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pH fluctuation in an intertidal beach in Bermuda[1]

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Abstract

Unusually high pH values up to 9.6 measured during low tide in a calcareous sandy beach were correlated with high in situ temperatures. Daily fluctuations of up to 1.5 pH units are limited to the topmost layer of sediment. Light, by controlling photosynthesis, is the causal factor in determining high pH at the surface; subsurface sediments do not respond to experimental light changes. Indications of such fluctuations are lacking in the literature. These fluctuations could influence community respiration.

Patterns of vertical distribution of pH in protected marine sediments are well established. In parallel with *Eh* and oxygen concentration, pH generally decreases with sediment depth, mainly due to bacterial sulfur reduction and carbon dioxide evolution during the decomposition of organic matter. Frequently a pH minimum is observed in the redoxpotential-discontinuity layer (Fenchel and Riedl 1970), below which pH increases slightly or may remain constant. Actual pH-depth profiles vary considerably with type of sediment (ZoBell 1946), environmental conditions (Bruce 1928; Fenchel and Jansson 1966), and time of year (Thorstenson and Mackenzie 1974).

The variability of pH of the interstitial environment is generally considered to be insignificant (Moore 1931; Pennak 1951; Pollock 1971; Pugh et al. 1974) and to have no effect on the various groups of meiofauna (Coull 1970; Ganapati and Rao 1962; Hartwig 1973; Jansson 1966; Tietjen 1969). Precipitation of sulfide prevents a drop in pH below 6.9 (Ben-Yaakov 1973), whereas the upper limit of the pH range is controlled by the buffering capacity of the carbonate system which, in its upper range, operates maximally at pH 9 (Pytkowicz 1967; Pytkowicz and Atlas 1975).

A temporal variation of pH, including surprisingly high readings at the surface of the sediment, was first recorded on a protected sandy beach in Bermuda (Wieser et al. 1974). We here examine this phenomenon more extensively at the same beach.

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Material and methods

The beach—Field measurements and field experiments were carried out in the central flat region of the intertidal sandy beach at Tuckers Town Cove, Bermuda. The sheltered beach consists of well sorted medium sand, (phi = 1.3–2.2: Farris 1976), composed exclusively of carbonate minerals. Stands of red mangroves (*Rhizophora mangle*) may influence the beach ecosystem by providing organic matter. During the semidiurnal tidal cycle the central flat region is exposed for 2–4 h twice a day and covered during high tide by water rarely exceeding 1 m in depth. The surface sand remains saturated with water during the whole low tide period and tide pools are scattered around in small depressions. The salinity of the interstitial water is 34.5–36‰ (Farris 1976). *Eh* drops to +100 mV within the first 2–5 mm (Wieser et al. 1974). The biological activity is most concentrated in the upper 1 cm of sediment (Wieser and

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Zech 1976). Our measurements were confined to fairly cloudless days to guarantee comparable conditions of solar radiation and to cancel out the effect of dilution of pore water by occasional rain showers.

Field measurements—pH was measured with a Radiometer specific ion meter (PHM 53) with a scale ranging from pH 0 to 10 and a smallest scale division of 0.1 unit. The spherical head of the glass electrode (Schott N 115) was 10 mm in diameter. A calomel half-cell (KCl, Schott B 281) served as reference. To cancel out the error of salt effects and to avoid long equilibration times (Pytkowicz et al. 1966), we calibrated the electrode system against open seawater (pH 8.2; 27.5°–29°C) from outside the inlet of the bay. Therefore our data are more accurately interpreted as being the differences between the pH of surface seawater and that of sediment, but agreement with a two-point calibrated electrode (E. Hartwig pers. comm.; Hartwig et al. 1977) showed the error to be negligibly small. The temperature dependence of the sensitivity of the electrode system was <0.01 pH unit per °C as determined experimentally and was not compensated for. The overall experimental error (± 0.1 pH unit) and the physical temperature coefficient of seawater of 0.01 pH unit per °C (Ben-Yaakov 1970; Gieskes 1969) lie within the range of ecological variability.

Temperature was measured simultaneously with pH using a mercury thermometer (0°–60°C) calibrated in 0.1°C. Continuous temperature measurements were made with thermistors (YSI thermolinear 703, 5°–45°C) embedded in 20-cm-long Plexiglas tubes with a 1-mm-thick metal knob at the end. The signals of four probes were amplified, multiplexed, and recorded on a miniscript (Goerz) printing 20° to 40°C full scale, calibrated to 2% against a precision grade mercury thermometer.

In highly stratified sediments considerable pH gradients in the uppermost millimeters are to be expected. By using a 10-mm-diameter glass electrode one takes advantage of the high potential stability but may fail to measure the true pH maximum at the very surface. However, when the glass electrode is pushed into the water-saturated sediment to a depth of about 1 cm, the head of the electrode obtains complete contact with the surface pore water carried down during insertion. Mixing with the interstitial water from slightly deeper levels and disturbance of the environment by the exposed electrode (e.g. light conditions) make long equilibration times unreliable. On the other hand, rapid equilibration of the proton activity between pore water and electrode is prevented by a film of water which forms over the electrode after washing with distilled water or seawater. Therefore we pushed the electrode into the sediment several times before commencing each series of 10 successive measurements in an area of about 10 cm in diameter. By this procedure, the surface pH at one spot (27.5°C) averaged 9.16 ± 0.09 (99% C.L.), while a mean of 8.81 ± 0.15 was obtained when the electrode was rinsed with distilled water before each measurement. An even more pronounced error was observed when the electrode was rinsed with seawater. This cannot be avoided in measurements in the sublittoral or during high tide, when water covers the sediment. Therefore we restricted our measurements to periods of low tide when the sediment was not covered by seawater.

The variation within each series of 10 pH measurements, expressed as 99% confidence limits of the mean, is due partly to the horizontal microdistribution of pH within the prescribed area and partly to random errors in measurement (different depth of insertion, water contact, equilibration time). Horizontal variation of pH within the whole study area could not be quantified, as many related parameters change rapidly with time and it was impossible to obtain enough measurements at any one time (*see Fig.* 3).

Field and laboratory experiments—To compare the effect of different intensities of incident solar radiation on pH and temperature without interference with

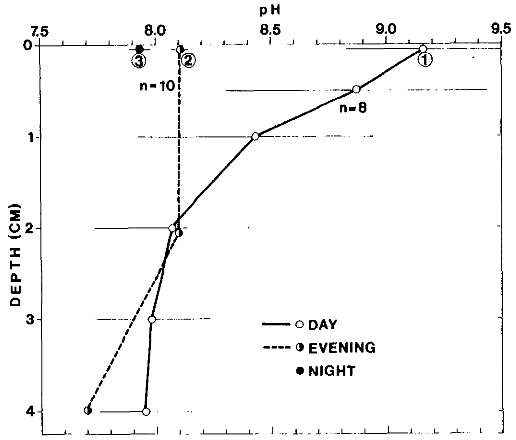

Fig. 1. Variation of pH with depth of sediment. 1—During daytime (values from Wieser et al. 1974); 2—evening, about 2 h after sunset (2030), single measurements in 2- and 4-cm depth; 3—night (0210). Horizontal bars represent 99% C.L. of means.

water and air exchange, we inverted a styrofoam box with two side walls removed over an area of sand in the flat region. This is referred to as shadow (*s*). All experiments simulated low tide conditions.

The laboratory experiments were conducted in a constant temperature room (20°C) at the Bermuda Biological Station with sediments collected at the study site. A 10-mm layer of sand was put into glass jars; the dark jars were enclosed in aluminum foil, with care taken that the samples remained saturated with water. Six neon lights illuminated the jars from the top at a distance of 20 cm. The samples were heated by the electric light and cooled by a ventilator.

In discussing the laboratory experiments, we will consider only the trends of the pH changes, as no attempts were made to simulate natural light conditions.

Results

Daily fluctuation and vertical distribution of pH—The pH of the surface sediment reaches maximum values, up to 9.6, at daytime low tide (Fig. 1). Shortly after sunset the pH decreases below that of seawater, and still lower readings are obtained during the night, when reducing conditions prevail up to the surface and the odor of hydrogen sulfide diffuses over the beach. Maximum daily fluctuations of up to 1.5 pH units are limited to the topmost 0.5 cm of sediment.

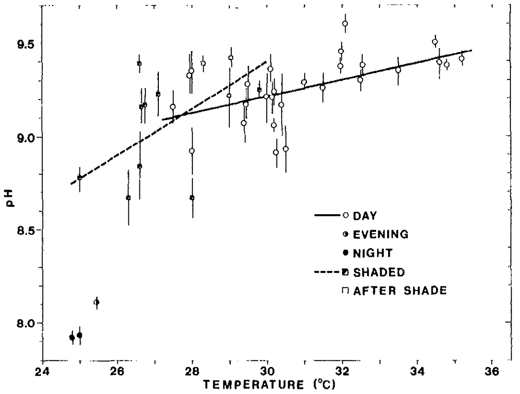

Fig. 2. Variation of pH of surface sand with temperature. Vertical bars represent 99% C.L. of means of 10 successive pH measurements. Solid line—regression for daytime values: $N = 270$; $P < 0.001$; $pH = 7.90 + 0.044 \times temp(°C)$. Dashed line—regression for values under shadow: $N = 90$; $P < 0.001$; $pH_s = 5.68 + 0.124 \times temp_s(°C)$. Regressions calculated with Bartlett's method of best fit (Simpson et al. 1960). Regression coefficients b (95% C.L., 0.034–0.054) and b_s (95% C.L., 0.079–0.173) are significantly different ($P < 0.05$, t-test). Increase of pH with temperature (=0.1 pH unit per °C) is also found in coastal waters and open oceans (Akaiyama et al. 1966; Ben-Yaakov and Kaplan 1968).

Correlation of pH with temperature and light—Correlations were highly significant between pH and temperature during low tide at midday (Fig. 2). Shadow inhibits the drastic rise of pH and keeps the temperature low (Table 1). Af-

Table 1. Means of pH and temperature of sediment surface during low tide, and effect of shading (*s*). Variance includes variability in time and space.

Date	N	pH	pH 99% C.L.	Temp (°C)
5 Sep	140	9.15	9.12–9.18	30.06
5 Sep_s	40	8.74	8.68–8.80	26.48
16 Sep	50	9.42	9.38–9.46	32.22
16 Sep_s	50	9.24	9.20–9.28	27.38
30 Sep	30	9.28	9.21–9.35	27.83
1 Oct	50	9.40	9.37–9.43	34.52

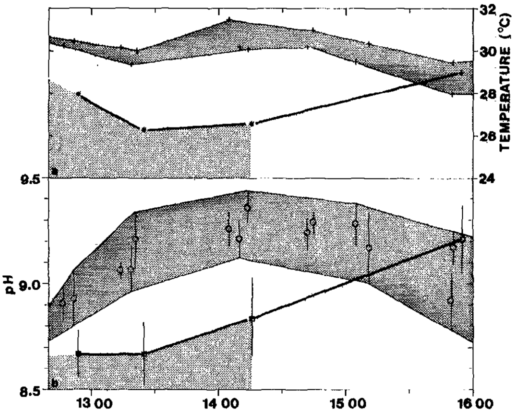

Fig. 3. Variation of temperature (a) and pH (b) with time during a low tide period at midday (+,○; dark bands indicate ranges), and effect of shadow (lower dark area); lines connect measurements under shade (*,▨) and after shade (+,□) at the same patch. Water receded at 1240 hours and flooded at 1600 hours. *See also Fig. 2.*

ter removal of our "experimental cloud," pH and temperature increased simultaneously (Fig. 3).

Field and laboratory experiments—To show whether temperature, solar radiation, or a combination of both is responsible for the high pH values of surface sediments, we varied one of the two factors experimentally and held the other constant.

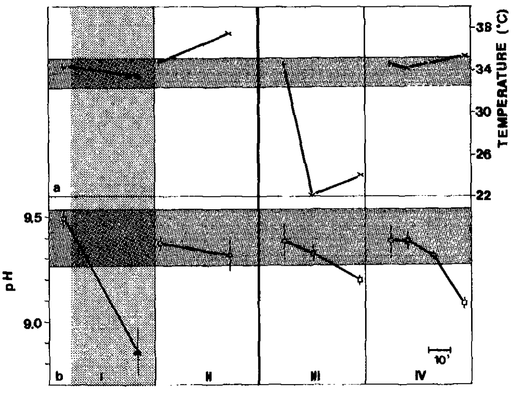

Fig. 4. Effect of temperature (a) and light on pH (b), field experiments. I—Dark bell jar; II—light bell jar; III—cooled jar; IV—reference jar. Darkened horizontal band circumscribes variability in situ. *See also Fig. 2.*

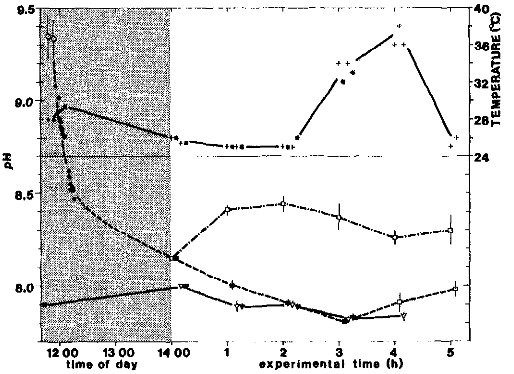

Fig. 5. Effect of temperature (a) and light on pH (b) in surface and subsurface sand (10-cm depth). Darkened area: field measurements. An initial decrease of about 0.03 pH·min^{-1} down to pH 8.5 was followed in a shaded place near the beach immediately after sampling. Open area: laboratory measurements. Dashed-dotted line—surface sand exposed to light; dashed line—dark surface sand (■) subsequently exposed to light (□); solid line—subsurface sand exposed to light (▽) and dark (▼). *See also Fig. 2.*

In one experiment in situ in which the conditions resembled those used in community respiration studies with light and dark bell jars, pH decreased by 0.6 pH units under the dark jar (Fig. 4, I) but remained constant under the light jar (Fig. 4, II).

In order to lower temperature without interfering with solar radiation, we partially immersed a glass jar containing a 10-mm layer of water-saturated surface sediment in ice water and exposed it to the sun on the beach. The sand was occasionally stirred with the thermometer to equilibrate temperature (Fig. 4, III). A control was treated identically except that it was not cooled (Fig. 4, IV). Regardless of temperature, pH remained relatively constant in both jars. The small decrease was probably due to the mechanical disturbance of the sediment system.

In the laboratory experiments light caused the pH of the surface sediment to increase, but no difference in pH could be detected between light-exposed and dark subsurface sands. Temperature changes had no effect on pH in either type of sediment (Fig. 5).

Discussion

General remarks—Records of high pH values in surface sediments are lacking in the literature. This is the more surprising as diurnal fluctuations in pH, reflecting the ratio of algal production to animal respiration, are well known in intertidal rockpools (Newell 1970) and various freshwater and marine environments (Talling 1976; and others). Are diurnal fluctuations of pH in marine sediments, as described here, exceptional, or is it merely that their general occurrence has so far remained undetected?

Any investigation excluding the actual surface from measurement (Bruce 1928; Ganapati and Rao 1962; Hartwig 1973; Jansson 1966; Pugh et al. 1974; Pytkowicz 1971) will miss the alkaline extremes in the beach ecosystem (Fig. 1). The dimensions of the glass electrode render measurements of the actual surface of the sediment difficult. With large electrodes our methodological considerations should be followed (*see above*).

Furthermore, any delay between sampling and pH measurement (Fenchel and Jansson 1966; Pamatmat 1968) will mask the occurrence of high pH values, since we found that the pH of surface sediment had dropped by 1.2 units within 2 h after sampling (Fig. 5). The relative stability of the pH of the subsurface sediment after sampling agrees with other observations (Fanning and Pilson 1971; Pytkowicz 1971; Thorstenson and Mackenzie 1974).

Light as the causal factor—The biological nature of the mechanism effecting the observed pH fluctuations was demonstrated by comparison of the reaction to light of surface and subsurface sediments (Fig. 5). Subsurface sediments have much lower photosynthetic potentials (Fenchel and Straaup 1971; Pamatmat 1968; Taylor and Gebelein 1966) and are therefore less susceptible to light-induced changes of pH. Changes of pH due to photosynthetic activity are restricted to the uppermost layer of sediments, because light penetrates maximally 2 to 7 mm into sand and mud (Gomoiu 1967).

Sedimentological and edaphic factors—The high pH values measured at the Bermuda beach expand the limits of the natural environment for marine sediments in the positive *Eh* range, given by Baas-Becking et al. (1960). They stated, however, that they were uninformed about the *Eh*-pH range of calcareous sediments. As the upper limit of pH is controlled by the precipitation of calcium carbonate, wide pH fluctuations may be restricted to certain types of sediment by such factors as grain size and magnesium content of the carbonate phase (Schmalz and Chave 1963), protective surface coatings (Pytkowicz 1971), and dissolved organic matter (Chave and Suess 1970; Berner et al. 1970).

However, some indications of changes of pH associated with light and photosynthesis even in noncalcareous sediments have been reported. Hopkins (1963) measured a difference of 0.4 pH units between shaded mud and the mud surface exposed to light. Kühl (1964) recorded pH values of up to 9.0 in a tide pool on a mud flat, while a shaded pool remained at pH 8.3. High pH values in stagnant tide pools (Amanieu 1969; Pfannkuche et al. 1975) and runoffs (Pugh et al. 1974) during tidal exposure during the day suggest that similar pH fluctuations may also occur at the exposed surface of sediments (Kühl 1971). However, local penetration of interstitial water from lower levels (Gardner 1975; Hopkins 1963; Kühl and Mann 1966; Ott and Machan 1971) may counteract the photosynthetic effect on pH.

Wide pH fluctuations are very probably limited to lenitic beaches, where there is no or very little exchange of the interstitial water (Pollock and Hummon 1971; Riedl and Machan 1972). In an investigation of freshwater sediments, light-dependent elevation of pH was observed even in the wash zone of running waters (Gnaiger and Gruber in prep.); pH values exceeding 10.0 were measured in exposed and water-covered sediments. Substantial pH fluctuations may therefore also be expected in subtidal marine sediments with a dominance of benthic over planktonic primary production (Sournia 1976).

Ecological implications—If the pH of sediments is to be used as an indicator of pollution (Leppäkoski 1968; Makemson 1973; Pugh et al. 1974), further knowledge of the dynamics of pH in the natural environment is needed. Enhanced respiratory rates and anoxic acid production, even in the aerobic surface film of polluted sediments (Makemson 1973; Patriquin and Knowles 1975), will drive pH to lower values and thereby interfere with the creation of alkaline conditions by photosynthetic activity.

High pH values may be considered a limiting factor confining a number of species to the lower, oligoxic or anoxic, layers at times when high pH, *Eh*, pO_2, and high temperature prevail at the sediment surface (Wieser et al. 1974; Wieser 1975).

pH fluctuations as observed in our study may be of importance in understanding sand beach energetics: "With increasing pH values, the concentration of free carbon dioxide and of bicarbonate decreases, and at pH 9.4, photosynthesis of marine green plants ceases even in bright sunlight, because there is no more carbon dioxide or bicarbonate available" (Rheinheimer 1972, p. 1460). Since values as high as 9.5 were not exceptional at the beach we studied, inhibition of primary production cannot be excluded at times of highest radiant energy input into the ecosystem. A conventional method for studying the energy metabolism of benthic communities is the use of light and dark bell jars. As shown in our field experiments, pH drops significantly in the sediment under the dark bell jar and thus may influence community respiration. This effect must be considered in any investigation in which this method is used.

References

AKAIYAMA, T., T. SAGI, T. YURA, AND K. KIMURA. 1966. On the distribution of in situ pH in the adjacent seas of Japan. Oceanogr. Mag. **18:** 83–90.

AMANIEU, M. 1969. Recherches écologiques sur les faunes des plages arbitées de la région d'Arcachon. Helgol. Wiss. Meeresunters. **19:** 455–557.

BAAS-BECKING, L. G., I. R. KAPLAN, AND D. MOORE. 1960. Limits of the natural environment in terms of pH and oxidation-reduction potentials. J. Geol. **68:** 243–284.

BEN-YAAKOV, S. 1970. A method for calculating the in situ pH of seawater. Limnol. Oceanogr. **15:** 326–328.

———. 1973. pH buffering of pore water of recent anoxic marine sediments. Limnol. Oceanogr. **18:** 86–94.

———, AND I. R. KAPLAN. 1968. pH-temperature profiles in ocean and lakes using an in situ probe. Limnol. Oceanogr. **13:** 688–693.

BERNER, R. A., M. R. SCOTT, AND C. THOMLINSON. 1970. Carbonate alkalinity in the pore waters of anoxic marine sediments. Limnol. Oceanogr. **15:** 544–549.

BRUCE, J. R. 1928. Physical factors on the sandy beach. 2. Chemical changes, carbon dioxide concentration and sulphides. J. Mar. Biol. Assoc. U.K. **15:** 553–565.

CHAVE, K. E., AND E. SEUSS. 1970. Calcium carbonate saturation in seawater: Effects of dissolved organic matter. Limnol. Oceanogr. **15:** 633–637.

COULL, B. C. 1970. Shallow water meiobenthos of the Bermuda platform. Oecologia **4:** 325–357.

FANNING, K. A., AND M. E. PILSON. 1971. Interstitial silica and pH in marine sediments: Some effects of sampling procedures. Science **173:** 1228–1231.

FARRIS, R. A. 1976. Systematics and ecology of Gnathostomulida from North Carolina and Bermuda. Ph.D. thesis, Univ. North Carolina.

FENCHEL, T., AND B. O. JANSSON. 1966. On the vertical distribution of the microfauna in the sediments of a brackish-water beach. Ophelia **3:** 161–177.

———, AND R. J. RIEDL. 1970. The sulfide system: A new biotic community underneath the oxidized layer of marine sand bottoms. Mar. Biol. **7:** 155–268.

———, AND B. J. STRAAUP. 1971. Vertical distribution of photosynthetic pigments and the penetration of light in marine sediments. Oikos **22:** 172–182.

GANAPATI, P. N., AND G. C. RAO. 1962. Ecology of the interstitial fauna inhabiting the sandy beaches of Waltair coast. J. Mar. Biol. Assoc. India **4:** 44–57.

GARDNER, L. R. 1975. Runoff from an intertidal marsh during tidal exposure—recession curves and chemical characteristics. Limnol. Oceanogr. **20:** 81–89.

GIESKES, J. M. 1969. Effect of temperature on the pH of seawater. Limnol. Oceanogr. **14:** 679–685.

GOMOIU, M. T. 1967. Some quantitative data on light penetration in sediments. Helgol. Wiss. Meeresunters. **15:** 120–127.

HARTWIG, E. 1973. Die Ciliaten des Gezeiten-Strandes der Nordseeinsel Sylt. 2. Ökologie. Mikrofauna Meeresbodens 21. 171 p.

———, G. GLUTH, AND W. WIESER. 1977. Investigation on the ecophysiology of *Geleia nigriceps* Kahl (Ciliophora, Gymnostomata) inhabiting a sandy beach in Bermuda. Oecologia **31**: 159–175.

HOPKINS, J. T. 1963. A study of the diatoms of the Ouse Estuary Sussex 1. The movement of the mudflat diatoms in response to some chemical and physical changes. J. Mar. Biol. Assoc. U.K. **43**: 653–663.

JANSSON, B. O. 1966. On the ecology of *Derocheilocaris remanei* Delamare and Chappius (Crustacea, Mysticocarida). Vie Millieu **17**: 143–186.

KÜHL, H. 1964. Über die Schwankungen der abiotischen Faktoren in der Elbmündung bei Cuxhaven. Helgol. Wiss. Meeresunters. **10**: 203–216.

———. 1971. On changes of the interstitial water after decomposition of organic matter. Smithson. Contrib. Zool. **76**: 171–205.

———, AND H. MANN. 1966. Änderungen im Chemismus des Interstitialwassers am Strand von Cuxhaven während einer Tide. Helgol. Wiss. Meeresunters. **13**: 238–245.

LEPPÄKOSKI, E. 1968. Some effects of pollution on the benthic environment of the Gullmarsfjord. Helgol. Wiss. Meeresunters. **17**: 291–301.

MAKEMSON, J. C. 1973. Oxygen and carbon dioxide in interstitial water of two Lebanese sand beaches. Neth. J. Sea Res. **7**: 223–232.

MOORE, H. B. 1931. The muds of the Clyde sea area. 3. Chemical and physical conditions; rate and nature of sedimentation and fauna. J. Mar. Biol. Assoc. U.K. **17**: 325–358.

NEWELL, R. C. 1970. Biology of intertidal animals. Logos.

OTT, J. A., AND R. MACHAN. 1971. Dynamics of climatic parameters in intertidal sediments. Thalassia Jugosl. **7**: 219–229.

PAMATMAT, M. M. 1968. Ecology and metabolism of a benthic community on an intertidal sandflat. Int. Rev. Gesamten Hydrobiol. **53**: 211–298.

PATRIQUIN, D. G., AND R. KNOWLES. 1975. Effects of oxygen, mannitol and ammonium concentrations on nitrogenase (C_2H_2) activity in a marine skeletal carbonate sand. Mar. Biol. **32**: 49–62.

PENNAK, R. W. 1951. Comparative ecology of the interstitial fauna of fresh-water and marine beaches. Ann. Biol. **27**: 449–479.

PFANNKUCHE, O., H. JELINEK, AND E. HARTWIG. 1975. Zur Fauna eines Süsswasserwattes im Elbe-Aestuar. Arch. Hydrobiol. **76**: 475–498.

POLLOCK, L. W. 1971. Ecology of intertidal meiobenthos. Smithson. Contrib. Zool. **76**: 141–148.

———, AND W. D. HUMMON. 1971. Cyclic changes in interstitial water content, atmospheric exposure, and temperature in a marine beach. Limnol. Oceanogr. **16**: 522–535.

PUGH, K. B., A. R. ANDREWS, C. F. GIBBS, S. J. DAVIS, AND G. D. FLOODGATE. 1974. Some physical, chemical, and microbiological characteristics of two beaches of Anglesey. J. Exp. Mar. Biol. Ecol. **15**: 305–333.

PYTKOWICZ, R. M. 1967. Carbonate cycle and the buffer mechanism of recent oceans. Geochim. Cosmochim. Acta **31**: 63–73.

———. 1971. Sand-seawater interactions in Bermuda beaches. Geochim. Cosmochim. Acta **35**: 509–515.

———, AND E. ATLAS. 1975. Buffer intensity of seawater. Limnol. Oceanogr. **20**: 222–229.

———, D. R. KESTER, AND B. C. BURGENER. 1966. Reproducibility of pH measurements in seawater. Limnol. Oceanogr. **11**: 417–419.

RHEINHEIMER, G. 1972. Bacteria, fungi and bluegreen algae, p. 1459–1469. *In* O. Kinne [ed.] Marine ecology, v. 1, Part 3. Wiley-Interscience.

RIEDL, R. J., AND R. MACHAN. 1972. Hydrodynamic patterns in lotic intertidal sands and their bioclimatological implications. Mar. Biol. **13**: 179–209.

SCHMALZ, R. F., AND K. E. CHAVE. 1963. Calcium carbonate: Factors affecting saturation in ocean waters off Bermuda. Science **139**: 1206–1207.

SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN. 1960. Quantitative zoology. Harcourt, Brace & World.

SOURNIA, A. 1976. Primary production of sands in the lagoon of an atoll and the role of foraminiferan symbionts. Mar. Biol. **37**: 29–32.

TALLING, J. F. 1976. The depletion of carbon dioxide from lake water by phytoplankton. J. Ecol. **64**: 79–121.

TAYLOR, W. R., AND C. D. GEBELEIN. 1966. Plant pigments and light penetration in intertidal sediments. Helgol. Wiss Meeresunters. **13**: 229–237.

THORSTENSON, D. C., AND F. T. MACKENZIE. 1974. Time variability of pore water chemistry in recent carbonate sediments, Devil's Hole, Harrington Sound, Bermuda. Geochim. Cosmochim. Acta **38**: 1–19.

TIETJEN, J. H. 1969. The ecology of shallow water meiofauna in two New England estuaries. Oecologia **2**: 251–291.

WIESER, W. 1975. The meiofauna as a tool in the study of habitat heterogeneity: Ecophysiological aspects. A review. Cah. Biol. Mar. **16**: 647–670.

———, J. OTT, F. SCHIEMER, AND E. GNAIGER. 1974. An ecophysiological study of some meiofauna species inhabiting a sandy beach at Bermuda. Mar. Biol. **26**: 235–248.

———, AND M. ZECH. 1976. Dehydrogenases as tools in the study of marine sediments. Mar. Biol. **36**: 113–122.

ZOBELL, C. E. 1946. Studies on redox potential of marine sediments. Bull. Am. Assoc. Pet. Geol. **30**: 477–513.

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