

THE MEIOFAUNA AS A TOOL IN THE STUDY OF HABITAT HETEROGENEITY: ECOPHYSIOLOGICAL ASPECTS. A REVIEW ⁽¹⁾.

by

Wolfgang Wieser

Institut für Zoophysiologie der Universität Innsbruck, Austria.

Résumé

L'analyse de l'hétérogénéité des sédiments marins peut être accomplie en utilisant différentes stratégies. Les principales sont les suivantes :

- mesures de variation des facteurs physico-chimiques ;
- évaluations de la répartition spatiale et temporelle des organismes vivant dans les sédiments (micro-organismes, méiofaune) ;
- recherche expérimentale sur les réponses des micro- et méioorganismes aux stimulus de leur environnement.

La dernière approche — qui est en fait écophysiologique — bien qu'encore peu développée est la plus prometteuse. Étant donné que les sédiments marins peu profonds constituent un écosystème d'une grande ancienneté et d'une grande diversité, on peut supposer que chacune des très nombreuses espèces qui y vivent sont adaptées non seulement aux écarts des combinaisons de facteurs sévissant dans l'ensemble de l'écosystème, mais aussi à un groupe spécifique de facteurs caractérisant la micro-niche dans laquelle l'espèce effectue son cycle. Dans cet article sont passés en revue les rapports entre organismes et sédiments marins qui sont répercutés sur les possibilités de survie des espèces méiobenthiques. Leur petite taille et leur faible possibilité de déplacement peuvent faire de ces animaux un instrument idéal pour explorer un environnement qui, par son hétérogénéité spatiale et temporelle, ne peut être décrit de manière satisfaisante à la suite de quelques mesures de variables physico-chimiques. En particulier, la distribution verticale des espèces de la méiofaune sera mise en parallèle avec leur résistance à la température, le pO_2 , le pH et la salinité, ainsi qu'avec une combinaison de ces facteurs. La conclusion principale qui peut être tirée de résultats encore trop peu nombreux est qu'au moins chez la plupart des habitants d'une plage subtropicale, les limites de tolérance aux hautes températures, alcalinité et faible pO_2 , sont très voisines des extrêmes écologiques notés pour ces facteurs dans les zones préférentielles de ces espèces. Le degré de correspondance est illustré de la meilleure manière par le fait qu'une différence de répartition verticale de quelques centimètres, quelquefois même de millimètres, se reflète généralement par une différence frappante dans les écarts de tolérance vis-à-vis des hautes températures, de l'alcalinité, ou du manque d'oxygène. La concordance entre la tolérance aux fluctuations de salinité et la répartition doit probablement être aussi étroite, mais s'appuie sur moins de documents. D'autre part, ni le taux d'acidité, ni les écarts de basse température de l'eau interstitielle ne semblent être des facteurs limitant la répartition de la méiofaune subtropicale.

Une connaissance plus détaillée des rapports entre la répartition des facteurs et de la faune d'une part, et les limites de tolérance des animaux d'autre part, devrait être utile pour prévoir les changements faunistiques susceptibles de se produire au cours de modifications survenant à l'intérieur de l'habitat et résultant, par exemple, de la pollution. De plus, le degré d'adaptabilité à l'environnement des principaux composants de la faune peut être un indicateur de la diversité globale et de la stabilité de l'habitat en question.

(1) Contribution no. 634 from the Bermuda Biological Station.

Introduction

Many ecological investigations lead to the trivial conclusion that, by virtue of its morphological and physiological specializations, a particular species or a particular population is capable of living where, indeed, it lives. The triviality disappears, however, if we ask ourselves *how close* is the degree of correspondence between the adaptive features of a species and its environment. If the question is put quantitatively, it may be discovered that, with respect to some factors, the species lives very close to the limits of its capabilities whereas with respect to other factors it is — so to speak — buffered by wider safety margins. In this way, the limiting or "master" factors that determine the distribution of a given species can be defined, and these in turn allow prediction of the effects of disturbance of the environment — for example through pollution — on the composition of the fauna (see also Jansson, 1967; Arndt, 1973).

The degree to which a species fits the environment can be determined by: a) studying its distribution in time and space, b) measuring the important ecological variables in the habitat and c) analyzing, in the laboratory, the responses of the species to these variables.

If the leading representatives of an ecosystem are analyzed in this way, a picture emerges that should be characteristic of the habitat in question. In old and stable habitats (in the sense of Sanders, 1968; Slobodkin and Sanders, 1969) one would expect the whole system to consist of sub-systems (microenvironments, niches, zones, etc.) each occupied by a characteristic set of species which fit more closely into their specific environment than the inhabitants of more recent and unstable habitats. This distinction is not generally applicable, of course, since even the most predictable of habitats harbors a heterogeneous collection of species of which some are always more eurytopic and more mobile than others, and quite a few which are not in equilibrium with their physical environment because of biological interactions (see Grassle and Sanders, 1973). All the same, it might be possible to characterize different habitats by comparing the ranges of environmental factors with the tolerance limits of the dominant species occupying these habitats. In favourable cases, certain rules of distribution may emerge and even exceptions to these rules may prove useful in shedding further light on the interrelationships between a habitat and its inhabitants.

Habitat and organisms

In the following, those relationships between organisms and marine sediments will be reviewed which are reflected in the survival ranges of meiofauna species. Their small size and low powers of locomotion may prove these animals to be ideal tools for probing an environment which, because of its spatial and temporal heterogeneity, cannot be described adequately on the basis of a few measurements of physical and chemical variables. This inherent difficulty in the physicochemical definition of marine sediments has been well expressed by Pugh et al. (1974, p. 333) : "The beaches have been shown to have a variable microbiology and chemistry, arising from the different physical conditions. The survey has, however, only consisted of a number of discrete samples both spatially and temporally. From experience we would now conclude that such analyses can never adequately describe a beach: they are powerless to reveal 'sources' and 'sinks' of various nutrients and effects on populations since the environment involves a dynamic equilibrium, extensively buffered against change in any direction, and in which the compo-

nents are so intricately interwoven that they are not revealed by such cursory glances".

Three factorial principles may be distinguished which are responsible for the "fine-grained" structure of intertidal and shallow water marine sediments:

a) *horizontal gradients*, comprising gradients of ecological factors between land and water or between the intertidal and the sublittoral;

b) *vertical gradients*, comprising gradients of ecological factors from the surface into the depth of the sediment;

c) *inhomogeneities*, comprising variations of ecological factors within a restricted site which are not due to gradients but to inhomogeneities in sediment composition, patchiness of food and to other biotic factors.

Both gradients and inhomogeneities possess not only a spatial but also a temporal dimension which has to be kept in mind if a complete analysis of sediment-organism relationship is attempted.

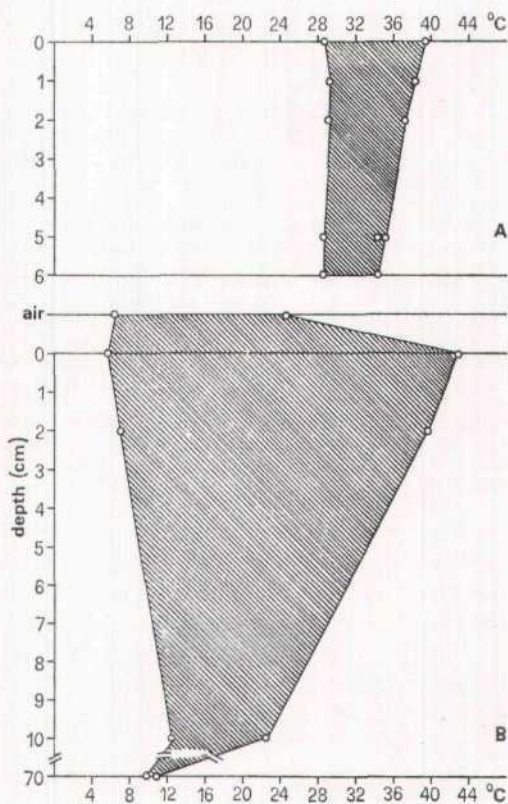
Temperature

There is an infinite variety of patterns for the horizontal and vertical distribution of temperature on beaches, and several attempts to describe them have been made (Bruce, 1928; Renaud-Debyser, 1963;

FIG. 1
Comparison between the temperature ranges of a subtropical and a temperate beach.

A: Tuckers Town Beach, Bermuda, mid-littoral. Vertical distribution of temperature as measured at low tide on several days in August 1973.

B: Askö Beach, Baltic, supralittoral. Diurnal range of temperature on a sunny day in May (based on data from Jansson, 1967b).



Johnson, 1965; Jansson, 1966, 1967b; Harris, 1972, and others). The vertical distribution of temperature on two very different types of beach is summarized in Fig. 1, from which two generalizations emerge:

- 1) the thermal environment becomes less extreme and more stable with depth;
- 2) the temperature maximum reached in the upper two cm or so on sunny days is more or less independent of the geographical

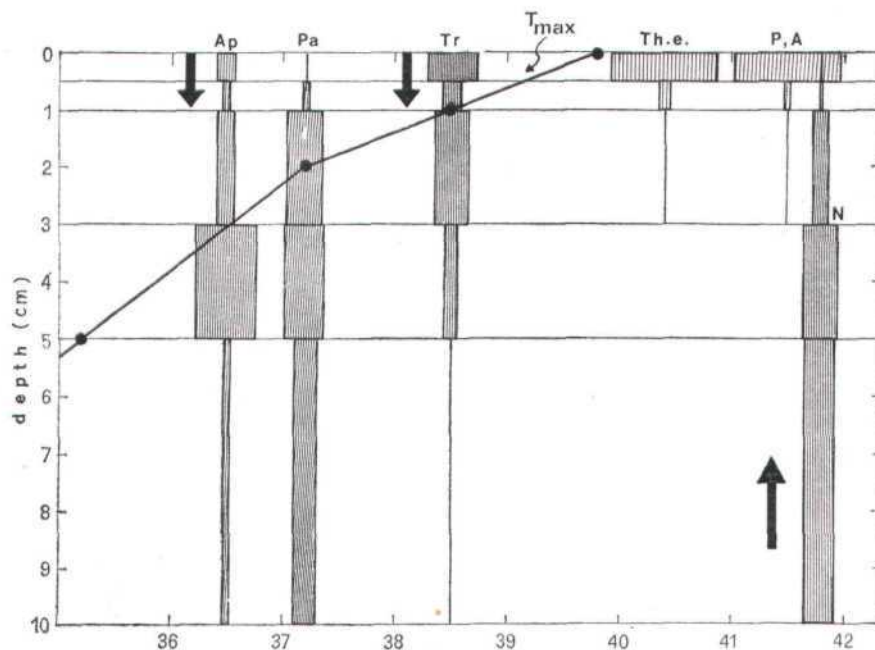


FIG. 2

Vertical distribution plotted against upper lethal temperatures at five hours exposure of several meiofauna species from Tuckers Town Beach, Bermuda.

The maximum temperatures recorded during the investigation period (August 1973) at various depths are also indicated (T_{max}) using the abscissa as a normal temperature scale. In several species, a discrepancy was observed between vertical distribution and LT_{50} . Two species occurred in greater numbers in zones in which the temperature may rise appreciably above their experimentally determined LT_{50} . One species, according to its LT_{50} , could have occurred much higher up than it was actually found. In these species, then there exists a « potential » or a « requirement » for vertical migration, the direction of which is indicated by arrows.

Ap = *Apodopsyllus africanus*; Pa = *Paramonhystera* n.sp.; Tr = *Tripyloides* n.sp.; Th.e. = *Theristus erectus*; N = *Nannolaimoides decoratus*; P, A = *Psyllocampus* n.sp. and *Amphiascoides subdebilis* (not separated).

location of the beach, but the temperature minimum and the diurnal (as well as annual) range of temperature is not (see also Jansson, 1971).

Again these seem to be trivial statements but, on their basis, the response of the fauna to differences in the thermal regimes of different beaches or of different zones of one particular beach cannot be predicted.

For example, the opinion has been expressed that «eurythermy

is one of the most remarkable characteristics of the subterranean littoral microfauna" (Delamare Deboutteville, 1960; see also Burbanck and Burbanck, 1967) and Fenchel (1969) considered the whole group of Ciliates to be little affected by temperature although, in a later publication, Lee and Fenchel (1972) reported some effects of temperature on the rate of growth of Ciliates from antarctic, temperate and tropical sediments. If eurythermy—in its widest sense—was indeed a general characteristic of the marine meiofauna, little correspondence between the distribution of species and their temperature tolerance would be expected. However, there are indications that such a correspondence, so well known in the marine macrofauna (Theede, 1973; v. Oertzen, 1973 and others), holds for the meiofauna too. For example, Boaden and Erwin (1971), in an investigation of beaches in Northern Ireland, report an upper thermal maximum of 34.3°C for *Protodrilus symbioticus* which lives near high water level, but of only slightly more than 25°C for *Turbanella hyalina* which lives near low water level. A similar correspondence between high temperature tolerance and distribution on a beach has been found in two species of the oligochaete genus *Marionina* by Lasserre (1971). A study relating high temperature tolerance and vertical distribution of the meiofauna in a subtropical low energy beach (Wieser et al., 1974) revealed a surprisingly good correspondence between these two variables for most of the species examined. If LT_{50} is plotted against vertical distribution (Fig. 2) it can be seen that, in general, the deeper a species occurs in the sediment, the lower its high temperature tolerance. There was a difference of 4.6°C between the maximum temperature recorded at the surface and at 5 cm depth on Tuckers Town Beach, Bermuda, in August 1973, and almost exactly the same difference in LT_{50} was found to occur between two species of Harpacticoids confined to the upper 5 mm of the beach (*Amphiascoides subdebilis*, *Psyllocamptus* n.sp.) and one species (*Apodopsyllus africanus*) that has its center of abundance at 3-5 cm depth and deeper. Whereas the finding that species inhabiting the upper layers of sediments also have the highest temperature tolerance is trivial, the finding that temperature tolerance is reduced in species that have their center of abundance a few cm below the surface is not. Moreover, there is a remarkable similarity between the highest temperature a species can endure for a short time (the LT_{50} values of Fig. 2 are based on one-hovir experiments) and the highest temperature likely to be experienced in its habitat (compare Fig. 1a and 2). The same observation was made by Jansson (1968) with respect to *Haploveljovskya subterranea* and other Turbellarians of Baltic beaches in which the upper limit of their tolerance range and the maximum temperatures encountered in their habitat nearly coincide between 25 and 28°C.

On the basis of these as yet very incomplete findings one conclusion may be drawn:

in many marine meiofauna species high-temperature tolerance is adjusted closely to the highest temperature to be expected in that zone of the beach in which the species has its center of distribution.

This corroborates the idea expressed by Hamilton (1973) that biological processes, in general, are adapted as closely as possible to the highest temperature occurring in the habitat of a given species.

However, Fig. 2 also indicates that the correlation between LT_{50} and vertical distribution is not perfect, which would indeed be surprising. Some additional factors to be considered in this respect will be discussed further below (p. 655).

As far as the response to *low* temperature is concerned, our knowledge is even scantier than that concerning *high* temperature. However, it appears that there is less correspondence between low-temperature tolerance of the meiofauna and the lowest temperatures likely to be experienced by the animals in their habitats. No systematic study in this direction was made in Bermuda but, on several occasions, sediment samples were kept in the refrigerator and many species of Nematodes, Ciliates and other groups were found to survive such a treatment for several days. The lowest water temperature to be expected around Bermuda in winter is about 17°C. In temperate beaches, all species tested so far survive sub-zero temperatures (Boaden and Erwin, 1971; Gray, 1965) and even freezing (Barnett, 1968; Gerlach and Schrage, 1971), although in nature they probably never encounter such extreme conditions.

Oxygen

The development of electrodes has made the measurement of oxygen availability and of redox potentials in sediments a fairly easy task. In consequence, an increasing number of papers is appearing in which the vertical or horizontal distribution of the meiofauna is correlated with gradients of oxygen availability or redox potential (Jansson, 1966, 1967, 1971; Fenchel and Jansson, 1966; Fenchel, 1969; Fenchel et al., 1967; Enckell, 1968; Riedl and Ott, 1971; Harris, 1972; Dinet, 1972; Giere, 1973; Wieser et al., 1974). Although oxygen availability and Eh are not strictly interdependent, it is usually assumed that Eh values below—100 mV indicate the unavailability of molecular oxygen for aerobic metabolism. The methods presently in use for measuring oxygen availability and redox potential suffer from two weaknesses:

firstly, they are not fine enough to give a true picture of the environment of organisms measuring less than 1 mm in length and only a few microns in diameter. Enckell (1968) has suggested that oxygenized and reduced areas in intertidal sediments may have a circumference of less than 1 mm;

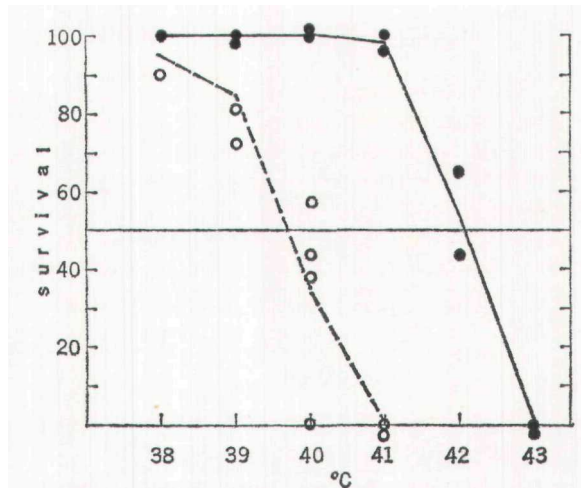
secondly, they are not sensitive enough to supply unequivocal proof of the absence of molecular oxygen at the site of measurement. The interpretation of short-term investigations is further hampered by long-term fluctuations of factors and fauna (Pugh et al., 1974). For example, the distribution of oxygen in the sediment may change in an unpredictable manner by diffusion through animal burrows and plant stems (Teal and Kanwisher, 1966; Teal and Wieser, 1966) or by convection due to locomotion of larger animals (Gordon, 1966; Davis, 1974). On the other hand, animals surviving anoxia for a certain length of time may regenerate their oxidative capacity by regular or irregular migrations to the surface.

Additional information on the role of oxygen as an ecological factor may be obtained from tolerance experiments. Since most species inhabiting low energy beaches (Fenchel and Riedl, 1970) are capable of surviving lack of oxygen for shorter or longer periods, it is advisable in tolerance experiments to combine anoxic conditions with a second stressor, for example high temperature. By this means, the effect of anoxia will become apparent in a sufficiently short time to prevent secondary effects of starvation, microbial growth, etc. (Wieser et al., 1974). If the responses of meiofauna species to a high temperature stress in the absence and in the presence of oxygen are compared, the following predictions can be made:

- a) species that are inevitably harmed by lack of oxygen are not likely to migrate at any time into lower, anoxic strata of the sediment;
- b) species which are unaffected by lack of oxygen are the most likely candidates for migrations between surface and deeper layers;
- c) species which are harmed by the presence of oxygen have to be obligate inhabitants of anoxic layers.

FIG. 3
Survival (percentage) of *Steineria* n. sp. at different experimental temperatures. Exposure time: 5 hours.

Full circles: normoxic water. Open circles: anoxic water. The line of 50 p. 100 survival (LT_{50}) is indicated.



One approach to the measurement of response to lack of oxygen is illustrated in Fig. 3: The LT_{60} of a species is determined both at saturation pO_2 and in the absence of (or with very little) oxygen. The difference between the two LT_{50} values, ALT, is a measure of the dependence of that particular species on oxygen. The larger ALT, the more oxiphilic the species. Fig. 4 illustrates the relationship between ALT and vertical distribution of some meiofauna species at Tuckers Town Beach, Bermuda. An analysis of the few species examined reveals the following: of the two dominant groups of inhabitants of the upper sediment layers, the Harpacticoids are much more dependent on oxygen than the Nematodes. No doubt this can be explained by the higher mobility of the Harpacticoids which allows them to escape at any sign of the onset of oxygen shortage. Apart from the surface-inhabiting *oxiphilic* group of species, a group of species occurs which is more or less insensitive to the amount of

oxygen present. These species may be called *facultative anoxi-* (or *microôxi-*) *bionts*. They are the most likely candidates for undertaking migrations, and thus effecting exchange of material, between the upper and lower layers of the sediment. Finally, the Nematode •*Paramonhystera* n.sp. is one of the new obligate *anoxi-* (or *microôxi-*) *bionts* so far found in marine sediments since at least some of its life functions are irreversibly damaged by normal pO_2 (ALT is negative). It is true that a few specimens of this species were also found close to the surface but, in this particular locality, the sediment proved to be reduced at a depth of only 1 cm (Wieser et al., 1974).

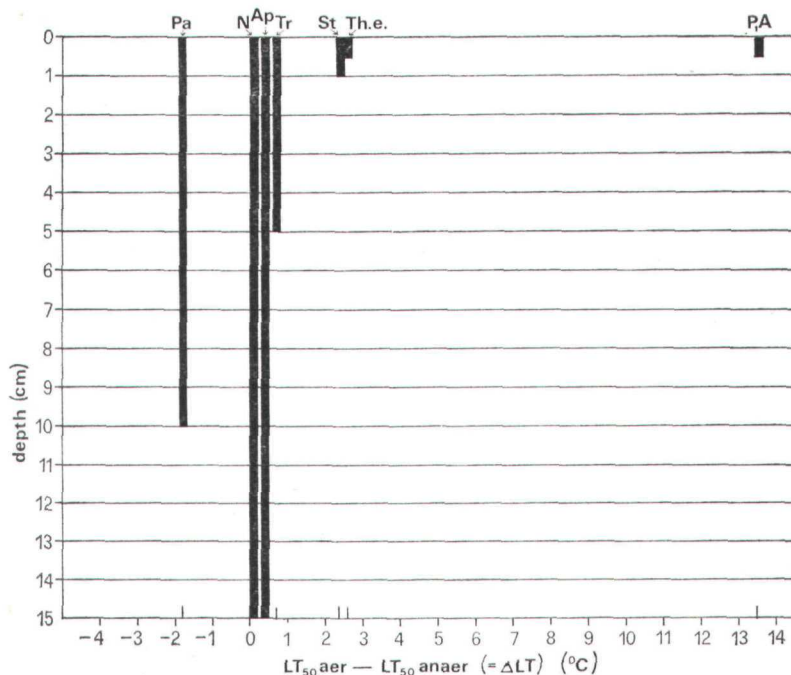


FIG. 4

Vertical distribution plotted against the degree of oxiphily in several species of meiofauna from Tuckers Town Beach, Bermuda. The degree of oxiphily is expressed as the difference of lethal temperature (ALT) between normoxic ($LT_{50\text{ aer}}$) and anoxic ($LT_{50\text{ anaer}}$) conditions. The height of the bars indicates the range of vertical distribution of approximately 90 p. 100 of the specimens of a given species. Abbreviations as in Fig. 2, plus St = *Steineria* n.sp.

The distribution of facultative and obligate anoxibionts is identical, so that distribution data alone cannot be used to distinguish one group from the other. It is impossible to say, therefore, which of the many species so far reported from the "sulfide system" (Fenchel and Riedl, 1970) are obligate or merely facultative anoxibionts. At any rate, a great number of micro- and meiofauna species, mainly comprising Ciliates, Turbellarians, Gnathostomulids and Nematodes, appear to be more or less regular inhabitants of anoxic sediments (Wieser and Kanwisher, 1961; Teal and Wieser, 1966; Fenchel, 1969; Fenchel and Riedl, 1970; Boaden and Platt, 1971; Atkinson, 1973; Ott and Schiemer, 1973; Boaden, 1975); some of these (so far the

most likely seems to be the "thiobiotic" *Gastrotrich Gigantodasys* sp. Maguire and Boaden 1975) may turn out to be true anoxibionts like *Paramonhystera* n.sp.

pH

Although it is well established that photosynthetic activity and temperature may render sea water quite alkaline (Baas-Becking et al.,

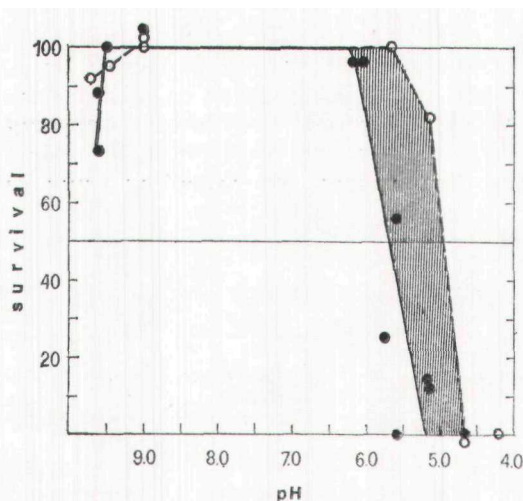


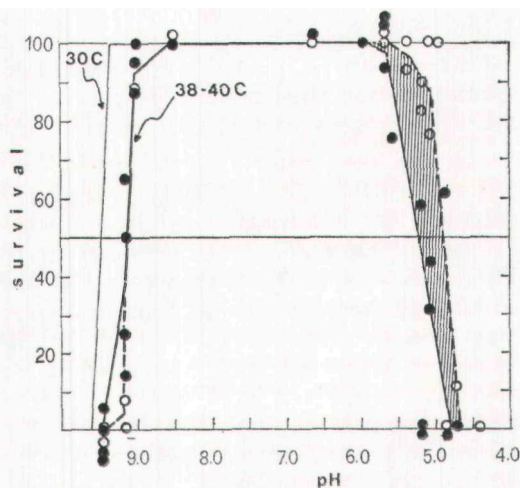
FIG. 5
Survival (percentage) of two Harpacticoids, *Psyllocamptus* n. sp. and *Amphiascoides subdebilis*, in sea water alkalized with NaOH or acidified with HCl.

Exposure time: 2 hours. Full circles: normoxic water, 38-40°C. Open circles: oligoxic water ($pO_2 = 2-8$ Torr), 30°C. For the latter experiments, sea water was made anoxic by gassing with oxygen-free nitrogen followed by acidification or alkalinization. Both pO_2 and pH were monitored continuously with electrodes. The increased range of survival under oligoxic conditions is indicated by shading. Each symbol denotes one experiment with 20 specimens.

1960), pH is usually considered a conservative factor in marine sediments with no effects on organisms (Delamare Deboutteville, 1960; Ganapati and Rao, 1962; Renaud-Debyser, 1963; Pollock, 1971; Hartwig, 1973). However, it has been shown recently that, at least

FIG. 6
Survival (percentage) of *Steineria* n.sp. in sea water alkalized with NaOH or acidified with HCl.

Exposure time: 2 hours. Full circles: normoxic water, 38-40°C. Open circles: oligoxic water ($pO_2 = 2-8$ Torr), 38-40°C. Survival in the alkaline region in normoxic water at 30°C is indicated by the regression line based on 18 experiments. Other conditions as in Fig. 5.



in subtropical low-energy beaches, high temperature and photosynthesis may combine during low tide to increase the pH of the superficial pore water to as much as 9.6 (Wieser et al., 1974). Tolerance experiments proved that pH-values of this magnitude must constitute a

barrier to migration into the surface layer for quite a few species. Since in nature high pH-values are usually correlated with high temperature, tolerance experiments should be carried out in the upper thermal range of a given species. Three of the most characteristic experiments of this kind are shown in Fig. 5-7 which suggest the following generalizations:

a) if carried out at a temperature not much lower than LT_{50} for the experimental period (two hours in the experiments shown) the upper limit of alkaline tolerance ($LD_{50 \text{ alk}}$) is closely correlated with the vertical distribution and the biology of the species concerned. This can be illustrated in a more general way by plotting $LD_{50 \text{ alk}}$ against the highest pH-values measured in the zone in which each species reaches the upper limit of its vertical distribution (ignoring the occurrence of a few specimens above this limit) (Fig. 8). Most species follow very closely the "iso-pH-line" which is the same as

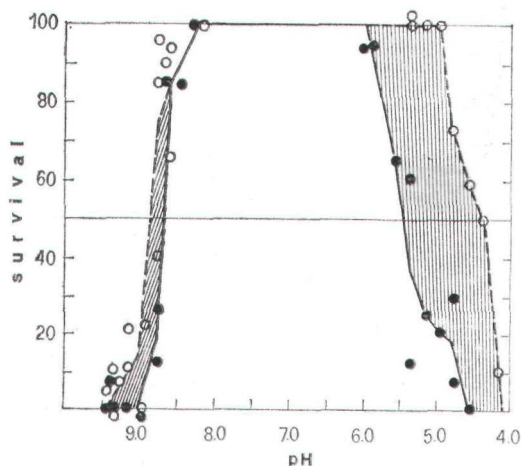


FIG. 7
Survival (percentage) of *Paramonhystera* n. sp. in sea water alkalized with NaOH or acidified with HCl.

Exposure time: 2 hours.
Experimental temperature: 35°C. Full circles: normoxic water. Open circles: oligoxic water ($pO_2 = 2.8$ Torr). Other conditions as in Fig. 5.

saying that there is hardly any superfluous alkaline tolerance in these species. From this, it may be inferred that alkaline resistance is such a costly process that it will not be maintained unnecessarily;

b) in the upper thermal range of anyone species, temperature has only little effect on $LD_{50 \text{ alk}}$ and $LD_{50 \text{ ac}}$. No difference could be detected, for example, in *Steineria* n.sp. between 38 and 40°C or in *Nannolaimoides decoratus* between 40 and 43°C (Wieser et al., 1974). This indicates that alkalinity is the dominant stressor as compared with high temperature. Larger temperature differences, however, may lead to differences in LD_{50} . In *Steineria*, for example, $LD_{50 \text{ alk}}$ increased from pH 9.15 to 9.5 when experimental temperature was lowered from 38 to 30°C (Fig. 6). This is important since it suggests that some species may migrate into the uppermost sediment layers when the temperature is low but avoid them when it is high;

c) pO_2 has no effect on $LD_{50 \text{ alk}}$, except for a slightly negative effect of normal pO_2 in the obligate anaerobe *Paramonhystera* n.sp. (Fig. 7). This again points to alkalinity as the overriding stress factor in this environment;

d) resistance to low pH-values does not seem to be highly adaptive

since even in anoxic sediments, due to the buffering action of organic and inorganic systems (Ben-Yaakov, 1973), the pH of pore water does not fall much below 7.0. It was suggested previously (Wieser et al., 1974) that differential sensitivity to low pH may be correlated with the feeding habits of a given species, but no information contradicting or supporting this speculation could be obtained. The effect of pO_2 on acid tolerance is quite different from that on alkaline tolerance since in all species investigated lack of oxygen *enhances* the former (Fig. 5-7). However, the basis of this effect is different in the obligate anaerobe *Paramonhystera* and in the three oxiphilic species tested.

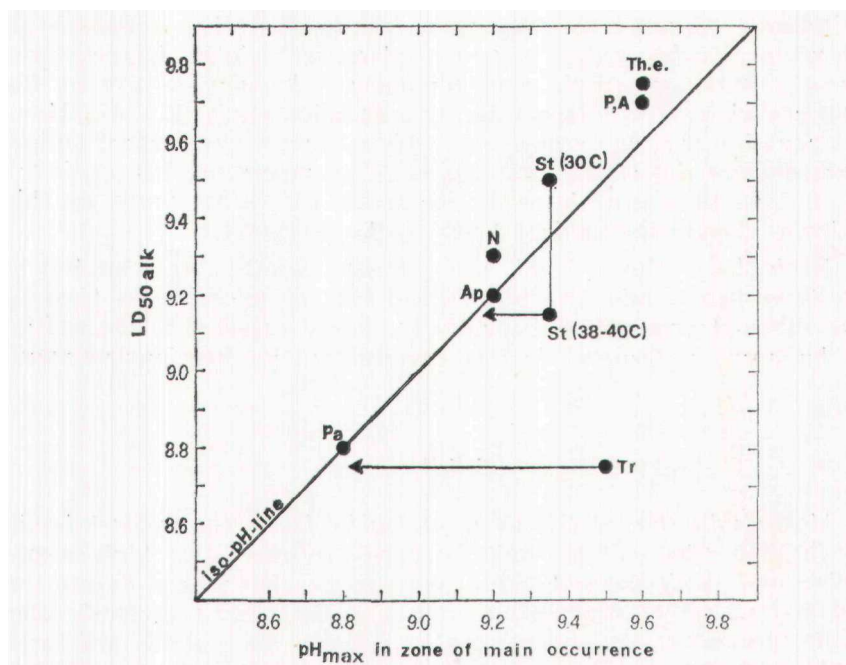


FIG. 8

Alkaline tolerance (expressed as $LD_{50 alk}$) plotted against pH measured in the zone of main occurrence of different meiofauna species from Tuckers Town Beach, Bermuda.

The distribution data are those of Fig. 2. In one case (St.), $LD_{50 alk}$ was determined at three experimental temperatures. Whenever a discrepancy occurs between pH tolerance and the pH-value measured in the habitat, this may be due to the fact that the determination of pH and that of vertical distribution took place on different days. In order to reach a zone in accordance with their alkaline tolerance, both *Tripyloides* (Tr) and *Steineria* (St) must carry out vertical movements on hot days. This requirement is indicated by arrows. Other abbreviations as in Fig. 2.

The oxiphilic species survive better because in the absence of oxygen they fall into a coma, in which state they resist lower pH-values better than if active and moving. As will be recalled, this was not the case with respect to temperature. *Paramonhystera*, on the other hand, does not fall into a coma and, in accordance with its behaviour under thermal stress, survives low pH-values better under anoxic than under normoxic conditions even when active.

Discrepancies between pH tolerance, vertical distribution and

measured pH values of the interstitial water may arise when vertical distribution and pH values are not determined on the same day. For example, the vertical distribution on which the data of Fig. 8 are based was determined on a fairly cool day, whereas pH measurements were made on the hottest days in order to get an idea of the extremes of pH fluctuations on the beach. Fig. 2 and 8 contain one major discrepancy, i.e. the distribution of *Tripyloides* n.sp. which, on the basis of its temperature and alkaline resistance, would not be expected to penetrate that far into the surface layers of the sediment. This suggests that *Tripyloides* is a particularly mobile species which may exploit the surface layers on cool days, avoiding them on hot days. A similar explanation can be given for the fact that, although on account of its fairly low alkaline tolerance at high temperatures ($LD_{50 \text{ alk}} = 9.15$), *Steineria* n.sp. should not be able to live in the upper cm where it was found during a zonation study (Fig. 4). However, zonation was determined on a day on which the surface temperature did not rise above 30°C and at this temperature $LD_{50 \text{ alk}}$ is 9.5 (Fig. 8) and thus just above the maximum pH values found on this particular day in the surface layer of the sediment.

Examples of this sort add stress to the fact that, with respect to high temperature and alkalinity, the limits of tolerance at least of some subtropical meiofauna species are finely adjusted to the spatial and temporal patterns of factors encountered in their environment.

Salinity

Most studies on salinity as an ecological factor for the meiofauna have been carried out in undersaturated sediments on high-energy beaches and above the water line on atidal beaches where, due to the combined effects of evaporation, rain and the mixing of freshwater runoffs, ground water and sea water, salinity fluctuations are large (see Jansson, 1971). To animals living in this kind of environment, the generalization expressed by Gray (1966) must apply that "interstitial species are euryhaline and well able to survive the conditions experienced in the field". It could not be otherwise. However, is it true that *all* interstitial species are euryhaline or would one expect to find more subtle adjustments to local conditions by meiofauna species living in different beaches or in different zones of one and the same beach? In accordance with the results of temperature- and pH-tolerance experiments, it may be predicted that species living on low-energy beaches or below the low-water line or in deeper sediment layers have lower salinity tolerances than species living on high-energy beaches, high above the water line and in surface layers of the sediment. Relationships of this kind are suggested by some experiments with animals from coarse substrates and atidal beaches in temperate areas. For example, the salinity tolerance of the low intertidal Gastrotrich *Turbanella hyalina* is less than that of the high intertidal Archiannelid *Protodrilus symbioticus*, occurring on the same beach (Boaden and Erwin, 1971). Another example is that of two species co-occurring in Baltic beaches, the Turbellarian *Coronhelmis lutheri* and the Harpacticoid *Parastenocaris phyllura*. The former

species is a proper interstitial form and has a wide salinity tolerance ranging from 2 to 28 p. 1000, the latter is confined to the ground water and tolerates salinity from 1 to 5 p. 1000 only (Jansson, 1968). Fenchel et al. (1967) reported a certain correspondence between the salinity regime of a beach in the Baltic and the fauna living in it. The backshore is characterized by low salinity and harbors some species (e.g. *Marionina praeclitelochaeta*) with low salinity preference; the middle shore is dominated by very euryhaline species (e.g. *Akteredilus monospermatus*) and, in the foreshore, euryhaline species or species with a preference for high salinity occur. The salinity preferences of the two Oligochaetes mentioned were also studied by Jansson (1962). However, as far as this group of animals is

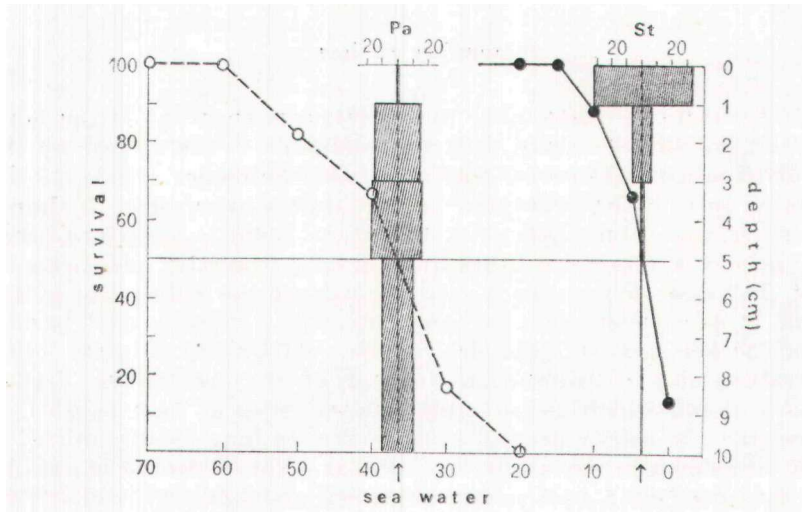


FIG. 9

Survival (left ordinate) of two nematodes, *Paramonhystra* n.sp. and *Steineria* n.sp., in diluted sea water (in percentage). Superimposed upon the survival curves are two columns illustrating the vertical distribution (right ordinate) of the two species. They are positioned in such a way that the center of each column coincides with the LD₅₀ value of the species it characterizes.

Conditions of tolerance experiments: 30°C, one hour exposure time. The width of the column represents the relative abundance of the species in each vertical zone. Each circle denotes mean values of 3-4 tolerance experiments with at least 20 specimens each.

cerned, one could argue that they are fairly recent immigrants from freshwater habitats and that their pattern of distribution on a beach does not reflect long-term adjustments to local conditions but rather the degree of their success in competing with marine immigrants.

In low-energy beaches and in water-saturated sediments, salinity fluctuations due to evaporation, rain and fresh-water influx from land are small and confined to the upper centimeters (Sanders et al., 1965; Johnson, 1967; Barnett, 1968). Heavy rain may drive the interstitial fauna down (Ganapati and Rao, 1962) but more often dilution of the pore water of the upper sediment layers is reported to have little effect on the fauna (Linke, 1939; Jansson, 1967b; Barnett, 1968). Since in saturated sediments even heavy rain does not affect the

salinity of the pore water below a depth of approximately 2 cm (Barnett, 1968), the question arises as to whether species living predominantly in deeper strata of the beach are more sensitive to dilution of the medium than inhabitants of the upper layers. That this is the case is illustrated by Fig. 9 which shows that in the surface species *Steineria* n.sp., LD₅₀ after one hour exposure to 30°C (the average temperature on rainy summer days at Bermuda) is about 4 p. 100 sea water, whereas in the lower-level forms, *Paramonhystera* n.sp. and *Apodopsyllus africanus* (the latter not shown in Fig. 9), it is between 35 and 40 p. 100 sea water. Thus again, a small difference in vertical distribution is reflected in a fairly large difference in range of tolerance.

A question of time

It is sometimes stated that "the tolerances observed in the laboratory do not always agree with the tolerance limits shown by the field distribution" (Jansson, 1968; see also Schlieper et al., 1952). This must be so if the time factor is not taken into account. It should cause no surprise, for example, that the ecological temperature range of an animal is more restricted than the experimental one, because, in the first case, temperature acts throughout the entire life of the animal, in the second one for only the short experimental period. One of the best known examples for the relationship between lethal temperature and exposure time is that of the freshwater Triclad *Crenobia alpina* which can tolerate temperatures as high as 25°C if they occur only briefly around midday and as long as the animal is able to cool down to approximately 10°C at night (Pattee et al., 1973). Thus the time factor, just as any other ecological factor, is of importance in determining the "ecological valence" (Kühnelt, 1955) of a species.

In some intertidal seaweed-inhabiting species of meiofauna, it was shown that the ability to tolerate anoxic conditions is closely

TABLE 1

Lethal temperature (LT₅₀) at three lengths of exposure, and differences of LT₅₀ (ΔT) between these time levels, for Nematodes and Harpacticoids from a low-energy beach in Bermuda. Time of measurement: August 1973 and 1974. All species were exposed to high temperatures in normoxic sea water, except *Paramonhystera* n.sp., which survived better under anoxic conditions.

Exposure time (hours)	LT ₅₀ (°C)			ΔT (°C)	
	1	5	10	1-5	1-10
<i>Theristus erectus</i>	41.7	40.4	37.8	1.3	3.9
<i>Steineria</i> n. sp.	—	42.1	—	—	—
<i>Psyllocamptus</i> n. sp.	43.4	41.5	—	1.9	—
<i>Amphiascoides subdebilis</i> ..					
<i>Apodopsyllus africanus</i>	38.4	36.5	35.4	1.9	3.0
<i>Tripyloides</i> n. sp.	40.7	38.5	36.5	2.2	4.2
<i>Nannolaimoides decoratus</i> ..	44.9	41.8	40.4	3.1	4.5
<i>Paramonhystera</i> n. sp. (anaerobic)	38.5	37.2	36.1	1.3	2.4

correlated with the duration of these conditions during low tide in the field (Wieser and Kanwisher, 1959). It may be assumed that, quite generally, the curves relating survival and exposure time must have features that signal adaptive responses of the species concerned. If, for example, the slope of the function relating LT_{50} and exposure time is flat, it may be predicted that the species is not subject to large

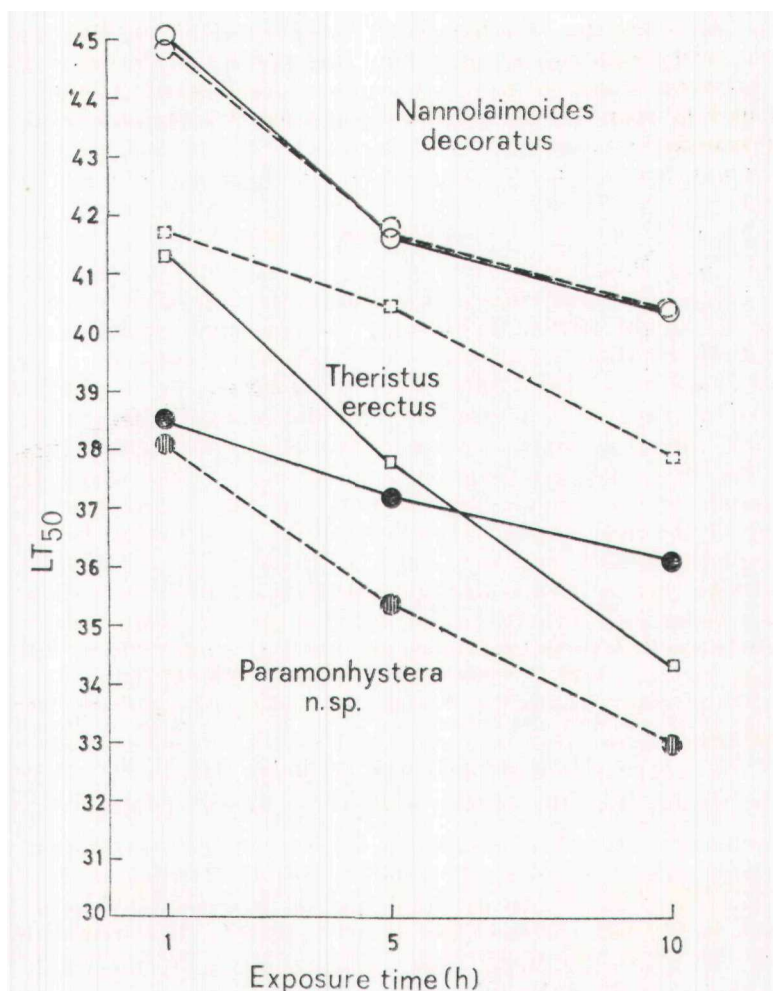


FIG. 10

Three response types of meiofauna species exposed to combination of high temperature and low pO_2 .

LT_{50} 's under oxic (broken lines) and anoxic (solid lines) conditions are plotted against exposure time (from Wieser et al., 1974).

temperature fluctuations in nature. This may be true of the anaerobic Nematode *Paramonhystera* n.sp. in which LT_{50} after 10 hours' (anoxic) exposure is only $2.4^{\circ}C$ lower than after 1 hour's exposure—the smallest difference in LT_{50} found in all the Bermuda species tested (Fig. 10 and Table 1). On the other hand, the largest differences in LT_{50} , and thus the steepest slopes in the LT_{50} : exposure time plot occurs

in two Nematodes, *Tripyloides* n.sp. and *Nannolaimoides decoratus*, which also show the greatest discrepancies between temperature tolerance and vertical distribution (Fig. 2 and 10).

These two Nematodes appear to belong to a group of species which is able to tolerate relatively high temperatures for a short time (for example, when low tide occurs around noon), avoiding longer spells by downward migration into the sediment. In this respect, they resemble the freshwater Triclad *Crenobia alpina* mentioned above. The function relating LT_{50} and exposure time must approach, at "infinite time" a value which is equivalent to the LT_{50} for the whole life cycle of the species. According to Hopper et al. (1973), this critical temperature, below which a species is able to complete its whole life cycle, is expected to lie between 33 and 35°C in a

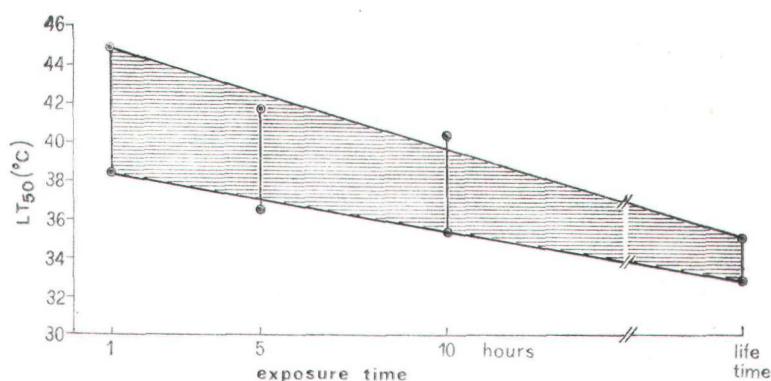


FIG. 11

The relationship between temperature tolerance (expressed as LT_{50} °C) and exposure time in some subtropical meiofauna species.

The ranges of LT_{50} at the exposure times of one, five and ten hours include all the species studied at Bermuda (see Table 1). The range at the «life time» value is that below which some Nematodes from a subtropical mangrove habitat were found to be able to complete their whole life cycle (Hopper et al., 1973).

number of subtropical meiofauna species. After an exposure time of 10 hours, the LT_{50} of all Bermuda species tested lies within a range of 35.4 and 40.4°C. An extrapolation of this relationship to "infinite time" would fall not far short of 33-35°C (Fig. 11), establishing this range as a fairly general upper thermal limit for the completion of life cycles in the subtropical meiofauna.

Tidal and diurnal migrations

Tolerance experiments discussed in the present paper and by Wieser et al. (1974) suggest that some meiofauna species adjust their vertical distribution to the fluctuating conditions of the environment. For example, species with relatively low alkaline- or high temperature-tolerance appear to move into the upper layers of the sediment on cooler days (*Apodopsyllus africanus*, *Tripyloides* n.sp., *Steineria* n.sp.). Conversely, one Nematode species, *Nannolaimoides decoratus*, was found to have a much higher temperature tolerance

than would have been expected on the basis of its vertical distribution (Fig. 2). In this case, one could resort to the historical-evolutionary explanation that *N. decoratus* is a tropical species that only recently has moved into this more northern habitat to which it has not yet adjusted fully. On the other hand, one could regard the discrepancy between vertical distribution and temperature tolerance as a "potential" which allows this species to migrate into the surface layers of the sediment, on particularly hot days when other species are driven into deeper layers.

Vertical migrations of marine meiofauna species were reported some 70 years ago by Bohn (1903) and Gamble and Keeble (1904), and again several times in recent years (Renaud-Debyser, 1963; Boaden, 1968; Boaden and Platt, 1971; Rieger and Ott, 1971; Westheide, 1966, 1972; Schmidt, 1968; Schmidt and Westheide, 1971 and others).

On high-energy beaches and in unsaturated sediments, the interstitial fauna has to follow the fluctuations of pore water with the tides (see, e.g. Jansson, 1966; Westheide, 1972). In saturated sediments on sheltered beaches, however, the vertical movements of the sediment fauna are more complex. There is always one group of species that does not move with the tide or photoperiod. These are mainly animals that are prevented from downward movements by their inability to tolerate reduced oxygen conditions for even a short time. In compensation, they have to be able to tolerate high temperature, alkaline conditions and reduced salinity during rainfall. To this group belong quite a few Harpacticoid Copepods (Barnett, 1968; Harris, 1972; Wieser et al., 1974) and Nematodes, e.g. *Theristus erectus* and *Steineria* n.sp., discussed in the present paper.

Amongst the migrating species, two groups may be distinguished: one that moves upwards and another one that moves downwards with approaching low tide (Boaden and Platt, 1971; Rieger and Ott, 1971). Examples for the former are the oldest known tidal migrant, the Turbellarian *Convoluta roscoffiensis* (Bohn, 1903; Gamble and Keeble, 1904), Nematodes (e.g. *Microlaimus criminalis* in the Adriatic: Rieger and Ott, 1971), and a few Copepods (Boaden and Platt, 1971; *Apodopsyllus africanus*, as discussed by Wieser et al., 1974 and in the present paper). A large group of species leaves the superficial layers as low tide approaches, amongst them Nematodes and Turbellarians (Rieger and Ott, 1971; Boaden and Platt, 1971) and, the best-documented case, the Polychaete *Hesionides arenaria* on North Sea beaches (Westheide, 1972). These vertical movements are controlled by directing stimuli, amongst which the following have been discussed: oxygen (Gray, 1966; Jansson, 1966, 1967c; Boaden and Erwin, 1971; Dinet, 1972), water turbulence and currents (Boaden, 1963, 1968), light (Gray, 1966, 1968; Jansson, 1968), gravity (Gray, 1968), temperature (Gray, 1965, 1966), salinity (Jansson, 1968; Pollock, 1971) and tidal periodicity (Boaden, 1963). The data presented in this review suggest that limiting factors like pO_2 , high temperature and alkalinity should be of the greatest importance in controlling the vertical migrations of the sediment fauna. What these stimuli achieve is to direct the animals into zones in which they find optimum conditions for feeding, metabolism and reproduction.

For example, many species moving up to the surface of the sediment at low tide must be considered to do so because of the presence there of photosynthesizing algae. Vertical movements with the tides are well known in Diatoms (Taylor, 1964; Palmer and Round, 1967) and it is suggested that quite a few species of meiofauna

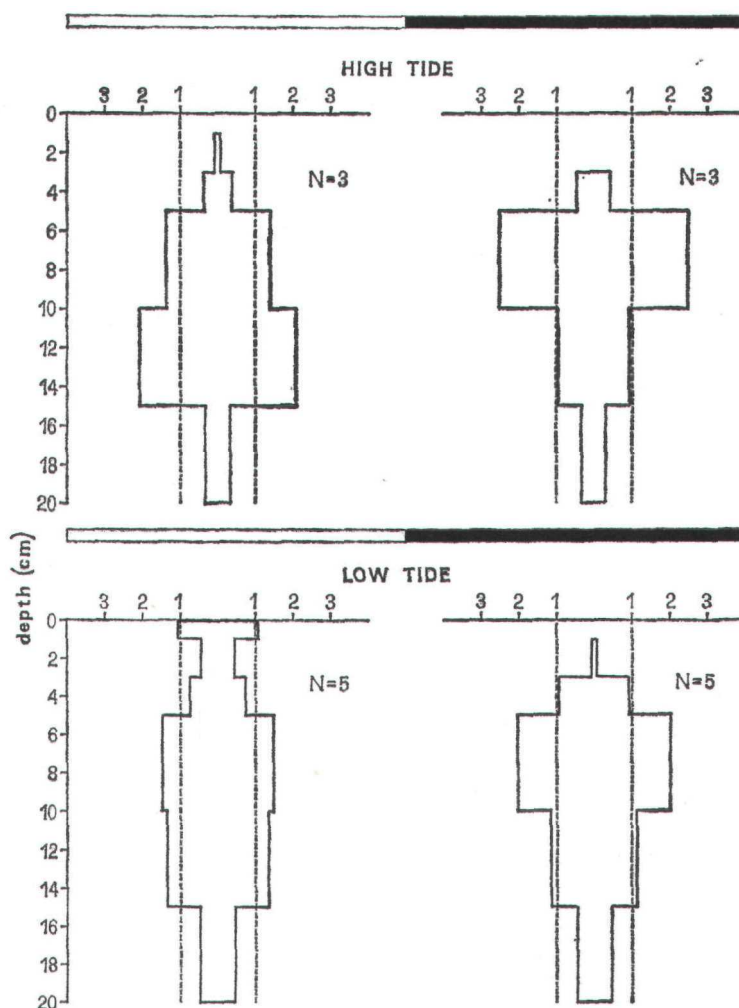


FIG. 12

Dynamics of vertical distribution of *Apodopsyllus africanus* at Tuckers Town Beach, Bermuda.

Different combinations of tidal and diurnal stages are represented. Black bars indicate night time. The width of the columns indicates the relative abundance of the species in multiples of the average density throughout the core.

migrate in synchrony with the Diatoms because they feed on them or on attached microorganisms. This suggestion has also been advanced by Boaden and Platt (1971). Such a dependence of animals of photosynthesizing algae is the more likely if it can be shown that the animals move to the surface when low water occurs during the day but not during the night. A combination of diurnal and tidal

rhythms in directing the vertical movements of Diatoms has been described by Palmer and Round (1967) and it also seems to determine the movements of the Harpacticoid *Apodopsyllus africanus* on Tuckers Town Beach in Bermuda (Fig. 12 and Gnaiger, unpublished). Other types of vertical movements of the meiofauna in intertidal sediments must be determined by the distribution of bacteria and yeasts (Westheide, 1968; Schmidt and Westheide, 1971). It is most likely that some members of the meiofauna are better adjusted metabolically to exploit these food sources under combination of environmental factors prevailing at high tide, others under conditions prevailing at low tide.

Another reason why the inhabitants of lower and anoxic strata of sediments move upwards during low tide may be that they are facultative anoxibionts that, after a critical length of time, have to repay their oxygen debt or, in some other way, recharge their oxidative potential. Again, *Apodopsyllus africanus* may be a case in point since its temperature tolerance is not affected by anoxia up to an exposure time of five hours, whereas it is harmed when exposed to anoxic water for 10 hours and longer (Wieser et al., 1974).

Finally, the synchronization of vertical movements with tidal or diurnal cycles may be determined by the contingencies of reproduction which require the members of heterosexual species to form aggregation during the reproductive period. This mechanism has been described in the Archiannelid *Trilobodrilus heideri* by Boaden (1963).

Conclusion

In the terms of modern physiology, the study of the survival of organisms under environmental stress is not considered an exciting field of study. However, in a group of animals as little known ecologically and physiologically as the meiofauna of marine sediments, it has its merits. Investigations into the relationship between the distribution of factors and fauna on the one hand, and the ranges of tolerance of the animals on the other, may help to answer the following two questions:

- 1) what are the factors limiting the vertical and horizontal distribution of the major faunal components of a habitat? Knowledge of this sort could be used for predicting faunal changes as a consequence of changes occurring in the habitat as, for example, through pollution;
- 2) is there a relationship between the degree to which the major faunal components of a habitat fit the environment and the overall diversity or stability of the habitat? If such a relationship was proved, tolerance limits could be used for drawing conclusions as to the ecology and history of a given habitat. This would be particularly useful in comparing localities in different climatic regions of the world.

The paucity of data does not permit the formulation of general rules but the Bermuda study at least provides a point of reference for future studies. The main conclusion to be drawn, on the strength of the experimental and field data discussed in this review, is that, in most species, the tolerance limits for high temperature, alkaline

conditions and low pO_2 are very close to the extremes for these factors occurring in the preferred habitat of the species. The degree of correspondence is illustrated best by the fact that a difference in vertical distribution of a few centimeters—sometimes even of millimeters—is usually reflected in a striking difference in the ranges of tolerance for high temperature, alkalinity or lack of oxygen. The correspondence between tolerance for, and distribution of, salinity may be equally close (see Jansson, 1968) but is less well documented. On the other hand, neither the degree of acidity nor the range of low temperature of the pore water appear to be factors limiting the distribution of the subtropical meiofauna.

From this, it can be predicted that any change in the environment that leads to changes in the oxygen regime or in the upper limits of temperature and alkalinity—like the introduction of cooling water from a power plant or of effluents from a pulp factory—can radically alter the composition of the fauna. This conclusion does not take into account the possibility of acclimatization to new environmental conditions: very little is known concerning such a faculty in the marine meiofauna. Short-term acclimatization to different temperatures did not affect the respiratory rate of the interstitial Nematode *Theristus erectus* (Wieser et al., 1974) and Jansson (1968) was unable to alter the salinity tolerance of the Oligochaete *Akteredrilus monospermatecus* by eight days acclimatization to a different salinity regime. On the other hand, the ability of a few inhabitants of brackish water sediments to adapt to changes in salinity and temperature was discussed by Arndt (1973). Indeed, it would have been surprising if no representative of the meiofauna showed any adaptive responses to long-term changes of, at least, some of the limiting ecological factors.

The second argument of a more general nature concerns the relationship between tolerance ranges of the meiofauna and the degree of diversity and stability of their environment. As stated by Gray (1974, p. 254): "Littoral sediments are unpredictable eurytopic environments and have reduced diversity because unpredictability overrides structural complexity as the major factor controlling diversity". However, within this type of habitat, the low-energy beaches, particularly those in climatic regions with narrow ranges of environmental factors, ought to be characterized by higher predictability, stability and faunal diversity than high energy beaches in regions with wide ranges of environmental factors. For example, Ott (1972) concluded that diversity of the Nematode fauna from deposits on a North Carolina beach was inversely related to *in situ* temperature ranges (see also Gray, 1974).

The combination of high stability and diversity should result in an increased subdivision of the habitat into microhabitats or niches, each being occupied by one species. It is a plausible speculation that, in such a habitat, the majority of species would be better adjusted to, and fit better into, the specific pattern of environmental factors characteristic of each microhabitat than the occupants of a low-stability low-diversity type of habitat. In consequence, the tolerance ranges of the better-adjusted species should fit more closely the ranges of ecological factors measured in their habitats than those of the less

well adjusted species. This would agree, e.g. with the contention that tropical species live closer to their upper thermal limit than forms from higher latitudes (Gonzalez, 1974; see also Mayer, 1914; Naylor, 1965). Of course, the ecophysiological distinction between stable and unstable habitats would not hold in those cases in which an unstable habitat is subjected to the influence of one or several extreme environmental factors which dominate the survival prospects of the organisms living in it.

No equivocal data are available for testing the hypothesis but the Bermuda study, at least, yielded results that provide an impressive example of close correspondence between biological and ecological limits as far as high temperature, alkalinity, pO_2 and perhaps even salinity are concerned. It remains to be seen whether, in habitats of lower stability and heterogeneity, the degree of correspondence between these variables is reduced. If so, data concerning the resistance of the meiofauna may provide the basis for conclusions as to the general ecological structure of marine sediments.

Acknowledgments

The original research referred to in this review was carried out in the course of a research project on the ecophysiology of the marine meiofauna at the Bermuda Biological Station for Research in the summers of 1973 and 1974. This project was supported by the « Fonds zur Förderung der wissenschaftlichen Forschung in Österreich », project no. 1852, and by a special grant of the Ministry of Education of Austria. The cooperation of the following friends and scientists is acknowledged: Jörg Ott, Fritz Schiemer, Erich Gnaiger and Gernot Bretschko. Thanks are also due to the Director, Dr. W. Sterrer, and to the staff of the Bermuda Biological Station who helped us in every way during our visits. Erich Gnaiger was also the recipient of an Exon fellowship, managed by the Bermuda Biological Station, which permitted him to extend his work at this Institution.

Summary

An analysis of the heterogeneity of marine sediments can be carried out by employing various strategies. The following may be mentioned:

- measurement of physico-chemical variables;
- recording of spatial and temporal distribution of organisms living in the sediments (microorganisms, meiofauna);
- experimental investigation of the responses to environmental stimuli of micro- and meio-organisms.

The last-mentioned—ecophysiological—approach is the least developed but offers the greatest promise. Since shallow water marine sediments represent an ecosystem of great antiquity and diversity it may be assumed that each of the multitude of species living in it is adapted not only to the range of factorial combinations prevailing in the whole ecosystem but also to the specific set of factors characteristic for the micro-niche in which the species carries out its life cycle. In this paper those relations between organisms and marine sediments will be reviewed which are reflected in the survival ranges of meiofauna species. Their small size and low powers of locomotion may prove these animals to be ideal tools for probing an environment which because of its spatial and temporal heterogeneity cannot be described adequately on the basis of a few measurements of physical and chemical variables. In particular the vertical distribution of meiofauna species will be matched against their resistance to temperature, pO_2 , pH and salinity, as well as to combinations of these factors. The main conclusion that can be drawn on the basis of as yet very few data is that at least in most inhabitants of a subtropical beach the tolerance limits for high temperature, alkaline conditions and low pO_2 are very close to the extremes for these factors occurring in the preferred zone of the species. The degree of correspondence is illustrated best by the fact that a difference in vertical distribution of a few centimeters, sometimes even of millimeters, is usually reflected in a striking

difference in the ranges of tolerance for high temperature, alkalinity, or lack of oxygen. The correspondence between tolerance for, and distribution of, salinity may be equally close but is less well documented. On the other hand, neither the degree of acidity nor the range of low temperature of the pore water appear to be factors limiting the distribution of the subtropical meiofauna.

A more detailed knowledge of the relationship between the distribution of factors and fauna on the one hand, and the ranges of tolerance of the animals on the other, should be useful in predicting faunal changes as a consequence of changes occurring in the habitat, as for example, through pollution. Furthermore, the degree to which the major faunal components of a habitat fit the environment may be indicative of the overall diversity and stability of the habitat in question.

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