

AN ECOPHYSIOLOGICAL APPROACH TO THE  
MICRODISTRIBUTION OF MEIOBENTHIC  
OLIGOCHAETA. I. PHALLODRILUS  
MONOSPERMATHECUS (KNÖLLNER)  
(TUBIFICIDAE) FROM A SUBTROPICAL  
BEACH AT BERMUDA\*

Olav Giere

*Zoological Institute and Zoological Museum, University of Hamburg,  
Martin-Luther-King-Platz 3, 2000 Hamburg 13, Fed. Rep. Germany*

ABSTRACT

Phallodrilus monospermathecus from a Bermuda beach showed a distinctly inhomogenous distribution due to dense aggregations of worms in the subsurface layers of the high-water line, whereas the lenitic eulittoral sand flats were only scarcely populated. The abiotic factor system in the various sample sites and layers was analyzed using mainly electrometrical in-situ methods. In order to find out the ecophysiological background of this distributional pattern, the tolerance of the worms to temperature, salinity, alkalinity, oxygen supply, and combinations of these parameters, was studied.

Results show that Ph. monospermathecus is extremely tolerant to each factor per se, even if it exceeds the naturally occurring range. However, rigorous parameter combinations often acted as multiple stressors and reduced survival time of the animals markedly. Judging from these experiments, the microdistribution in the field can be explained by restriction to layers with moderate temperatures and relatively stable salinity, by preference for well oxygenated sand and avoidance of unusually high alkalinity.

These studies represent the first part of an investigation comparing ecological conditions for meiobenthic oligochaetes in different climates.

INTRODUCTION

Marine oligochaetes from eulittoral beaches exhibit a markedly inhomogenous distributional pattern (Jansson 1962, 1968 ; Giere 1970, 1971, 1973; Lassère 1971, 1975). The complicated interaction of abiotic ecological parameters on the species distribution can be elucidated by ecophysiological experiments which achieve a more general aspect if conspecific populations with different environmental background are studied. The interstitial tubificid Ph. monospermathecus is common both in temperate European as well as in the subtropical to tropical beaches of Ber-

---

\*Contribution no. 725 from the Bermuda Biological Station

muda, and, therefore, is an apt representative for these problems. Thus, it is hoped to get more information about the divergences in meiobenthic ecosystems from different climates, and also, to estimate the range by which a meiofauna species shifts its physiological capacity to adapt to different ecological situations.

#### MATERIAL AND METHODS

During two stays at the Bermuda Biological Station I had the occasion to study the species in a shallow tidal cove. This report is the first part of a comparative investigation to be later completed by similar studies on Baltic and North Sea shores. The Bermuda work was connected with a research program on the ecophysiology of meiofauna in a subtropical beach initiated by Wieser (Wieser et al. 1974; Wieser 1975).

The investigated beach consisted of rather uniform calcareous sand both in the slope (about 6 m wide) and in the shallow intertidal flat (Fig. 1). Average grain size was 250  $\mu\text{m}$ . Exposure to atmosphere was much influenced by a sand bar which extended into a slightly elevated southwestern part. Especially on the low-lying northeastern part of the cove ("sand flat"), many puddles of highly concentrated sea water were developed during ebb-tide. More physiographical details of Tucker's Town Cove will be given as part of the results (see also Wieser et al. 1974; Wieser 1975; Farris 1975; Gnaiger 1976).

10 cm<sup>2</sup> deep sediment cores were taken with a perspex corer of 50 cm<sup>2</sup> surface area. From this the oligochaetes were quantitatively extracted by elutriation in subsamples of 50 to 100 cm<sup>3</sup>. Temperature, alkalinity and redox-potential were recorded with thin electrodes inserted into the different layers of the sediment. Salinity was measured by a refractometer. In addition to this, representative samples were analysed for grain size composition. The tolerance experiments were conducted with 20 specimens each in small vials kept in water baths at different temperatures. Salinity gradients were established by adding to normal, filtered sea water (35 ‰ S) rain water or sea salt, increased alkalinity by addition of NaOH. Fully oxygenated (normoxic) sea water was attained by intensive aeration, oxygen-deficient (hypoxic) sea water (7 % saturation) by flushing with nitrogen under continuous control of pH-values (Wieser et al. 1975).

Tolerance is defined as lethal time for 50 % or 100 % of the animals tested (LT 50, 100). Differences in survival times ( $\Delta\text{LT}$ ) are in most cases based on the averaged results of replicate experiments. The worms were regarded as dead when no movement was detected after gentle shaking of the vials and additional exposure to light stimuli. Experiments were usually discontinued after 12 h, in some cases after 24 h, in order to rule out undesirable secondary effects due to accumulation of metabolic wastes and lack of food in the vials. Thus, the results account only for short-term reactions.

RESULTSField Studies on Distribution of Factors and Fauna

Based on numerous vertical cores along a grid of sampling stations, a characteristic pattern of abiotic factors and oligochaete fauna became apparent (Fig. 1 and 2):

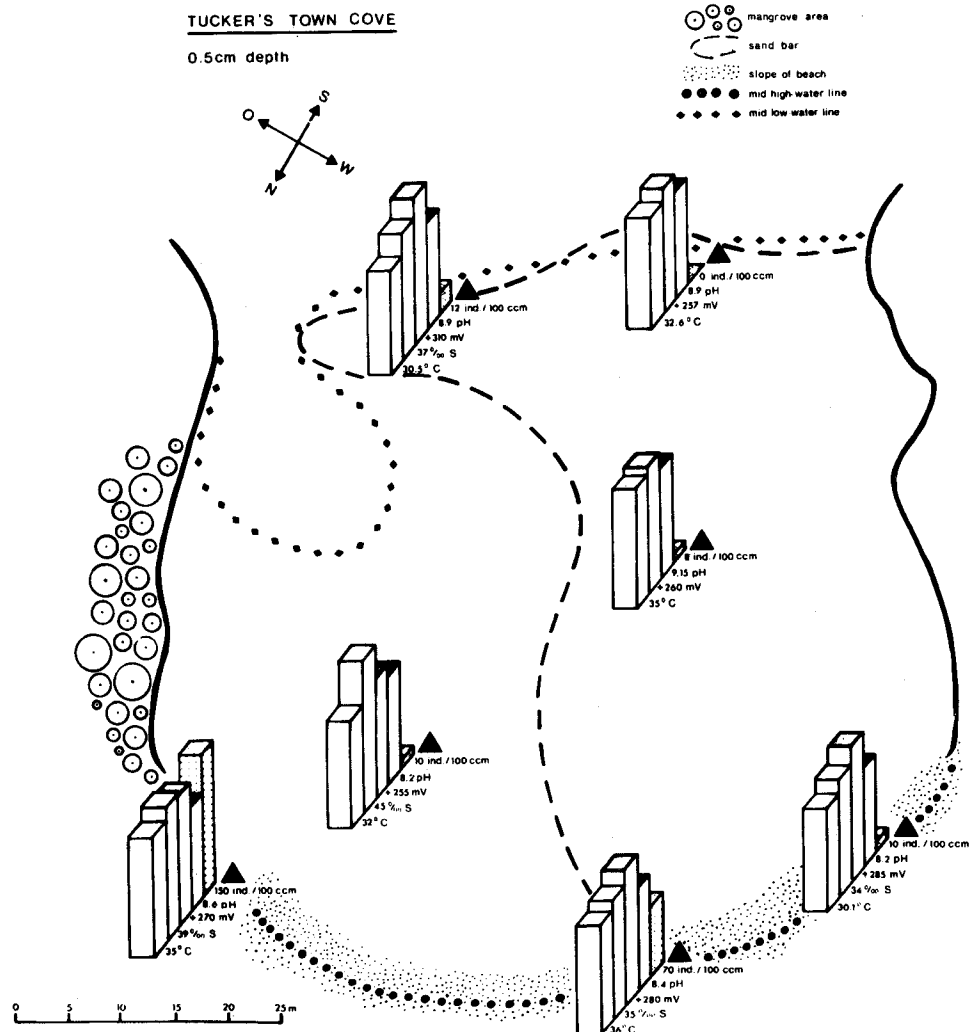


Fig. 1. Distribution of abiotic factors and Phallo-drilus monospermathecus in surface sediments

In the superficial sediment layer (0.5 cm depth, Fig. 1) the abiotic system at ebb-tide was fairly similar both in the sand flat, the sand bar and the high-water line: a combination of

markedly high pH-values (mostly exceeding 9.0, in some recordings up to 9.5; see Wieser et al. 1974; Gnaiger 1976) with relatively high salinities (35‰ to 40‰S, sometimes up to 45‰S), warm temperatures (30° to 35°C) and good oxygen supply (Eh-values about +250 mV). The slope of the beach differed from the tidal reaches mainly in having lower pH-values, probably due to less assimilation activity of diatoms in the dryer surface sediments.

However, the distribution of *Ph. monospermathecus* displayed a distinct difference between slope and lower tidal areas: where-

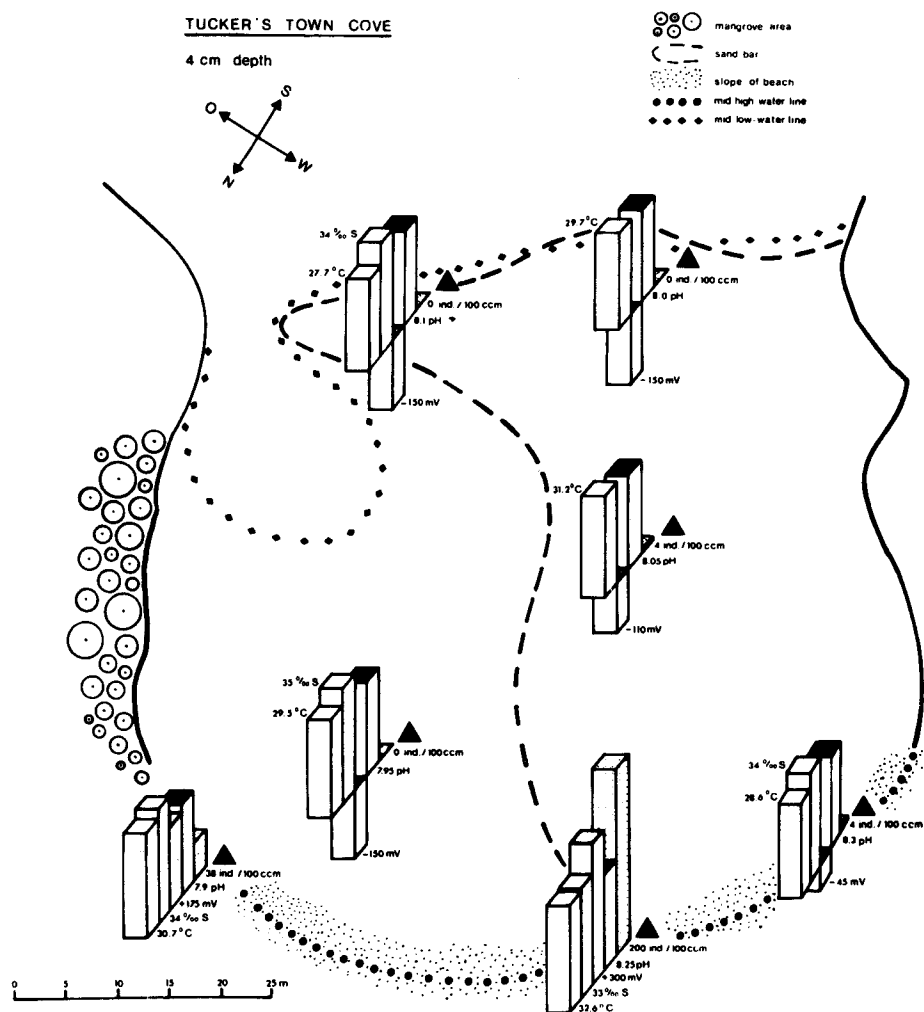


Fig. 2. Distribution of abiotic factors and *Phallo-drilus monospermathecus* in 4 cm depth

as most parts of the high-water line were inhabited by dense populations (often  $>100$  ind./ $100\text{ cm}^2$ ), the mid- and low-tide samples contained very poor numbers of this tubificid (0-10 ind./ $100\text{ cm}^2$ ). Also in the southwestern corner of the high-water area, populations were similarly small.

Examining the situation in a depth of 4 cm (Fig. 2), marked differences between the lower flats and the higher slope of the cove became visible both in the abiotic system and in the oligochaete distribution. In this depth, the almost horizontal mid-tide and low-tide parts (decline about 20 cm per 70 m), being very smoothly overflowed by the tidal currents, proved to be totally anoxic (greyish colour, Eh-values mostly appr. -50 mV) and contained high concentrations of  $\text{H}_2\text{S}$ . The same was valid for the exceptional southwestern site of the high-water line where a high input of decaying plant material combined with a diminishing slope resulted in a negative redox-potential.

In clear contrast were most of the slope stations. Here, the tidal waves percolate at high-water: good to sufficient oxygen conditions (positive Eh-values) throughout the upper 8 to 10 cm despite a rich content of organic debris. The generally lower and fairly stable overall range of the other abiotic factors evidently reflected the subsurface position of the layers examined. Salinity proved to be fairly consistent throughout the sediment column due to a neglectable influx of fresh water. Temperature regularly decreased with depth in a smooth gradient of not more than  $3^\circ$  to  $4^\circ\text{C}$ . Reduction of alkalinity corresponded with the diminishing assimilation of diatoms.

The response of *Ph. monospermathecus* to the abiotic situation in the deeper horizons (Fig. 2) is an almost complete avoidance of the lower tidal areas. This is in striking contrast to the rich aggregations of worms in the aerated subsurface layers along the high-water line (up to 200 ind./ $100\text{ cm}^2$ ). Only in the southwestern sample, where sediment layering was basically identical with that of the flat, tubificids were rare.

#### Resistance Experiments

The experimental work should answer two main questions: 1) What impact have combined (stress-)factors compared to that of one single stressor? 2) Does a specific factor dominate other parameters in mainly determining the animals' distribution?

To start with temperature (Fig. 3), *Ph. monospermathecus* showed an extremely wide tolerance range. In normal oxygen-, salinity- and alkalinity-conditions, it seemed to cover a span from unnaturally low  $6^\circ\text{C}$  up to  $30^\circ\text{C}$  without any apparent impairment. Below  $30^\circ\text{C}$ , hypoxia had little effect on the viability of the animals (see p. 7 and Table 1). Even beyond  $35^\circ\text{C}$ , the decrease in survival rates was not very distinct before approaching the  $39^\circ\text{C}$ -mark which evidently was the upper thermal resistance limit even for short-term exposure.  $40^\circ\text{C}$  caused severe damage and almost instantaneous death.

In order to test the combined effect of temperature with other abiotic parameters, salinity- and pH-conditions were modulated in further experiments. The extremely high tolerance of this species even in a multifactorial stress situation was emphasized by the fact that up to  $30^\circ\text{C}$  *Ph. monospermathecus* kept its full viability during almost the entire experimental time, even in

water of adverse salinity- or pH-range if oxygen was present (Fig. 3). Beyond 35°C, the combined effect of relatively high temperature and low salinity, a situation well possible after heavy showers, resulted in a rapid decrease of life time and terminated at 39°C in LT-values of approximately 1 h only (solid triangles). High temperature combined with high alkalinity (pH 9.5), often to be recorded after long insolation at ebb-tide (Gnaiger 1976), caused a similarly high mortality even at normal salinities and had an even aggravated impact in the warm, highly

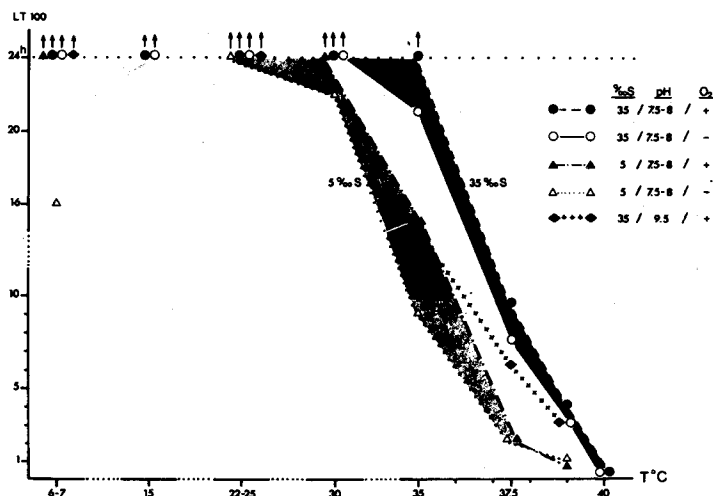


Fig. 3. Thermal resistance of *Ph. monospermathecus* from Bermuda at different environmental conditions

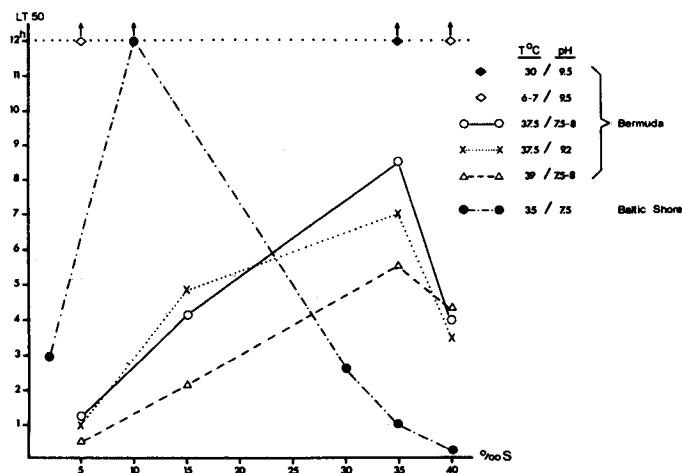


Fig. 4. Salinity tolerance of *Ph. monospermathecus* in normoxic water of varying temperature and alkalinity

saline water of the surface layers at ebb-tide exposed to the sun (diamonds). Finally, extremely low temperatures plus oxygen deficiency and low salinity reduced life time too (open triangles). But, whatever factor combination was tested, the upper thermal threshold remained rather constantly at 39°C as in the one-stressor experiment. Hypoxic conditions caused only a slightly more pronounced decline in survival times (greyish and black fields in Fig. 3.; see Table 1).

Plotted against salinity gradients, Fig. 4 shows *Ph. monospermathecus* again to be not severely affected by just one stress factor (e.g. pH 9.5, solid diamond) if temperature stayed at 30°C. Still at 6°C, the survival rate was amazing, since even extreme salinities like 5 ‰ and 40 ‰S did not heavily deteriorate viability (open diamonds). However, beyond the 30°- to 32°C-threshold, even good oxygen supply and normal pH conditions could not rule out a loss in viability. At 37.5°C, this reduction was lowest in natural sea water of 35 ‰S, increased in the range of 15 ‰ to 5 ‰S, and heaviest approaching 40 ‰S (open circles). Correspondingly, at higher alkalinities (pH 9.2, crosses) or temperatures (39°C, triangles), the deterioration of survival was even more pronounced.

Compiling the impact of oxygen within this factor pattern, a decrease of LT-times due to oxygen deficiency was particularly noticeable in a range slightly beyond "normal" environmental conditions (i.e. 30°-35°C; 35 ‰S; 8.0-8.5 pH). Near the upper threshold of viability for each single factor (i.e. 39°C; about 40 ‰S; 9.5 pH), life-spans uniformly approached to minutes or some few hours (Fig. 3 and Table 1). These results on the affect of hypoxia, however, are still tentative and need further examination and differentiation.

TABLE 1 Survival of *Ph. monospermathecus* in Different Oxygen Concentrations

|                | temp. | normoxic | hypoxic | LT 100  |
|----------------|-------|----------|---------|---------|
| pH 7.5-8/35 ‰S | 30°   | 24 h     | 24 h    | -       |
|                | 35°   | 24 h     | 21 h    | 3 h     |
|                | 37.5° | 9 h 30'  | 7 h 30' | 2 h     |
|                | 39°   | 4 h 45'  | 3 h 15' | 1 h 30' |
|                | 40°   | 15'-20'  | 10'-20' | 5'-10'  |
| pH 9.5/35 ‰S   | 39°   | 2 h      | 1 h 20' | 40'     |

#### DISCUSSION

Coincident occurrence of several abiotic stressors seems to be much more pronounced in many subtropical and tropical low-energy-beaches than in boreal shores. Higher temperatures accelerate development of oxygen deficiency and heighten alkalinity. Increased evaporation augments salinity, and leads to water losses in the sediment. Sudden heavy showers dilute the sediment water at ebb-tide drastically. In these situations, survival of *Ph. monospermathecus* will be restricted to a much narrower range of resistance than evident from one-stressor-experiments. This explains the distinct distributional pattern of the species in

Bermuda which can well be linked together with the ecophysiological short-term reactions revealed in the experiments (Fig. 5).<sup>1</sup>

Though in all areas of the beach the surface layers harboured basically the same positive and negative factors, their influence on the settlement of *Ph. monospermathecus* is different. In the mid- and low-tide regions of the cove, the worms in the uppermost layers cannot avoid the adverse impact of extreme factors which prevails the positive moment of good oxygen supply.

#### TUCKER'S TOWN COVE

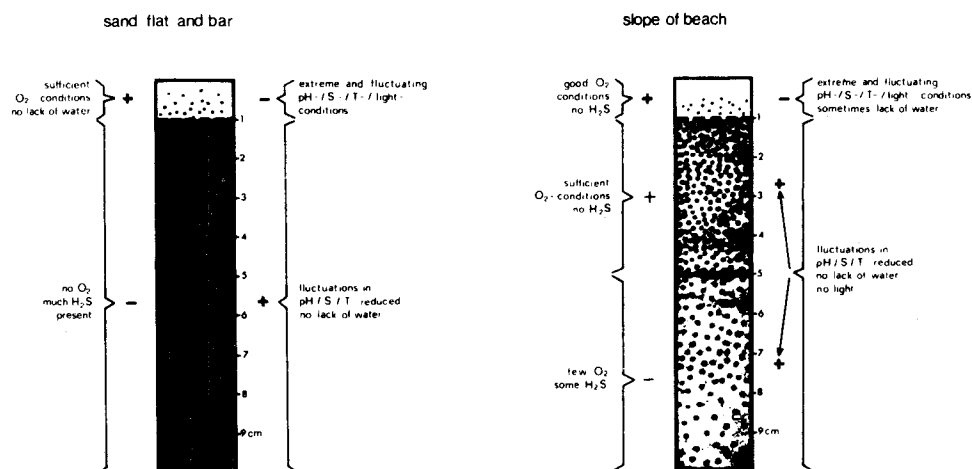


Fig. 5. Schematic interpretation of the factor system determining distribution of *Ph. monospermathecus* on a subtropical beach of Bermuda

In the deeper horizons, lack of oxygen and high concentrations of poisonous  $H_2S$  rule out every other possible favourable influence and strictly limit any vertical extension of the population. Thus, in the intertidal reaches and in the southwestern part of the slope, occurrence is restricted to the uppermost layers and, due to the suboptimal conditions here (multiple-stressor situation), few worms are to be found. In the better aerated slope, the subsurface layers give shelter from the rigorous fluctuations of most abiotic factors. Since, here, the worms are still sufficiently supplied with oxygen, they can readily utilize the richly accumulated organic matter.

A limiting factor, characteristic for tropical and subtropical calcareous sands and to that extent unknown in the mostly siliceous beaches of boreal regions, is high alkalinity of the surface sediments which, at summer conditions, regularly exceeds the threshold of good viability for *Ph. monospermathecus* (Fig. 4). The alkalinity to be one of the most important abiotic factors in the Bermuda beaches was already stated by Wieser (1975) for other animals. Even in temperate areas, v. Oertzen and Schlungbaum (1972) and Theede (1973) found a close correlation

between high alkalinity and reduced resistance to oxygen deficiency.

It can be interpreted as an additional adaptation to overcome sudden changes in the abiotic environment that Ph. monospermathecus has a well developed "immediate response" reaction (Kinne 1970) to physiological shocks. This was found already by Jansson (1962) for Baltic populations and in the Bermuda-experiments it was indicated by similar survival times independent of previous acclimation (24 h).

However, if acclimation acts for longer periods than seem to apply here, it is still possible that Ph. monospermathecus exhibits also a "meaningful" reaction which would correspond with the results of Kähler (1970). The basis for this potential would be a well developed ability of osmoregulation, found also in other marine interstitial oligochaetes (Lassère 1969, 1971, 1975; Tynen 1969) and indicated by the effective regulation of body volume observed in my experiments.

The resistance data confirm the euryoecous nature of Ph. monospermathecus to be expected from a cosmopolitan species (Tynen 1969). But they also reveal that the Bermuda-animals had a maximal resistance to temperature and alkalinity variations at 35 ‰ which is about the average salinity in their natural environment, whereas at low salinities survival in warm weather was reduced (Fig. 4). In contrast to this, results from the Baltic shore showed those populations to have optimal resistance just in the mesohaline range (about 10 ‰), their original habitat salinity and a substantially lower survival rate at 35 ‰ (Fig. 4). Since maximal resistance and optimal range usually are closely correlated (Kinne 1964, 1970, 1971), the two populations probably have a diverse preferential behaviour for salinity. The same seems valid for temperature, since the resistance of Baltic populations at 35°C was very reduced, even in their optimal salinity, whereas the Bermuda-animals at this temperature and in their usual salinity range showed no impairment at all. On the other hand, it was not before 6°C that temperature acted as an additional stressor. Survival at these very low temperatures (which the worms will never encounter in their subtropical environment) means that at its lower range thermal resistance is almost the same as in the boreal populations (see also Jansson 1962, 1967, 1968).

The indications of different preference ranges between populations of diverse environmental background do not necessarily contradict Jansson's data (1962, 1968) which signified a stable preference of Ph. monospermathecus for low salinities despite a one week's treatment in high salinity. It is possible (Kinne 1964, 1970), that animals possibly attain only the initial phase of stabilization during this short period of acclimation which might not be sufficient for a shift of their preference behaviour. However, the population on Bermuda certainly could establish by long-term isolation a steady state (Kinne op. cit.) and has acclimated to the subtropical conditions. This would not support the general ranking of Ph. monospermathecus as a brackish-water species, as suggested by Pfannkuche (1974).

### CONCLUSIONS

The results for Ph. monospermathecus corroborate the generalized statement of Wieser (1975) for other meiofauna members from subtropical regions: the upper temperature tolerance is closely adjusted to the highest temperature to be expected in the field. As with temperature, tolerance in general was very wide if just one parameter acted as stressor. But, apparently, there is no single master-factor predominantly responsible for the viability of the worms. It is the interdependent and interacting effect of several main parameters aggravated by subtropical conditions which confines the animals' distribution. Thus, interpreting the abiotic system in terms of tolerance limits, certain principles of field distribution in subtropical climate could be derived.

It remains an interesting task to further correlate these results with the distribution and ecophysiology of corresponding populations from boreal climates. Judging from the data on thermal resistance, subtropical and boreal populations seem to have kept the same extremely wide range of genetically fixed tolerance. However, exposure to different environments for long periods of time, apparently caused new and diverse steady state reactions with probably also different stable preferences. This leads in each population to a meaningful resistance adaptation adjusting them to their respective ecological situation. Though the nature of this adaptive process is yet unknown, it is assumed to be non-genetic (Kinne op. cit.), since the fairly uniform euryoecous background is an optimal genetical basis for the world-wide distribution of this meiobenthic oligochaete. Maintenance of a wide physiological and ecological potential and ability of non-genetical adaptation to the array of local life conditions seems to be a significant predisposition for any wide-spread distribution, so typical for this species and many other members of the interstitial fauna.

### ACKNOWLEDGEMENTS

It is gratefully acknowledged that the work at the Bermuda Biological Station For Research was supported by the Deutsche Forschungsgemeinschaft (1975) and by a fellowship from Exxon (1976). I thank Mrs. L. Seitz-Hildebrand for her careful drawing of the figures.

### REFERENCES

- Farris, R.A. 1975. Systematics and ecology of Gnathostomulida from North Carolina and Bermuda, Diss. Univ. North Carolina, Chapel Hill.
- Giere, O. 1970. Untersuchungen zur Mikrozonierung und Ökologie mariner Oligochaeten im Sylter Watt. Veröff. Inst. Meeresforsch. Bremerh. 12, 491-529.

- Giëre, O. 1971. Beziehungen zwischen abiotischem Faktorensystem, Zonierung und Abundanz mariner Oligochaeten in einem Küstengebiet der Nordsee. Thalassia jugosl. 7, 67-77.
- Giëre, O. 1973. Oxygen in the marine hygroscopical and the vertical microdistribution of oligochaetes. Mar. Biol. 21, 180-189.
- Gnaiger, E. 1976. pH and temperature fluctuations in an intertidal beach in Bermuda: An experimental approach. (in press).
- Jansson, B.O. 1967. The importance of tolerance and preference experiments for the interpretation of mesopsammon field distributions. Helgol. wiss. Meeresunters. 15, 41-58.
- Jansson, B.O. 1968a. Quantitative and experimental studies of the interstitial fauna in four Swedish sandy beaches. Ophelia 5, 1-71.
- Kähler, H.H. 1970. Über den Einfluss der Adaptationstemperatur des Salzgehaltes auf die Hitze- und Gefrierresistenz von Enchytraeus albidus (Oligochaeta). Mar. Biol. 5, 315-324.
- Kinne, O. 1964. Non-genetic adaptation to temperature and salinity. Helgol. wiss. Meeresunters. 9, 433-458.
- Kinne, O. 1970. Temperature: Animals - Invertebrates. In: O.Kinne (ed.), Mar. Ecol. 1, Environmental Factors, Pt. 1. Wiley, London, 407-514.
- Kinne, O. 1971. Salinity: Animals - Invertebrates. In: O.Kinne (ed.), Mar. Ecol. 1, Environmental Factors, Pt. 2. Wiley, London, 821-995.
- Lassère, P. 1969. Régulations énergétiques entre le métabolisme respiratoire et la régulation ionique chez une Annélide Oligochète euryhaline, Marionina achaeta Hagen. C.R. Acad. Sci. Paris, 268, 1541-1544.
- Lassère, P. 1971. Données écophysiologiques sur la répartition des Oligochètes marins meiobenthiques. Incidence des paramètres salinité, température, sur le métabolisme respiratoire de deux espèces euryhalines du genre Marionina Michaelsen 1889 (Enchytraeidae, Oligochaeta). Vie Milieu Suppl. 22, 523-540.
- Lassère, P. 1975. Métabolisme et osmorégulation chez une Annélide Oligochète de la méiofauna: Marionina achaeta Lassère. Cah. Biol. mar. 16, 765-798.
- Oertzen, J. -A. v. and Schlungbaum, G. 1972. Experimentell-ökologische Untersuchungen über O<sub>2</sub>-Mangel und H<sub>2</sub>S-Resistenz an marinen Evertebraten der westlichen Ostsee. Beitr. Meereskunde 29, 79-92.

- Pfannkuche, O. 1974. Zur Systematik und Ökologie naidomorpher Brackwasseroligochaeten. Mitt. Hamburg. Zool. Mus. Inst. 71, 115-134.
- Theede, H. 1973. Comparative studies on the influence of oxygen deficiency and hydrogen sulphide on marine bottom invertebrates. Neth. J. Sea Res. 7, 244-252.
- Tynen, M.J. 1969. Littoral distribution of Lumbricillus reynoldsoni Backlund and other Enchytraeidae (Oligochaeta) in relation to salinity and other factors. Oikos 20, 41-53.
- Wieser, W. 1975. The meiofauna as a tool in the study of habitat heterogeneity: Ecophysiological aspects. A review. Cah. Biol. mar. 16, 647-670.
- Wieser, W. et al. 1974. An ecophysiological study of some meiofauna species inhabiting a sandy beach at Bermuda. Mar. Biol. 26, 235-248.