the prey was noted.

Aedes larvae were added to cultures for food and were consumed by E. berenice. Mosquito pupae and adult T. verticalis were infrequently eaten by previously non-fed, older naiads. Immature Trichocorixa, Chironomus, Ceratopogonidae, Ephydra and Eochrus were consumed, but mature Gammarus, Daphnia magna and immature mayflies (Leptophlebia) were not eaten. All naiads were separated in cultures to prevent cannibalism.

## CHAPTER IV

## DISCUSSION

In the high salt marsh zone, pools of water retained in shallow depressions are alternately flooded by high spring and exposed during neap tides. Consequently, several environmental factors, chiefly salinity and temperature not only undergo rapid diurnal change but also exert selective controls on community structure.

These factors are more extreme and more variable in the high marsh than in adjacent areas. Upper pools may completely evaporate during drought, or freeze completely during cold periods. The deeper lower pools contained water, algal and vascular plant growth through the year.

Tidal flooding, rainfall, run-off and drought altered the condition of life in the high marsh pools. At times these pools passed from polyhaline to near oligohaline in a few days time, and from exposed hypersaline conditions to flooded euhaline situations within a few hours. Water temperatures may increase by 15 or more degrees from sunrise to mid-day in summer. In winter, ice cover, low water temperatures, increased  $H_2S$  production and salinity fluctuations from oligohaline to euhaline can occur. Purple sulfur bacteria indicated limited amounts of oxygen present and the production of sulfide by microbiological decomposition of organic matter (Van Niel and Stanier, 1959). At times, throughout the year anerobic conditions were observed with the resulting black substrate, sulfide deposits and  $H_2S$  production.

This environment contained a relatively small number of insect species. Of the 8 insect orders found in the pannes, only 3 were represented by 2 or more species. More species of Diptera were found than insects from other orders, but the Hemiptera and Coleoptera with 3 species each, followed the Diptera in abundance. Within the Hemiptera, 2 semi-aquatic forms and 1 aquatic species were found. However, the Coleoptera were represented by 3 aquatic species. The orders Odonata, Trichoptera, Collembola and Lepidoptera were represented by one species each, and of the four, only Erythrodiplax berenice (Odonata) was found throughout the year. These findings support the assertion that this tidal marsh is a rigorous environment (Cooper, 1974).

Both T. verticalis and E. berenice are permanent inhabitants of the high marsh pannes, and may be important contributors to their community structure and function. Both insects complete their life cycles within the marsh, and though both fly as adults, they remain in the marsh system throughout the year.

These insects represent different trophic levels (Fig. 29), and dissimilar degrees of aquatic adaptation. E. berenice is strictly carnivorous and the trichocorixid is omnivorous. Dragonfly naiads possess gills and do not have to surface for air. T. verticalis must break the water surface film to renew the plastron air, but in contrast to the Erythrodiplax, they remain aquatic as adults.

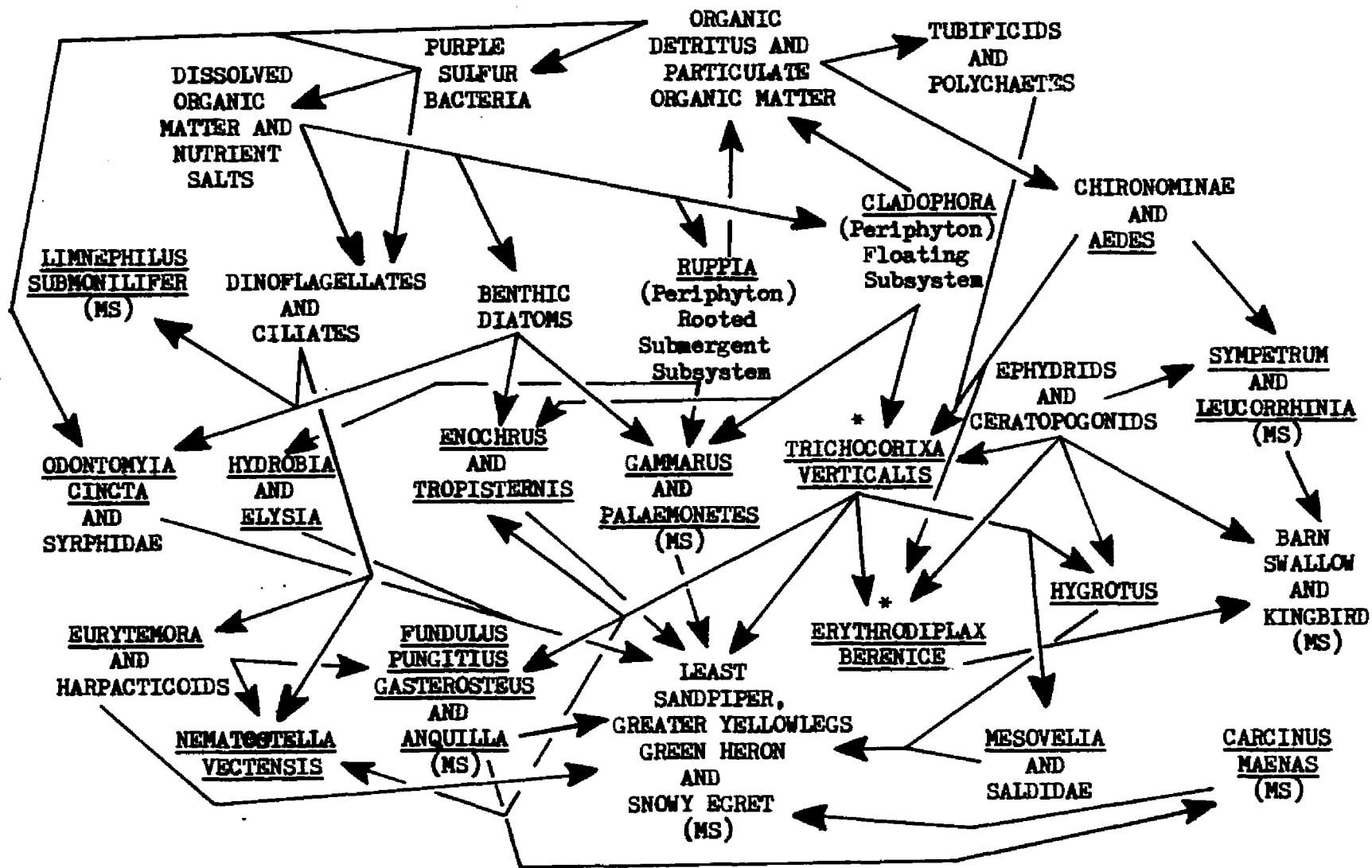
Trichocorixa verticalis is the only aquatic salt marsh hemipteran at Adam's Point. Adult notonectids were found

Figure 29. Diagramatic representation of some major food web components in a high salt marsh panne system, Adam's Point, N. H.

(MS) = Migrating subsystem

\* = Study species

Arrows denote observed trophic relationships



infrequently on a seasonal basis but were accidental and unable to survive. All developmental stages of T. verticalis are tolerant of the rigorous environmental extremes of the high salt marsh, thus enabling them to maintain continual populations in the pannes.

Trichocorixids are omnivorous, preying on certain animals (Chironomus, Ceratopogonids, and Oligochaeta), but also feeding on detritus and algae. Thick detrital ooze and abundant filamentous Cladophora provides a substantial and stable food supply for this salt marsh boatman.

Trichocorixa verticalis make up 2.6 - 23.1 % of shore-bird food items (Table 8). Boatmen concentrated in drought-reduced pools were easily accessible to multispecific shorebird and wader aggregations. They are preyed on by panne-inhabiting fish as well. Observational and experimental analysis of Fundulus heteroclitus food habits indicates a high utilization of trichocorixids (67 % for 10 fish analysed).

Trichocorixa inhabit the floating algal mat within a surface to 12.5 cm depth curve, which is often an area of greatest salinity change (Figs. 19 and 20). Their euryhaline nature allows them to rest and feed on the algal filaments, where they remain protected somewhat from fish below and birds above this mat. In aquaria, boatmen were readily available to predatory Fundulus heteroclitus, Pungitius pungitius and Anguilla rostrata when an algal mat was absent.

Salt marsh neustonic and benthonic invertebrates prey on boatmen in the pannes. Of the neuston, the wolf spider, Pardosa sp., and the water treader, Mesovelia mulsanti, are

both active predators at the water surface, seizing corixids on contact. Immature Mesovelgia and salpids feed on the eggs and young of T. verticalis while submerged, thus utilizing this food source at all levels of development and habitat. Both predators were observed capturing surfacing corixids that were concentrated in drought-reduced pools.

The benthos contained invertebrates, including E. berenice naiads, that fed on corixids. The 3 beetles at Adam's Point are predacious as larvae and fed on the bugs. Unlike Hygrotus (Dytiscidae), the 2 Hydrophilidae (Enochrus and Tropisternus) feed on detritus and algae as adults. Adult Hygrotus crawl in bottom silts with numerous trichocorixids, though their larvae inhabit the algae.

In the Cladophora, the anemone, Nematostella vectensis (Coelenterata) fed on immature T. verticalis along with smaller copepods. Although plankters were an observed food source, they typically eat fly larvae and Hydrobia (Harris, personal communication). This anemone was observed catching adult corixids (4.0 - 5.0 mm length), but the prey would escape after a brief struggle.

Trichocorixids swim to the surface frequently during periods when blackened substrate, H<sub>2</sub>S odor, bacterial blooms and sulfur deposits were most obvious. They surface and dive in such rapid succession as to produce a conspicuous sprinkle effect on contact with the water surface. Under simulated panne and algal mat conditions, (Fig. 14), T. verticalis produced double swimming and surfacing activity peaks which seem to correspond to diurnal oxygen curves reported by salt



marsh researchers (Bradshaw, 1968; Nicol, 1935; Richards, personal communication). An increase in swimming and surfacing activity concomitant with periods of decreased oxygen as reported above and conversely, decreased activity at mid-day oxygen saturation, was noted in the marsh. It seems likely that the degree of swimming and surfacing could be correlated with dissolved oxygen.

The boatman apparently renews its  $O_2$  supply at the water surface nearly instantaneously, a behavior pattern that may enable it to avoid predation. Corixids provide a part of the diet of shorebirds, and it seems likely that animals remaining at the surface for extended time would be most easily captured by birds and fish. For example, dark, conspicuous and inactive floating Odontomyia larvae make up a sizable portion (5.4 - 95 %) of food items for 4 of the 6 shorebirds analysed (Table 7) even though these larvae were not sampled that abundantly (Table 9). Furthermore they are large (10 - 30 mm in length) and stiff with a calcium carbonate impregnated integument, which might make them less palatable. Since corixids may comprise a significant portion of food for Fundulus heteroclitus, it appears that rapid renewal of  $O_2$  at the surface is highly adaptive.

It seems likely that T. verticalis responds to low  $O_2$  by leg-pumping behavior or "fanning", that according to Thorpe (1950) was observed by Comstock in 1887, who suggested that the exposed surface of the bubble might be acting as a physical gill to the extent of assisting in the removal of oxygen from the surrounding water. Air stores (bubbles) of Naucoris and

Notonecta, insects which set up water currents by leg-pumping behavior, are far more efficient as physical gills than is Hydrophilus which has no ventilating (fanning) movements (Wigglesworth, 1972).

T. verticalis remained attached to the algae and fanned the air bubble at variable rates, by pumping the metathoracic legs in unison. This activity increased just prior to the surfacing and swimming peaks at morning observations (1000 to 1200 hrs), and just slightly after the same peaks during nocturnal (2200 to 2400 hrs) measurements (Fig. 14). By this activity, corixids can obtain enough oxygen even at higher summer temperatures, without actively swimming to the surface (Wigglesworth, 1972). This increase in leg-pumping rates might correspond to possible periods of decreasing oxygen saturation as indicated by salt marsh  $O_2$  curves in floating algal sub-systems (Bradshaw, 1968; Nicol, 1935; Richards, personal communication). This behavior would help to supplement the  $O_2$  bubble uptake without increasing the surfacing activity, and would be adaptive for conserving energy and reducing the vulnerability of this animal to predators by allowing it to remain longer within the algal filaments. The demand for oxygen may change with salinity changes, and as the range of natural conditions for a species expands or contracts (Macan, 1974), this boatman has extended its range of natural conditions into the salt marsh and is well adapted to satisfying such demands.

My observations of T. verticalis agree with those of Davis (1966), who reported that the eggs of Trichocorixa

reticulata are highly tolerant of high water temperatures and a wide range of salinities, which may be sufficiently high to withdraw most of the water from the unhatched eggs. In summer, eggs of T. verticalis hatched in salinities between 0.0 and 50 o/oo and between temperatures of 20 to 36 C. Eggs in fall and winter can tolerate hypersalinites and freezing conditions.

The staggered (delayed) development of trichocorixid eggs is an adaptation for population maintenance in the alternately exposed and reflooded high marsh pannes, and ensures that one re-flooding does not cause all the eggs to hatch. If annihilation of the active stage is inevitable sooner or later, there may be selective pressure in favor of a species like T. verticalis that breeds rapidly and produces resting eggs possessing staggered developing characteristics. These boatmen can survive waterless periods in the egg, and can strike a compromise between a quick return to the active stage when water comes and the avoidance of annihilation should water coverage not last long enough for completed development (Macan, 1974).

Responses of T. verticalis to both constant and variable temperatures and constant salinity combinations indicate that they are eurythermal and euryhaline. At variable temperatures, immature boatmen are more euryhaline than the adults. Nymphs tolerated salinities between 0.0 and 55 o/oo, while adults reached an LT 50 at salinities above 40 o/oo. Adult boatmen can fly from upper pools when conditions become limiting. During dry periods when hypersaline water was present in the upper high marsh, large concentrations of adult

boatmen were found in the deeper pannes (sites 4, 5) where the water was at lower temperatures and salinities (Fig. 10). The immatures (wingless) are unable to escape the more highly stressed upper pannes, and therefore the observed high tolerance level could increase chances for survival of nymphs. The egg, which is a highly adaptive stage, can survive among hypersaline-moisture laden Spartina stems.

Animals living in the algal subsystem are subjected to wide salinity variation within narrow depth limits (halocline), due to fresh water layering and slow diffusion during calm conditions (Fig. 20). T. verticalis occurs throughout the pannes in the surface algae and bottom silts. Within both microhabitats, conditions of uniform surface to bottom salinities are the exception, and often marked salinity differences exist between the surface and bottom layers (Figs. 19 and 20). Nicol (1935) noted also such salinity layering in the pools of the Aberlady Bay salt marshes.

Mortalities of immature and adult T. verticalis were lowest within 2 separate salinity ranges (0.0 - 5.0 and 25 - 30 o/oo) at both constant and uncontrolled variable temperatures (Figs. 25, 26 and 27). In general mortalities increased within the 10 - 15 o/oo level before decreasing toward a separate mixohaline (25 - 30 o/oo) salinity realm. High survival of this insect within both oligohaline and mixohaline conditions, would be a beneficial adaptation to the diurnal and seasonal salinity changes in the pannes. In fact, it might be that such tolerance would indicate better survival under more constantly varying factors like temperature (Figs. 25 and 26) than where this factor was controlled and constant (Fig. 27).

A difference in tolerance limits existed between fall collected boatmen and those collected and tested in the summer (Figs. 25, 26 and 27). Summer T. verticalis were more tolerant of higher temperature and salinity combinations. Similarly, fall (winter) and summer collected eggs show tolerance differences. T. verticalis lay eggs mostly in autumn, though less frequently, pairing and egg laying were noted in the summer. Summer eggs developed and hatched soon after oviposition, whereas, most fall eggs (Sept.), could be held 3 to 4 months at room temperatures before they hatched.

According to Cobben (1968), many corixids have ovarian maturation and egg deposition in late autumn or during relatively mild winter periods (0 - 4 C). T. verticalis, that releases diapause eggs in the fall and nondiapause eggs in the summer but have no over-wintering adults, resembles the 5th category of Cobben (1968), where, if female hemipterans are chilled prior to egg laying, they oviposit as soon as the temperature rises and such eggs develop at once. Low temperatures were effective in preventing diapause in ripe, but not yet deposited and fertilized eggs, and the sensitivity of such eggs to chilling is expressed much earlier than in eggs released before colder water temperatures prevail (Cobben, 1968). It is likely that this would explain why some T. verticalis late autumn eggs hatch soon after exposure to increased temperatures, while many delay development for several weeks to months. Certainly more work could be done with this boatman to test this possibility.

In the case of increased tolerance of summer eggs for higher salinity and temperature, the eggs are acclimated to these higher levels while in the female. Immature and adult summer generations show also an upper level tolerance for higher salinities and temperatures, and although field acclimation probably plays a role here, other possibilities (genetic aspects) should be considered. The adaptive meaning of these differences can be related to the ambient conditions prevailing, but differential tolerance to seasonal temperature and salinity levels might be caused by the effect of specific genes, and by the degree of heterozygosity (Battaglia, 1967). This area deserves further investigation.

Acclimation represents the essential means for temperature compensation, and temperature acclimation could produce an unspecific resistance to other environmental stress, such as salinity in this case (Kinne, 1967). The animal able to tolerate variable and adverse supranormal temperatures could probably compensate for higher salinities and shift the upward limit of lethal temperature and salinity upward. This might help explain the increased tolerance of summer acclimated and tested T. verticalis over those in fall (late Oct. and Nov.) (Figs. 25, 26 and 27).

For T. verticalis the conditions discussed above could exist, and in some aspects probably do. The variable tolerance levels for animals subjected to extreme seasonal environmental factors would help insure continued survival of boatmen populations throughout the year. Only those animals capable of adjustment to diurnal and seasonal fluctuations of salinity

and temperature could maintain local populations and permanently inhabit the high salt marsh pannes.

Differential rates of development of T. verticalis were noted during spring sampling of the upper sites (1 - 3) when compared to the lower sites (4 - 6) at Adam's Point. April sampling in site 3 yielded a 15.7: 68.7: 14.4: 0.9 % ratio of the first 4 size classes (instars 1st to 4th; 1.0 mm: 1.5 mm: 2.0 mm: 2.5 mm length) from a total of 200 corixids measured. Similar methods on the same date at sites 4 and 5 yielded only 2 T. verticalis of 1.0 mm length (recent hatched 1st instars). Large egg samples at both site areas showed a similar difference of development relationship. I can only speculate as to the causes for such obvious differences, but it is possible that more extreme salinity and temperature conditions at the upper sites could initiate development sooner than in the more constant conditions of the lower pannes (sites 4 - 6).

Erythrodiplax berenice is the only Odonata completing its life cycle in the high marsh at Adam's Point, although several species are transient inhabitants as adults. The eggs and naiads are tolerant of wide ranging salinities and temperatures, and are part of the floating Cladophora community. Other adult odonates (Sympetrum and Leucorrhinia) inhabit the marsh at different times, but their eggs and immatures do not survive in the pannes.

E. berenice is a predator in both adult and immature stages. Naiads feed on a wide variety of salt marsh invertebrates, including immature T. verticalis. Adults feed on Aedes

and probably other salt marsh dipterans to some extent. They remain with the upper zones of Spartina alterniflora and S. patens, where dense swarms of adult mosquitoes are found. Population peaks of adult E. berenice are synchronized with high productivity of this dipteran food source (Fig. 28). Numerous larvae and other soft bodied invertebrates of the algal mat provide a substantial food supply for the polyphagous naiads. As a relatively large, unselective and efficient predator, it seems likely that this insect has limited competition for the rich and varied primary consumers of the Cladophora.

Naiads wait for more active prey to move within reach of the labium, which is rapidly extended and contracted, seizing and holding the food to be crushed by the mandibles. Actively swimming organisms such as Artemia salina, Aedes sollicitans and immature T. verticalis are accepted as food items by these naiads, and the latter two are possibly preyed on in the marsh. Six to 8 mm long Artemia were seized, held, and completely devoured by the young of E. berenice, within 4 to 5 minutes. In most cases the larvae of Aedes are eaten as readily as were the Artemia. Adult T. verticalis are rarely seized by these immature dragonflies, and in a few attempts noted, much of the hemelytra, head and leg parts were left. Less active swimmers but abundant Diptera (Chironomus, ceratopogonids & Ephydra subopaca) and tubificid oligochaetes are eaten, but larger active and hard shelled amphipods are rejected.

E. berenice naiads are part of the floating algae community (Table 9), and though they seem to disappear from algae samples at adult emergence peaks in 1975 (Fig. 28), I



found them at a density of 11.3 per m<sup>2</sup> and represented throughout the year (Tables 3 and 4). There were probably eggs and possibly early nymphs present in the Cladophora throughout the summer in 1975.

They remain relatively immobile, and concealed from predatory fish and birds while remaining within the algae. No naiads were found among stomach contents of fish and birds from the marsh (Table 7), in sharp contrast to open water swimming T. verticalis and floating dipteran larvae (Odontomyia). Insectivorous birds, including kingbirds and swallows, often feed in the Spartina and take adult dragonflies during emergence periods.

In the Anisoptera, the rectal chamber of the nymphs is a highly specialized respiratory device with muscles which produce regular expansion and contraction movements (Pennak, 1953). With tracheal gills, they generally remain submerged and do not need to surface for air. Under anerobic conditions in culture, I have observed E. berenice with the chamber opening (posterior) pushed up and just above the water surface. It seems likely that during low oxygen saturations, this respiratory behavior could prevent mortality. Under normal conditions, they remain submerged, slowly crawling about in the algal mat, but occasionally move quickly using abdominal muscular pulsations forcing a jet of water from the rectal chamber. Regular respiratory pulsations of the abdomen were observed, and could be used as a measure of activity (dormancy release and mortality).

The naiads of Erythrodiplax were generally in the deeper pannes (sites 4, 5 and 6) where standing water and algal mat were continually maintained. On 3 occasions, naiads were collected from shallow, open pannes of upper sites 2 and 3 that were subjected to various degrees of exposure during drought-neap tidal periods. Naiads were found following tidal flooding of previously exposed upper sites, where during short dry periods algae blanketed the substrate, retaining hypersaline (40 - 70 o/oo) moisture.

E. berenice is eurythermal and euryhaline, as they survived temperatures and salinities of 30 - 38 C and 0.0 to 90.0 o/oo. They were starved in laboratory culture in oligosaline to hypersaline conditions at 0 to 15 C, and under such conditions they survived periods between 1 and 3 months. Another Odonata, Somatochlora semicircularis Selys (Corduliidae) is able to survive weeks or months of drought in microclimates of saturation humidities, under stones, logs, moss mat, and deep in the bases of sedge clumps in Irwin Pond, Colorado (Willey and Eiler, 1972). Since E. berenice can remain starved and inactive, and is eurythermal and euryhaline, it seems likely that it is adapted to at least conditions of partial exposure in the lower-level pannes, and might possibly survive drying in the upper-level pannes beneath moisture laden algae as well.

It would be most interesting to investigate the loss of body water of E. berenice under experimental desiccation at variable temperatures and salinities. The rate of water loss from an insect at any given temperature is due to cuticle permeability and the vapor pressure gradient between the cuticle

and the air which is directly affected by air movements (Bursell, 1964). The observed inactivity of E. berenice and that reported for Somatochlora by Willey and Eiler (1972), may be significant in the reduction of air movements that might upset the vapor pressure gradient and thereby increase the movement of water across the cuticle. In agreement with Willey and Eiler (1972), I observed reduced activity that might tend to limit the exposure of nymphs to predators, such as birds feeding during dry periods. Possibly, besides an inactive nymphal stage, a resistant egg might play some role in the survival of this dragonfly during droughts. Though I observed oviposition in the floating algae, acquisition and testing of eggs remains to be done with E. berenice.

Earlier, I referred to certain temporary inhabitants of the high marsh as representing a migrating subsystem (Copeland, Odum and Moseley, 1974). They migrate into the marsh from other habitats and produce species outbreaks. Larval Trichoptera (Limnephilus submonilifer), and adult Odonata (Sympetrum vicinum) are examples of insects utilizing the available salt marsh resources during limited periods of the productive season. In the spring (March - May) larval caddisflies inhabit the freshened upper pannes, but following emergence, the adults do not stay in the marsh. In contrast, only adult Sympetrum (dragonflies) utilize the same upper Spartina zone as E. berenice adults, but during September - October, immediately following the occurrence of Erythrodiplax (Table 6).

For E. berenice the two apparent emergence periods correspond to the late spring and summer increase in primary production and concomittant increase in salt marsh herbivores and dipteran prey species (Aedes) (Fig. 28). Since the Sympetrum outbreak follows that of E. berenice, competition for a similar food source within the same habitat would be avoided. Cameron (1972) stated that predaceous insects in the salt marsh respond numerically to prey abundance, and suggested that they are host-specific. With this in mind, it seems likely that both adult dragonflies could be utilizing the same adult mosquito food source that fluctuates in abundance from May - November. An obvious similarity of behavior (short flights) and habitat (Spartina patens and dwarf S. alterniflora), which is also the area of highest mosquito density, exists between the two odonate species. It would be interesting if a more critical study of the salt marsh food sources of adult E. berenice and S. vicinum could be accomplished.

I was unable to find any reference to salt marsh inhabitation by caddisfly larvae of Limnephilus submonilifer. In some Trichoptera, including L. submonilifer, the ability to undergo diapause, oviposit apart from water, and form a gelatinous matrix protecting eggs and larvae from desiccation and freezing, form important adaptations to temporary vernal pools (Wiggins, 1973). Sexual maturity is delayed by summer diapause of adults, when they remain concealed in the woods. This allows the caddisfly to survive summer dry periods near temporary freshwater pools, so would appear to allow it to inhabit salt marsh pannes, which are temporarily flooded and

freshened in the spring, but become highly saline and exposed in the summer.

According to the life history of L. submonilifer reported by Wiggins (1973), it seems likely that the eggs are laid on debris and plant stems in the S. patens zone, and hatch in a gelatinous matrix there. They would break diapause and leave the gelatinous matrix when flooded by rain and low salinity water in early spring. The larvae develop in the spring-freshened pannes, containing an abundant diatomaceous food source, with limited competition and predation. Adults emerge from the marsh before late spring and early summer temperature and salinity increases overcome them. Such adaptive stages would permit larvae to develop in the marsh quite apart from the woodland habitat of the diapausing adults. By the time spring salinities have increased, the adults have emerged. Sexually mature adults break diapause in late summer (Wiggins, 1973), and a gelatinous matrix would protect their eggs from autumn and winter salinities and freezing conditions.

When referring to brackish water animals in general, Nicol (1935) stated that the larger numbers are derived directly from the marine fauna, and only a few come from fresh water, and of those few, the majority belong to the Insecta. From the species composition of high marsh macrofauna at Adam's Point, insects in 7 orders represent about 56 % of the total number of identified aquatic species of all organisms collected, and so insects are more dominant by species numbers than all other animals and certainly those organisms exclusively of marine origin. An analysis of the taxonomic list of adult organisms

collected from intertidal marsh by Wall (1973), indicates a similar dominance of insect species (71 % of all species listed). If one were to separate those animals of the high marsh pannes by fresh or marine predominance, certain abundant non-insects such as tubificid oligochaetes, ostracods, aquatic Acarina, Rotifera (observed during this study), Hydrobia and Turbellaria would not be included as strictly marine (Pennak, 1953).

In his environmental classification of the invertebrate kingdom, Pennak (1953) listed various taxonomic categories by marine, fresh water and terrestrial environments. Insects are listed as "Chiefly terrestrial, but with abundant fresh-water representatives." Only one group, the Archiannelida (Dinophilus gardineri) found in the pannes at Adam's Point, are listed as exclusively marine by Pennak (1953), and the remaining groups are represented and scattered under various headings from "Predominantly marine but with a few freshwater species; predominantly fresh-water and a few marine species," to "Chiefly terrestrial, but with abundant fresh-water representatives and a few marine species (insects),".

In this respect, fresh water animals, in contrast to marine, have frequent and regular occurring devices for withstanding unfavorable environmental conditions (resting eggs, cysts, desiccation adaptations and habits). Some specialized animals manage to avoid rigorous predation or competition by having the ability to withstand extremes of physical and chemical conditions such as wide salinity ranges and disappearance of water (Macan, 1974). Such special adaptations as occur

among marine animals are restricted chiefly to intertidal species, and are for the most part, merely special behavior patterns rather than distinctive morphological adaptations (Pennak, 1953).

I have observed this adaptive relationship in the resting egg of T. verticalis, which is resistant to high salinities, periods of panne exposure, and freezing. The naiads of Erythrodiplax berenice have been collected in a dormant and inactive stage under winter ice, and can remain relatively inactive at variable temperatures and salinities in a starved condition.

Diapause has been referred to for various developmental stages of insects, including odonate naiads. Macklin (1963) showed that Pachydiplax longipennis probably has diapause under normal conditions, and of 2 naiads reared under similar conditions of photoperiod and temperature (18 to 21 C), one placed at a lower temperature (5.6 C) for 5 days completed its total growth 40 days sooner than the other maintained at 18 to 21 C. It was assumed that the animal subjected to the low temperature met its diapause development requirements more readily and then proceeded to emerge in a shorter period of time. Corbet (1956) (in Macklin, 1964) found what appeared to be a diapause in Anax imperator which was induced by changing the photoperiod. It seems possible that a true diapause allows E. berenice naiads to survive inactively and withstand extreme conditions in salt marsh pannes. It would be interesting if further research could be done in this area.

Pennak (1953) mentioned the habits of some freshwater invertebrates that bury themselves in the substrate to remain in a torpid state during dry or cold conditions. This might be the case for infaunal pupae and adults of certain salt marsh forms including some insects (Coleoptera, Hygrotus and Tropisternus) that suddenly appear as active adults following their absence in winter.

During my simulated panne experiments, a succession of invertebrates, including T. verticalis, were observed following a period of solid ice formation. At warmer temperatures, thawing occurred and gradual succession of organisms began to appear (copepods, tubificid oligochaetes, T. verticalis and turbellarians). Trichocorixids survived freezing in the egg stage, and this seems likely for the other forms mentioned above.

In common with the limited numbers of other brackish-water species, a small number of aquatic and semi-aquatic insects are capable of surviving and completing a life cycle in the salt marsh pannes. When one considers their species dominance in this intertidal environment, the question of their relative absence from coastal and open ocean systems becomes more interesting. In relation to their terrestrial and fresh water origin, insects have devices for withstanding the unfavorable environmental conditions of the shallow, lentic, intertidal pannes. Insects can certainly withstand the salinities and temperatures of the ocean habitats, but it seems likely that more frequently variable and greater depths, including more unstable surface conditions and currents might provide



a partial answer to this question. Insects are dependent on water surface contact for respiration, and or emergence to adult stage, and the relative facility for this is apparent in the salt marsh in contrast to the open ocean.

Cameron (1972) and Foster and Treherne (1976) concluded that salt marsh insects have specialist feeding strategies similar to insects of terrestrial environments. This does not appear to be the case with the two aquatic insects (freshwater origin) studied here or for other associated insects of the panne system (Fig. 29). In the high tidal panne as with the terrestrial salt marsh, the primary energy flow between autotrophic and heterotrophic levels is through the detritus rather than grazing food chain. The omnivorous water boatman is similar to other panne invertebrates in its importance as a consumer of primary production. E. berenice naiads, though strictly carnivorous, agree with this generalist feeding strategy, but as terrestrial adults, their feeding biology is little known. Although I have contributed some information on the ecology of this marine dragonfly, much basic knowledge has yet to be obtained. This fact is reinforced by its absence from the comprehensive review of marine insects by Cheng (1976).

Though the two species studied here will tolerate fresh water, they were found only in coastal marine environments. From prior literature, and this study, the two insects investigated at Adam's Point are restricted to coastal distribution and are well adapted to living in the salt marsh. In both cases, they are the only species in their respective

families found in the high marsh pannes, and with E. berenice, the only species of the order, Odonata. It would seem that a reduction of interspecific competition would follow from the successful invasion and adaptation to the intertidal marsh. From the fresh water systems where numerous insect species abound, including many Corixidae and Libellulidae, to open coastal systems where closely related crustaceans dominate, T. verticalis and E. berenice must be considered successful in their adjustment to survival in the intertidal salt marsh.

## LITERATURE CITED

- Axtell, R. C. 1976. Coastal horse flies and deer flies (Diptera: Tabanidae). Pages 415-445 in L. Cheng, ed. Marine insects. American Elsevier Publ. Co., N. Y.
- Barbour, M., R. Craig, F. Drysdale, and M. Ghiselin. 1973. Coastal Ecology: Bodega Head. University of California Press, Los Angeles, Calif. 338 pp.
- Barnes, R. S. K., A. E. Dorey, and C. Little. 1971. An ecological study of a pool subject to varying salinity (swampool Falmouth): an introductory account of the topography, fauna and flora. *Journal of Animal Ecology* 40:709-734.
- Battaglia, B. 1967. Genetic aspects of benthic ecology in brackish waters. Pages 547-577 in G. H. Lauff, ed. *Estuaries*. AAAS Publ. 83. Washington, D. C.
- Bayly, I. A. E. 1972. Salinity tolerance and osmotic behavior of animals in athalassic saline and marine hypersaline waters. *Ann. Rev. Ecol. Syst.* 3:233-268.
- Beadle, L. C. 1943. Osmotic regulation and the faunas of inland waters. *Biol. Rev.* 18:172-183.
- Bedford, J. J., and J. P. Leader. 1975. Hemolymph composition in the larva of the dragonfly, *Uropetala carovei*. *J. Ent.* (A)50(1):1-7.
- Bent, A. C. 1926. Life histories of North American marsh birds. *Bull. U.S. Nat. Mus.*, No. 135, Washington, D. C.

- Bent, A. C. 1927. Life histories of North American shore birds, Pt. 1. Bull. U.S. Nat. Mus., No. 142, Washington, D. C.
- Bent, A. C. 1929. Life histories of North American Shore birds, Pt. 2. Bull. U.S. Nat. Mus., No. 146, Washington, D. C.
- Berner, L., and W. C. Sloan. 1954. The occurrence of a mayfly numph in brackish water. *Ecology* 35:98.
- Borrer, D. J. 1942. A revision of the Libelluline genus Erythrodiplax. Ohio State Univ. Grad. Sch. Stud., Biol. Series, Contrib. Zool. Ent., 4: XV 1-286.
- Borrer, D. J. 1951. New records of Maine dragonflies (Odonata). *Ent. News* 62:209-217.
- Borrer, D. J., and D. M. DeLong. 1971. An introduction to the study of insects. Holt, Rinehart and Winston, N. Y. 812 pp.
- Borrer, A. C. 1975. Environmental requirements of selected estuarine ciliated protozoa. National Environmental Research Center. Office of Research and Development, EPA Corvallis, Oregon. 49 pp.
- Bradshaw, J. S. 1968. Environmental parameters and marsh foraminifera. *Limnol. Oceanogr.* 13(1):26-38.
- Breeding, C. H., F. D. Richardson, and S. A. Pilgrim. 1974. Soil survey of New Hampshire tidal marshes. Res. Rep. No. 40. N. H. Agr. Expt. Sta. Univ. N. H. Durham, N. H. 94 pp.

- Britton, W. H. 1923. The Hemiptera or sucking insects of Connecticut. P. IV. Guide to the insects of Connecticut. State Geol. Nat. Hist. Surv. (Conn.) Bull. 34.
- Brown, E. S. 1948. The ecology of Saldidae (Hemiptera-Heteroptera) inhabiting a salt marsh, with observations on the evolution of aquatic habits in insects. *Journal of Animal Ecology* 17:180-188.
- Bursell, E. 1964. Environmental aspects: Humidity. Pages 323-361 in M. Rockstein, ed. *The physiology of insecta*. Vol. 1. Academic Press, New York.
- Butler, P. M., and E. J. Popham. 1958. The effects of the floods of 1953 on the aquatic insects fauna of Spurn (Yorkshire). *Proc. R. ent. Soc. Lond.* (A)33:149-158.
- Cameron, G. N. 1972. Analysis of insect trophic diversity in two salt marsh communities. *Ecology* 53(1):58-73.
- Cheng, L. (ed.) 1976. *Marine Insects*. American Elsevier Publ. Co., N. Y. 581 pp.
- Cobben, R. H. 1968. Evolutionary trends in Heteroptera P. I Eggs, architecture of the shell, gross embryology and eclosion. Centre Agr. Publ. Documentation Wageningen, The Netherlands. 475 pp.
- Comstock, J. H. 1950. *An introduction to entomology*. Comstock Publ. Co., Ithaca, N. Y. 1064 pp.
- Cooper, A. W. 1974. Salt marshes. Pages 55-98 in H. T. Odum, B. J. Copeland, and E. A. McMahan, eds. *Coastal ecological systems of the United States*. Vol. II. Conservation Foundation and NOAA Office of Coastal Environment, Washington, D. C.

- Copeland, B. J., H. T. Odum, and F. N. Moseley. 1974.  
Migrating subsystems. Pages 422-453 in H. T. Odum,  
B. J. Copeland, and E. A. McMahan, eds. Coastal  
ecological systems of the United States. Vol. III.  
Conservation Foundation and NOAA Office of Coastal  
Environment, Washington, D. C.
- Davis, C. C. 1966. Notes on the ecology and reproduction of  
Trichocorixa reticulata in a Jamaican salt-water pool.  
Ecology 47:850-852.
- Dexter, R. W. 1947. The marine communities of a tidal inlet.  
Ecol. Monogr. 17(3):261-294.
- Dukes, T. D., T. D. Edwards, and R. C. Axtell. 1974.  
Associations of Tabanidae (Diptera) larvae with plant  
species in salt marshes, Carteret County, North Carolina.  
Environmental Entomology 3(2):280-286.
- Edmondson, W. T., and G. G. Winberg. 1971. A manual on  
methods for the assessment of secondary productivity in  
fresh waters. IBP Handbook 17. Blackwell Sci. Publ.  
Oxford. 358 pp.
- Fish, C. 1964. Environmental relationships of benthos in  
salt ponds (plant relationships). Tech. Rep. No. 3,  
Vol. 1, p. 6-1 to 10-1. Graduate Sch. Oceanogr. Univ.  
Rhode Island, Kingston, R. I.
- Foster, W. A., and J. E. Treherne. 1976. Insects of marine  
saltmarshes: problems and adaptations. Pages 5-42 in  
L. Cheng, ed. Marine insects. American Elsevier Publ.  
Co., N. Y.

- Gardner, A. E. 1956. The biology of dragonflies. Proc. S. London Ent. Natur. Hist. Soc. 1954-55:109-134.
- Gloyd, L. K., and M. Wright. 1959. Odonata. Pages 917-940 in W. T. Edmondson, ed. Fresh-water Biology. John Wiley and Sons, Inc., N. Y.
- Gosner, K. L. 1971. Guide to identification of marine and estuarine invertebrates: Cape Hatteras to the Bay of Fundy. John Wiley and Sons, Inc., N. Y. 693 pp.
- Gustafson, J. F., and R. S. Lane. 1968. An annotated bibliography of literature on salt marsh insects and related arthropods in California. Pan-Pacific Entomologist 44(4):327-331.
- Howe, R. H., Jr. 1920. Manual of the Odonata of New England. Thoreau Mus. Nat. Hist. Mem. 2:1-138.
- Hungerford, H. B. 1948. The Corixidae of the Western Hemisphere. Univ. Kans. Sci. Bull. 32:1-827.
- Hutchinson, G. E. 1931. On the occurrence of Trichocorixa Kirkaldy (Corixidae, Hemiptera-Heteroptera) in salt water and its zoogeographical significance. Am. Nat. 65:573-574.
- Johnson, A. W., and K. L. Hays. 1973. Some predators of immature Tabanidae (Diptera) in Alabama. Environmental Entomology 2(6):1116-1117.
- Kinne, O. 1967. Physiology of estuarine organisms with special reference to salinity and temperature: General aspects. Pages 525-540 in G. H. Lauff, ed. Estuaries. AAAS Publ. 83. Washington, D. C.

- Lauff, G. H. (ed.). 1967. Estuaries. Washington, D. C., AAAS, 757 pp.
- Leech, H. B., and H. P. Chandler. 1956. Aquatic Coleoptera. Pages 293-371 in R. L. Usinger, ed. Aquatic insects of California. Univ. Calif. Press.
- Macan, T. T. 1974. Freshwater ecology. John Wiley and Sons, Inc., N. Y. 343 pp.
- Macklin, J. M. 1963. Growth rate of Pachydiplax longipennis and Erythemis simplicicollis as influenced by environmental factors. Proc. North Central Branch, E.S.A. XVIII:138-139.
- Macklin, J. M. 1964. Notes on the life history of Anax junius (Drury) (Odonata: Aeshnidae). Proc. Ind. Acad. Sci. 72:154-163.
- Miller, W. R., and F. E. Egler. 1950. Vegetation of the Wequetequock-Pawcatuk tidal marshes, Connecticut. Ecol. Monogr. 20(2):143-172.
- Miller, N. C. E. 1956. The biology of the Heteroptera. Leonard Hill Limited, London. 162 pp.
- Moens, J. 1973. Study of the water balance in larvae of Aeshna cyanea (Muller) by means of measurement of changes in total body weight, with special reference to the method (Anisoptera: Aeshnidae). Odonatologica 2(2):91-98.
- Needham, J. G., and H. B. Heywood. 1929. A handbook of the dragonflies of North America. Charles C. Thomas Publisher, Baltimore, Maryland. 378 pp.
- Nicol, E. T. 1935. The ecology of a salt-marsh. J. Mar. Biol. Assoc. 20:203-261.



- O'Meara, G. F. 1976. Saltmarsh mosquitoes (Diptera: Culicidae). Pages 303-333 in L. Cheng, ed. Marine insects. American Elsevier Publ. Co., N. Y.
- Osburn, R. C. 1906. Observations and experiments on dragonflies in brackish water. *Am. Nat.* 40:395-399.
- Pennak, R. W. 1953. Fresh-water invertebrates of the United States. Ronald Press Co., N. Y. 769 pp.
- Peters, W., and R. Ulbrich. 1973. The life history of the water-boatman, Trichocorixella mexicana (Heteroptera: Corixidae). *Can. Ent.* 105:277-282.
- Recher, H. F. 1966. Some aspects of the ecology of migrant shorebirds. *Ecology* 47(3):393-407.
- Redfield, A. C. 1972. Development of a New England salt marsh. *Ecol. Monogr.* 42:201-237.
- Sailer, R. I. 1948. The genus Trichocorixa (Corixidae: Hemiptera). Pages 289-407 in H. B. Hungerford, ed. The Corixidae of the Western Hemisphere (Hemiptera). Vol. 32. *Kans. Univ. Sci. Bull.*
- Schoffeniels, E. 1950. La regulation de la pression osmotique et de la chloremie chez les larves d'odonates. *Archs int. Physiol.* 58:1-4.
- Scudder, G. G. E. 1969. The fauna of saline lakes on the Fraser Plateau in British Columbia. *Verh. Int. Ver. Limnol.* 17:430-439.
- Scudder, G. G. E. 1976. Water-boatmen of saline waters (Hemiptera: Corixidae). Pages 263-289 in L. Cheng, ed. Marine insects. American Elsevier Publ. Co., N. Y.

- Smith, R. F., and A. E. Pritchard. 1956. Odonata. Pages 106-153 in R. L. Usinger, ed. Aquatic insects of California. Univ. Calif. Press.
- Sutcliffe, D. W. 1960. Osmotic regulation in the larvae of some euryhaline Diptera. Nature, London 187:331-332.
- Sutcliffe, D. W. 1962. The composition of hemolymph in aquatic insects. J. Exp. Biol. 39:325-343.
- Teal, J. J. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43:614-624.
- Teal, J., and M. Teal. 1969. Life and death of the salt marsh. Little Brown and Co., Boston. 278 pp.
- Thorpe, W. H. 1932. Colonization of the sea by insects. Nature 130:629-630.
- Thorpe, W. H. 1950. Plastron respiration in aquatic insects. Biological Rev. 25:344-390.
- Tones, P. I., and U. T. Hammer. 1975. Osmoregulation in Trichocorixa verticalis interiores Sailer (Hemiptera: Corixidae)-an inhabitant of Saskatchewan saline lakes, Canada. Can. J. Zool. 53(9):1207-1212.
- Usinger, R. L. 1956. Aquatic Hemiptera. Pages 182-228 in R. L. Usinger, ed. Aquatic insects of California. Univ. Calif. Press.
- Usinger, R. L. 1957. Marine insects. Pages 1177-1182 in J. Hedgpeth, ed. Treatise on Marine Ecology and Paleocology. Geol. Soc. Amer. Mem. 67.
- Vagenas, G. 1969. An ecological study of the Hampton-Seabrook, N. H. salt marsh. M. S. Thesis. Botany Dept. Univ. of New Hampshire. 74 pp.

- Van Niel, C. B., and R. Y. Stanier. 1959. Bacteria. Pages 16-46 in W. T. Edmondson, ed. Fresh-water Biology. John Wiley and Sons, Inc., N. Y.
- Walker, E. M. 1953. The Odonata of Canada and Alaska. Univ. Toronto Press. 292 pp.
- Walker, E. M., and P. S. Corbet. 1975. The Odonata of Canada and Alaska. Vol. 3, Part III. Univ. Toronto Press. 307 pp.
- Wall, W. J. 1973. Intertidal sand and salt marsh invertebrate fauna associated with the bloodsucking Diptera of Cape Cod, Massachusetts. Environmental Entomology 2(4):681-684.
- Wells, H. W. 1961. The fauna of oyster beds, with special reference to the salinity factor. Ecol. Monogr. 31(3): 239-266.
- White, III, H. B., and W. J. Morse. 1973. Odonata (dragonflies) of New Hampshire: an annotated list. Res. Report No. 30. N. H. Agr. Expt. Sta. Durham, N. H. 46 pp.
- Wiggins, G. B. 1973. A contribution to the biology of caddisflies (Trichoptera) in temporary pools. Life Sci. Contr., R. Ont. Mus. No. 88. Bryant Press Limited. 28 pp.
- Wigglesworth, V. B. 1972. The principles of insect physiology. Chapman & Hall, London. 827 pp.
- Willey, R. L., and H. O. Eiler. 1972. Drought resistance in subalpine nymphs of Somatochlora semicircularis Selys (Odonata: Corduliidae). The American Midland Naturalist. 87(1):215-221.
- Wright, M. 1943. The effect of certain ecological factors on dragonfly nymphs. J. Tenn. Acad. Sci. 18:172-196.