CYCLIC CHANGES IN INTERSTITIAL WATER CONTENT, ATMOSPHERIC EXPOSURE, AND TEMPERATURE IN A MARINE BEACH[1]

Leland W. Pollock
Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts 02543

and

William D. Hummon
Department of Zoology, Ohio University, Athens 45701, and Systematics-Ecology Program, Woods Hole

ABSTRACT

Seasonal, tidal, and spring-vs.-neap changes in water content, atmospheric exposure, and temperature were studied within the interstices of a porous, semiprotected beach. Semidiurnal tides were nearly equal in amplitude and reached 120 cm from spring low to high. Overall mean grain size was 660 μm and mean sorting, 500 μm, with finer, better sorted, and more layered sand in the upper beach. Pore space averaged 36.5%.

Water content at low tide reached minima of 10% pore-space saturation in shallow sands of the upper beach; most sand above the minimum water table lost >50% of its water. The upper beach drained more completely at neap than at spring tides. Draining occurred more slowly than filling, and deeper sediments drained more slowly than shallow ones, resulting in a progressive landward delay of up to 4 hr in the water table's "low tide." Little seasonal variation was noted.

Beach temperatures were basically those of the sea surface, modified by duration of exposure. Temperatures of sea and water table followed a gradual cycle of seasonal change, averaging 1C/week. Daily temperature variations exceeding 5C were confined to the upper 10 cm of sand in mid- and upper beach areas. Neap tides exposed the upper beach for long periods and produced thermal extremes.

Salvat's concept of environmental zones along fine-sand beaches was modified and applied to both superficial and depth vectors at this coarse-sand beach.

INTRODUCTION

A labyrinthine capillary system of spaces exists between grains of beach sand, providing habitat for small animals referred to as the interstitial meiofauna. In marine habitats the extent and depth to which tidally active water circulates is determined by beach slope, amplitude of tidal changes, and dimensions of the interstitial spaces (Callame 1963; Jansson 1967*a*). Thus, intertidal beaches range from relatively impermeable, flat, fine grain size habitats, with circulation restricted to surface areas, to porous, steeper, larger grain size habitats, allowing circulation to depths >1 m at high tide. Ecological studies on relatively nonporous beaches have been numerous (*see* Salvat 1967; McIntyre 1969). But information on conditions within porous intertidal beaches is scarce (*see* Jansson 1971; Pollock 1971), though it is in such beaches that meiofauna are most abundant and diverse (McIntyre 1969).

Unlike many macrofaunal beach inhabitants that maintain direct or indirect contact with the sedimentary surface only during portions of each tidal cycle, the meiofauna are totally dependent on conditions within the beach. Since interstitial animals pass between sedimentary parti-

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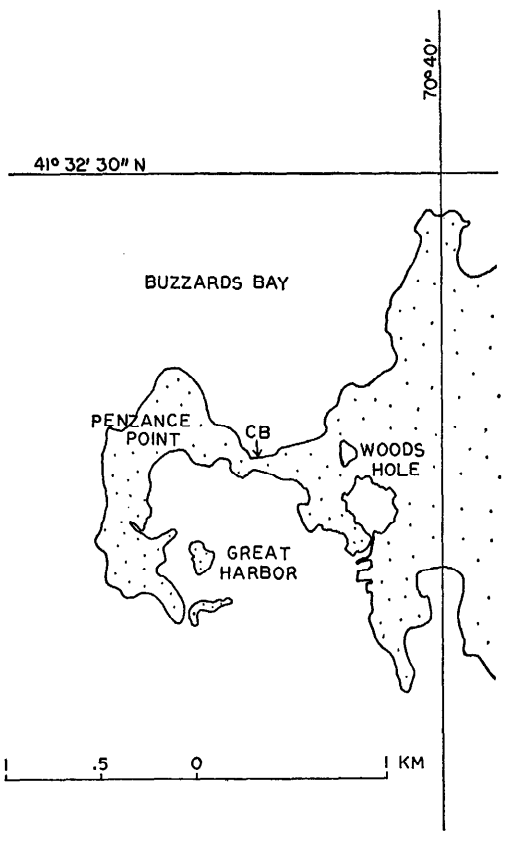

FIG. 1. The region surrounding Woods Hole, Massachusetts. CB—Crane's beach.

cles without moving the particles themselves, the dimensions of the pore spaces and necks define the upper size limits of this habitat; but meiofauna are entirely dependent on an aqueous medium for activity, so the lower size limit of the habitat is determined by the amount of water remaining in pore spaces at low tide. The actual habitat of intertidal meiofauna has constantly changing dimensions as pore spaces drain and fill with the tides.

Most published information on interstitial parameters is limited to isolated observations made at low tide. Such studies consider neither the hidden nor the delayed effects of cyclic tidal changes and consequently may misinterpret the effects of such parameters on faunal distribution and abundance. Our purpose was to explore the influences of seasonal and tidal variations in water content and atmospheric exposure in a beach, as well as the changes in temperature resulting from their interplay. We also studied the effect on each of differences in amplitude between spring and neap tides. This paper is part of a broader survey of conditions within the interstitial habitat of a porous tidal beach (Pollock 1970*a*, *b*; Hummon 1967, 1968, 1969).

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AREA AND METHODS

Crane's beach (41° 31′ 41″ N, 70° 40′ 41″ W) is on Penzance Point, a peninsula extending westward 1.5 km from Woods Hole, bordered on the north by Buzzards Bay and on the south and east by Great Harbor (Fig. 1). This beach (Fig. 2) faces Buzzards Bay at the narrowest portion (100 m wide) of the neck joining Penzance Point to Woods Hole proper. It extends 150 m along the head of a small cove. A series of seawalls provides shelter toward the west, and the east end blends into a rocky point. A longshore sandbar covers the mouth and much of the interior of the cove, protecting lower portions of the beach (20 m wide—mean low water to supralittoral fringe) from severe surf.

Observations were confined to a transect (Fig. 3), 20 m from the southwest end of the beach, extending from the mean low water to above spring high water and from the beach surface down to the depth of the low tidal water table (i.e., the level of interstitial saturation at low tide). The resultant vertical triangle measured 18 m along the surface of the sand and about 1 m deep at the highest station.

Tides are semidiurnal and nearly equal in amplitude. Along the Buzzards Bay shore, mean spring tides range from −14 to 140 cm and mean neap tides from 17

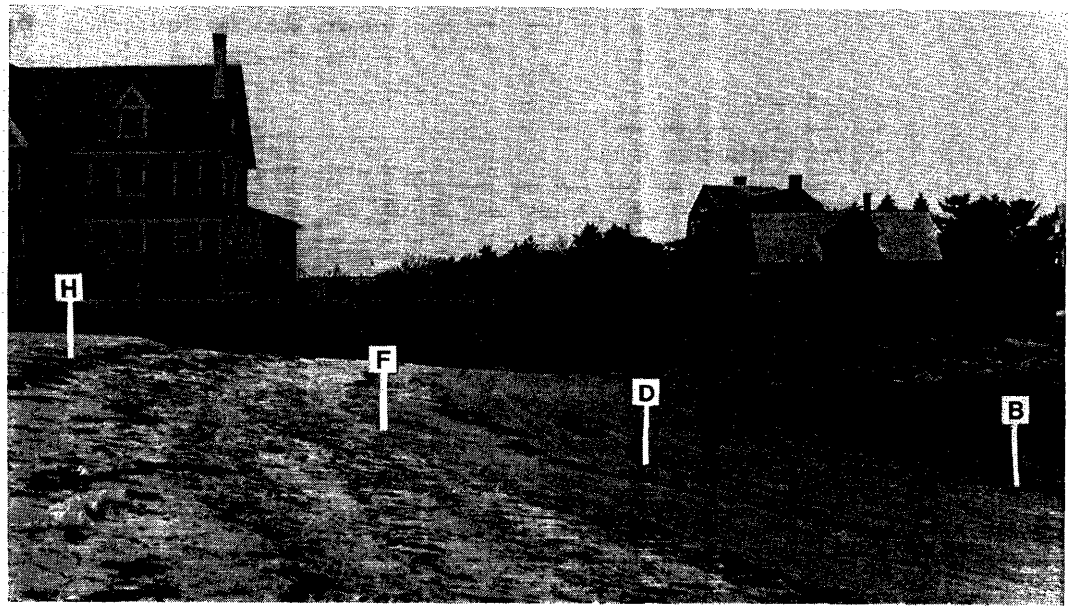

FIG. 2. Crane's beach at low tide, spring 1969. Markers B–H refer to station locations (*see text*).

to 96 cm elevation; the mean tidal level is 61 cm. Winds are generally westerly–southwesterly in summer and northwesterly in winter. Onshore winds raise tidal levels a few cm and produce waves ranging from 15–25 cm, occasionally 60 cm. Swashes from these waves reach beach elevations nearly as high as the wave crests themselves. Winds also affect the exposed beach by increasing evaporation of water from the superficial sand layers.

Nine stations were placed at elevations of 8, 31, 54, 69, 85, 107, 130, 153, and 176 cm above mean low water and are termed stations A–I (Fig. 3). The mean low water reference was estimated on the basis of a series of observed and predicted high and low tide levels ($n = 20$), with adjustments for wind and waves. Although distances between stations varied somewhat between collections, tidal exposure (i.e., elevation above mean low water) remained constant for each station. Samples were taken at each station from the sand surface to the low tidal water table at depths of 1–3, 4–6, 8–10, 14–16, 22–24, 26–28, 32–34, 38–40, 44–46, 51–53, 58–60, 65–67, 72–74, 81–83, and 90–92 cm. Maximum depths sampled range from 14 cm at station A to 90 cm at station I. The asymmetry in this pattern results from stratified sampling used in concurrent analyses of faunal distribution. Stations were located in the field by sightings with a hand level to a surveyor's range pole placed at a supralittoral reference point and calibrated in elevation above mean low tide. Horizontal distances between stations were measured for construction of beach profiles.

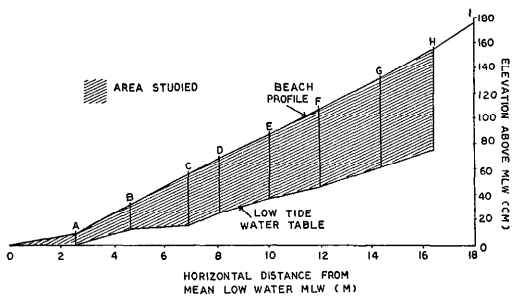

FIG. 3. The vertical transect at Crane's beach, including stations A–I.

Sand samples ($n = 307$) were taken in 2–3 subsamples (10 cm^3 each) from the beach during routine faunal sampling.

Following extraction and counting of the fauna, this sand was subjected to granulometric analysis by wet-sieving through screens of –2, –1, 0, 1, 2, 3, and 4 phi (mesh openings of 4,000, 2,000, 1,000, 500, 250, 125, and 62.5 μm). Calculation of mean phi and sorting phi follows Inman (1952); translation of phi measurements into micrometers follows Hummon (1969). Sand less than –2 phi was excluded from the analysis, since most fauna was absent from substrata consisting primarily of such coarse material. Only trace amounts of sediments measured greater than 4 phi and in general these were disregarded.

Emery and Foster (1948) found a progressive delay in the occurrence of low tide in the water table from the low tidal line toward landward stations. A preliminary survey at Crane's beach revealed the importance of compensating for this time lag if truly low tidal conditions were to be measured throughout the beach. As a result, landward stations were sampled up to 2.25 hr after seaward stations. Some error probably occurred from not sampling precisely at low tide of the water table at each station, but it was far less than that resulting from failure to compensate at all.

Seasonal changes in interstitial temperature and water content were assessed from data gathered at intervals of 2 to 3 weeks from late May 1967 through April 1969 ($n > 1{,}000$ for each). Temperatures were measured with a portable thermometer by a thermistor inserted at appropriate depths into the walls of excavations at each station. Readings are accurate to ±0.25C. Records of the temperature of the air at Woods Hole and open seawater in Buzzards Bay were supplied by W. Anderson and J. Chase of the Woods Hole Oceanographic Institution. Water content of samples of sand was estimated by the volume-displacement method (Hummon 1969; *see also* Hulings and Gray 1971).

To study changes in interstitial conditions during tidal cycles, the temperature and water content of sand and elevation of the water table and seawater were measured periodically at several stations throughout a complete spring tidal cycle (13 May 1968) and again throughout a neap tidal cycle a week later (20 May 1968). At 0.5-hr intervals, the depth of the water table was recorded in excavations at stations A–I. Every 1.5 hr temperature and water content of unsaturated portions of stations B, D, F, and H were measured at 10-cm depth intervals.

TABLE 1. *Effect of tides on mean grain sizes (A) and sorting (B) during calm weather at Crane's beach*

	No. of samples	Differences in A (μm) $\bar{X}$	Differences in A (μm) SD	Differences in B (μm) $\bar{X}$	Differences in B (μm) SD
Low tide (control)					
upper beach	6	47	11	54	42
Incoming tide					
upper beach	6	175	235	178	155
midbeach	15	126	118	142	93
lower beach	4	138	158	125	137
Outgoing tide					
upper beach	7	152	231	204	173
midbeach	12	141	129	206	165
lower beach	7	154	151	63	46

RESULTS

Mean of mean grain sizes, based on samples from 36 locations in Crane's beach, was 660 μm (SD, ca. 180 μm). The mean sorting (measure of grain-size dispersion about the mean) for these samples was 504 μm (SD, ca. 160 μm). The beach has a coarse substratum of poorly sorted sand, somewhat finer, better sorted, and more layered in the upper beach area than in the lower.

The effect of tidal activity on grain sizes and sorting is small compared to some beaches (e.g., Strahler 1966), but it is nonetheless persistent and dynamic. Table 1 shows differences in mean grain size and sorting between duplicate samples matched for elevation and depth, but collected 25 cm apart laterally. On incoming tides, the first sample was taken at low tide and its duplicate beneath shallow waters of the rising tide; on outgoing tides,

the first sample was gathered beneath high tide waters and its duplicate at low tide. Controls were collected from various depths in the upper beach area during a period of low tide. All samples consisted of triplicate 10-cm³ subsamples. The results suggest that even in calm weather, the passage of a tide up or down produces greater and more variable change in mean grain size and sorting than is found in lateral duplicates taken without an intervening tide. The least disturbed area, the midbeach, was reshuffled sufficiently on incoming tides that the change in mean grain size averaged 126 ± 30 μm compared to controls that averaged $74 \pm 3\mu$m. One exception, the lower beach on an outgoing tide, shows changes in sorting and dispersion around the mean comparable to those occurring in lateral samples taken on the same low tide. This may be related to the longshore bar beyond the base of the beach, which calms water lying between it and the lower portion of the beach.

It is not surprising therefore that the results of 8 midbeach samples ($n = 44$), taken at intervals of 3 weeks, show considerable variation as a result of tidal reworking. Mean change in the mean grain size was 70 ± 23 μm, whereas mean change in sorting was 208 ± 21 μm, suggesting that the same sand was being reworked in widely different ways over an extended period of time.

A year-long series of profiles, taken at intervals of about 3 weeks, shows constant variability, with average changes of 3.2 ± 0.7 cm elevation every 3 weeks in the upper beach area, 4.1 ± 0.8 cm in the midbeach area, and 4.8 ± 0.9 cm in the lower beach area. The average profile ranged from 10.5 to 11.9% and gives little indication of the dynamic flux that regularly occurs.

A series of sand samples (100 cm³ each) was taken from surface, middle, and water table depths of the lower, mid-, and upper beach areas. The 9 samples, analyzed in triplicate ($n = 27$) by the volume-displacement technique, contained a mean of $36.5 \pm 0.5\%$ pore space.

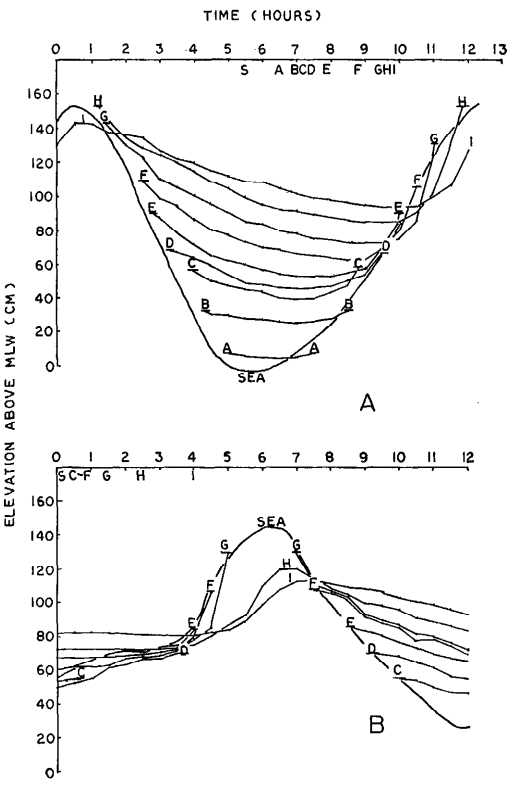

FIG. 4. Tidal changes in elevation of seawater and the water table at stations A–I. A. Spring cycle, 13 May 1968; B. Neap cycle, 20 May 1968. Letters along the abscissa indicate the times at which lowest elevation was reached at each station.

Water content

Spring and neap tidal changes in the elevation of seawater and the water table are shown in Fig. 4. Curves representing each station are identified by letter and indicate the location of the water table from first exposure by ebbing spring tide (Fig. 4A) through the low at midday, and continuing until stations were covered again by flooding seawater, and from neap low tide (Fig. 4B) through the afternoon high and then past the night low.

Differences between spring and neap tidal circulation of water are illustrated in Fig. 5. Lines representing intervals of 3 hr indicate the approximate period within a 12-hr tidal cycle that portions of the

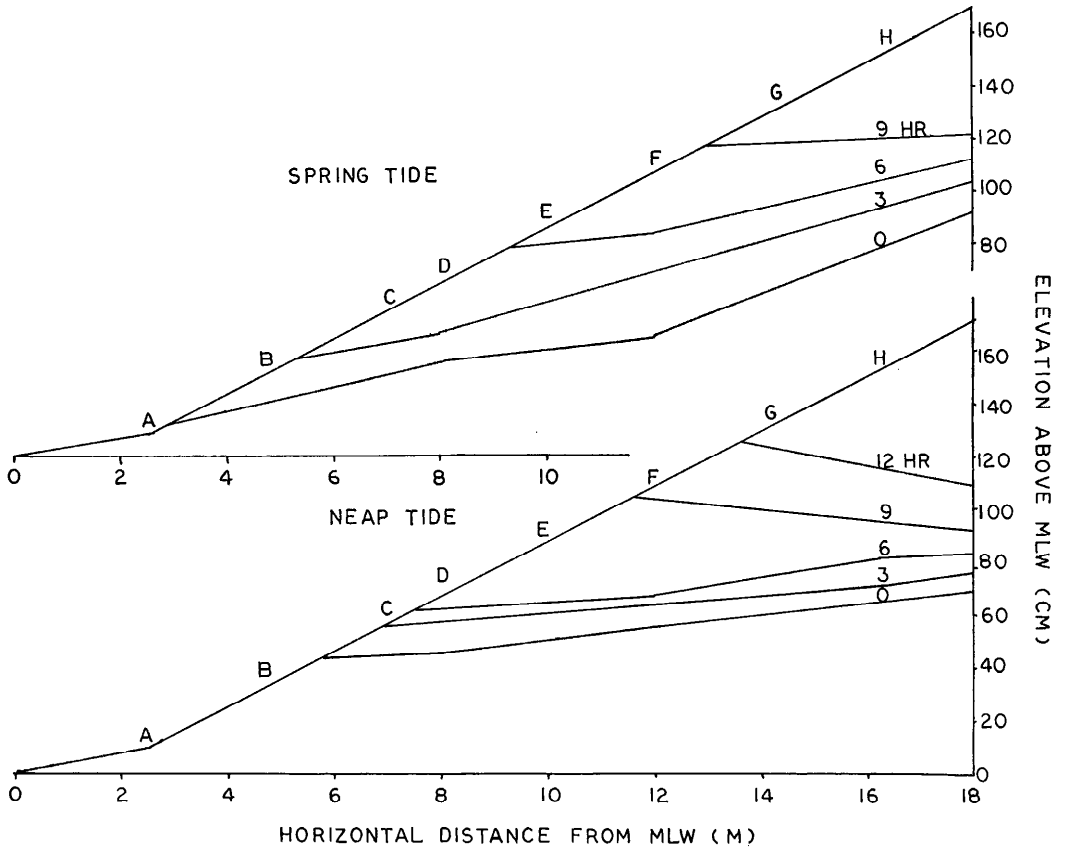

FIG. 5. Comparison of spring and neap tidal drainage throughout the transect. Lines indicate hours of each tidal cycle during which regions are less than 50% saturated.

beach remained less than 50% saturated by interstitial water. The regions most affected by these differences were shallow depths at higher stations and deeper portions of all stations. Although during the neap tidal cycle, the upper 30 cm at station H never exceeded 30% saturation, greater depths at the same station filled and drained to some extent. All depths in the remaining station lost less water in the neap cycle than they did during the spring tide. The range of amplitude of the water table throughout the beach was generally less in neap tide than in spring (*see* Table 2).

The progressive delay in low tide at the water table from the lower beach toward the landward interior is illustrated in Fig. 4. Letters along the abscissa indicate the approximate times at which deepest water table levels (i.e., station "low tides") were recorded at each station and in the adjacent seawater. Low tide at stations H and I occurred 4 hr after the seawater had reached its nadir during the spring tidal series (Fig. 4A). In contrast to progressive delays in movement of the water table

TABLE 2. *Tidal ranges in amplitude of the water table (in cm) at Crane's beach*

		Stations					
	Sea	D	E	F	G	H	I
Spring tide (13 May 1968)	166	31	37	54	67	85	75
Neap tide (20 May 1968)	108	26	32	49	72	60	45

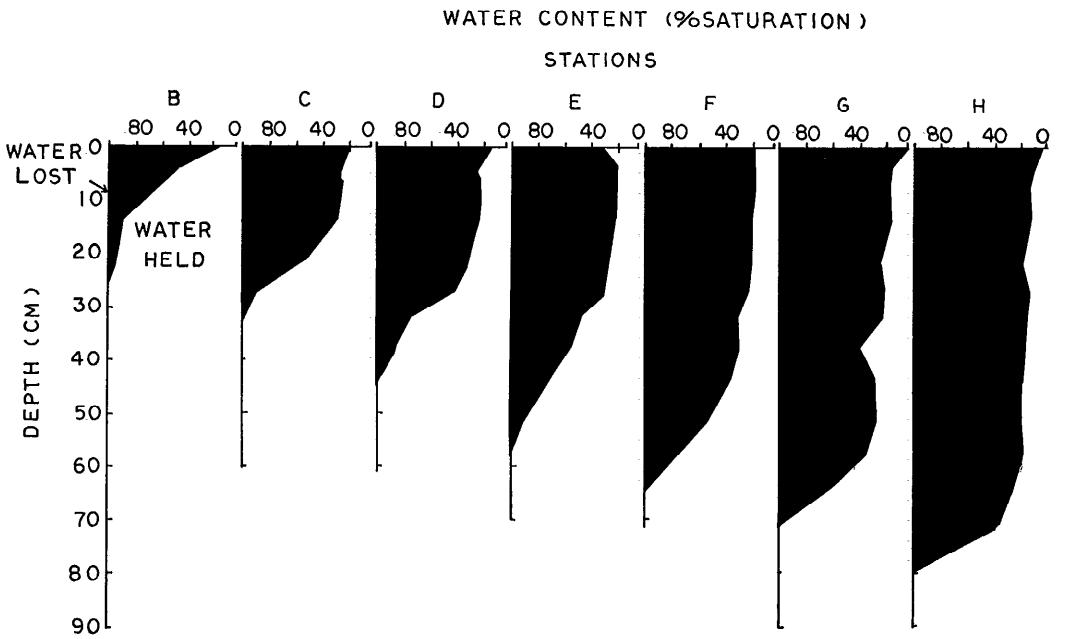

FIG. 6. Average range of tidal change in water content expected at 10-cm depth intervals at stations B–H (*see text*).

from seaward to landward during the spring cycle, only the upper beach (stations G, H, and I) was affected during the neap cycle (Fig. 4B). Throughout the lower portion of the beach, low tide in the water table co-occurred with low tide of the seawater.

Although in nature sandy soil rarely becomes totally devoid of water (Kramer 1949), a tidal range in water content from 100% saturation to less than 10 was a frequent occurrence near the sand surface in the upper beach. An estimate of the lower limits of water depletion, including compensation in field sampling for lags in water movement, was averaged from low tidal water contents measured from April through July 1968. Although variations are expected to result from spring–neap tidal cycle alternations, Fig. 6 indicates the relative severity of water depletion. Average lowest water content reached at intervals of 10-cm depth at each station appear along the right side of each graph. At high tide, stations were flooded with seawater, so vertical lines on the left indicate high tide conditions of fully saturated water content. The black area between represents the range of variation in water content expected at each station over a tidal cycle. Only the upper half of the beach lost more than 80% of its water saturation, although nearly all of the beach lost over 50%.

The rate of water loss and duration of exposure to low saturation may be as important as the minimum levels of saturation. Change in water content measured through spring and neap tidal cycles in 10-cm depth intervals at stations D, F, and H are shown in Fig. 7. Patterns of spring and neap drainage were generally similar. Superficial layers drained nearly completely upon emersion and filled

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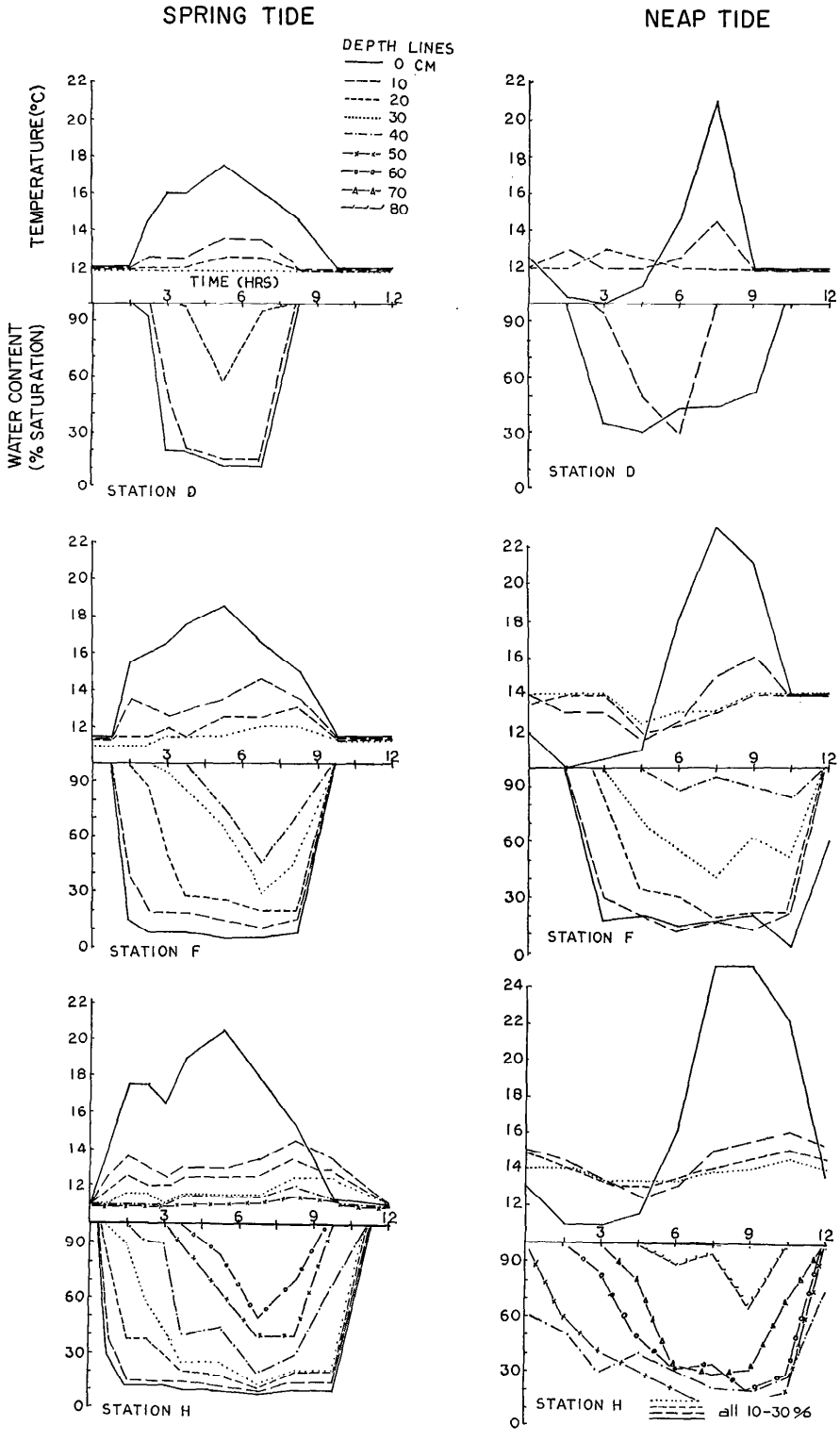
FIG. 7. Tidal changes in water content and temperature at 10-cm depth intervals at stations D, F, and H. Spring cycle, 13 May 1968; neap cycle, 20 May 1968.


SPRING TIDE
NEAP TIDE
DEPTH LINES
0 CM
10
20
30
40
50
60
70
80
TEMPERATURE(°C)
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STATION D
STATION D
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all 10-30%

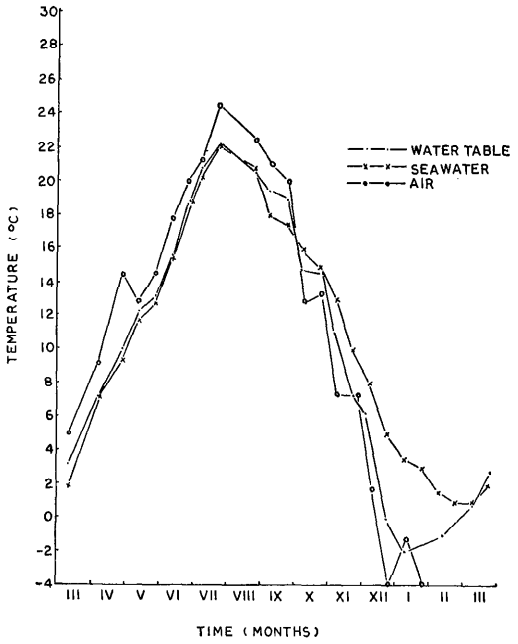

FIG. 8. Annual temperature changes in atmosphere, seawater, and water table at Crane's beach, 1968–1969.

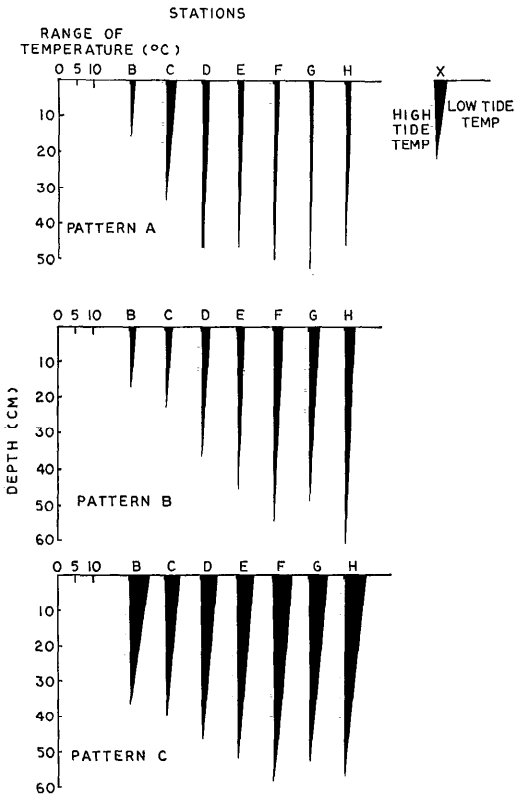

FIG. 9. Patterns of tidal variations in temperature at 10-cm depth intervals at stations B–H (*see text*).

quickly with the incoming tide, whereas deeper layers drained far more slowly than they filled. Left-hand skewness of graphs from greater depths illustrates this phenomenon.

A time gradient of immersion-emersion, existing from the superficial sand in the upper beach to greater depths toward the lower beach, was reflected in the duration of exposure to a given level of water content. Figure 5 (*see above*) represents the duration of exposure to 50% saturation throughout the beach during a spring and a neap tide. The portion of the beach that was less than 50% saturated for more than half of each 12-hr cycle included the uppermost third at spring tide and the uppermost half at neap tide.

Temperature

Temperatures in the water table approximated those in adjacent seawater (Fig. 8). Temperatures in the water table ranged from –2.0C to 22.3C, with an average rate of change of about 1C/week.

Ranges in temperature variation from that of the adjacent seawater over a tidal cycle are illustrated in Fig. 9. With characteristics of seawater dominating conditions at flood tide, vertical lines to the left represent high tidal temperatures. Low tidal temperatures, as differences from the high, are indicated on the right; the black area represents the range of temperatures expected to occur during a full tidal cycle.

Tidal variations in temperature throughout the year could be grouped into one of the patterns shown in Fig. 9—although the actual values differed with each collection. The range between temperatures of the sand surface and those of the water table at any station at low tide was narrow in fall and winter (patterns A and B), but larger during spring and summer (pattern C). Variations were generally less

than 3C between depths of 20 cm and the water table at all seasons.

Daily changes in temperature at stations D, F, and H (*see* Fig. 7) indicate that large temperature differences were limited to the surface 10 cm of sediment; at greater depths they remained within a few degrees of the water table temperature throughout spring and neap tidal cycles.

The range of temperature increase during daytime low tides was directly related to duration of exposure to harsh atmospheric conditions. The fact that lowest spring low tides in Buzzards Bay occurred at midday during summer increased the severity of exposure; the lag in water table drainage within the beach also prolonged exposure to atmospheric conditions. Temperature in exposed sediments continued to increase regardless of local low tide and decreased only as the flooding tide approached.

DISCUSSION AND CONCLUSIONS

Water content

Intertidal, interstitial water is derived from seawater and limited quantities of freshwater. Beach slope, porosity, and grain size of the sediment, capacity for water retention of different types and sizes of sediment, tidal and wave activity of seawater, abundance of precipitation, and evaporation by the atmosphere all determine the abundance of water held in intertidal sediments (Bruce 1928; Graton and Fraser 1935; Jansson 1967*b*; Johnson 1967; Rullier 1957).

With the diurnal flow and ebb of tidal water to counter the pervasive atmospheric influence at Crane's beach, the latter factor was of overwhelming importance only at the sand surface in the upper beach. Evaporation undoubtedly drew some interstitial water regularly from upper beach sediments and more broadly over the superficial few centimeters of sand during midsummer. The beach experienced little rainwater runoff other than precipitation falling directly onto the beach during low tide.

The permeability of sediment controls water movement through interstitial spaces; confined dimensions of capillary spaces result in increasingly limited water movements (Emery and Foster 1948; Ruttner-Kolisko 1961 1962). Brafield (1964) related water circulation through sand to the proportion of the sediment less than 250 μm in diameter. Although fine sediments lose little more than superficial water during ebb tide, coarser sediments, such as those at Crane's beach, undergo extensive drainage. Despite the relatively great permeability of sands on this beach, movements of deeper interstitial waters were noticeably restricted and lagged behind movements of adjacent seawater.

The degree and rate at which portions of the beach fill during tides also is related to the amount of time that overlying seawater remains at a higher elevation. Inward water pressure, caused by flooding spring tides, which rose quickly at Crane's beach (ca. 24 cm/hr), was sufficient to saturate the most interior portions of the beach. Both the rate (ca. 15 cm/hr) and magnitude of change in amplitude was reduced during neap tide. With the consequent reduction of water flow, interior sections filled and drained much less extensively than during spring tides.

A gradient of flow from overlying seawater into the beach filled interstitial spaces rapidly. Drainage, however, occurred much more slowly than filling (*see* Fig. 7) and resulted from gravity flow alone. "Suction" of the descending water table was countered by water retention through capillarity within interstitial spaces. Although 50% of the interstitial water was lost quickly, it took far longer for the remaining water to be lost.

Kramer (1949) described four conditions in which water is found in soils: Gravitational water drains by gravitation alone and is lost and regained quickly; capillary water held around and among particles moves far more slowly; hygroscopic water forms thin films around sedimentary particles and is extremely difficult to remove; finally water can be present as vapor. Ap-

parently water lost quickly in most of our samples represented gravitational water, and capillary water loss produced the gradually diminishing levels below 50% saturation. Losses of interstitial water even at the surface of the beach stabilized at levels of ca. 10% saturation (Fig. 7), probably an approach to the minimal, tightly held films of hygroscopic water.

Temperature

Temperatures of seawater, the water table, and deeper portions of the interstitial habitat were similar and showed little tidal variation. They followed gradual seasonal climatic changes and were dominant in determining temperature throughout the beach during flood tide. For about 12 hr of each day (i.e., while the beach was filled with water), temperatures at all sites approximated those of the seawater-water table measured at low tide. At low tide, temperatures of superficial sands exceeded those of the seawater-water table in the late morning and afternoon but fell below those of the seawater-water table at night (as reported for atidal beaches by Jansson 1967*c*). Probably the underlying nocturnal-high tidal pattern of temperature change within the beach followed a seasonal change similar to that shown in Fig. 8 for seawater-water table. Increased temperatures apparently occurred only during daytime portions of low tidal cycles.

Broad changes in temperature were related to the difference between temperatures in the atmosphere and in the water table, as well as by the period of exposure to air. During low tide, thermal insulation by the sediment and evaporative cooling at the beach surface damped significant influence of even extreme atmospheric conditions below a depth of 10–20 cm (below 5 cm in a fine grain beach, Johnson 1965).

In early spring and fall, when sea and air temperatures are similar, the daytime temperature of the interstitial habitat remained nearly constant regardless of tidal exposure. As daytime air temperatures rose in late spring and summer, a lesser but proportional rise in low tidal interstitial temperature occurred. In winter, when air temperature was lower than that of seawater, temperature in the superficial sand of the upper beach dropped several degrees below that of seawater. At such times water in the upper 10–15 cm of the beach froze. Tidal movements of water and insulation provided by snow cover (sometimes 70.5 cm thick) prevented more extensive freezing of interstitial water. From spring through fall atmospheric influence was strongest during daytime low tides. In winter, nighttime low tidal conditions may have been slightly more severe.

Decreased water table amplitude during neap cycles affected temperatures throughout the beach. Superficial layers of sand high on the beach were exposed for several days at a time, allowing temperatures there to reach extremes. On the other hand, temperatures in deeper portions of the beach remained under the influence of seawater temperature longer at neap tide.

Temperature changes depended on the extent to which atmospheric conditions could modify the ordinarily dominant temperature of sea and interstitial water. For this reason, patterns of tidal variation in temperature are closely related to changes in water content.

Salvat (1964, 1967) provided a useful classification of zones along the intertidal surface of fine grain beaches. He described four areas along the lower to upper beach axis, characterized by water conditions (paraphrased from Salvat 1967):

Zone of dry sand—sediment above the level of neap high tides which is emergent during several successive tidal cycles. Under the effects of meteorological conditions, this sediment, which loses its gravitational water on emersion, also may lose its capillary (or retention) water. It sustains strong thermal variations and is distinguished from other areas by irregular immersion.

Zone of retention—sediment reached by all tides. It loses gravitational water at

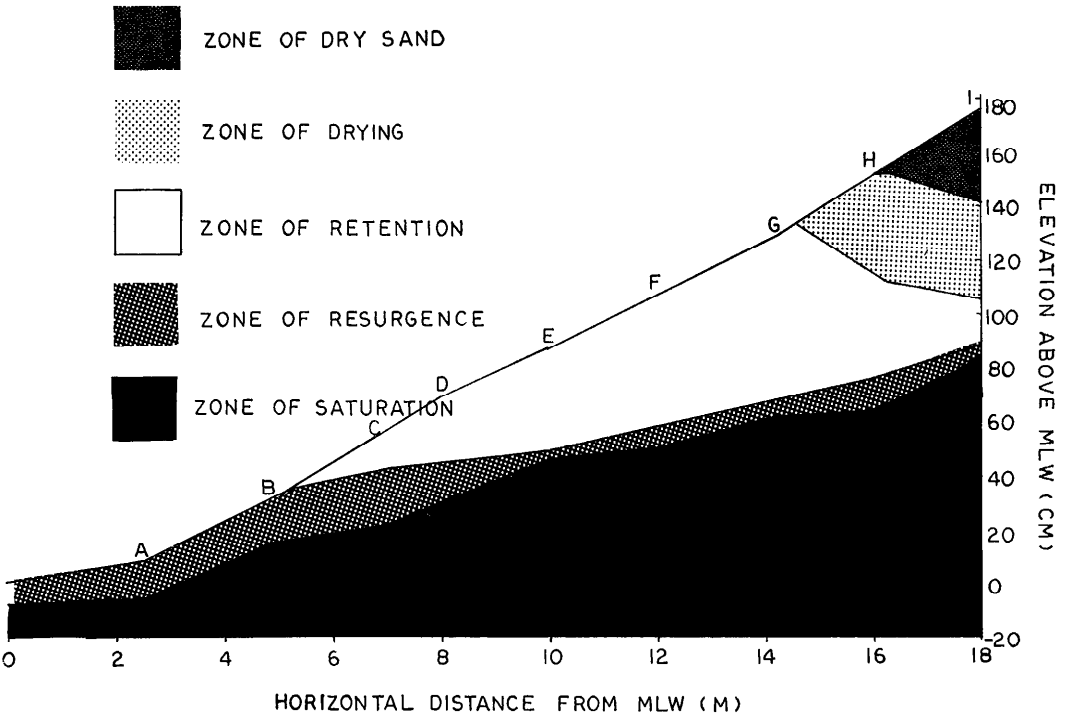

FIG. 10. Environmental zones at Crane's beach.

emersion, but it conserves water of retention. Sediment in this zone displays an absence of very fine sediment, slight accumulation of organic materials, and relatively loose packing. Consequently, great porosity and permeability allow extensive circulation and interstitial water replenishment. Thermal variations can be important during emersion.

Zone of resurgence—the site of intensive circulation of interstitial water during high tide as well as low. During tidal ebb, gravitational water from the zone of retention drains through the sediment of this region, appearing at the surface of the beach as streams. Such resurgence continues as long as the level of interstitial water is above the level of tidal water. Circulation is inverse when the height of tidal water exceeds that of interstitial water. During emersion, the lowering level of interstitial water causes a similar lowering in the level of resurgence, causing superficial sediments in this area to lose their gravitational water. Sediment of this zone is characterized by slight accumulation of very fine fractions and organic materials and reduced porosity through a more compact arrangement of sand grains.

Zone of saturation—sediment continually saturated by water, showing weak porosity and permeability. Circulation is greatly reduced because considerable very fine sediment and a large accumulation of organic material clogs interstices.

To describe the situation at Crane's beach, we have extended Salvat's classification by dividing his zone of dry sand into the zone of drying and the zone of dry sand. The zone of drying is distinguished by irregular water replenishment during spring high tides or during storms, while the zone of dry sand is restricted to regions almost never receiving seawater.

This sequence of environmental zonation can be applied successfully not only to horizontal vectors along the surface of Crane's beach but to vertical axes of con-

TABLE 3. *Environmental zones at Crane's beach*

Zone	Water content	Temperature
Zone of dry sand	Almost never receives seawater; affected by precipitation but usually very low; hygroscopic water held	Highly variable due to strong atmospheric influence; high in summer, low in winter
Zone of drying	Extensive drying; low and irregular; capillary water usually lost	Wide variations
Upper	Tidally or regularly varying; 100–15% saturation; gravitational water lost	Can be great (up to 10C) in summertime low tides
Zone of retention	Tidally or regularly varying; 100–40% saturation	Little tidal variation
Lower	Gravitational water lost	
Zone of resurgence	High saturation; little variation; some gravitational water lost	Nearly constant; follows gentle seasonal cycle

ditions as well. In fact, so well do Salvat's definitions of surface zones on fine grain beaches apply to depth zones in a larger grain beach that changes in the terminology used above are not required.

Vertical characterizations at our stations along the lower to upper beach axis differ from one another in proportions of each of these zones (Fig. 10, Table 3). Low tidal elevation varies through spring and neap cycles and with local weather conditions, so resurgence and saturation predominate in lower beach stations. Decreased fluctuations in the amplitude of the water table within the beach confine the extent of the zone of resurgence at more landward stations. The zone of retention dominates the entire beach but diminishes rapidly above the high tidal region. The zone of drying includes the range between high tidal levels in spring and neap tides, while dry sand areas occur only above the spring high levels.

Within the inhabited zones, the parameters studied here form a double gradient from low to high beach and from the sand surface to greater depths. This network of physical conditions including grain size, water content, and temperature provides a broad matrix for possible niche specialization. Grain sizes extend from a poorly sorted mixture of large and small sizes low on the beach to more uniform medium grains in the upper beach and from the constantly reworked superficial sediments to more stable conditions at greater depths. Both water content and temperature extend from extremes in upper beach superficial sand to more moderate conditions both lower on the beach and deeper in the sand.

The results of granulometric analyses from the beach are of particular interest because of the diversity of grain sizes present. Material represented in the study transect included grains ranging from very fine sand to cobble—as one would expect in a region dominated by glacial till from a terminal moraine. Fully two-thirds of the tardigrade and gastrotrich species encountered could be found at one time or another in sands ranging from 200 to 3,000 μm. It was not clear whether the reduced grain size variability associated with the remaining species was the result of size preference choice by the animals or was fortuitous. Nevertheless, the generalization remains that most species of these two faunal groups tolerate broad ranges of grain size.

Comparable generalizations can be drawn for effects of water content and temperature. The zone of retention and the zone of resurgence are most heavily populated in densities, often in excess of 100 meiofaunal animals/cm^3 of sediment. Meiofauna are apparently unable to withstand the drying and high temperatures in the zones of drying and of dry sand; few were found in the zone of saturation, their occurrence probably being limited by a lack of oxygen resulting from decreased circulation (Gordon 1960; Brafield 1964).

Incorporating dynamic tidal aspects into our study of these physical parameters permits a more realistic assessment of the intertidal beach as habitat for meiofauna. The moderate variations in water content and temperature suggest that the interior of a porous sandy beach such as Crane's beach may be less physically rigorous than any other intertidal habitat. The zones of

retention and resurgence probably represent an environment little more extreme than shallow sublittoral sediments. In addition, the capillary network of interstitial spaces provides a tremendously expanded intertidal surface area for meiofaunal activity. A cross section through a coastal region of porous sediments would reveal that potential meiofaunal habitats are limited to the surface few centimeters of subtidal sediments (McIntyre 1969), expand to occupy large areas and depths within an intertidal area, and then plane off to a rather limited range surrounding the region of continental groundwater flow (Delamare-Deboutteville 1960).

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