TIDAL MARSH WILDLIFE AND THEIR HABITATS

Franklin C. Daiber

College of Marine Studies
and
The School of Life and Health Sciences
University of Delaware

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INTRODUCTION

Man has had an interest in tidal marshes for many centuries. They have provided him with a source of food for himself and his domestic animals as well as material for shelters. They have served as a buffer against storm damage inflicted against upland structures. Also they have been a source of obnoxious insects as well as disease dissemination. Of late years tidal marshes have been looked to as sites for industrial development, recreation, homes, waste disposal and sources of raw materials. As a result, the tempo of interest in tidal wetlands has stepped up with a corresponding increase in interaction and conflict.

Tidal marshes are a dynamic zone between the sea on one hand and the uplands on the other. They are under the profound influence of the flood and ebb of the tide, subjected to tidal erosion and sedimentation and the ingress of all manner of marine organisms. On the other hand there usually is an inflow of fresh water from upland sources and terrestrial animals have easy access to this semi-aquatic habitat.

Because these tidal wetlands are a meeting place between the sea and dry land they acquire characteristics derived from both, yet they display an individuality that clearly sets them aside as a unique habitat. Vegetational types are evident which are not found elsewhere. Therefore, distinctive plant-animal interactions become evident which have been characterized by Shanholtzer (1974) and Kraeuter and Wolf (1974) for the vertebrates and invertebrates respectively.

Teal (1962) delineated the vegetation of a Georgia tidal marsh and placed the animals associated with such vegetational zonation into three general categories: (1a) terrestrial animals living in the marsh, (b) terrestrial or freshwater species living on the landward edge; (2) aquatic species with their center of abundance in the estuary, (a) estuarine species limited to the marsh low water level, (b) species in the streamside marsh, (c) estuarine species found well into the marsh; (3) marsh species with aquatic ancestors, (a) species with planktonic larvae and (b) species living entirely within the marsh. Teal recorded 57 percent of the aquatic species (2a and 2b) occupying the lowest portions of the marsh where exposure at low tide is the shortest. Those living on the marsh are living at one edge of their species distributions; their numbers maintained by migrations from the water and by adaptations and tolerance levels. Those living above the mud are subjected to great environmental stress and those penetrating farthest into the marsh have adapted burrowing habits. The remainder are tolerant enough to inhabit the entire marsh. Teal estimated the terrestrial species comprise almost half the marsh fauna, yet have made few adaptations to marsh living and are much less important in community energetics than the aquatic species. In the same vein, when Kraeuter and Wolf (1974) set aside those animals found in the creeks and pools and similar areas, only a few species remain to dominate the marsh surface.

Much work has been done on the game species (waterfowl) and furbearers (muskrats) that are characteristic numbers of

the tidal wetlands fauna (see Daiber, 1974, 1977, for reviews).
Among the non-game species various taxonomic groups have
attracted a good deal of attention, the salt marsh mosquitos
(see numerous articles in various entomological journals), the
Foraminifera (Lee and Muller, 1973; Phleger, 1970, 1977), and
the fiddler crabs (Teal, 1958; Crane, 1975). Other groups such
as the mites (Luxton, 1967), insects in general (Davis and
Gray, 1966), beetles (Evans, et al., 1971), amphipods (Phillips,
1978), passerine birds (Tomkins, 1941; Marshall, 1948;
Johnston, 1956) have received only spotty examination. Others
like the protozoa (other than Foraminifera), oligochaetes, and
nematodes have received essentially no attention. Herein exist
many interesting studies of species composition and population
dynamics.

While attention is focused on the local scene it seems
desirable to establish a broader perspective. By so doing,
attention can be called to the many interesting studies that
have been carried out examining tidal wetland species of which
nothing is known from this region. The present paper will
review various parameters and their interactions that influence
marsh animal distributions which in turn influence facets of
life histories such as breeding, feeding and behavior. No
attempt will be made to be all inclusive, whole groups of animals
will not be covered such as the Foraminifera (see above citations
for review).

MOLLUSCA. PELECYPODA:

The Ribbed mussel, Geukensia demissus (Dillwyn 1817)
(= Modiolus demissus), is an obvious member of the marsh fauna
if one searches along the creek banks and drainage ditches
looking for this corregated shelled mollusc partially protruding
from the marsh muds. It is restricted to such locations and is
a passive feeder, ingesting material only as the flooding tide
brings particulate matter past the incurrent siphon. During
1961, as part of a class exercise in Canary Creek marsh,
Delaware, the average mussel density was $45.5/m^2$ within a one
meter zone bordering drainage ditches. Beyond this the numbers
declined to $6.0/m^2$ in the short Spartina alterniflora within
a 10 m distance from the ditches. The mussel has been examined
in the Sapelo Island marshes of Georgia where random samples
gave an estimated population density of $7.8/m^2$ for the inhabited
portions of the marsh. They were most dense near the heads of
small creeks, an average of 52 animals/m^2 being common in
certain marsh types (Table 1). The tall Spartina (1-3 m) --
Creek Head marsh, which occupies only six percent of the total
marsh area, contained 46 percent of population by weight. The
medium Spartina (0.5-1.0 m) levee had a reported density
one-seventh of the tall Spartina -- Creek Head marsh but the
levee, occupied 3.5 times as much area and contributed the
second largest percentage of total weight (Table 1) (Kuenzler,
1961).

Clumped distributions within uniform marsh areas were a
striking feature of the Sapelo Island mussel populations in that

Table 1. Population distribution and density of _Geukensia demissus_ from the Sapelo Island marshes. (From Kuenzler, 1961, by permission of the editor of _Limnology and Oceanography_.)

No.	Marsh Type Description	% of Total Marsh	#/0.2m^2 X̄	#/0.2m^2 Variance	Density/m^2 #	Density/m^2 Wt.	% Total Population #	% Total Population Wt.
1	Muddy Creek banks	4	0		0	0	0	0
2	Tall Spartina edge	9	0		0	0	0	0
3	Medium Spartina levee	21	1.14	12.32	5.7	4.35	17	22
4	Short Spartina low elevation	16	1.24	9.29	6.2	3.0	15	12
5	Short Spartina high elevation	20	0.08	0.11	0.4	0.15	1	1
6	Salicornia spp. Distichlis spicata	9	0.23	0.37	1.1	0.40	2	1
7	Juncus roemarianus	4	2.64	26.4	13	6.15	9	7
8	Tall Spartina creek heads	6	10.4	146	52	31.6	47	46
9	Medium Spartina medium elevation	11	1.11	5.72	5.6	4.55	9	12
	Total	100					100	100
	Mean		1.33		6.66*	4.11		

*The difference in density of 6.66/m^2 and 7.82/m^2 reported in the text was due to the mat not being sieved. Mussels less than 25 mg were not recovered but did constitute 18 percent of the total number.

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sample variances were larger and more numerous in densely
populated marsh types such as the creek heads where they often
exceeded one meter in diameter or paralleled the creeks for
many meters.

Kuenzler reported the vertical distribution to be approxi-
mately 200-240 cm above mean low water. The center of biomass
was situated at 220 cm with the maximum density probably at
this same level. It was calculated a mussel at the 220 cm
elevation would be covered by 77 percent of the flood tides
or about 18 percent of the time. The greater density by weight
at low and medium elevations was thought to be made possible by
longer feeding times. When comparing growth rates, it was
always greater in the low marsh types (Short Spartina, low
elevation; Tall Spartina, creek heads) than in higher marsh
types (Medium Spartina, levee; Salicornia-Distichlis; Medium
Spartina, medium elevation).

Lent (1967a, 1967b, 1968, 1969) elaborated on the signifi-
cance of intertidal distribution and air-gaping in the Ribbed
mussel. He compared those mussels typically found in tidal
marsh muds with those located on exposed surfaces such as
bridge pilings. There was a significant difference in the shell
length-height ratios; bridge mussels being longer than marsh
mussels. Lent (1967b) attributed the difference between
habitats to the crowding effect of clumping in the marsh.

Kuenzler (1961) and Lent (1967b) found an excellent
correlation between shell height and the cube root of the
shell-free, dry body weight. However, Lent did not find any

relationship between the shell weight-meat weight ratios and intertidal height. Since the mussel is exposed during part of the tidal cycle and air-gapes during exposure, respiration could be carried on and such exposure would thus not reduce meaty tissue weight as rapidly. Air-gaping by increasing the efficiency of aerial respiration would permit a greater landward penetration of the intertidal zone.

In his 1968 paper, Lent pointed out median survival times in gaseous environments to be proportional to the volume of oxygen present. Lent reported oxygen tension during exposure at 15 mm Hg and 110 mm Hg while inundated (Figure 6, 1968). Lower rates of respiration in air were explained by these lower oxygen tensions of the mantle cavity fluid in air-gaping mussels. Although the rate was lower in air than when submerged, more oxygen was consumed because of extended exposure (82% aerial exposure, Kuenzler, 1961). Mussels survived for long periods exposed as long as they were protected from dessication.

Dessication and temperature changes are environmental parameters with which the exposed mussels are confronted. Lent (1969) considered the mussel to possess a high tolerance to dehydration and a very high enzyme thermostability. Temperature had a significant effect on the rate of dessication at low but not at high humidity (Lent, 1968). Dessication resulted from water loss by air-gaping and was a physical phenomenon in which a surface to volume relationship caused small mussels to reach a median lethal weight loss of 36-38% more rapidly than large mussels.

Mussels can survive over a temperature range of at least 56°C with a recorded minimum of -22°C (Lent, 1969). An upper LD50 for a 10 hour heat stress fell between 36.4 and 37.8°C with the large mussels more labile to thermal stress than small animals (Lent, 1968). Such temperature tolerance would explain the geographic distribution ranging from Prince Edward Island in the north to South America.

Salinity limits are wide but not firmly established. The lower limit is at least 3°/oo. Mussels can survive water losses of 36-38% by dessication and have at least 71% of their tissue water frozen (Lent, 1969). Therefore the upper limit must be high. Intact animals were able to survive direct transfer into a salinity of 75°/oo from an environmental salinity of 30°/oo. Lent reported Guekensia to be isomotic between 9 and 43°/oo. Waugh and Garside (1971) reported the mussel to be an osmoconformer at higher salinities but changing to osmoregulation below 10°/oo.

Mussels living in moist marsh mud occupied a higher intertidal height than those living on exposed bridge pilings. When the intertidal position of bridge mussels was examined as a function of shell size the population fell within an ellipse (Figure 1). The intertidal range was greatest for medium size mussels and was reduced for both larger and smaller groups. Lent (1968) considered this ellipse to be a geometric form within which the natural population could live. The upper surface was generated by the physical factors of dessication and thermal stress whereas predation and competition are biotic factors determining the lower surface.
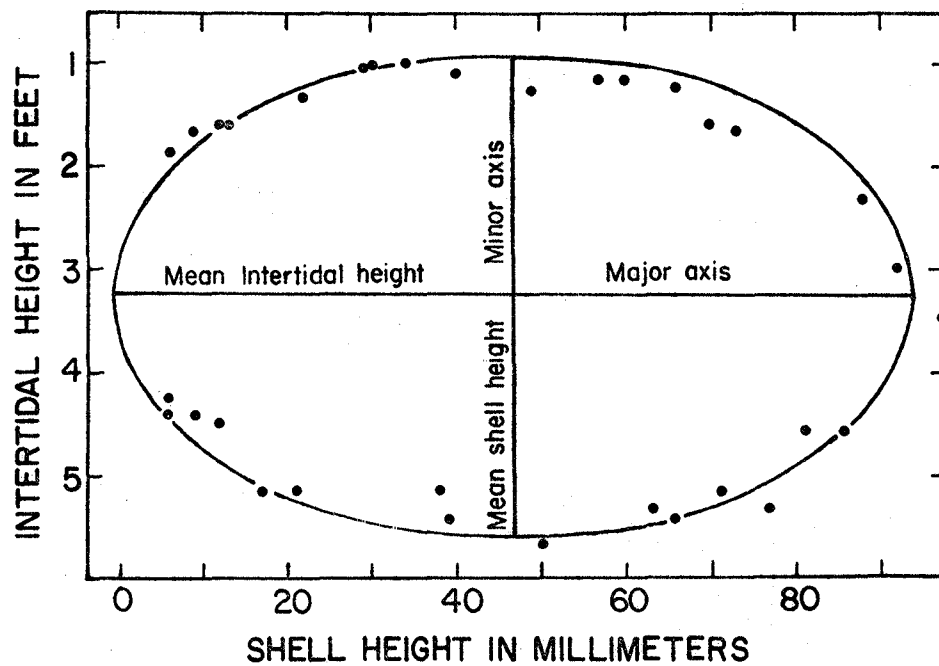
Figure 1. Intertidal height as a function of shell height for
33 mussels on the periphery of the distribution of
Canary Creek bridge. (From Lent, 1968, by permission
of the editor of Biol. Bull.)

Lent (1969) proposes air-gaping in the mussel to be a significant behavioral adaptation which permits aerial respiration and penetration of the higher intertidal zone. In addition it is physiologically and biochemically adapted in that it is both eurythermal and euryhaline. These two adaptations provide a tolerance toward dessication, salinity variation, thermal stress, and possibly anaerobic conditions. However, there is no obvious morphological adaptation thus the pelecypod body plan precludes further landward penetration.

An ongoing study of another marsh surface bivalve Cyrenoidea floridana depicts an interesting parallel to the gaping behavior of Geukensia demissa. So far this small bivalve which gets up to 9 mm in length has been found to have a Delaware distribution restricted to the southern portion of the state, not extending beyond the Great Marsh of Lewes. This clam appears to alternate between air-gaping and keeping the valves closed when the animal is exposed to air. Humidity must be quite high in the clam's habitat as individuals tend to be found where there is a thin covering mat of algae and organic debris. Laboratory observations record air bubbles being trapped in the mantle cavity of the juveniles and older individuals. These bubbles and the abundance of periostracal hairs increasing the shell surface area give a positive buoyancy to the clam. Because of the type of reproduction one might expect the young to be clustered near the adults. Preliminary results suggest this is not the case. The clams tend to be distributed among the short Spartina alterniflora and

Distichlis spicata plants of the higher reaches of Canary Creek marsh. Sampling has demonstrated a negative correlation between adult clam and stem densities but a positive association between juveniles and stems. Dispersion of the clam appears to be brought about by the positively buoyant clams floating in the very gently flowing water as it floods over the marsh surface. The plant stems probably provide impedence to the water flow causing the juveniles to be lodged between or swept up against the stems, thus increasing their densities where the stems are the densest (P. Kat, personal communication).

GASTROPODA:

The Coffee bean snail, *Melampus bidentatus*, is an abundant member of the tidal marsh fauna and has received the attention of numerous workers over the years. Hauseman (1932) found few snails where tides flood the tall marsh grass and where fiddler crabs are common, with snails more numerous above the high tide mark. According to Holle (1957), *Melampus* can be found only in salt marshes flooded by normal tides and avoids tidal submersion by climbing grass stems or debris. In contrast, Hackney (1944) reported *Melampus* as common on the mud flats of Beaufort, North Carolina.

Dexter, in a series of papers on the marine molluscs of Cape Ann, Massachusetts region (1942, 1944, 1945), related *Melampus* distributions to vegetation. In 1942, he often found individuals in small groups under solid objects, occasionally finding the snail in the upper margins of thatch grass or

Spartina glabra (= S. alterniflora) marsh. Small clusters of
Melampus were found in the Spartina patens marshes of Little
River (1944). Dexter was of the opinion in his 1945 paper
that the high marshes of Spartina patens, located for the most
part above mean high water, were the only important habitat
for Melampus bidentatus.

During a 1961 class exercise in Canary Creek marsh where
dwarf Spartina alterniflora dominated the vegetation the mean density
of Melampus was $645.2/m^2$. The very large standard deviation
of 497.2 suggested a very uneven distribution of snails across
the marsh surface, tending to decrease toward the marsh borders.
It was noted that those sampling sites located in areas devoid
of vegetation had very few or no snails. The inference is the
snails crawled up the grass stems to avoid inundation, a
pattern of behavior that has been observed many times. Parker
(1976) reported similar densities for various marshes bordering
both sides of Delaware Bay (Delaware: Canary Creek 693 $\pm$ 340;
New Jersey: Dras Creek 445 $\pm$ 184, Fortesque 420 $\pm$ 175.

In his study of the Poropotank River area of Virginia,
Kerwin (1972) found the Coffee bean snail associated with the
brackish water marshes dominated by Spartina alterniflora-
Scirpus robustus stage and Spartina cynosuroides; and with the
salt marshes dominated by Spartina alterniflora (short form),
S. patens-Juncus-Distichlis zone, in the Distichlis zone and
in the upper levels of the area dominated by the dwarf form
of Spartina alterniflora of Woods Hole area of Massachusetts.
They go on to say Melampus occurred largely in the upper two-

thirds of the zone lying above mean high water of neap tides
(MHWN) and below the mean high water of spring tides (MHWS)
but was also found in the zone lying between MHWS and the
extreme upper limit worked by any tides (Figure 2). They
described the snail as occupying the upper 12 percent of the
intertidal zone which was bathed for only eight of the 354.4
hours (or 2.3 percent) of each semilunar cycle. Apley et al.
(1967), Apley (1970), and Russell-Hunter et al. (1972)
described the reproductive cycle of the snail as being
synchronized to summertime spring tides.

Melampus bidentatus tends to be isosmotic. Russell-Hunter
et al. (1972) submerged early egg masses in water with salinities
of 25-110% sea water and found these masses to act like osmo-
meters. Kerwin (1972) recorded Melampus densities of $0.23/m^2$
in the Poropotank River, Virginia, brackish marsh where the
salinity range was $4.11-9.38^{\circ}/oo$. In that same marsh where the
salinity was higher ($9.38-14.72^{\circ}/oo$) snail densities were
$7.24/m^2$. No Melampus was recorded in the fresh and slightly
brackish marshes with salinities below $4.11^{\circ}/oo$. Parker (1976)
recorded much the same pattern for the Delaware Bay marshes;
larger numbers in areas of higher salinities. Parker provided
some information on the brackish water snail, Detracia
floridana, a snail easily confused with Melampus. Detracia
abundance tended to increase with declining salinities,
apparently totally absent in the highly saline marshes.

Utilizing the aging procedure employed by Apley (1970),
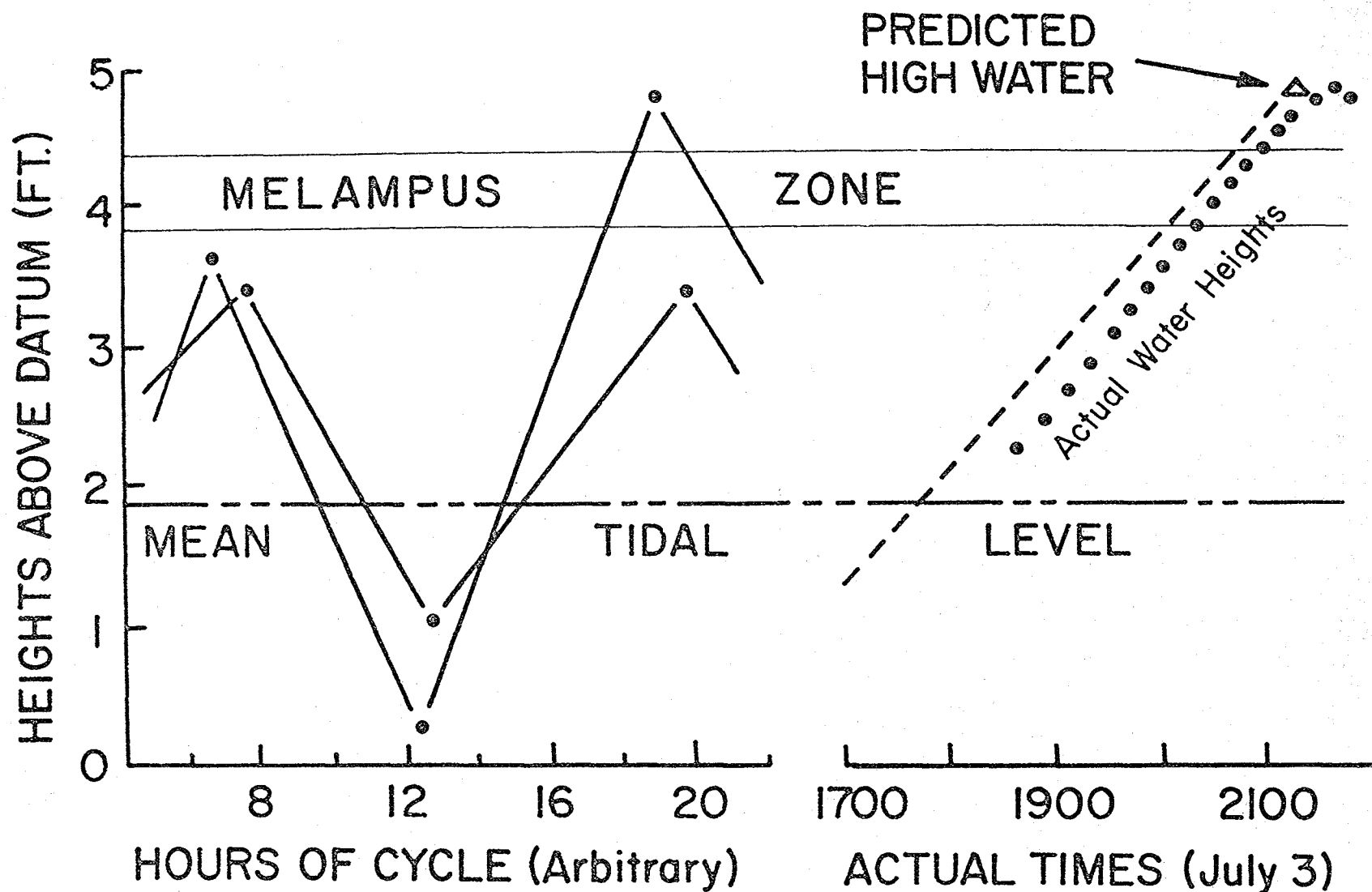Parker (1976) demonstrated a general pattern of increasing length

Figure 2. The relation of the vertical zone (3.9 to 4.4 ft above datum) occupied by
natural populations of Melampus at Little Sippewisset, typical ranges of spring
(-0.02 to 4.77 ft) and neap (0.9 to 3.28 ft) tides, and the observed time
course of actual tidal heights during one high water of springs. Note that the
mean level of all tides (MTL) does not necessarily correspond to mean sea level
(MSL). (From Figure 8 in Russell-Hunter et al., 1972, by permission of the
editor of Biol. Bull.)

in millimeters within each age class along a decreasing salinity gradient. This was particularly evident in those samples taken from the Broadkill River marshes. Laboratory observations by Parker clearly portrayed the euryhaline nature of the snail. Larvae were highly active at salinities ranging from 15 to $40^O/oo$, slightly less so at $10^O/oo$ and they showed a markedly reduced activity at $5^O/oo$. Approximately 90 percent of the larvae survived for 10 hours in salinities varying from 2.5 to $40^O/oo$. None survived in fresh water. Parker has reported the adults to be osmoconformers over the salinity range of 8 to $51^O/oo$. Above and below these levels osmoregulation might be indicated. However, Parker pointed out the apparent regulation may be merely avoidance reaction as the animals were less active, withdrew into their shells and there was a copious mucus flow above and below $8-51^O/oo$.

ARTHROPODA. CRUSTACEA:

Fiddler crabs are an obvious scurrying faunal component of tidal marshes. Pearse (1914) identified three characteristics strongly associated with these crabs, having watched 13 species in North and South America and in the Philipines. (1) Fiddler crabs are diurnal, whereas other crabs are nocturnal as well. (2) A substrate specifity is displayed giving rise to zonation in habitat selection. (3) Fiddler crabs feed on tidal flats during low tide with greatest activity on the ebbing flow. Frantic activity by the crabs was reported by Pearse as the tide began to flood. Crabs retreat to their burrows during high tides

and prolonged flooding, hastily gathering mud pellets to plug
the entrance as the tide floods over the marsh surface. They
open their burrows but will remain in them during extended
periods of low tides which tend to dry out the tidal flats.
Drying tends to inhibit the feeding process for the crabs.

Marsh crabs can be divided into three behavioral groups
associated with tidal cycles (Teal, 1959). (1) _Eurytium_
limosum, _Panopeus_ _herbsti_, _Sesarma_ _reticulatum_ are active when
the tide is high or when the sky is cloudy and the sun is not
shining. When the marsh is uncovered at low tide they are
in their burrows, near the top, either exposed to air or in
the water. Crichton (1960) described _Sesarma_ _reticulatum_
clearing mud from its burrow as the tide receded, depositing
it at either side of the entrance where a complete canopy was
frequently formed. (2) _Uca_ _pugnax_ and _U_. _minax_ are active
principally when the tide is out and do feed under water when
the tide is high or in tide pools during low tide. (3) _Uca_
pugilator and _Sesarma_ _cinereum_ are active only in the air.
_U_. _pugilator_ is in its burrow at high tide while _S_. _cinereum_
climbs above the water level. The first group is found in
the low marsh at the low tide level and the second group
occupies an intermediate zone. The third group, with one
exception, is located at the high tide level. Teal found
colonies of _Uca_ _pugilator_ just above the low tide level on the
creek banks of the Georgia marshes. Crabs in the first group
build burrows with numerous openings which allow the burrows to
fill with water. _Uca_ _pugnax_ and _U_. _minax_ dig burrows with single

openings but seldom plug them. Uca pugilator almost always plugs its burrow entrance at high tide and thus remains in a pocket of air. However, Teal considers the air pocket incidental to the primary need for a hiding place.

Tidal flooding plays a profound role in the lives of these crabs beyond the daily ebb and flow. Uca minax digs a burrow downward to the point where the chamber is at low tide water level (Gray, 1942). This species excavates new burrows during prolonged low water periods or when the burrows are filled with water from extended flooding. In either case, the burrow is dug to a depth to assure flooding of the chamber. Teal (1958) suggests predation may be influencial in restricting the distribution of Uca pugnax at the lower intertidal levels. This species frequently remains outside its burrows as the tide is flooding while Uca pugilator almost never does. The former is therefore more subject to predation by aquatic organisms.

While Pearse (1914), Gray (1942) and Teal (1958) point out the importance of substrate and tidal flooding in the lives of fiddler crabs, specific associations between crabs and vegetation are also evident. Gray describes Uca minax habitat at Solomons, Maryland, as a high water sand and mud substrate sparsely covered by Spartina cynosuroides and Paspalum sp. Uca minax is found in association with 15 species of marsh plants, occurring with five species more than 20 percent of the time in the Poropotank River marshes of Virginia: Spartina alterniflora, 87.8%; Scirpus robustus, 32.9%; Distichlis spicata, 31.7%; Spartina patens, 24.4%; and S. cynosuroides, 20.7%.

High population densities are reported in the tall and short
S. alterniflora and at the edge of the D. spicata-S. patens
community with densities ranging from 0-76 burrows/m^2 (Kerwin,
1971).

Schwartz and Safir (1915) described the burrowing of Uca
pugnax where there was dense vegetation cover, while U.
pugilator burrowed in sparse vegetation or where it was absent.
Teal (1958) found U. pugnax prefers to burrow where there is
vegetation cover and is thus found to be most numerous in the
Short marshes wherein the Spartina is 10 to 50 cm tall on firm
substrate containing varying amounts (40-70%) of sand and the
Medium marshes with Spartina one meter tall on soil that is
soft with small amounts of sand (0-10%). Gray (1942) and Teal
(1958) found Uca minax in certain of the Short Spartina high
marshes where the grass is very short (10-20 cm) and the sand
content is about 30% and water tends to stand. Uca pugilator
was found primarily in the Salicornia-Distichlis marsh and on
the tidal creek banks. The former is high, sandy marsh with
sparse vegetation and covered only by spring tides. In both
situations, U. pugilator seems to be attracted to sparse or
absent vegetation.

The large burrows of the Marsh crab Sesarma reticulatum
have been reported within five meters of the tidal water of
Canary Creek marsh of Delaware and associated with Spartina
alterniflora (Daiber and Crichton, 1967). Crichton (1960)
considers this marsh crab responsible for patches of bare mud
along the creeks and ditches as it crops the cordgrass and

undermines the roots. Frequently these bare areas are swathes separating several feet of lush tall _Spartina_ _alterniflora_ further back on the marsh surface. At other times, they border directly on the bare mud of the stream bank. It is in these swathes that the burrows are the largest and most numerous. The number of burrow openings range from one to ten per square yard with four to five being an average. Crichton considers this burrowing activity to enhance the erosive action of the water and to keep the banks low enough so the tides can flood over the marsh surface.

Salinity plays some part in fiddler crab distributions. The description of the habitat for _Uca_ _minax_ in Solomons Island, Maryland (Gray, 1942) which included _Spartina_ _cynosuroides_, would suggest this to be a brackish water species. Kerwin (1971) found _U_. _minax_ widely distributed in brackish and salt marshes of the Poropotank River, Virginia, where the salinities were greater than $2^{o}/oo$ and less than $16^{o}/oo$ (Table 2).

Miller and Maurer (1973) reported _Uca_ _pugnax_ from high salinities $(21-29^{o}/oo)$ while _U_. _minax_ was most abundant in lower salinities and even into fresh waters $(0-12^{o}/oo)$ of three Delaware tidal streams. An examination of Table 3 shows a shift in abundance for the two species between 15 and $18^{o}/oo$ for the Broadkill River; i.e., _U_. _pugnax_ and _U_. _minax_ being more abundant at 18 and $15^{o}/oo$, respectively. A similar shift in abundance is shown between 23 and $25^{o}/oo$ and 18 and $20^{o}/oo$ for the Mispillion and Murderkill Rivers respectively. Miller and Maurer displayed a significant (at 0.005) positive correlation

Table 2.

PERCENT OF TOTAL SAMPLES, MEAN DENSITY PER SQUARE
METER, AND THE MEAN SALINITY RANGE IN EACH MARSH
TYPE IN WHICH UCA MINAX BURROWS OCCURRED. (Modi-
fied slightly from Table 1, Kerwin, 1971, by
permission of the editor, Ches. Sci.)

Marsh Type	Frequency %	Density (No./m^2)	Salinity (O/oo)
FRESH	0.0	0.0	0.3 - 0.8
SLIGHTLY BRACKISH	0.0	0.0	0.8 - 4.1
BRACKISH	71.4	7.9	4.1 - 9.4
SALT	83.8	14.3	9.4 - 14.7
TOTAL AREA	66.7	12.4	0.3 - 14.7

Table 3.

Abundance of fiddler crabs in relation to salinity in three Delaware rivers.
(Table 1, Miller and Maurer, 1973, by permission of the editor, Ches. Sci.)

	Broadkill River			Mispillion River			Murderkill River		
Sta-tion	No. *U. pugnax*	No. *U. minax*	Salinity ‰	No. *U. pugnax*	No. *U. minax*	Salinity ‰	No. *U. pugnax*	No. *U. minax*	Salinity ‰
1	0	0	29	30	0	27	30	0	21
2	0	0	29	30	0	26	30	0	21
3	31	0	29	30	0	27	30	0	21
4	25	1	29	30	0	26	30	0	21
5	45	1	29	26	0	26	27	3	21
6	45	2	25	29	4	26	18	12	21
7	37	0	24	20	1	26	23	7	21
8	23	17	23	10	10	25	19	11	21
9	17	7	21	8	20	23	16	14	20
10	16	8	20	8	22	21	6	24	18
11	32	18	18	0	22	15	7	23	11
12	4	13	15	0	0	13	3	27	9
13	3	9	12	0	30	10	6	24	6
14	6	36	9	0	0	5	0	30	5
15	1	35	8	0	0	4	0	30	3
16	0	30	5	0	0	1	0	0	1
17	0	32	1	0	0	0	0	0	0.5
18	0	4	0	0	0	0	0	0	0
19	0	3	0	0	0	0	0	0	0
20	0	2	0	0	0	0	0	0	0

between abundance and increasing salinity for Uca pugnax and
a significant negative correlation for Uca minax in all three
rivers. They went on to say that the mid-point of the crabs
distributions, where both species were equally abundant was
approximately at 12, 11 and 8°/oo in the Broadkill, Mispillion
and Murderkill Rivers, respectively. Further examination of
Table 3 would suggest the points of equal abundance for both
species to be closer to $18-25^{O}$/oo, depending on the river
examined. The authors speculated that such mid-points may be
the areas where neither species is favored by competitive
advantage or where both are equally adapted to salinity regardless
of competition.

Something other than salinity may be playing a role in
such distributions. Students of the present author reported
numerous U. pugnax and few U. minax from one area of the
Blackbird Creek marsh in Delaware where the stream salinity was
recorded at $4-5^{O}$/oo. This is supported by Teal (1958) and
Kerwin (1971) who suggest substrate as well as salinity and
competition influence fiddler crab distributions. Both Teal
(1958) and Miller and Maurer (1973) suggested U. pugilator
has a preferred salinity range between that of U. minax and
U. pugnax.

Teal (1958) tested the salinity tolerance for the three
species of Uca by placing them in finger bowls with differing
salinities ranging from 0°/oo to 58°/oo. It was only in the
0 to 7°/oo salinity that there was a difference in survival.
All species survived for three weeks at the higher salinities

and in an experiment where the salinity was varied between 0 and $30^{\circ}/oo$ on an alternate day basis. At $0^{\circ}/oo$, 50 percent of U. minax had not died at the end of three weeks when the experiment was terminated, 50 percent of U. pugilator died at the end of three and one-half days, while 50 percent of U. pugnax died within one and one-half days. At $7^{\circ}/oo$, 50 percent of the other two species survived over the test time of 10 days.

Teal (1958) also provided these three crab species with a choice of freshwater or a salinity of approximately $30^{\circ}/oo$. Both sexes of U. minax showed a statistical preference for fresh water over salt. The males of both U. pugilator and U. pugnax showed a significant preference for salt over fresh water. The females of both species were found more often in salt water but the differences were not statistically significant. In all cases the females showed a less strong preference (Table 4).

When examining U. pugnax and U. pugilator at higher salinities, Green et al. (1959) found both species to be hypo-osmotic regulators. The sera for those crabs in 100 percent sea water were 12 percent lower in osmotic concentration and for those animals in 175 percent sea water, 22 percent lower than their respective media. Lockwood (1962), in a discussion of osmoregulation among the crustacea, considered U. minax, U. pugilator and U. pugnax to belong to that group of animals wherein the blood is hypo-osmotic to the medium in highly saline water and hyperosmotic in low salinities. It is apparent that

Table 4.

PERCENT OF MALES AND FEMALES OF THREE SPECIES
OF FIDDLER CRABS WHICH PREFER FRESH OR SALT
WATER ($\sim 30^{o}/oo$) IN A 24-HOUR EXPERIMENT.   (P
IS PROBABILITY THAT RESULTS IN ROW ARE NOT
DIFFERENT.)   (Table III, Teal, 1958, by per-
mission of the editor, Ecology).

Percent Preferring

	Fresh Water	Sea Water	P
U. minax			
male	68	32	0.001
female	60	40	0.024
U. pugilator			
male	40	60	0.02
female	48	52	0.6
U. pugnax			
male	20	80	0.001
female	35	65	0.058

these three species have different salinity preferences, wide
ranges of tolerance and differing abilities of adjusting to a
salinity range within the framework of being hypo- and hyper-
osmotic regulators.

There is general agreement about substrate preferences by
fiddler crabs. This specificity gives rise to fiddler crab
zones in habitat selection (Pearse, 1914; Gray, 1942; Teal,
1958; Kerwin, 1971). Uca pugnax burrows in mud (Pearse, 1914)
and Teal (1958) found it on the levee marsh and short Spartina
low marsh where the sand content was 0 to 10 percent as well
as where the sand content was greater. He concluded U. pugnax
distribution is determined by a preference for a vegetated
muddy substrate and salt water. In contrast, both Pearse (1914)
and Teal (1958) recorded U. pugilator with a preference for
sand. Teal found this species to be dominant in the Salicornia-
Distichlis marsh where the soil was 80 to 95 percent sand.
However, in the short Spartina high marsh where the sand content
is 40 to 70 percent, Teal reported U. pugilator did not burrow
to any appreciable extent. In laboratory tests it burrowed
in sand above the water level, presumably because such burrows
below the water would be more apt to collapse. Teal concluded
U. pugilator preferred sandy habitats but could not colonize
all such habitats because of competition with the other species
of Uca. Both Gray (1942) and Teal (1958) found U. minax
displaying a preference for sand and mud with the sand content
exceeding 30 percent (Teal). The soil had to be wet and the
salinity could vary over a wide range. Gray (1942) reported the

presence of <u>Spartina</u> <u>cynosuroides</u> coinciding with the presence

of <u>U</u>. <u>minax</u> and Teal concluded the species prefers a mud or

variable substrate and fresher water.

Results indicate <u>Uca</u> <u>minax</u> prefers substrates of high

energy value, i.e. high organic content. This appears to be

the case even though such substrates characteristically have

the lowest oxygen levels. Substrate oxygen is not considered

to be critical to habitat selection and this species can revert

to an anaerobic mode of respiration during those times when it

is submerged in the water of the burrow (Teal and Carey, 1967).

Therefore, organic materials for feeding would be the primary

component in habitat selection (Whiting and Moshiri, 1974).

Interestingly, Teal (1959) considers <u>U</u>. <u>minax</u>, which does not

possess any temperature acclimation, has a lower respiratory

rate and is more dependent on oxygen tension, to be greatly

limited in distribution in a typical salt marsh. However, as

Teal points out, competition probably plays an important role in

<u>Uca</u> distributions.

In addition to amounts of organic material and sediment

particle size, the differentiation of feeding mechanisms among

fiddler crabs had a bearing on crab distributions (Miller, 1961).

There are two general processes of feeding involved: flotation

and the coordinated action of the mouth parts. There is a copious

use of water from the gill cavities to flood the buccal cavity

during feeding. There is always the need for water replacement.

To continue feeding the crab must have access to an external

water supply to replenish its respiratory water. The inclusion

of the flotation process is one major factor keeping Uca from living in a terrestrial habitat. Pearse (1914) comments about these crabs scooping up mud with the chilipeds, feeding on the tidal flats as the tide ebbs. They will remain in their burrows when the flats dry out, feeding apparently being inhibited.

Uca pugnax has been observed to leave its burrow during feeding, dip its thorax to take up water, finding insufficient water, return to the burrow and a source of respiratory water to take up feeding again. This may explain the high degree of burrow territoriality observed for Uca pugnax. Such territoriality has not been observed for U. minax which feeds in muddier areas away from the burrow. The need for water for the flotation process for U. pugilator which inhabits sandy areas has more pronounced effect on this crab's movements. The crab may have to feed at the water's edge away from the burrow should water not remain in the burrow during low tide.

Of these three fiddler crabs Uca minax has the least modified mouth part hairs. It prefers to feed in low areas where the mud is very fluid. The material carried to the mouth is very fine and little sorting is needed before ingestion. The presence of flat-tipped hairs on the second milliped meropodites of U. minax is believed to enhance the sorting process and to enable it to live in a coarser substrate where food is less available. The modification of hair tips into a spoon shape on the second maxilliped meropodites of U. pugnax enables this crab to feed in coarser substrates. The luxuriant

fringe of plumose hairs on the outer edges of the second
maxillipeds and on the maxillae enables U. pugnax to feed on
a muddy substrate.

The greatest modification of the hairs of the mouth parts
occurs in Uca pugilator, greatly increasing the efficiency of
the mouth parts to sort out coarse material. In addition to
having to select against coarse mineral material, fiddler
crabs are also faced with the greater paucity of food materials
in a sandy habitat. In Uca pugilator the efficiency of sorting
is further enhanced by a cleaning action which involves drawing
sand particles over the bristled surface of the first maxilliped
basal endites by the second maxillipeds. This cleaning process
retains the bulk of the food particles which are washed by
respiratory water toward the base of the buccal cavity.

The import of this is U. minax cannot efficiently sort out
coarse material and must thus have access to abundant food
material on a silty substrate. The more advanced mouth parts
of U. pugnax enable it to have a wider distribution, living in
the sandy areas of a new marsh. The reduced ability of U.
pugnax to sweep sand particles clean of food probably restricts
its ability to live on a sandy beach. The highly modified mouth
parts of Uca pugilator enable it to live in sandy areas. When
U. pugilator feeds in a marsh it cannot separate out the fine
silty material and is not as efficient in getting food as when
it sweeps the sand grains of food particles in a coarse
substrate (Miller, 1961).

INSECTA:

Insects are a common component of the tidal marsh fauna,
occupying a variety of habitats. Relatively few families can
be classed as pests and those noxious to man are of considerable
economic importance and thus have received a great deal of
attention. Much work has been devoted to the control of salt
marsh mosquitos, beginning with Smith (1902) who recognized the
relationship between mosquito distributions and zonation of
salt marsh vegetation. He advocated filling those depressions
on the marsh surface adjoining the uplands where mosquitos breed,
or ditching so tidal action could circulate water through such
areas.

Tidal inundation has been identified as a factor limiting
the distribution of Aedes species of mosquitos on Delaware salt
marshes (Connell, 1940). Young larvae fail to appear in
portions of the marshes flooded by tides as frequently as 25
days per lunar month. Abundant breeding can be expected only
in portions of Spartina alterniflora marsh where the frequency
of tidal inundation is less than eight days per lunar month.
Table 5 depicts the relationships between vegetation and
insect numbers for Aedes sollicitans and Aedes cantator, wherein
most of the mosquitos were taken in the Spartina patens zone.
LaSalle and Knight (1974) found the Juncus marshes in Carteret
County, North Carolina, to be subjected to a higher rate of
tidal flooding during the mosquito breeding season than the
marshes examined in Pamlico County. Consequently, there was a
much lower level of Aedes breeding in the former area than in

Table 5.

AVERAGE NUMBER OF AEDES LARVAE AND PUPAE PER DIP FROM
THE SALT MARSHES OF EGG ISLAND, NEW JERSEY (From
Ferrigno, 1958).

	Aver. number of larvae and pupae per dip		
VEGETATION	A. cantator	A. sollicitans	TOTAL
Spartina patens	0.31	6.95	7.26
S. alterniflora	0.01	0.37	0.38
Mixed	0.29	2.42	2.71

Pamlico County. The higher flooding frequency in the Carteret County marshes probably accounted for the presence of <u>Anopheles</u> and <u>Culex</u> mosquitos which were as abundant as or more so than, <u>Aedes</u>. Ferrigno (1958) demonstrates the relationship between flooding and water depth on the success of mosquito breeding caused by Snow geese feeding activity (Table 6). In addition, the restriction of regular tidal flushing in vegetational zones for agricultural purposes has an impact on the numbers of mosquitos produced (Table 7). Diking enhances the growth of salt hay, <u>S</u>. <u>patens</u>, by preventing flooding with salt water. Later reflooding produces great broods of mosquitos, mostly <u>Culex</u> <u>salinarius</u> and <u>Aedes</u> <u>sollicitans</u>.

There appears to be some uncertainty from the earlier literature about the relationship between tidal flooding and vegetation zonation on one hand and the distributions of larval greenhead flies (Tabanidae). Hansens (1952) found them in the wetter portions of the salt marsh while Gerry (1950) described development as taking place primarily in the upper marsh reached only by the higher tides. He went on to say evidence indicates that larvae originate in the creeks from which they migrate to thatch piles at the head of the marsh. Wall and Doane (1960) found various species of tabanids well distributed over the surface of various Cape Cod marshes. Bailey (1948) rarely found <u>Tabanus</u> <u>nigrovittatus</u> where there was standing water on the marshes in the vicinity of Newbury, Massachusetts. Jamnback and Wall (1959) found the larvae associated with several species of salt marsh vegetation but most abundant in <u>Spartina</u>

Table 6.

Mosquito breeding at stations affected by feeding Snow geese in
New Jersey marshes.   (From Ferrigno, 1958)

Description of eat-outs

Percent Denuded within 70 foot Radius of Station Marker		Vegetation Type	Water Depth in Inches	Number of Larvae-Pupae per dip	total	Number of dips
A	10-30	S. patens	0-2	12.71	6607	520
B	10-40	S. alterniflora	0-6	1.56	2119	1355
C	50-90	S. patens-S. alterniflora	1-8	0.05	25	460
D	50-90	S. alterniflora	1-6	0.03		490
E	100 (Ponds)	S. patens-S. alterniflora	5-24	0.002	3	1401

Table 7.

The numbers of mosquito larvae and pupae sampled from natural and diked salt marshes of the Caldwalder Tract, New Jersey. (A portion of Table 2, Ferrigno, 1959.)

| Vegetation Type | Average number larvae-pupae per dip | | Seasonal totals | |
	Culex salinarius	Aedes sollicitans	Dips	Larvae-Pupae
UNDIKED				
S. alterniflora	0	0.0001	8280	1
S. patens	0.11	2.74	1080	3293
P. virgatum	0.003	0	600	2
Woodland swamp	0.02	0.01	840	620
DIKED				
S. alterniflora	0.26	4.22	360	1701
S. patens	0.72	3.54	2760	13376
S. cynosuroides	2.94	4.66	240	1988
P. virgatum	0.21	0.75	1320	2219
D. spicata	0	3.52	600	2761
J. gerardi	0	2.86	240	780
Typha	2.01	0.21	120	707

alterniflora and S. patens. Contrary to Gerry (1950), they
believe the larvae can survive in water for a long time.
Olkowski (1966) found most larvae among the S. alterniflora
of Delaware marshes with fewer individuals present as ground
elevation increased toward the Spartina patens zone. The
mature larvae were presumed to be dispersed to higher ground by
tidal action.

More recent work gives additional insights into the
distributions of tabanid flies. Dukes et al. (1974a) working
in Carteret County, North Carolina, and Meany et al. (1976)
working on Great Sippewissett Marsh, Massachusetts, found
Tabanus nigrovittatus and Chrysops fuliginosus larvae distributed
throughout the lower salt marshes occurring in highest densities
in areas below mean high tides and dominated by Spartina
alterniflora. The preference for low marsh was most marked for
C. fuliginosus (Tables 8 and 9). The less abundant Chrysops
atlanticus were also characteristic of low marsh areas. The
abundance of larvae decreased progressively toward slightly
higher elevations with concurrent decrease in Spartina alterni-
flora and increase in the irregularity of flooding. The authors
reported areas of S. cynosuroides, D. spicata and J. roemarianus
yielded decreasing numbers of larvae, in that order. However,
examination of Table 8 would suggest the order of D. spicata
and J. roemarianus be reversed. Dukes et al. did point out
that larvae can be found in the high Juncus marsh, particularly
in interspersed patches of other vegetation, which is indicative
of more frequent flooding. In mixed vegetation, as the proportion

Table 8. Recovery of Tabanid larvae from soil in various plant associations in four salt marshes in Carteret County, North Carolina, 1972. (Part of Table 3 from Dukes, et al., 1974, by permission of the editor of Environmental Entomology.)

	Samples		Larvae	
	Total number	Percent with larvae	Total number	Average/ sample
Newport River				
Spartina alterniflora	179	77.1	521	2.95
Distichlis spicata	27	25.9	12	.44
Juncus roemarianus	47	26.1	29	.62
S. cynosuroides	13	53.8	17	1.31
S. alterniflora & D. spicata	15	46.7	14	.93
J. roemarianus & D. spicata	5	40.0	7	1.40
Totals and overall average	286	44.9	600	1.28
Hoop Hole Creek				
Spartina alterniflora	11	36.4	6	.54
Juncus roemarianus	14	7.1	1	.07
S. alterniflora & D. spicata	5	40.0	3	.60
S. alterniflora & J. roemarianus	5	40.0	3	.60
S. alterniflora, D. spicata & J. roemarianus	5	40.0	2	.40
None	3	0	0	0
Totals and overall average	43	27.2	15	0.37
North River				
Juncus roemarianus	16	50.0	14	.87
S. alterniflora & J. roemarianus	4	50.0	6	1.50
Totals and overall average	20	50.0	20	1.19
Davis Peninsula				
Spartina alterniflora	10	40.0	5	.50
Distichlis spicata	6	16.7	1	.17
Juncus roemarianus	37	16.0	7	.19
S. alterniflora & D. spicata	4	0	0	0
S. alterniflora & J. roemarianus	2	50.0	1	.50
J. roemarianus & D. spicata	14	28.6	7	.50
S. alterniflora, D. spicata & J. roemarianus	4	25.0	1	.25
None	16	0	0	0
Totals and overall average	93	22.0	22	0.26

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Table 9.

MEAN NUMBERS OF TABANID LARVAE/M^2 FOR THE 1972-1973 AND 1974 SAMPLING PERIODS
FOR THE GREAT SIPPEWISSETT MARSH, MASSACHUSETTS. ONLY THE NUMBERS FOR THE
CONTROL AREAS ARE SHOWN, EXCLUDING THE RESULTS FROM FERTILIZATION TEST PLOTS.
C. ATLANTICUS WAS RECORDED IN LOW NUMBERS FROM THE TEST PLOTS BUT NOT
RECORDED FROM THE CONTROL PLOTS. (Modified from Table 1, Meany, et al., 1976.,
by permission of the editor, Journal of Applied Ecology.)

	1972-73		1974	
	Low Marsh	High Marsh	Low Marsh	High Marsh
Tabanus nigrovittatus	28.4 ± 4.3	22.3 ± 4.6	37.7 ± 8.3	12.5 ± 2.5
T. lineola	5.7 ± 2.7	2.4 ± 1.2	1.2 ± 0.9	1.2 ± 1.2
Chrysops fuliginosus	28.5 ± 4.5	3.8 ± 1.5	35.6 ± 7.7	0
C. atlanticus	0	0	0	0

of S. alterniflora decreased, the numbers of tabanid larvae also decreased. Sample sites in two of the marshes where there was no vegetation yielded no Tabanid larvae. This concurs with Bailey's (1948) observation that Tabanus nigrovittatus larvae are rarely collected where the marsh peat is devoid of vegetation.

In another paper (Dukes et al., 1974b) the larvae of the Sheep fly Chrysops fuliginosus (82%) and the Greenhead Tabanus nigrovittatus (18%) were found widely distributed throughout a Newport River, North Carolina marsh dominated by Spartina alterniflora. A natural drainage ditch had no apparent influence on distributions. The results were not always consistent with earlier work. Sampling methods have varied and Dukes et al. believe this to be an important factor. However, they propose surface topography to be equally important. The marsh studied was regularly inundated by the tide with no opportunity to dry out. They consider this contrary to many northern marshes dominated by Spartina patens and the entire Newport River marsh was portrayed as being equivalent to the ditch margins of the northern S. patens marshes.

Various authors have reported ditching increases available breeding areas for the Tabanidae in a tidal marsh (Bailey, 1948; Hansens, 1949). Walls and Doane (1960) found the greatest numbers of punkies (Ceratopogonidae) along the edges of the bays and drainage ditches where tall S. alterniflora was the dominant cover or from the moist mud where other vegetation dominated but not from dry or hard soil. Rockel (1969) described the changes

in marsh physiography resulting from ditching New Jersey marshes and the impact on intertidal organisms. Following ditching there was almost a one foot depression on the banks bordering the ditches. With such a soil contour, flooding tides normally covered the marsh to a distance of seven yards from the ditches with plants and animals submerged longer and more frequently than at higher levels. Rockel reported soil drainage to be more complete close to the ditches with the percent of soil water increasing at higher elevations. Soil organic matter and surface thatch increased with elevation, the latter tending to reduce evaporation and soil aeration. The salt water table was closer to the soil surface at higher elevations during ebb tides. There was increasing cordgrass density but decreasing plant height with an increase in elevation. Both Greenhead flies, Tabanus nigrovittatus, and Deer flies, Chrysops spp., exhibited population peaks in marsh areas which were about 0.2 foot below mean high water (MHW). Ditching, by producing more surface area below MHW, provided more marsh offering optimum conditions for larvae of the various biting flies. The impact of ditching was emphasized by Rockel (1969) who stated that 42% of a marsh surface is altered with ditches spaced at 100 foot intervals.

Vertical distributions become evident from the literature. Several authors (Bailey, 1948; Hansens, 1949; Wall and Jamnback, 1957) report Tabanus in the upper strata of marsh soil, usually the topmost one and one-half inches. There are apparent species differences in population concentrations. Rockel and Hansens
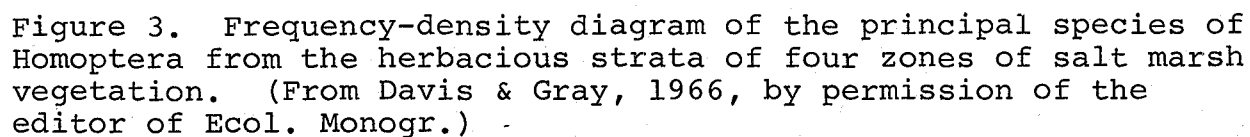
(1970a) found populations of Tabanus nigrovittatus and Chrysops

spp. were highest below mean high water level on gently sloping

banks where the cordgrass was about two feet tall. In their

paper of 1970b the Deerfly Chrysops fuliginosus emerged

primarily well below mean high water whereas T. nigrovittatus

emerged from elevations only slightly below MHW. Rockel and

Hansen (1970a) found the Striped horsefly Tabanus lineola and

the T. nigrovittatus variant known as "T sp 3" (and tentatively

identified in Freeman and Hansens, 1972, as T. n. simulans)

mostly at higher elevations where short marsh grass grows. In

contrast, Meany et al. (1976) found T. lineola appeared equally

between low and high marsh samples. Freeman and Hansens (1972)

found the larvae of T. nigrovittatus and T. lineola in more open

marsh areas of short grass with T. lineola more abundant in

the wetter locations. A greater variance was reported with

their finding "T sp 3" more prevalent in the tall grass areas

bordering ditches.

Rockel and Hansen (1970a) suggest Tabanus females oviposit

primarily on vegetation of a certain height which would influence

larval distributions. Emergence appeared to be synchronized

with the tide because the lowest areas that support vegetation

were exposed long enough to allow hardening of the exoskeleton

to permit adults to fly or to climb stems before reflooding

(1970b). They found no evidence of larval migrations (1970a).

This is in sharp contrast to Gerry's (1950) statement where he

indicated the flies originated in the open creek and migrated

to thatch piles in the higher areas near the marsh edge. Gerry

considered the reported similarity of prevalence of both

mosquito and biting fly concentrations in the upper marsh which

is less frequently flooded can be an asset in terms of control

of both flies and mosquitos. Since then, Dukes et al. (1974a)

believe any control measures directed against the larval stages

of tabanids would be inadvisable because such measures would

have to be applied to extensive areas with possible adverse

impacts on the marsh ecosystem.

Insects in general display an association between the

extent of tidal flooding and vegetation zonation. Tide-elevation

influences, primarily the length of the hydroperiod, determined

the distribution of insect dominants at more stations set up

within the North Carolina marshes examined by Davis and Gray

(1966). The Homoptera were most important and had a more nearly

zonal distribution pattern than did species from the other

insect orders (Figure 3). Homoptera numbers decreased as other

orders increased with the transition from low marsh to high

marsh elevations.

Evidence for zonation among the Homoptera has been enhanced

with the recent work of Foster and Treherne (1975, 1976). They

found the intertidal aphid, Pemphigus trehernei restricted to the

roots of the aster, Aster tripolium, growing in low marshes near

the edges of creeks and salt pans in the marshes of Scolt Head

Island, Norfolk. Gray (1971, in Foster and Treherne, 1975)

classified salt marsh communities containing Aster tripolium

into high, mid, and low marshes. High marshes are almost

removed from tidal influence while mid marshes are reached by

Figure 3. Frequency-density diagram of the principal species of Homoptera from the herbacious strata of four zones of salt marsh vegetation. (From Davis & Gray, 1966, by permission of the editor of Ecol. Monogr.)

all high spring tides and can be distinguished from low marshes
by the presence of <u>Plantago</u> <u>maritima</u>. Low marshes are inundated
by high neap and spring tides.

Foster and Treherne (1975) reported a relatively high
percent of air space near the creek edges where these root
aphids were most abundant (Figure 4). Only small aphid
populations were found in soils with less than 10 percent air
space (Figure 5). Adult aphids were about one millimeter in
diameter and were associated with cavities of at least that
size. These cavities were categorized and arranged in
decreasing order of importance:

(1) Cavities formed by cracking from drying and erosion

(2) Cavities formed by decaying roots

(3) Cavities formed by burrowing of other animals

(4) Cavities formed around mollusc shells and pebbles.

Cavities (1) and (3) were usually confined to edge regions while
cavities (2) and (4) were found in all marsh areas and were
generally water filled.

First instar aphids penetrated the edge soils of the low
marshes considerably earlier than the non-edge areas. In eight
trials with 12 aphids at each site, the mean number of aphids
floating $\pm$ S.E. was 0.88 $\pm$ 0.23 (7.3%) at the edge sites and
6.75 $\pm$ 0.59 (56.3%) at the non-edge sites, a highly significant
difference ($X^2 = 47.8$, P < 0.001).

Foster and Treherne found that aphid populations in
mid-marsh areas do not show an equivalent edge effect. Such
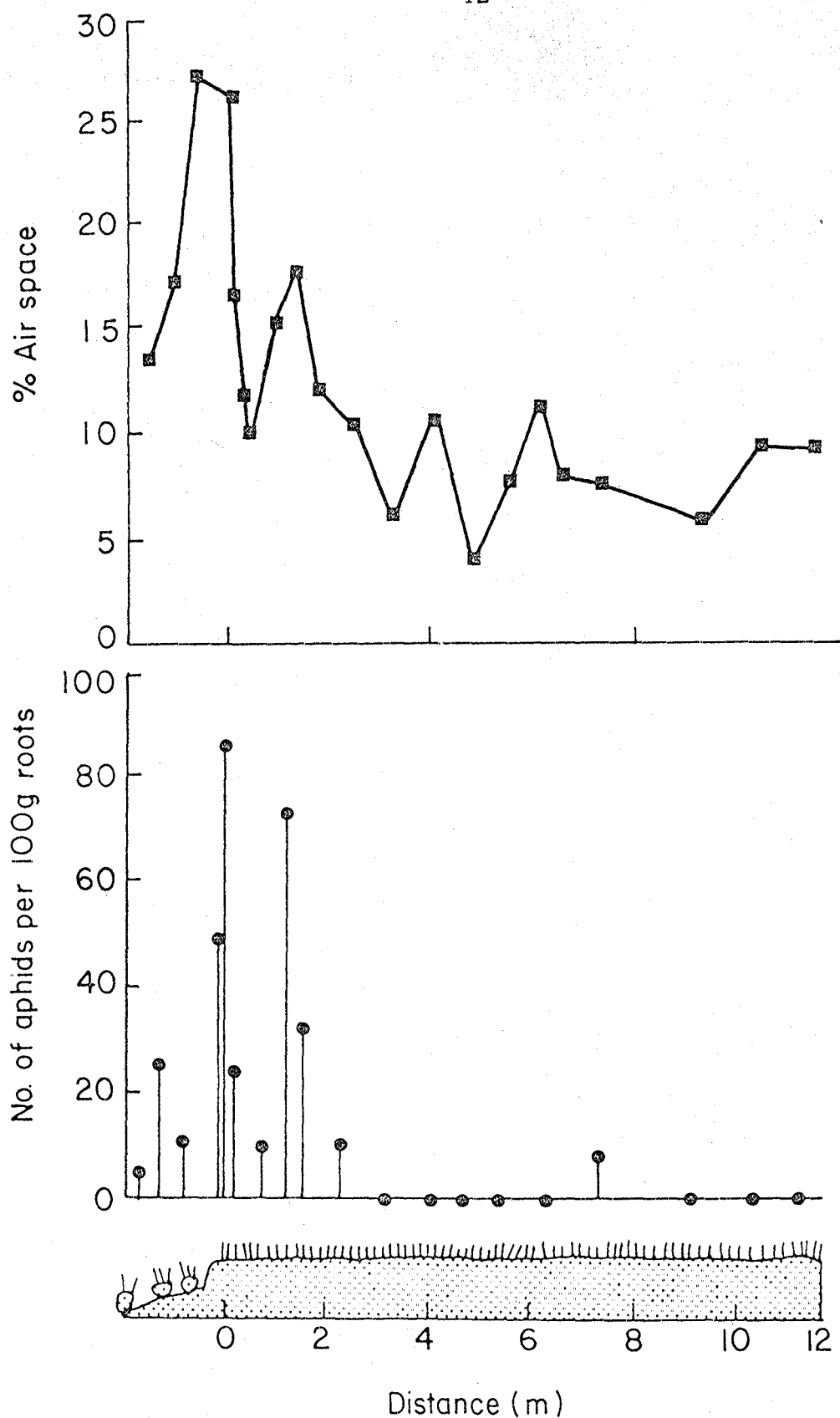sites did not support high aphid concentrations, the maximum

Figure 4. Aphid density and percent soil air-space along a transect on Missel Marsh East, May 26, 1971. All measurements are of single samples. Percent air space was measured by field method. (From Foster & Treherne, 1975, by permission of the editor, Oecologia.)
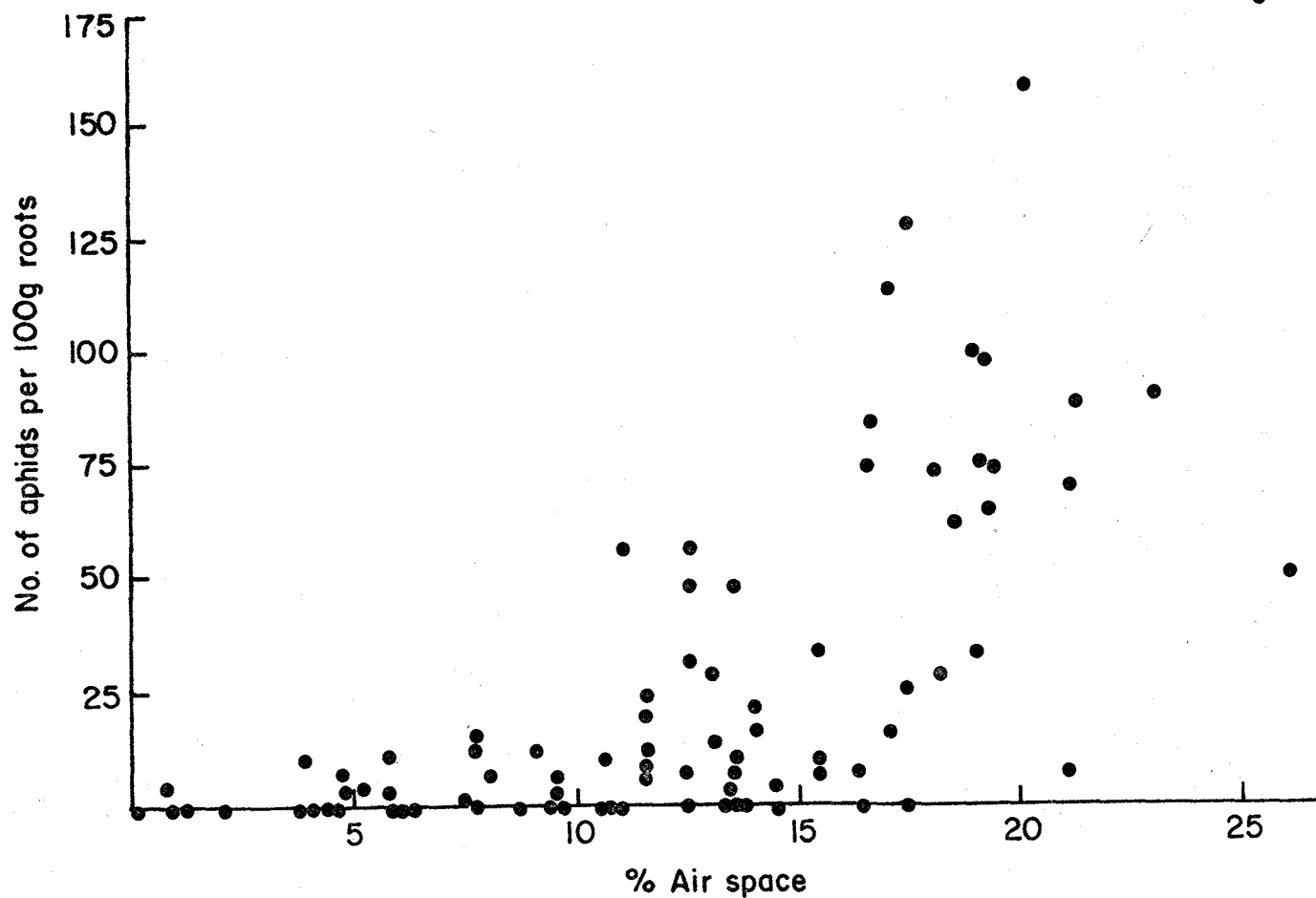
Figure 5.   Relationship between aphid density and percent air space in the soil.   Measurements
made in various sites on Scolt Head in 1970 and 1971.   Percent air space measured
by field method.   Aphid density expressed as numbers per 100g fresh weight of aster
roots.   (From Foster and Treherne, 1975, by permission of the editor, Oecologia.)

number per core was 20. The mid-marsh soils are more mature,
have a higher organic content, have smaller air spaces, and the
large cracks associated with the clay soils do not appear in
mid-marsh sites. The small pore size probably limits the
aphid populations in the mid-marsh.

Foster and Treherne (1975) suggest that for a salt marsh
aphid population to maintain itself, there must be appropriate
spaces within the soil physically to accommodate these non-
burrowing insects, and within such spaces conditions must be
suitable for survival. While there is an enormous potential
for parasitic exploitation of Aster tripolium by the aphid only
a small portion of the plant's distribution is available. The
edge regions appear more accessible to dispersing aphids along
the edges. The greater interplant spacing and larger bare areas
may enhance aphid landings along the edges in these low marshes.
In addition, the greater number of cavities along the edges
would be attractive to these animals.

Other works report on intertidal insects that are regularly
inundated by the flooding tide. Larsen (1951) reported marsh
beetle distributions were strongly influenced by soil type
and vegetation, changing as vegetation invaded bare areas.
Evans et al. (1971) described their observations of four species
of beetles (Bledius spectabilis, Heterocerus fenestratus,
Dichirotrichus pubescens and Cillenus lateralis) which were
confined effectively to the upper regions of the banks of the
drainage channels of the Scolt Head Island, Norfolk salt
marshes, in that region between the anaerobic mud of the lower

bank which was usually covered by a film of algae and the
dense marsh vegetation, mainly Halimione portulacoides
(Figure 6). There were no apparent interspecific differences
in beetle distributions within this zone. The beetle area
was usually well drained and identified by the castings produced
during burrowing. This area differed considerably from the
damper muds back from the drainage channels (Figure 7).
The area is covered intermittently by high tides to a depth of
one meter for seven days in every fortnight. Submergence was
reported to last about 3-4 hours at the highest tides.

Evans et al. (1971) portray B. spectabilis burrows, and
presumably Cillenus lateralis, being excavated to a depth of
2-5 cm but not penetrating beyond an average depth of 9 cm
(Figure 8). H. fenestratus burrowed to a depth of only 1-2 cm,
while Dichirotrichus pubescens did not burrow but lived in
surface cracks.

Submergence responses were found to induce an apparent
anoxic condition (Figure 9). There was a linear relationship
between submergence and recovery for H. fenestratus followed
by a more rapid recovery (Figure 10). The authors suggest the
use of physiological responses to submergence imply the
subterranean mode of life largely prevents direct exposure of
the beetles to sea water in natural conditions.

A significant proportion of H. fenestratus was found to
be vulnerable to flooding and this can be related to the shallow
burrows this beetle excavates. This in turn can be related to
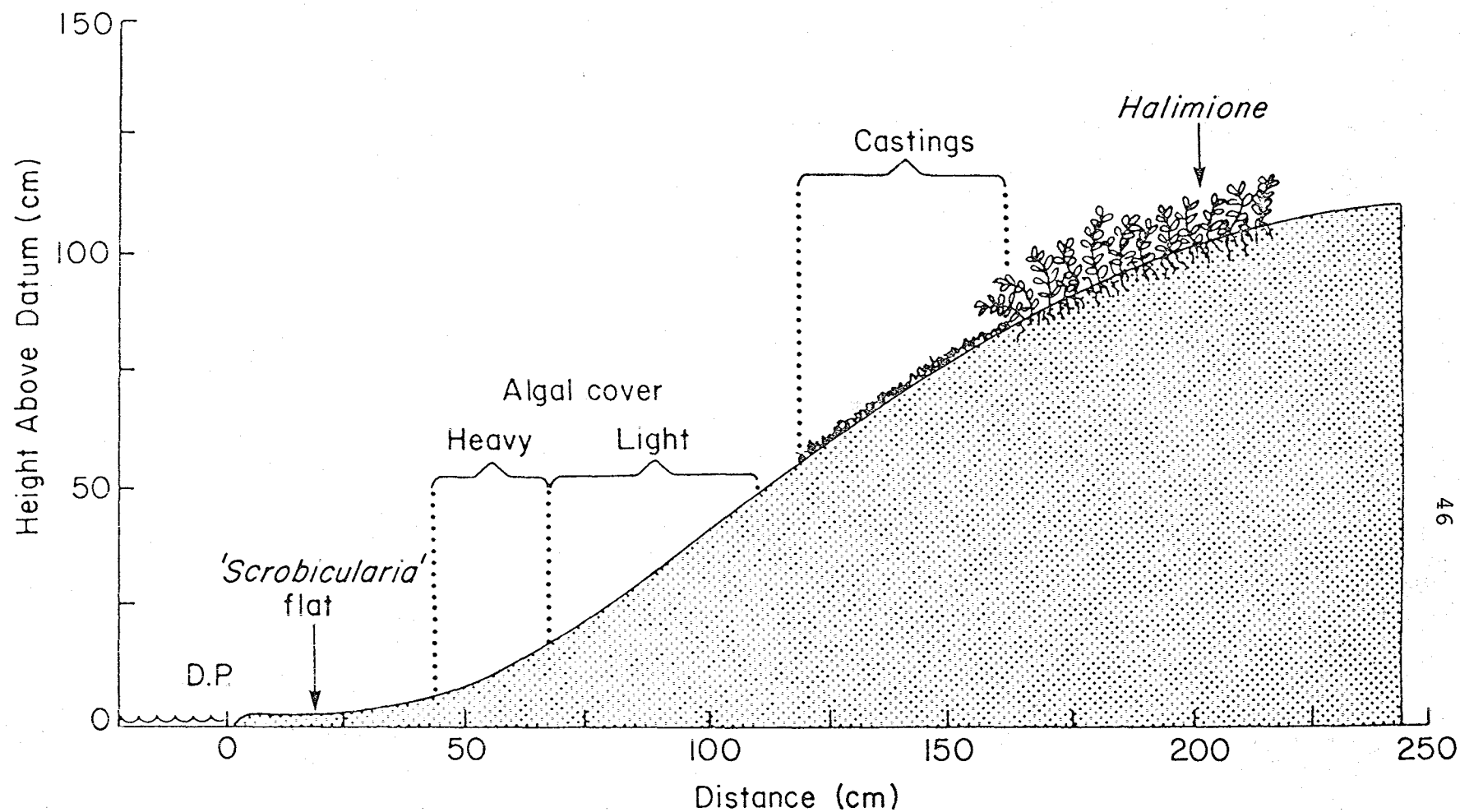the mode of respiration in which the delayed onset of deep

Figure 6. Section of the Hut Drain bank, showing region inhabited by Bledius spectabilis, Heterocerus fenestratus, and Cillenus lateralis (shown by castings). 'D.P.' marks water level of lowest high tide, August/September 1968. (From Evans et al., 1971, by permission of the editor, J. mar. biol. Assoc. U.K.)
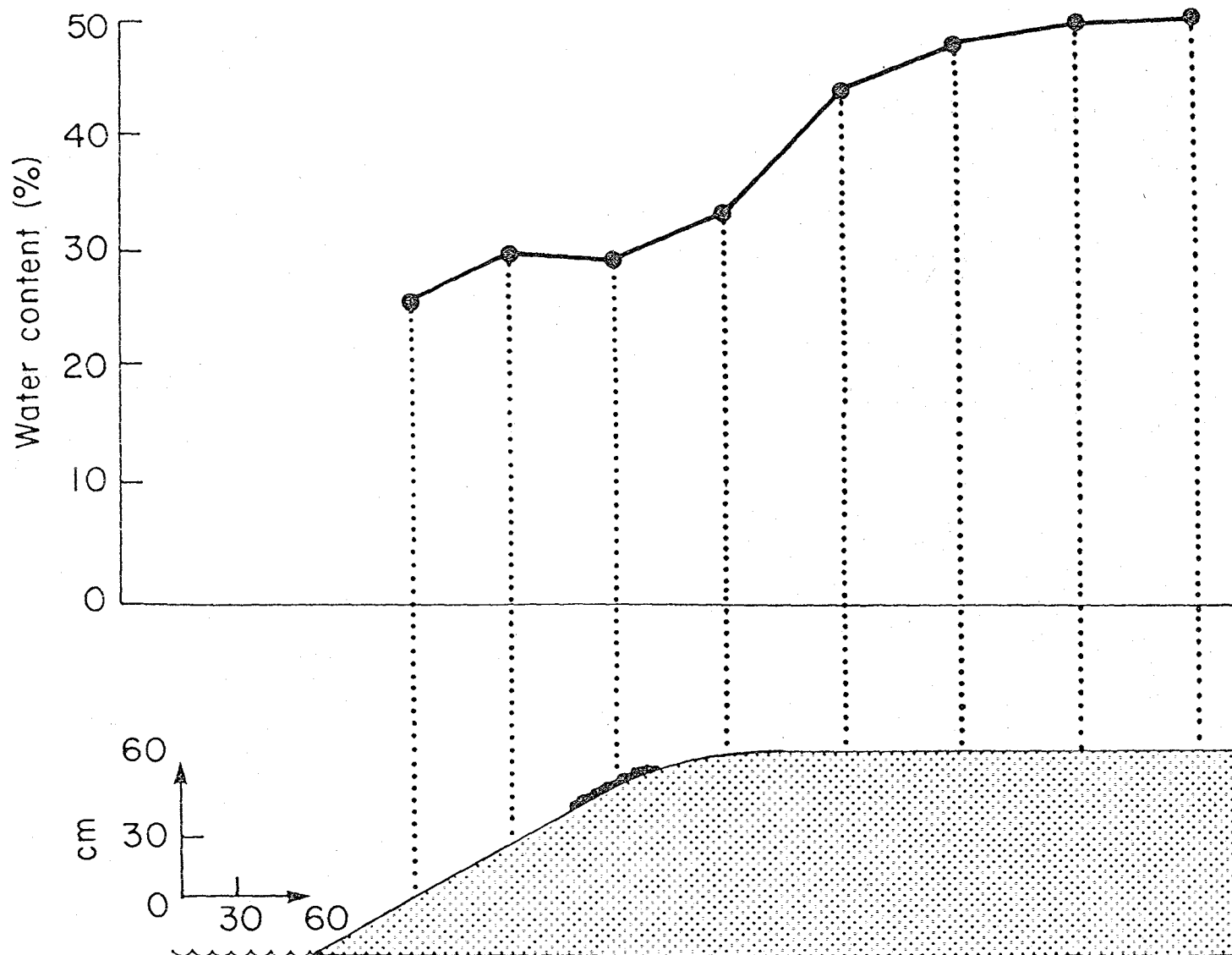
Figure 7. Water content in the top 10 cm of mud in a section of Hut Drain bank. The beetle area is represented by casting. (From Evans et al., 1971, Figure 4, by permission of the editor, J. mar. biol. Assoc. U.K.)
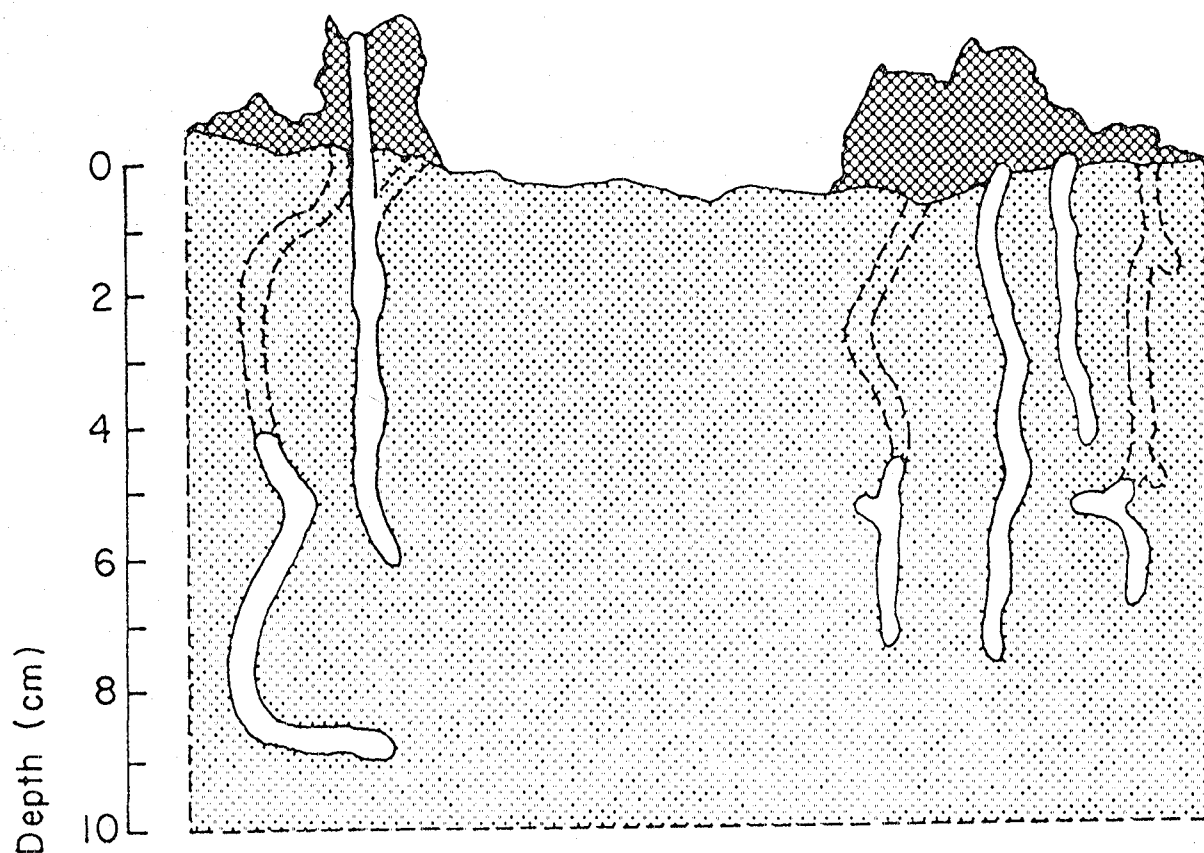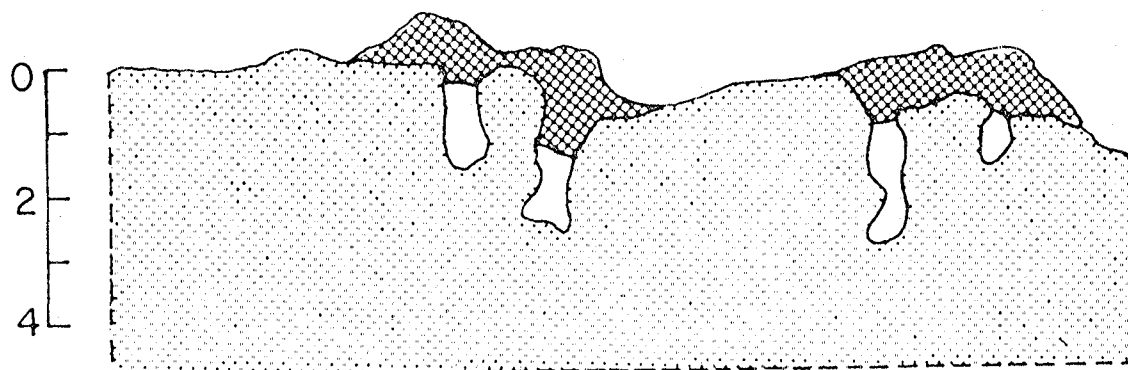
A. *B. spectabilis*

B. *H. fenestratus*

Figure 8. Diagram of burrowing activities of (a) Bledius
spectabilis and (b) Heterocerus fenestratus, following intro-
duction of six specimens of each species into 'soil cells.'
The solid lines represent open burrows and the broken ones
regions of the burrow system previously excavated and subsequently
refilled. (From Evans et al., 1971, Figure 6, by permission of
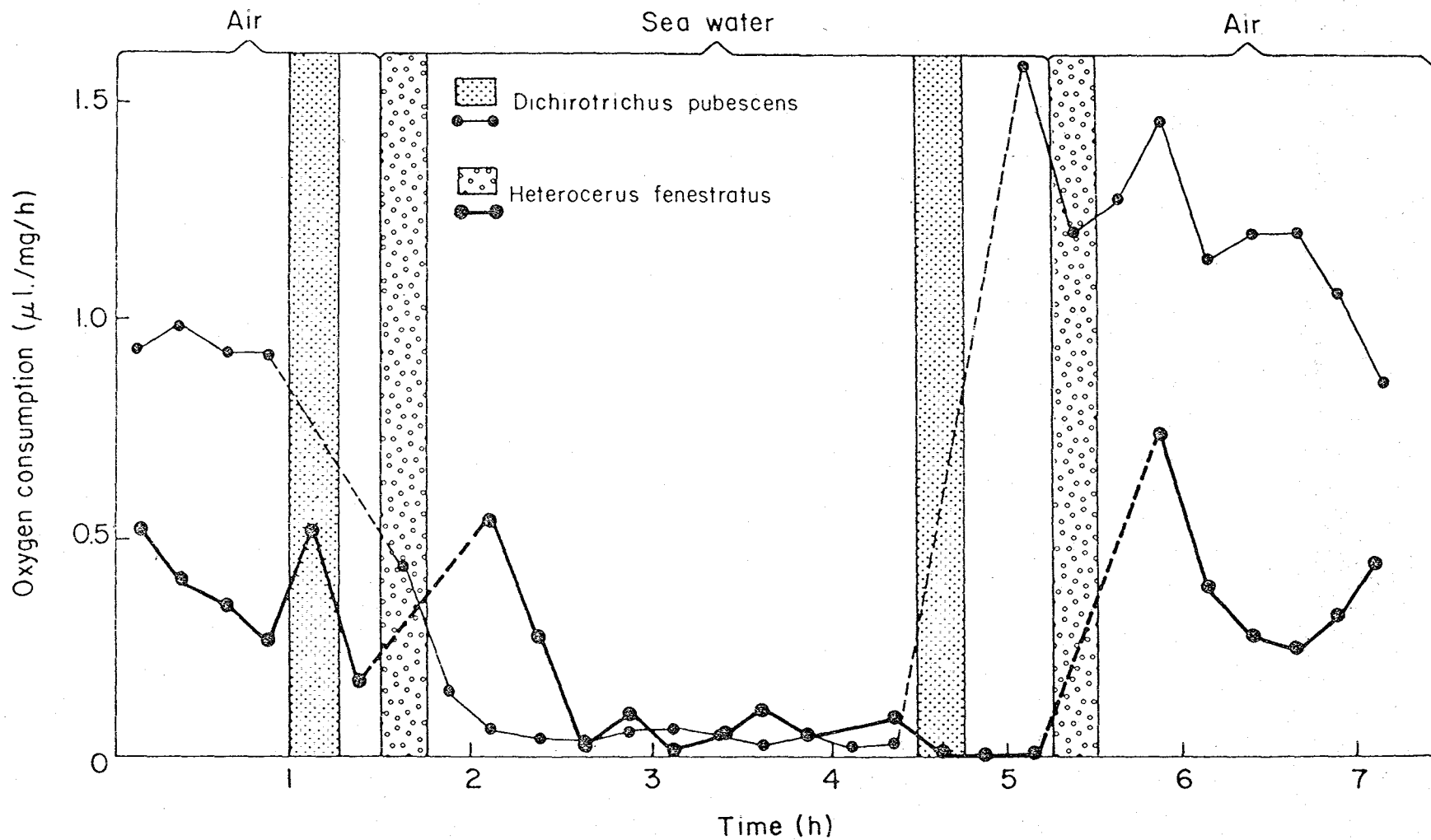the editor, J. mar. biol. Assoc. U.K.)

Figure 9. The effect of submergence in sea water on the oxygen consumption of five adult *Dichirotrichus pubescens* and thirty *Heterocerus fenestratus*. The shaded area indicates the equilibrium period allowed on introduction and removal of sea water from the manometer flasks. (Modified from Figs. 12 and 13 in Evans et al., 1971, by permission of the editor, J. mar. biol. Assoc. U.K.)
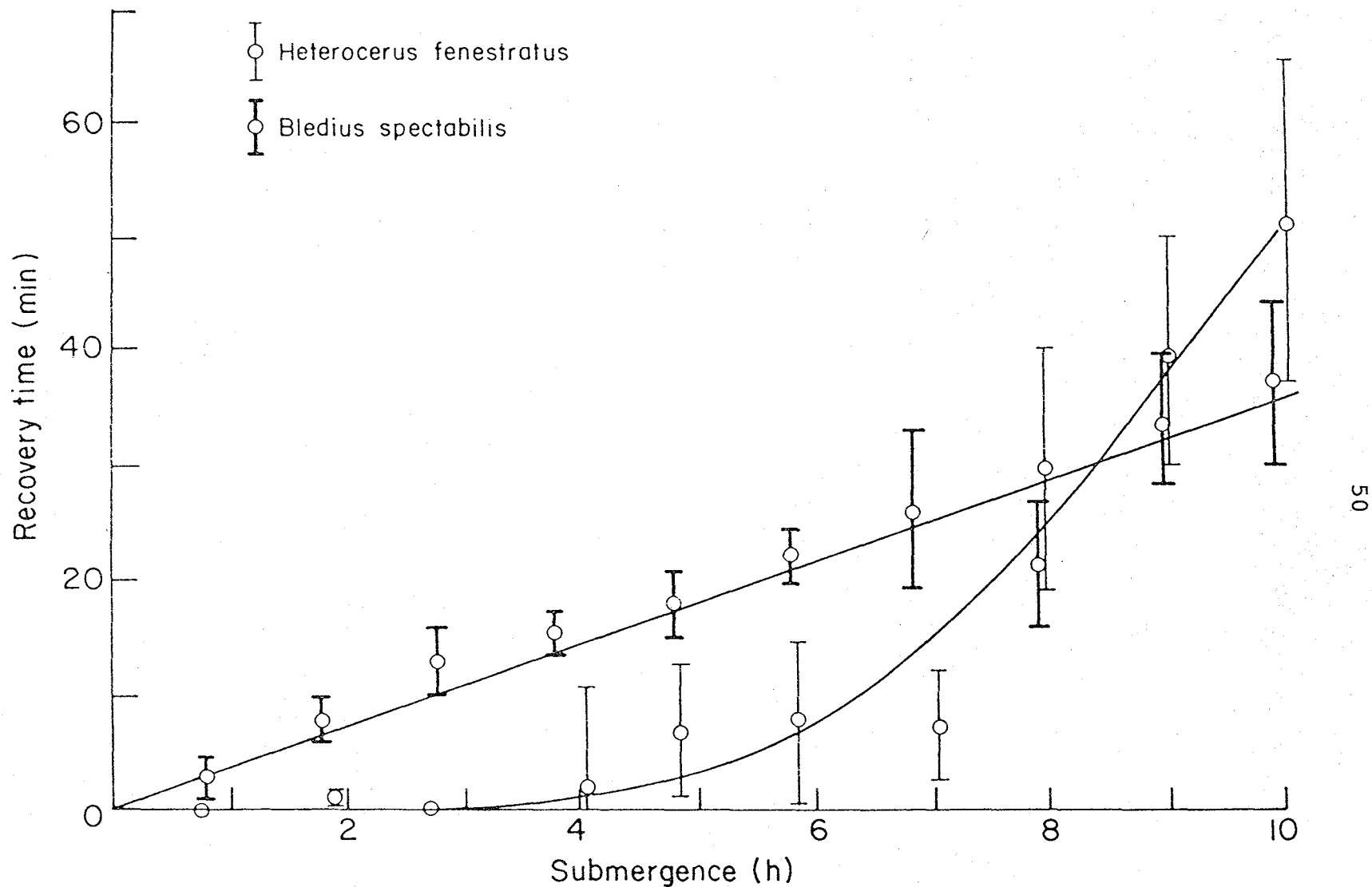
Figure 10. Recovery time for Bledius spectabilis and Heterocerus fenestratus from anoxia induced by varying periods of experimental submergence in sea water. (Modified from Figs. 9 and 11, Evans et al., 1971, by permission of the editor, J. mar. biol. Assoc. U.K.)

anoxia during the first four hours of submergence for H. fenestratus would ensure minimal recovery periods. This is in contrast to the other three species that had a greater and earlier decline in oxygen consumption during submergence but a quicker initial response in recovery (Figures 9 and 10). Apparently, the behavioral and burrowing activities permit this group of insects to survive and flourish in an area of the salt marsh that is regularly inundated by the tides and further work (Treherne and Foster, 1977) provides additional insights into behavioral patterns and survival of these insects.

Dicheirotrichus gustavi is widespread on the soft shores of the intertidal zone in the British Isles. On salt marshes, the adults apparently live in cracks in the mud and do not burrow. During tidal emergence D. gustavi exhibited well defined nocturnal activity. Maximum activity occurred after dusk and decays exponentially until dawn when it abruptly terminated by individual beetles retreating into soil cavities (Figure 11). This circadian activity insured that the majority of the population avoided direct submergence during the first few tidal coverages of the marsh surface of a rising tide sequence. The first tidal coverage, in a sequence of spring tides, occurred shortly before dawn when minimal numbers of adult beetles were exposed to sea water. The second and third critical tides each occurred 12.5 hours later, the second just before dusk while the insects were subterranean (Figure 12). Both field and experimental observations indicated that at least two tidal submergences are required to suppress nocturnal activity on the
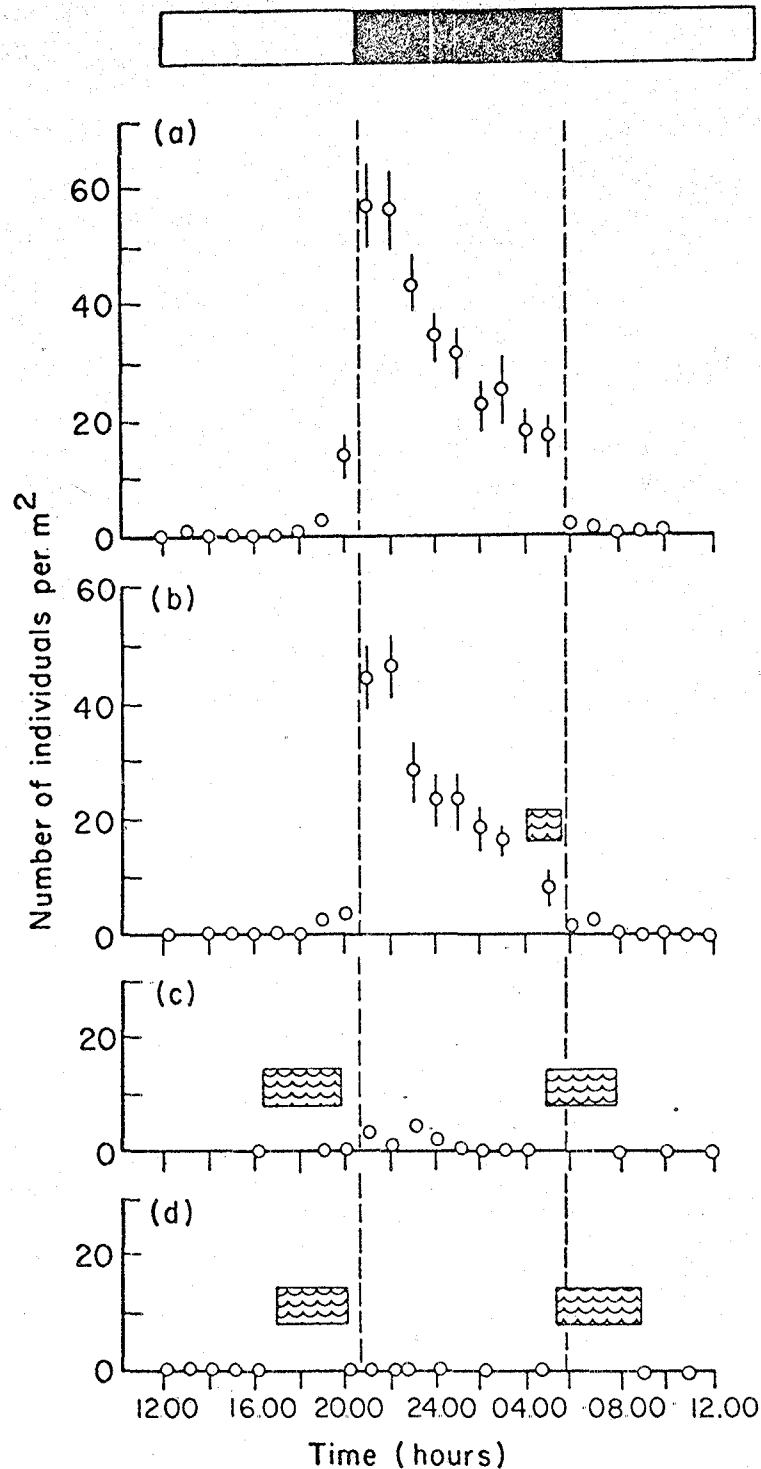
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Figure 11. Surface activity of Dicheirotrichus gustavi, in the
twenty experimental plots illustrated in Fig. 1, (a) before
(31 July 1975) and (b-d) during a period of tidal submergences
(horizontal bars) in a sequence of rising tides ((b): 2 Sept. 1975;
(c) 3 Sept. 1975; (d) 4 Sept. 1975). The open circles indicate the
mean number of individuals on the soil surface and the vertical
lines the extent of twice the standard error of the mean. Dawn and
dusk are indicated by the broken lines. (From Treherne & Foster,
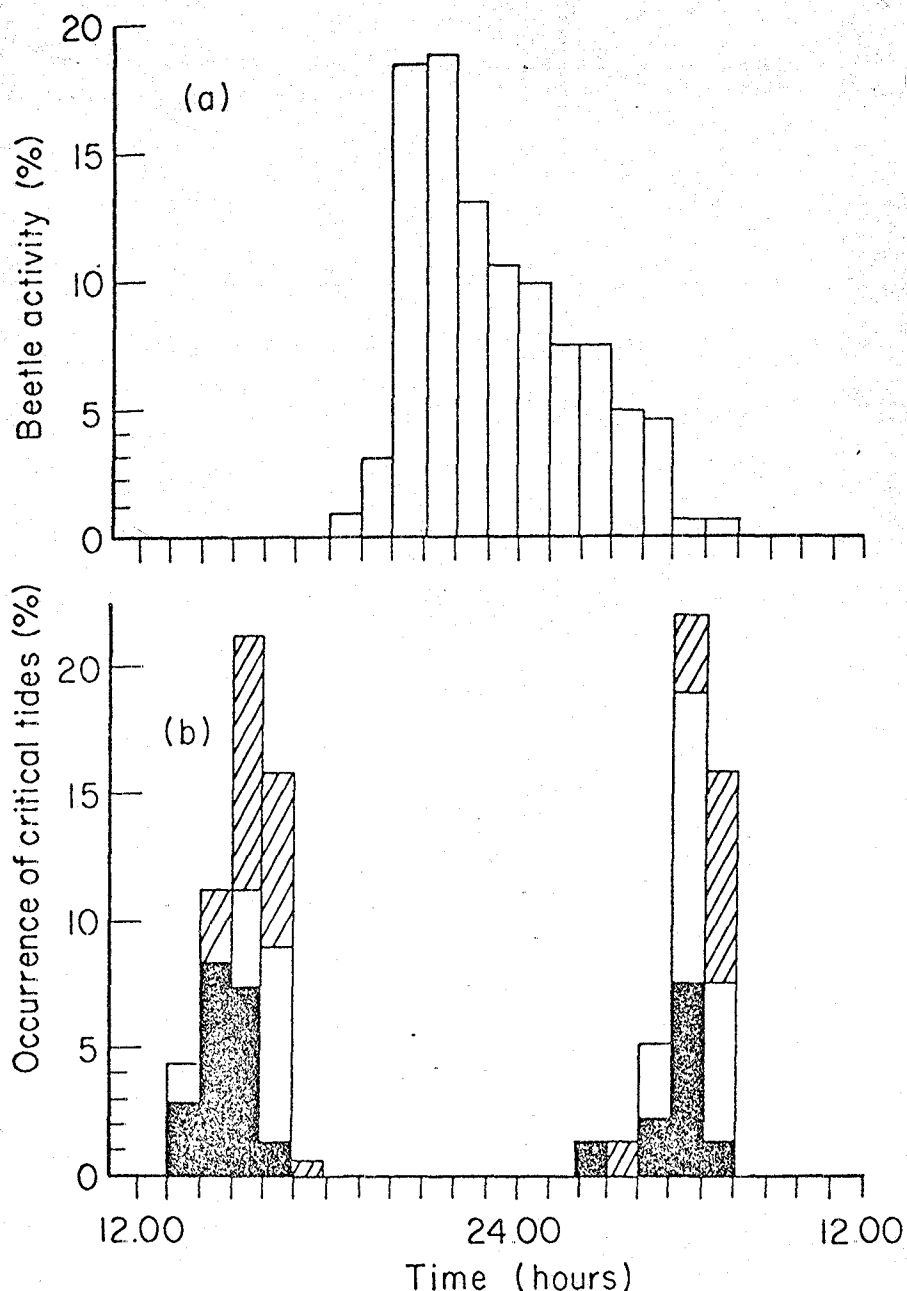1977, by permission of the editor of the J. Anim. Ecol.)

Figure 12. Timing of 'critical' tides (first tides to cover the beetle area after a period of emergence) in relation to beetle activity. It is assumed that tides of 20.7m above the Chart Datum just cover the beetle area (as on 3 Sept. 1975). A first 'critical' tide is any tide exceeding 20.7m which comes after at least three non-flooding tides. The second and third 'critical' tides follow the first at about 12.5 h intervals. (a) Hourly beetle activity in the field. Pooled data from (Fig. 2(a),(b),(c)) expressed as a percentage of the total number of beetles observed during this period. (b) Hourly occurrence of 'critical' tides in 1975 and 1976, expressed as a percentage of the total number of 'critical' tides. First 'critical' tide, solid columns; second 'critical' tide, open columns; third 'critical' tide, hatched columns. (Data from Admiralty Tide Tables.) (From Treherne & Foster, 1977, by permission of the editor of J. Anim. Ecol.)

soil surface. This change in behavior did not seem to be related to changed soil character but from direct experience of changed conditions in the cavities of submerged soil. Reversion to nocturnal surface activity followed an absence of two tidal submergences.

While Evans et al. (1971) found four species effectively confined to the upper intertidal regions of the banks of the Scolt Head marsh drainage channels they found no apparent interspecific differences in distribution within this zone. The mud is aerobic and brown with a quantity of organic material. In contrast, Larsen (1951) described beetle distributions to be very restricted, strongly influenced by soil types and vegetation, replacing each other in successive biotypes. As soon as conditions changed on those Danish marshes at Skallingen, beetle species distributions changed in accordance to their specific demands. As a rule different communities were kept in pure formations as were the plant communities. However, populations intermingled as an area passed through a transition period. Larsen (1951) established three groupings of beetles based on soil and plant associations.

1. Bare algal clay flats. _Bledius_ _spectabilis_ was associated with bare sand with a clay covering and an algal layer covering 20-60%, soil water content 20-25%, abundant in the tidal zone which is covered by water each day. _Bledius_ _taurus_ has much the same substrate requirements but is found with a high soil water content and prefers loose sand outside the tidal zone. _Bledius_ _diota_ and _Trogophlous_ _schneideri_ are

associated with no vegetation, high water content (20%), and high salinity (30-100°/oo).

    2. Bare humid sand flats. Bledius arenarius was found on pure sand, no clay, no algal mats or other vegetation with a salinity of 5-20°/oo and a water content of 10-20%.

    3. Tolerating plant covered soil. Bledius trichornis found mainly in overgrown biotypes and sandy places with varied salinities, 0-60°/oo. Dichirotrichus pubescens can be found in sandy places but prefers clay and dense vegetation. Heterocerus flexuosus was found in many places except where the sand was pure and bare. It invaded muddy banks with an algal mat and areas of pure sand covered by clay and overgrown with vegetation.

    At least three of the beetles described by Evans et al. (1971) are found in Larsen's (1951) categories 1 and 3, and still they are confined to a particular zone in the Scolt Head Marsh with no apparent differences within the zone. The divergence probably can be explained by the response of these beetles and the aphids (Foster and Treherne, 1975, 1976) to submergence.

AVES.

    There is a definite relationship between bird distributions in a salt marsh and the interplay between vegetational zonation, tidal flooding and salinity as it affects feeding and reproductive activities. Urner (1935) identified the ava fauna specialized to nest and feed in salt marshes in relation to the

marsh wetness, creek and pond depth, salinity and accessibility of the tides. Both he and Ferrigno (1961) called attention to changes in bird populations following any alterations in these various parameters.

The resident Clapper rail, Rallus longirostris waynei of the Georgia salt marshes displayed distinct distributional preferences within the dominant grass, Spartina alterniflora (Oney, 1954). This grass could be divided into three categories. A Tall Grass zone was located on the edge of natural drainage ditches, creeks and rivers with a soft mud substrate and an average plant density of 110/square yard, two to four feet tall. The Short Grass zone was found in the lowest parts of the Georgia marshes, had a high sand content with an average plant density of 362/square yard, five inches to two feet tall.

The square-back marsh crabs, Sesarma, the primary food of the rail, were most abundant in the Tall Grass zone. The fiddler crabs, Uca, and the periwinkle, Littorina irrorata, of secondary and tertiary food value, were found in the Medium and Short Grass zones, respectively. However, during his three year study, Oney found a definite nesting preference for the Medium Grass zone: 118 nests measured, 30 were in the Tall Grass zone, 87 or 74% were in the Medium Grass zone and only one nest was recorded for the Short Grass zone. Furthermore, his prior studies in 1949 and 1950 indicated the bird's preference for the medium type grass bordering the Tall Grass zone along a small ditch or creek. The average distance from a nest to the creek at low tide was 458 feet with a range of

3-1200 feet. The average nest was 20 feet from a change in vegetation zone with a range of 3-80 feet. Earlier, Stewart (1951) had called attention to the importance of the edge between vegetation zones in placement of Clapper rail nests. Working in the Eastern short marshes of Maryland, he found a high correlation between nest densities and the amount of edge between the tall (and dense) and the short (and sparse) growth form of Spartina alterniflora. Lower correlations were derived from pure stands of short and tall Spartina. Stewart recorded nest density in the best edge at 2.5 $\pm$ 0.3/acre with nests within 15 feet of the creeks.

Changes in vegetational cover can affect Clapper rail nesting. Ferrigno (1957) reported a decrease in observed nests on the Coney's area but an increase on the Keye's area, both in Cape May County, New Jersey. He attributed the decrease at Coney's to the development of large barren areas which had been formerly covered with Spartina alterniflora. Possible causes given were either adverse weather conditions or over-population of fiddler crabs killing the vegetation by burrowing activities. Rafting of debris by storm tides may have smothered the vegetation.

Several references call attention to the height of nest placement and the impact of inundation on hatching success of the rails. In his early work on the life histories of North American marsh birds, Bent (1963) located the second nestings of the Clapper rail, Rallus longirostris crepitans, on higher drier ground covered with only a few inches of water at high tide.

He went on to say that most nests were built in small clumps of grass along creek banks in soft wet mud: nest heights varied 8-12 inches above the mud, probably high enough to escape ordinary high tides but not spring tides. King rail nests were usually found in the shallow water portion of the marsh with water depths of 4-24 inches. The nest height above water was dependent on water depth; the shallower the water, the lower the nest (Meanley, 1969). Most nests of the resident Clapper rail of Georgia were 8-9 inches off the ground with the average distance from the ground to egg level at 14.8 inches with extremes of nine to 30 inches. These nests could be covered by as much as 12-19 inches of water and still support a hatch (Oney, 1954). Earlier, Stewart (1952) found 1951 hatching success of the first sets of eggs in the Chincoteague, Virginia marshes to be less than 45 percent compared to 94 percent in 1950. Due to high storm tides during the early part of the nesting season, production of young was greatly staggered. Ferrigno (1957) clarified the impact of storm tide flooding on hatching success (Table 10). On May 10, 1955, there had been a high tide with strong winds but little nest damage since the birds had just begun to nest. High tides of June 8-11, resulted in virtually complete nest destruction. There was subsequent renesting as evidenced by a later hatching peak. There were high lunar tides in 1956 but with no wind. Although 14 percent of the nests were destroyed by a flood tide on June 8, 83 percent of the first nests hatched successfully in that year.

Table 10.

CLAPPER RAIL NEST CENSUS DURING 1955 AND 1956
IN CAPE MAY COUNTY, NEW JERSEY.
(From Table 1, Ferrigno, 1957.)

Area	Number of observed nests		Number destroyed (by tides)		Number hatched successfully	
	1955	1956	1955	1956	1955	1956
CONEY'S	29	20	9	4	20	16
KEYE'S	7	10	3	1	4	9
TOTAL	36	30	12	5	24	25

The Clapper rail has been described primarily as a resident of the more saline low marshes (Stewart, 1951; Oney, 1954). In contrast, the King rail, Rallus elegans, and Virginia rail, R. limicola, are essentially inhabitants of the fresh and brackish marshes; numbers varying with vegetation (Bent, 1963; Meanley, 1969). They are common in the coastal marshes of Louisiana, abundant in the South Carolina low country fresh and brackish marshes, especially where the the giant cut grass Zizaniopsis miliacea and the fiddler crab, Uca minax, are present. The grass provides good nesting cover with a nest density as high as one per acre. In the Chesapeake Bay area, the King rail is most abundant where the big cord grass, Spartina cynosuroides is dominant, providing good cover.

Both the King and Clapper rails species occur in transition areas, especially in the lower reaches of brackish marshes where interbreeding sometimes produces hybrids. In Delaware they were taken in the Broadway meadows located between Flemings Landing and Woodland Beach. In that section at Taylors Gut where mixed populations occurred, the dominant vegetation was Spartina alterniflora and Scirpus robustus with the salinity range reported at 5.7-7.2°/oo. Inland at Flemings Landing, the dominant vegetation was Spartina patens and Distichlis spicata with a salinity range of 3.7-4.4°/oo and only the King rail was observed. Only Clapper rails were found at Woodland Beach with S. alterniflora and S. robustus as the dominant vegetation and a salinity range of 7.5-7.6°/oo.

Both rails establish nesting territories but there is no evidence that either species confines its feeding to a territory. Instead, they forage in areas adjacent to or in the preferred nesting areas. The King rail often takes advantage of muskrat runs in its search for food. Both rails search along creek banks where the Clapper rail finds its preferred food the marsh crab Sesarma or the fiddler crab. The King rail frequently repairs to a favorite feeding site, such as the top of a muskrat house, for dismemberment and ingestion of the food item (Oney, 1954; Meanley, 1969).

While both rails can be identified with the low marshes, Bent (1929) described the Eastern willet, Catoptrophorus semipalmatus, as a decidedly coastal bird, seldom seen far from coastal marshes, beaches and islands. He described the nesting area as being on sand islands overgrown with tall grass or on dry uplands close to marshes. Vogt (1938) was a bit more specific in his observations in the Fortesque, New Jersey marshes. He recorded most nests in the dense Spartina patens of the high marsh, near the boundary with Spartina alterniflora or Typha augustifolia. In addition, Vogt found the Willet most abundant where S. patens was regularly mowed or burned, presumably making it easier for the birds to feed. This clamorous bird was also found to be abundant where wintering Brant or Greater Snow geese had grazed S. patens in the absence of eel-grass (Zostera marina). Stewart and Robbins (1958) reported breeding densities of 10.5/100 acres of brackish hay marsh during a 1956 survey of Dorchester County, Maryland. In

contrast to earlier observations these workers described the habitat as a strip along the tidal creek 220 yards wide.

The Willet takes most of its food from within the established territory. Some trips are made to the bayshore or uplands and, when the water level is right, the marsh ponds are visited, the birds picking food from the grass blades. However, the extent of this off-territory feeding is affected by the wind (Vogt, 1938).

The casual visitor to a salt marsh seldom sees the secretive rails as they slip through the vegetation but, during the first half of the summer, a visitor can be announced by the clattering presence of the Willet. However, as the summer progresses these clamorous calls decline to silence although the bird can still be seen flying over the expanses of grass or walking along a creek bank. Black ducks can be put to flight during the early summer nesting season but waterfowl typically are most obvious during the fall migration flights and over the wintering areas.

Thirteen major types of waterfowl habitat have been categorized by Stewart (1962) in the upper Chesapeake Bay area; six in open tidewater areas, five marsh types and two in the coastal plain interior were designated as river bottoms and impoundments. The five marsh habitats were distinguished by salinity distributions which in turn had an influence on vegetational composition. Stewart considered the brackish estuarine bays to be the most important habitat for waterfowl populations as a whole. Fresh estuarine bays, brackish estuarine marshes and estuarine river marshes also attracted large numbers

of waterfowl (Table 11). While Stewart considered the brackish estuarine bays to be the most valuable waterfowl habitat, the marshes bordering such bays had fewer recorded species (10) than the less saline fresh estuarine bay marshes (13) and estuarine river marshes (12). The three marshes with one or two designated principal species had higher numbers of secondary species. It is evident that nine species were restricted to certain marsh habitats while seven were recorded from all five types. The Black duck was the most ubiquitous, being classed as a principal species for all five marsh habitats. Making an arbitrary selection of those seven species found throughout the marshes and using estimated population size data available from Stewart, Table 12 depicts the population distributions for four of the seven species. The widely distributed Black duck seemed to be more associated with the open bays or agricultural lands during migration and wintering. Large breeding populations were found along the shallow brackish estuarine bays and associated marshes. In contrast, while the recorded population was low (Table 12) the great majority (99%) of Green-wing teal were found in the tidal marshes. Stewart indicated the same pattern for the Blue-wing teal. It should be pointed out that waterfowl numbers within a particular type of habitat vary from location to location.

Vegetation dominance and distributions as well as salinity levels had an influence on waterfowl distributions by providing food and nesting sites. _Spartina_ _alterniflora_ was the predominant plant in the coastal embayed salt marshes located back of the

Table 11.

PRINCIPAL (P) AND SECONDARY (S) WATERFOWL SPECIES ASSOCIATED WITH VARIOUS TYPES OF UPPER CHESAPEAKE BAY MARSHES DURING 1958-1959. (Derived from Stewart, 1962.)

	Coastal Embayed Marsh		Salt Estuarine Bay Marsh		Brackish Estuarine Bay Marsh		Fresh Estuarine Bay Marsh		Estuarine River Marsh	
	P	S	P	S	P	S	P	S	P	S
CANADA GOOSE	X			X		X	X			X
BLACK DUCK	X		X		X		X		X	
SNOW GOOSE		X								
MALLARD		X		X		X		X	X	
GREEN-WING TEAL		X		X	X			X	X	
BLUE-WING TEAL		X		X	X			X	X	
SHOVELER		X		X		X		X		
AMERICAN WIDGEON		X		X	X			X		X
HOODED MERGANSER		X				X				X
COMMON MERGANSER								X		X
RING NECK DUCK								X		X
AMERICAN COOT		X						X		X
PINTAIL		X		X		X		X	X	
GADWALL				X		X		X		
WHISTLING SWAN								X		
WOOD DUCK									X	
	2	9	1	8	4	6	2	11	6	6
		11		9		10		13		12

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Table 12.

POPULATION DISTRIBUTION OF WATERFOWL ASSOCIATED WITH VARIOUS TYPES OF UPPER CHESAPEAKE BAY MARSHES DURING 1958-1959.

(Derived from Stewart, 1962 --- Tables 44, 45, 76, 84.)

Percent of total population*

Waterfowl	Total Population (X 1000)	Coastal Embayed Marsh 21,000 acres	Salt Estuarine Bay Marsh 113,000 acres	Brackish Estuarine Bay Marsh 47,000 acres	Fresh Estuarine Bay Marsh 30,000 acres	Estuarine River Marsh 67,000 acres
BLACK DUCK	317	12	10	3	3	5
CANADA GOOSE	---					
MALLARD	148	6	1	3	5	7
GREEN-WING TEAL	10	32	23	13	6	25
BLUE-WING TEAL	---					
AMERICAN WIDGEON	196	8	5	4		--
PINTAIL	---					

*The percentage figures are averaged values derived from five observation periods from October 2, 1958 through March 16, 1959.

The difference between the total percentage figure for each waterfowl species and 100% indicates the birds were observed on the open waters of the adjoining bays and areas other than in the marshes.

barrier beaches. The Black duck was the only species that was common and widely distributed while the Canada goose was numerous along tidal creeks and guts. Canada and Snow geese were most numerous on extensive cord grass areas or mud flats. Pintails, Shovelers, Blue-wing teal and American widgeon preferred open ponds with poor drainage or stable water levels in artifically created ponds. Scattered pairs of Black ducks along with a few Mallards and Blue-wing teal nested in these marshes. They preferred marsh islands rather than shore zone marshes and all nests found by Stewart (1962) were in the drier more elevated areas.

The salt estuarine bay marshes were characterized by a high salinity and narrow tidal fluctuation. Widgeon grass Ruppia maritima, salt grass Distichlis spicata, salt marsh cord grass Spartina alterniflora, salt meadow cord grass S. patens, the bulrush Scirpus robustus and Juncus roemarianus were the common plant species. The Black duck was the only common and widely distributed waterfowl. All others were scarce.

The brackish estuarine bay marshes comprised a complex mosaic of ponds, creeks and marshes. The principal plant species were Ruppia, Distichlis, Spartina cynosuroides, S. alterniflora, S. patens, Scirpus olneyi and Juncus roemarianus depending on the locale. There was a diverse fauna with raccoons and crows as important waterfowl predators. As in the coastal marshes, the Black ducks and Green-wing teal were generally distributed showing a definite preference for tidal creeks and ponds in drainage systems with marginal mud flats exposed at low tide.

The American widgeon and Gadwells concentranted on stable ponds with beds of widgeon grass or musk grass (Chara sp.). The Hooded mergansers were restricted to the larger tidal creeks while Canada geese preferred the larger ponds. Large numbers bred in these marshes with the Blue-wing teal restricted almost entirely to the marsh meadow (presumably Spartina patens).

The fresh estuarine bay marshes had next to the smallest total recorded acreage but a much greater diversity of vegetation. Along with this vegetation variety, Stewart recorded the greatest numbers of waterfowl species, though eleven of the 13 were classed as secondary (Table 11) and most of the population was located on the bays adjoining these fresh estuarine bay marshes (Table 12) rather than in the marshes themselves. As with some of the other marsh types, the Canada geese were found on the larger ponds while the Black ducks and teals were found in well drained areas of creeks and ponds with exposed mud flats.

The vegetation varied with salinity in the estuarine river marshes of the upper Chesapeake. This was an area with a great variety of emergent vegetation and possessed a greater tidal fluctuation than some other marsh types. The greatest concentrations of waterfowl, including many dabbling ducks, were located here between the fresh and brackish water habitats where excellent cover and food was available.

An examination of the numerous tables in Stewart (1962) depicting waterfowl food habits in the upper portion of Chesapeake Bay discloses a relationship between the horizontal salinity-

vegetational distribution and food habits. A greater variety
of food species was consumed as salinities decreased from one
marsh type to another. Presumably this was a reflection of
increased diversity and availability associated with less saline
areas. However, there may be more than availability playing a
part in the food habits of waterfowl associated with tidal
marshes. By using two criteria, timing of usage and relative
quantity of food per unit area remaining after usage, Owen (1971)
ascertained the winter feeding habits of White-fronted geese
in England to be highly selective in the choice of vegetation
zone. By both criteria, the Agrostis zone which is the lowest
grassy area and dominated by Agrostis stolonifera was preferred
to all others. Lolium perenni, Festuca rubra, Hordeum
sicalinum and Juncus gerardi were found at higher elevations, and
were consecutively grazed later in the season. Selection of a
zone was not absolute however; when large numbers of geese were
present all zones were occupied. Owen presented evidence that
plants may be selected on basis of protein, fiber and carbohydrate
content. If so, Puccinellia maritima was considered to be
preferred by White-fronted geese over Agrostris and Festuca.

Among the passerine species the magnitude of flooding
influences habitat selection for both the Coastal Savannah
sparrow Passerculus sandwichensis alaudinus and the Eastern
Sharp-tailed sparrow Ammospiza c. caudacuta. Both are found at
the higher marsh elevations. The former is found in the Salicornia
associes, less so among the Distichlis spicata. The Sharp-tailed
sparrow is found in the drier Spartina patens zone with some

nests on the ground but most of them are at varying heights
above ground level, presumably above summer high water levels
(Bent et al., 1968).

Adequate feeding grounds and suitable nesting cover within
easy flight of the feeding grounds provided two components of
a suitable habitat for both the Northern Seaside sparrow,
Ammospiza m. maritima (Bent et al., 1968) and Macgillvrays
Seaside sparrow, Ammospiza maritima macgillivraii (Tomkins,
1941). The latter is the breeding Seaside sparrow of South
Carolina and Georgia and in this locale these two requirements
are often separated by a short distance. Food requirements were
far stronger than nesting needs in determining habitat limita-
tions with population shifts caused by erosion of feeding sites.
Feeding grounds were the wet banks of salt creeks where Spartina
alterniflora grows rankest, the ponds that are at the heads of
salt creeks and the patches of S. alterniflora located on the
outer beaches that were flooded by tides. Tidal flooding of
the feeding grounds made them unsuitable for nesting sites.
Nests were built in a variety of places; a few inches above the
mud in Sporobolus-Paspalum to three feet in Spartina or Juncus
and up to five feet in Baccharis. Nesting preferences appeared
to follow this same order with the taller shrubbery the least
desirable site.

Much attention has been focused on the Song sparrows
Melospiza melodia of the salt marshes of the San Francisco Bay
region (Marshall, 1948; Johnston, 1956a, 1956b). These
investigators discussed habitat, abundance, annual cycles,

population structure and maintenance, and concluded that tidal

flooding and vegetational zonation were the determining

influences. Song sparrow distributions were more circumscribed

than vegetation distributions as birds are less tolerant of

drying (Marshall, 1948). Scirpus acutus and Typha latifolia

were dominant plants in the brackish marshes comprising a large

portion of the region. Scirpus californicus and Typha latifolia

grew upstream beyond the tidal flow while Scirpus acutus, being

more tolerant of salt, graded into the Spartina (largely

S. foliosa) marshes. There was no interruption of linear

sequence of breeding Song sparrows through these transitions

and birds of any intermediate zone did not sort out into

different plant associations in the brackish marshes (Marshall,

1948).

Both Marshall (1948) and Johnston (1956a,b) noted the Song

sparrow occupied territories strung out along the tidal sloughs,

exercising definite preferences for vegetation types and not

dispersing over the marsh surface. Marshall called attention to

differences in territorial spacing. Sparrow pairs were about

48 yards apart along the bayshore and about 52-70 yards

between pairs along the brackish marsh sloughs, depending on

the width of fringe plants, 15 and 5 yards respectively. The

birds used the tallest plants whether it was Scirpus acutus,

Spartina or Grindelia in the center of patches of these species

for song and calling perches. Plants on levees were visited but

territory headquarters were always at slough margins. Flooded

areas behind these levees, or any stagnant areas where tidal flow

had been cut off, were avoided as were low, dense growing stands of Scirpus campestris. The birds would visit drained Salicornia patches but did not establish territories in such locations.

Marshall (1948) went on to describe the relationship between Song sparrow distributions and the salt marsh vegetation dominated by Spartina foliosa, Salicornia ambigua, and Grindelia cunefolia. Spartina was found at the lowest elevations, Salicornia was covered only by the highest tides while Grindelia grew on the levees and elevated banks of the sloughs in the Salicornia zone. Song sparrow pairs were spaced at 76 yards, single file, along each bank in the Spartina marsh (Marshall, 1948) with an average territory width of 30 feet (Johnston, 1956b). In the Salicornia-Grindelia marsh, pairs were 30-100 yards apart, being closer together where the Grindelia was widest (Marshall, 1948). Johnston (1956b) disagreed somewhat since he found larger territories at the heads of the sloughs where the height and amount of vegetation, especially Grindelia, was reduced. He described the Spartina zone territories as being larger than those in the Salicornia and, during periods of high numbers, actual densities were 8-10 pairs per acre.

The breeding season is influenced by tidal heights (Johnston, 1956a) with the salt marsh song sparrow breeding about two weeks earlier than the upland form. This seems to be an adaptation to marsh life wherein the birds nest mainly during the lower tidal conditions existing in March. Late nests

suffered high mortality from the extended high run of tides
in April to June. Nests were placed off the ground, most
commonly in Salicornia, Grindelia, Distichlis or Spartina.
Any nest less than five inches above the ground would be flooded
out. Average nest height above ground was 9.5 inches for the
whole marsh and 12 inches in the low marsh. The birds usually
tried to put the nests in the highest vegetation but not always.
Johnston is of the impression that predators may exert some
selective pressure on the upper limit of nest height. No nests
were used more than once with nests of the season scattered
about in the territory. Generally an increase in vegetation
height during the growing season enabled the birds to nest at
successfully higher levels. Such action paralleled the increased
height of tides during the breeding season.

Marshall (1948) described the Song sparrow to be the only
ground foraging bird of the San Francisco Bay salt marshes, dropping
down through a Grindelia plant from a singing perch. In fact,
the species was limited to areas covered by tides where flows
are unimpeded. Both Marshall and Johnston stressed the Song
sparrow distributions are limited by vegetation, tidal water,
accessibility of the ground for foraging, habitat selection and
the sedentary nature of the populations. Such characteristics
favor the maintenance of integrity and distinctness of Song
sparrow populations in the salt marshes of the San Francisco Bay
region.

Sibley (1955) described the responses of salt marsh birds
to extreme tides in the San Francisco Bay area at times other

than nesting periods. White-crowned, Savannah and Song sparrows
and Long-billed marsh wrens were concentrated along the levees.
When flushed they did not fly out over the flooded marsh.
Willets and the Least and Western sandpipers settled on floating
debris. The Clapper, Sora, and Virginia rails, normally not
seen at low or average tidal conditions, were quite evident
clinging to Spartina stems or huddled in clumps of emergent
vegetation. Predators availed themselves of these concentra-
tions as California and Ring-billed gulls, Marsh hawks and
Short-eared owls were reported hunting along the levees and over
clumps of emergent vegetation.

MAMMALIA.

A number of small mammals have been associated with the
fringes of salt marshes (Paradiso and Handley, 1965). Shure
(1970, 1971) found a definite relationship between small mammal
distributions and the topographically controlled pattern of
barrier beach vegetation of a New Jersey marsh habitat. The
Meadow mouse Microtus pennsylvanicus was the most abundant,
constituting 97 percent of the captures associated with the dense
herbacious cover of the marshes of the bay shore dominated by
Spartina patens. Zapus hudsonius, Meadow jumping mouse and
Peromyscus leucopus, the White-footed mouse were fairly
abundant, the former being most evident in the brackish marshes
and upland borders. Peromyscus, the Masked shrew Sorex
cinereus and the House mouse Mus musculus were taken occasionally
in the salt marsh but primarily at trap sites in the marsh-upland

border. There is a change in small mammal distributions
during successional stages of a salt marsh (Figure 13). Shure
(1971) suggests the role of vegetation preference and inter-
specific relations as contributing factors and seems to
prefer the latter.

Microtus distribution is related to tidal flooding wherein
Shure (1971) found a significantly greater number of Meadow
vole in the drier more dense S. patens vegetation in contrast
to the lower wetter S. alterniflora. This preference was
further borne out by the significantly greater number of trap
captures from the Spartina patens covered spoil piles bordering
drainage ditches than from other marsh locations. Several
authors (Harris, 1953; Johnston, 1957) comment on the
willingness of Microtus to swim. Such behavior must be related
to unusual conditions such as storms because Shure (1971)
showed a significant restriction of Microtus movements caused
by the presence of mosquito control ditches wherein the vole
apparently had a reluctance to swim across such a waterway that
ranged up to one meter in width. This reluctance was further
substantiated by Shure recording significantly smaller recapture
distances in a brackish marsh than a salt marsh area. The
brackish marsh was highly compartmentalized by ditches and
most Microtus were repeatedly recaptured with the same
compartment.

Several authors (Harris, 1953; Fisler, 1965; Rudd et al.,
1971) comment on the presence of a home range for Microtus in
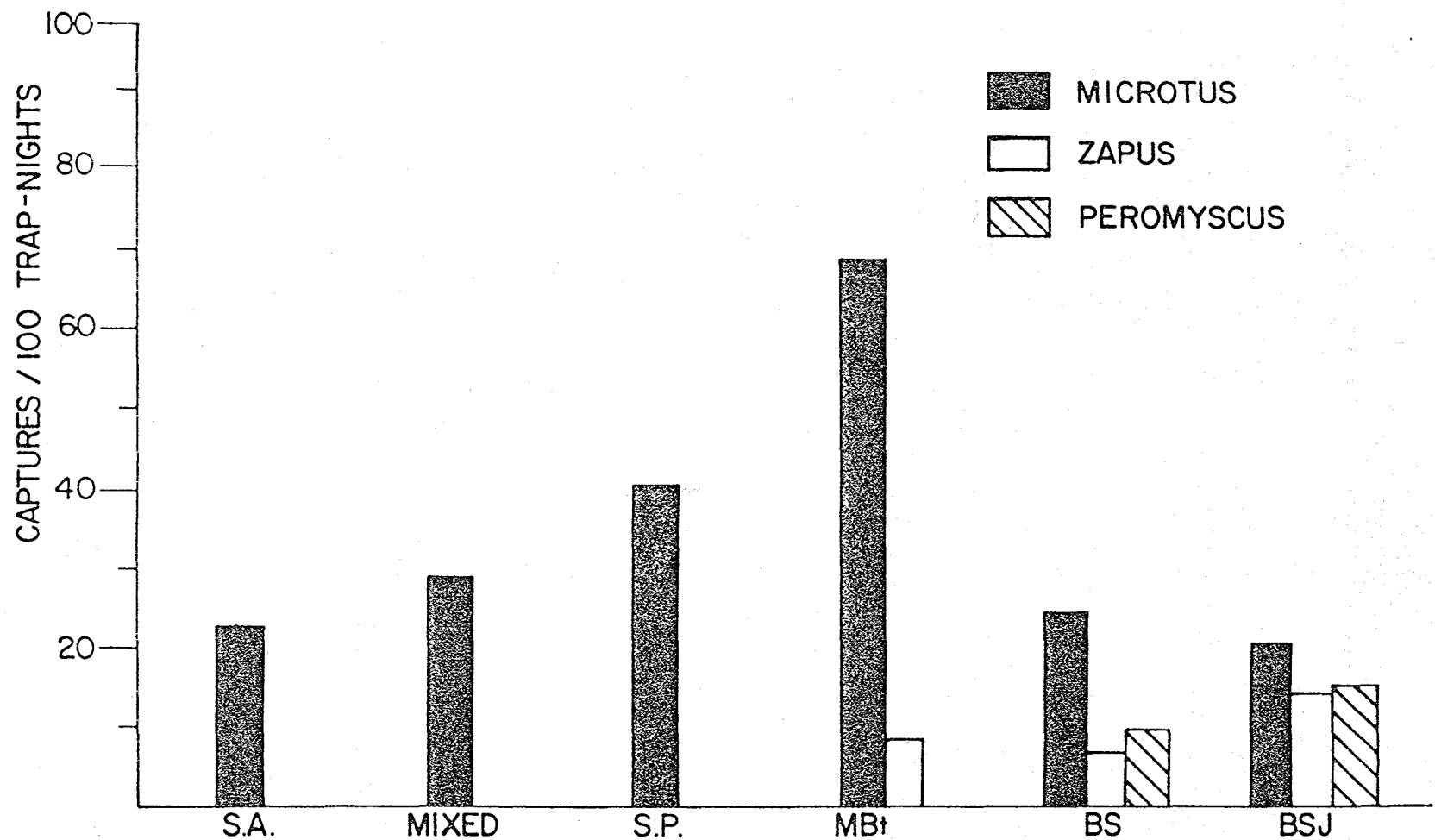a tidal marsh with Harris identifying the size at one quarter to

Figure 13. Capture rates of small mammals in communities representing seral stages in tidal marsh succession. The initial salt-marsh stage has been divied into mixed and homogeneous areas of Spartina alterniflora (SA) and Spartina patens (SP). Other seral stages include brackish marsh (MBt) and mixed herb-shrub savannahs (BS, BSJ). (From Figure 3, Shure, 1971, by permission of the editor of Amer. Midl. Nat.)

one half acre. Feeding is presumed to occur within that home
range and recent observations in Canary Creek marsh on the
frequent recapture of the same individuals and the presence of
feeding remains on grass in the same general location would
tend to confirm the presence of Microtus to a restricted area.

All of these mammals are inconspicuous marsh fringe
inhabitants. The Muskrat, Ondatra zibethica, is a much more
obvious animal, conspicuous by its houses dotting the marsh
surface and its aquatic runs among the vegetation. Much has
been written about its activities both in fresh and brackish
water marshes. Ditching for mosquito control which presumably
lowered water levels is reported to have an adverse effect on
vegetation needed for muskrat food and house construction
(Stearns et al., 1939, 1940). Important muskrat foods such
as Scirpus olneyi and Spartina cynosuroides have been replaced
by species such as Hibiscus oculiroseus, marsh mallow,
Kosteletzkya virginia, salt marsh mallow, Solidago remprevirens,
seaside goldenrod, Bidens trichoxperma, tick seed sunflower
and Aster novi-belgii, presenting a brilliant picture but of no
value to the muskrat (Figure 14).

Aerial views of Muskrat, Ondatra zibethicus, activity tend
to display discrete sites for feeding with the house or feeding
platform being the focal point. During the fall it is hard
from such aerial views to distinguish between feeding activity
and harvesting or grass for house construction. Errington (1963)
has very ably documented the presence of home range and
territorialism among muskrats and in addition has described the

0" — 5,807' ABOVE LOCAL MEAN LOW WATER

– MEAN GROUND ELEVATION – MARSH ————————————— -2.58"

– MEAN GROUND ELEVATION – MUSKRAT HOUSES -4.56"

5" –

– MEAN WATER LEVEL – UNDITCHED AREA   SCIRPUS -6.54"

80%

MEAN WATER LEVEL – MUSKRAT HOUSES -9.11"

10" –

MEAN WATER LEVEL – DITCHED AREA -11.62"

20%   HIBISCUS
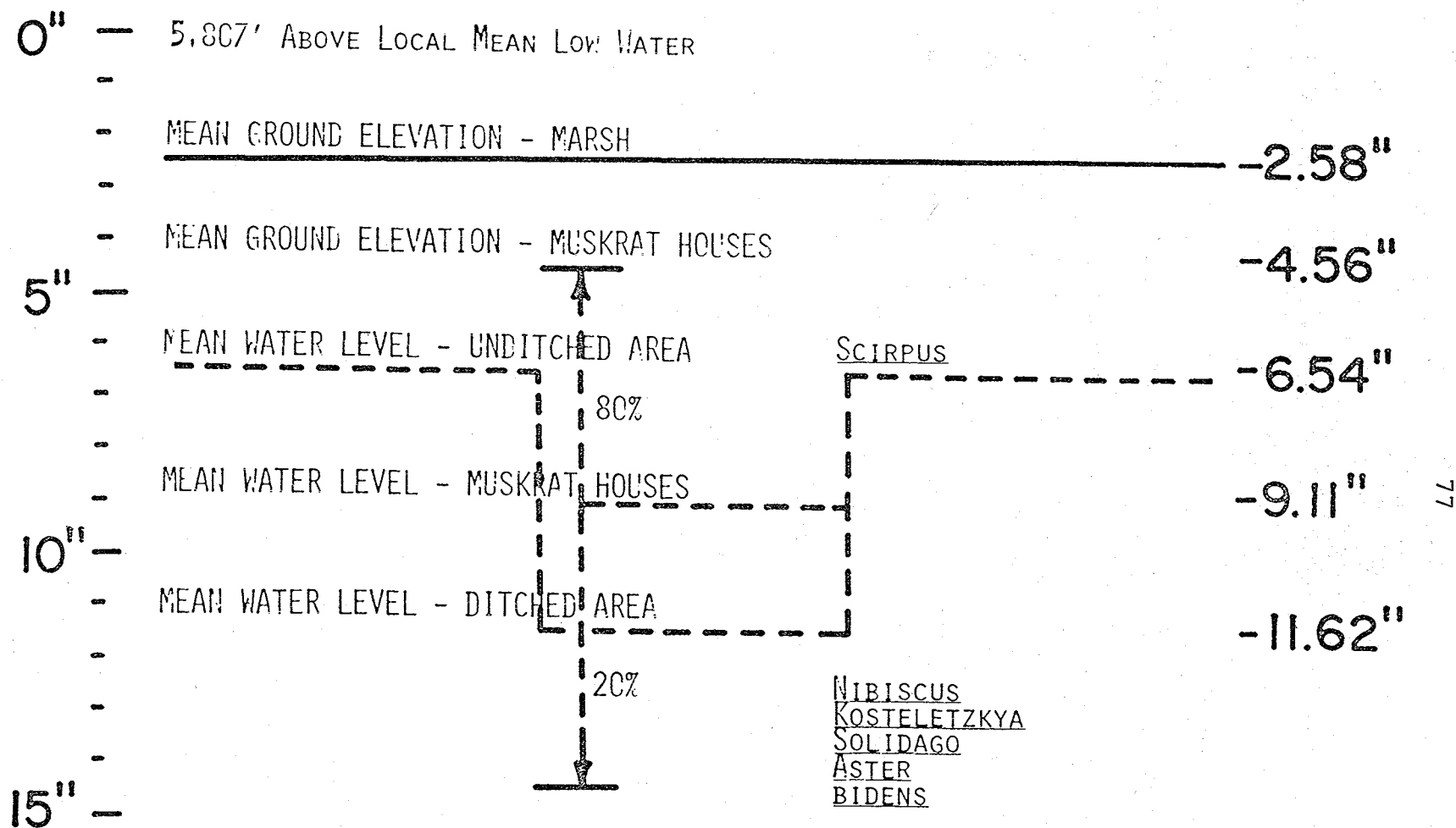KOSTELETZKYA
SOLIDAGO
ASTER
15" –   BIDENS

Figure 14.   Water levels in ditched and unditched tidal marshes as related to
muskrat houses and vegetation.   (From Stearns, et al., 1939.)

increased intraspecific strife induced by continued compression of home range and territory resulting from the expansion of the population. He described instances of animals apparently suffering from malnutrition repeatedly being captured within a limited area degraded by overgrazing.

Muskrat food and populations decrease as salinity increases (Harris, 1937; Dozier, 1947; Dozier et al., 1948). The Muskrats prefer the less saline types of vegetation such as the three-square sedges, Scirpus olneyi, S. robustus, S. americanus, and the cat-tails Typha. Less favored foods are Spartina cynosuroides, S. alterniflora, S. patens, Distichlis spicata and Juncus roemarianus. Dozier et al. (1948) reported the heaviest muskrats, with average weights of 2.25 and 2.26 lbs., consuming Group I plants (Scirpus olneyi, S. americanus, Typha (salinity 0.0-5.0^{o}/oo)) and Group II vegetation (S. olneyi, Typha (5-10°/oo)). Those feeding in higher salinity areas on Group IV vegetation (S. patens, S. alterniflora, S. olneyi and Typha (15.0-25.0^{o}/oo)) and Group V plants (S. patens, S. alterni-flora and Juncus roemarianus (25.0-43.0^{o}/oo)) had average weights of 2.16 and 2.20 lbs, respectively. On the surface, this weight differential does not appear significant. However, even casual observation reveals the divergence in plant distributions and numbers of muskrat houses along a salinity gradient. Dozier (1947) made a special point about the impact of salinity on tide water muskrat production. The animals were found in the upper reaches of tidal streams and were abundant where tidal influence was reduced. Diked areas or marshes that were flooded by high

salinity water during storms or through evaporation tended
to have reduced muskrat populations through loss of food plants
and drinking water.

Palmisano (1972) portrayed the interaction between vegeta-
tion types, salinity, extent of flooding and drought on the
distribution and abundance of the muskrat in Louisiana coastal
marshes. Palmisano recognized four major plant communities:
(1) saline marshes adjacent to the Gulf of Mexico dominated by
relatively few salt tolerance species, (2) brackish marshes
forming a broad zone of moderate salinity where plant growth
was vigorous, (3) intermediate, slightly brackish marshes,
and (4) fresh water marshes. Muskrats occurred in all the
coastal marshes examined; however, population densities varied
greatly. Brackish marshes composed of a mixed community of
Scirpus olneyi and Spartina patens were a preferred habitat
(Table 13). Although Palmisano recorded approximately equal
percentage values for southeastern and southwestern Louisiana,
population densities were much higher in the southeast. The
saline marshes in the southeast contained populations equal
to overall average density. The saline marshes of the southwest
were poor muskrat habitat, possibly because of their well
drained nature. The intermediate marshes had below average
population densities but high or average levels in restricted
areas adjacent to the brackish marshes. The fresh water marshes
exhibited the lowest densities of any type; 31.4 percent of the
total area examined supported only 4.1 percent of the total
houses counted. Populations were recorded at their highest

Table 13.

Acreage of marsh vegetative types in coastal Louisiana, percent of acreage surveyed and percent of houses counted. (Modified from Tables 2, 3, 4, Palmisano, 1972.)

Marsh Type	Southwestern			Southeastern			Total		
	Acreage	Percent Surveyed		Acreage	Percent Surveyed		Acreage	Percent Surveyed	
		Acres	Houses		Acres	Houses		Acres	Houses
Saline	45,507	2.6	1.0	753,130	22.2	20.8	798,637	12.4	14.2
Brackish	463,938	37.5	70.3	722,202	36.1	70.0	1,186,140	36.8	72.6
Intermediate	368,703	31.5	25.0	283,076	7.2	3.7	651,779	19.4	9.1
Fresh	390,757	28.4	3.7	830,769	34.5	5.5	1,221,526	31.4	4.1
Total	1,268,905	100.0	100.0	2,589,177	100.0	100.0	3,858,082	100.0	100.0

during periods of high precipitation and low salinity. The
greatest house counts were recorded in February when water
levels were generally high, temperatures low and the spring
breeding season about to begin.

Palmisano reported wide population fluctuations in localized
areas with rapid increases for 3 to 4 years followed by sharp
declines to almost zero in a few months. Such a decline was
observed in the brackish marshes in December 1971 following
two dry summrers. The other marsh types were not as severely
affected by the drought with populations actually increasing in
a few locations. These marshes served as important reservoirs
for muskrats during periods of stress in the brackish marshes.
In December 1971, when populations were below normal, non-brackish
marshes accounted for over 50 percent of the houses recorded.
During normal years less than 20 percent were recorded outside
the brackish marsh zone.

Mammals respond to storm tides on a salt marsh much as do
the birds; Norway rats and meadow mice are often found in the
same clumps of grass with birds (Sibley, 1955). Extremely high
tides that drive small mammals from cover occur during the
winter months in the San Francisco Bay area (Johnston, 1957;
Fisler, 1965; Rudd et al., 1971). At such times only 4-5
inches of vegetation remain exposed, mostly Grindelia cuneifolia,
a woody perennial growing along the elevated banks of tidal
sloughs. During flooding conditions, these mammals use the
emergent vegetation, floating debris, or move to higher ground.
Since high ground is some distance from centers of mammal

populations, most animals use emergent vegetation or floating

debris. Some are lost and a number of young are drowned in

the spring (Johnston, 1957). Swimming ability plays a part.

The shrew Sorex vagrans swims and dives well and most nests are

on high ground greater than six feet above mean sea level.

Rudd et al. (1971) found the greatest numbers of Sorex sinuosus

at the interface between the Salicornia ambigua marsh and the

Baccharis pilularis and grasses of the levees and found no

difference in numbers between a dry summer marsh and a flooded

winter marsh. The Meadow mouse Microtus californicus swims

and dives well (Johnston, 1957) but prefers to hide in what

emergent vegetation exists (Fisler, 1965). Since the mouse does

not normally move out of its home range during and after a storm

tide, only a rare combination of factors would reduce or

displace a population. Such a reduction was reported by Stark

(1963) wherein only those voles with home ranges on higher ground

survived several hours of winter storm tide and rain. Later

observations by Rudd et al. (1971) depicted a significant decrease

in the M. californicus population from a summer dry marsh to

an inundated winter marsh. They suggested the decrease could

be explained by drowning, increased predation or exclusion

caused by the high numbers of Peromyscus maniculatus or Mus

musculus. Harris (1953) was not clear in his own mind how

Microtus pennsylvanicus survived high water in the Blackwater

Refuge marshes of Maryland. It was not evident whether high tides

cause the voles to move to muskrat houses from the marsh surface

or whether the tides restrict the Microtus to the vicinity of the

houses, thereby making concentrating signs of their activity
as well as making it easier to take in traps. Harris considered
movement to high ground (landward edge of the marsh, islands
in the marsh or muskrat houses) as means for survival but if the
mice had to travel any distance exposure to predation would be
increased. While he acknowledged the mice's ability to swim
and dive with ease and that some did drown, Harris found it
difficult to accept that Microtus could scramble from one Spartina
culm to the next for any length of time and still survive.
Fisler found few mice in the Spartina foliosa, more in Salicornia
ambigua and the largest concentrations in the Grindelia growing
on the levees. This preference for high ground by M. californ-
icus agrees with the association between Microtus pennsylvanicus
and high marsh Spartina patens in New Jersey (Shure, 1970, 1971).
However, Johnston (1957) and Rudd et al. (1971) found Microtus
nests at all levels of the marsh surface, the breeding season
occurring during the fewest excessive tides.

The Norway rat, Rattus norwegicus was described by Johnston
(1957) as an excellent swimmer and diver but suffering consider-
able losses of young because its nests are located on the ground.
Apparently during the non-breeding season the Norway rat is
better able to survive (Stark, 1963). In contrast, the Harvest
mouse is a poor swimmer; its fur wets easily and it does not take
to the water readily. It normally nests above ground in old
sparrow nests and Johnston did not observe any nests being
flooded out. This may explain why Rudd et al. (1971) found only
a slight increase in Reithrodontomys raviventris numbers moving

from their characteristic <u>Salicornia</u> <u>ambigua</u> habitat to the
higher levees when the marshes are inundated during winter
high and storm tides.

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