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An ecophysiological approach to the microdistribution of meiobenthic Oligochaeta. II. *Phallodrilus monospermathecus* (Tubificidae) from boreal brackish-water shores in comparison to populations from subtropical beaches*

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Abstract

Phallodrilus monospermathecus, a typical interstitial oligochaete from Baltic and North Sea beaches, shows a characteristic microdistribution preferring the moist layers usually slightly above ground water which are sufficiently supplied with water and oxygen, protected against wave action and devoid of hydrogen sulfide. – Ecophysiological experiments testing the resistance against temperature, salinity, alkalinity, and hypoxia proved the populations to be extremely euryecous tolerating single factors far beyond their natural range. However, combinations of adverse factors reduced the tolerable limits, especially those of salinity, considerably. – In boreal climate, the habitat fluctuations for many physiographical factors apparently lie well within the tolerable range of the populations. Hence, the distributional pattern of *Ph. monospermathecus* from Baltic and North Sea beaches must be ascribed mainly to long-term and preference reactions and probably also to biotic factors (food supply, competition), and is less definable by short-term tolerances. This is in contrast to conspecific populations from Bermuda beaches. Here, the subtropical climate shifts the maximal oscillations of physiographical parameters close to the tolerance limits which makes the field distribution of the population explicable already by short-term survival tests (GIERE, 1977a). – Considering the differing distributional limits of *Ph. monospermathecus* in their climatically diverse habitats, the nature of ecophysiological adaptation in this ubiquitous meiobenthic species is discussed.

Zusammenfassung

Ein Versuch einer ökophysiologischen Deutung der Mikroverteilung meiobenthischer Oligochaeten. II. *Phallodrilus monospermathecus* (Tubificidae) von borealen Brackwasserküsten im Vergleich zu Populationen von subtropischen Stränden

Phallodrilus monospermathecus, ein häufiger interstitieller Oligochaet der Strände von Nord- und Ostsee, besitzt eine charakteristische Mikroverteilung, bei der neben ausreichendem Salz- und Sauerstoffgehalt die Feuchtigkeit und die Umlagerung des Sediments von Bedeutung sind. Toleranzexperimente mit Popula-

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tionen von Nord- und Ostsee zeigten, daß die Kapazitätsgrenzen dieser borealen Populationen, im Gegensatz zu denen von subtropischen Tieren, deutlich über den in der natürlichen Umgebung vorkommenden Werten für Salzgehalt, Temperatur, pH und Sauerstoff liegen. Dies unterstreicht die große Euryökie der weltweit verbreiteten Art. Somit scheint hier die Mikroverteilung der Art besonders durch Langzeitreaktionen und Präferenzverhalten sowie durch biotische Faktoren (Nahrung, Konkurrenz etc.) bestimmt und kaum durch kurzfristige Toleranzreaktionen erfaßbar. Dies steht in Gegensatz zu Populationen aus Bermuda, wo die abiotischen Extremwerte (besonders von Temperatur und Salzgehalt) bis nahe an die Toleranzgrenzen der Art reichten und – auch schon in Kurzzeittests nachweisbar – die Verteilung der Population bestimmten (GIERE, 1977 a). Ausgehend von den klimatisch unterschiedlichen Grenzwerten in den verschiedenen Populationen von *Ph. monospermathecus* werden die Grundlagen der ökophysiologicalen Adaptation dieser meiobenthischen Art diskutiert.

Introduction

The occurrence of the common interstitial oligochaete *Phallodrilus monospermathecus* (KNÖLLER) both in subtropical and boreal climate (Bermuda, Baltic and North Sea resp.) poses the problem whether these geographically and climatically separate populations exhibit a differing tolerance range for key factors such as temperature, salinity, oxygen and pH conditions. The pertinent results from the Bermuda populations (GIERE, 1977 a) correspond well with the characteristic and inhomogeneous microdistribution of this littoral worm.

By corresponding tolerance experiments and field distributional studies with populations from the German sea shores, a direct comparison of the micro-environment in different climatical regions is possible. Moreover, these studies could elucidate some general problems involved in ecological adaptation of species with wide-spread distribution.

Material and Methods

Each time 20 specimens from the lenitic Baltic shore at Karschau (Firth of Schlei; salinity range in sediment 5–12‰ S) and from the shore line of the North Sea flats at Keitum (Isle of Sylt; average interstitial salinity 18‰ S) were tested in small vias at different temperatures, salinities, alcalinities and oxygen tensions. Tolerance was defined as lethal time for 50% or 100% of the animals (LT 50; LT 100). Salinity variations were accomplished using natural habitat water and aged fresh water; only in a few cases artificial sea salt was added. Results always represent average values from 2 to 5 replicates. Before exposing the worms to extreme temperatures and/or salinities, they were acclimated to intermediate conditions. (For further technical details see GIERE, 1977 a.)

In order to study the field distribution, horizontal and vertical samples were taken with perspex corers of 20 cm² width in profiles perpendicular to the beaches from about 1 m below the flat/slope – transition area (high-water line on the North Sea shore at Keitum) up to about 10 m above it. In addition to studies at the lenitic Firth of Schlei (Karschau), we sampled also the exposed beach of the Baltic at Weidefeld, near the mouth of the Schlei. Preference for moisture content of the sediment was tentatively tested in a perspex trough with medium sand, offering moistures from 0% (dry) to about 19% (full saturation).

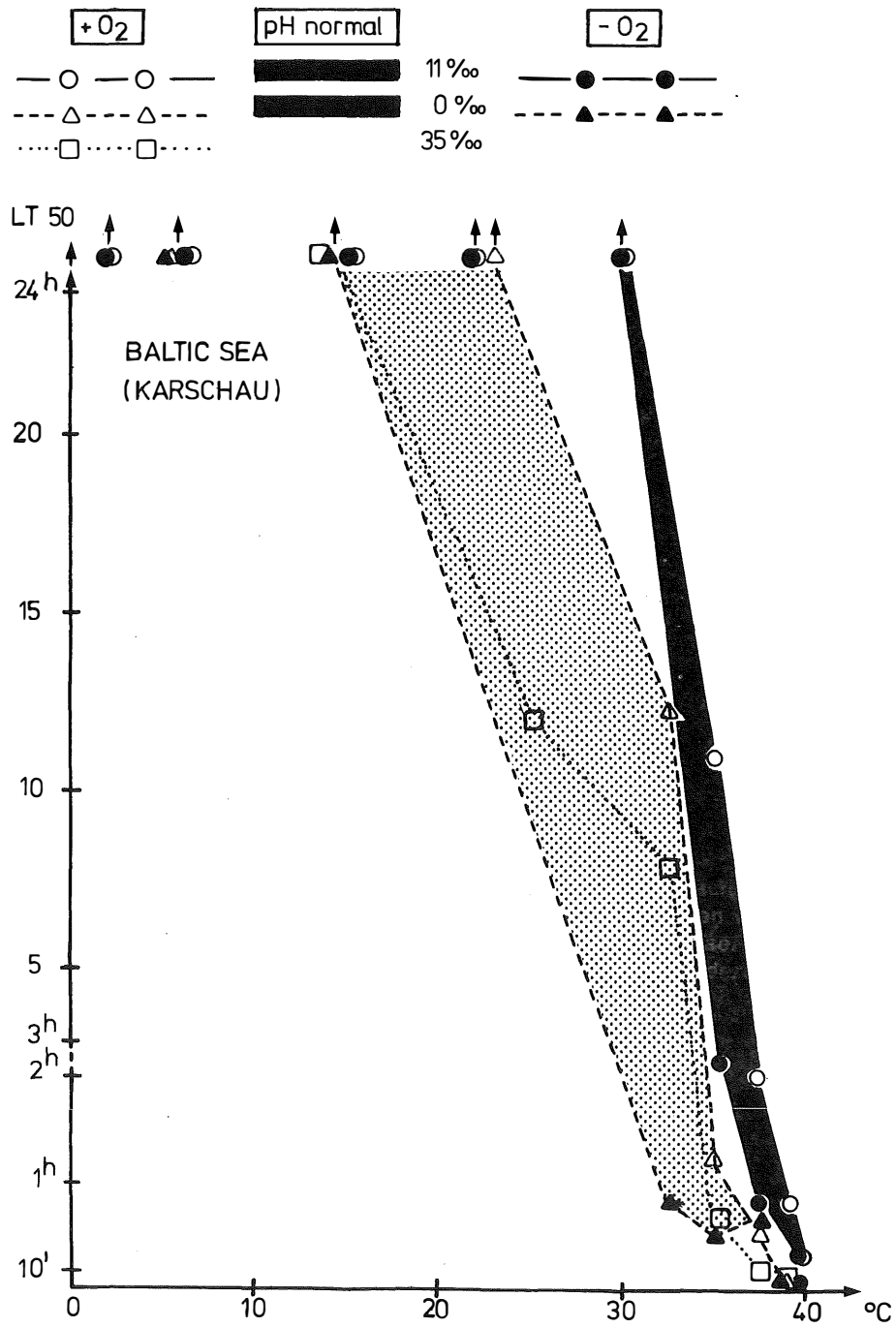


Figure 1
 Temperature tolerance of *Ph. monospermathecus* (Baltic population): Survival (LT 50) at various salinities and oxygen conditions

Results

1. Laboratory Experiments

Survival times of *Ph. monospermathecus* from Karschau (Fig. 1) in habitat-salinity conditions (11‰ S) are practically only restricted by temperatures higher than 30°C (circles in Fig. 1). A marked decrease starts when approaching 37.5°C. Around 39° to 40°C, extremely short tolerance times indicate the upper thermal threshold for life of the species.

Enhanced influence of rain and ground water can dilute the normally mesohaline water down to fresh water values. Even then, the worms survive temperatures normal for boreal climate (below 30°C; triangles in Fig. 1). Survival at 32.5 °C was still about 12 h. Thus, the course of the survival curve at 0‰ S is similar to that in normal brackish salinity conditions, though the general decline in this extreme stress situation is shifted and commences already at somewhat lower temperatures.

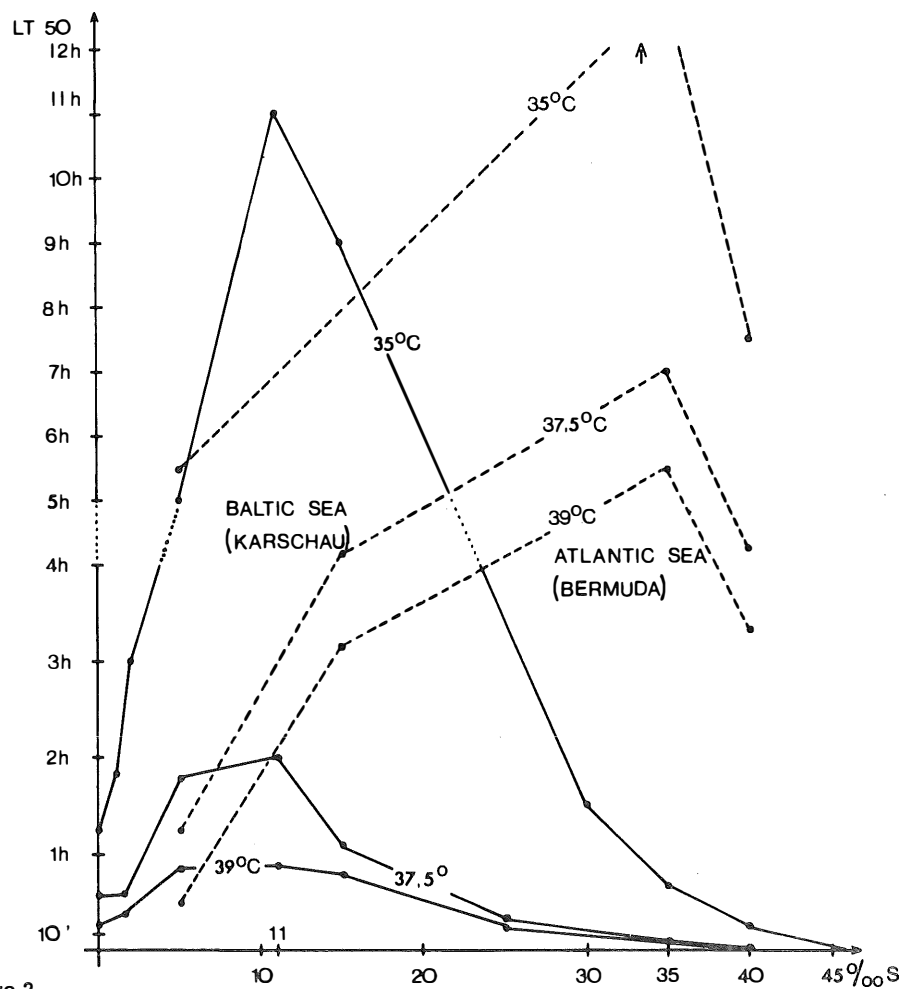


Figure 2

Salinity tolerance of *Ph. monospermathecus* (Baltic and Bermudian populations): Survival (LT 50) at various temperatures

In 35‰ S, the same steep decrease of LTs, however at even lower temperatures, is to be monitored (at 25°C – 12 h; 32.5°C – 8 h; 35°C – 40'; 37.5°C – 8'). Though this salinity is never to be encountered by the animals in the Baltic habitat (maximal salinity recorded here: 19‰ S), it is tested here for comparative reasons to the Bermuda populations. The fairly good survival even under these extreme salinity conditions stresses the amazingly euryecous nature of the species. The important role low temperatures attain for salinity tolerance is indicated by the fact that at 15°C the worms could survive for more than 24 h even at 45‰ S.

The influence of oxygen depletion as an additional stress factor becomes markedly evident at 0‰ S: In this milieu, already governed by one stress factor (reduced salinity), a maximal discrepancy between normoxic (open triangles in Fig. 1) and anoxic (black triangles) conditions could be found at about 32.5°C to 35°C (as indicated by the grey field in Fig. 1). Near the 39° to 40°C-threshold, stress due to anoxia does not clearly contrast with thermal limitation eventually resulting in almost instantaneous death. If, however, salinity conditions are regular (11‰ S) and oxygen depletion represents the only stress factor, this impairment can be ruled out to a high degree (black circles in Fig. 1), the "difference-field" (dark field in Fig. 1) between normoxic and anoxic conditions being rather narrow.

On the North Sea shore, salinities up to the thirties will occasionally occur whereas dilution down to fresh water levels is unknown. Hence, the pertinent tolerance rates indicate a far better adaptation to high salt contents (at 35°C and 35‰ S: LT 50 more than 4 h) than to fresh water where a rigorous restriction was to be monitored (at 35°C and 0‰ S: LT 50 only 20 min).

Plotting some temperature results from the Baltic populations against salinity (Fig. 2), the interdependence between these ecofactors and their mutual impact on the tolerance become more evident. Despite the significant tolerance differences with varying temperatures, in each case survival is greatest at 10‰ S to 12‰ S: It is the average salinity of the biotope which extends survival in an otherwise adverse situation.

Increased pH-values, in contrast to temperature, do not consistently exhibit an impact as additionally adverse parameters (Table 1).

Although there emerges a general trend towards less tolerance at higher alcalinities, especially in the populations from Karschau this tendency is not consistent, since the worms also survived in pH higher than realistic in the sediment where values up to about 9 have been recorded.

Table 1

Effect of increased pH on the survival of *Phalodrilus monospermathecus*

| | LT 50 | pH 7–8 | pH 9.2 | pH 9.5 |
|---------------------------------------|-------|---------|---------|---------|
| Karschau: 0‰ S/35°C/O ₂ – | | 0 h 37' | 0 h 52' | 0 h 25' |
| Karschau: 5‰ S/35°C/O ₂ – | | 3 h 0' | 4 h 10' | 3 h 50' |
| Karschau: 30‰ S/35°C/O ₂ – | | 2 h 35' | 1 h 20' | 0 h 50' |
| Keitum: 35‰ S/35°C/O ₂ + | | 4 h 12' | – | 1 h 50' |
| Bermuda: 35‰ S/39°C/O ₂ + | | 5 h 30' | – | 2 h 0' |

2. Field Results

Both sampled beaches from the Baltic displayed a fairly clear pattern of physiological parameters: The relatively steep and exposed slope of Weidefeld beach was characterized by well sorted medium to coarse sand (500 to 1000 μm , PFANNKUCHE, 1977), good oxygen supply throughout, and absence of a redox-potential discontinuity layer (RPD-layer). Ground water salinity ranged from about 15‰ S near the water line to about 3–5‰ S fifteen meters above WL. The sediment at the higher reaches of the slope was rather dry in the upper layers (often less than 5 weight-% water content, see Fig. 3 B).

The sandy shore of the Schlei at Karschau (about 8 m in width) is characterized by a very inhomogeneous mixture of fine and medium sand with gravel lying over a layer of clay. Influx of ground water can be very strong, the ground water level (GWL) fluctuating heavily depending on the prevailing winds (for details see PFANNKUCHE, 1977). The rich interstitial fauna is dominated by nematodes and oligochaetes.

The sandy high water (HW)-area and supralittoral of Keitum/North Sea (about 13 m in width) emerges from the silty to muddy wadden flats and physiographically represents a very inhomogeneous substrate with irregular layering of strata with different sediment and oxygen conditions. Below the HW-line, only a very thin oxidized layer covers the reduced, black, silty sand rich in H_2S (details see in GIÈRE, 1970, 1971). Apart from a substantial number of marine oligochaetes, this beach is inhabited by a rich meiofauna with preponderance of numerous nematodes and turbellarians.

With respect to the general inhomogeneity and oxygen conditions, the Bermuda beach which is considered here for comparative reasons (see Discussion), is similar to that in Keitum although climatical and sedimentary conditions are principally different (details in FARRIS, 1976; GIÈRE, 1977 a; WIESER et al., 1974; WIESER and SCHIEMER, 1977).

Despite the apparent differences between the boreal beaches in beach profile and grain size composition, the distribution pattern of *Ph. monospermathecus* is basically the same:

As evident especially in Weidefeld (Fig. 3), the animals are always concentrated in supralittoral sandy layers ("hygrosummal" acc. to WISZNIEWSKI, 1934) near the GWL and only scarcely inhabit the permanently submersed layers below WL (comp. JANSSON, 1962). The extent to which the water content determines the distribution of the worms is demonstrated by Fig. 3 A and B, where in Sept. 1977 the water and ground water level were unusually high due to a period of strong wind blowing from the sea. The *Phallodrilus* populations were found to have followed the risen GWL and were encountered higher up the beach than usual, whereas the surface horizons in the lower parts, exceptionally submersed and exposed to the wave splash, now were abandoned by the worms. In contrast to this, the low water-level in July 1975 apparently made the animals leave the upper horizons from 3 m upwards and migrate downwards into the moist sand. Now, even the lowest parts of the slope and the beginning flat, not submersed by water, were populated up to the surface.

On the North Sea beach at Keitum (Fig. 3 C), the physiographical situation is complicated by two new factors: oxygen deficiency and unsuitable sediment structure. Anoxia (and H_2S) strictly repels *Ph. monospermathecus* (GIÈRE, 1977 a; PFANNKUCHE, 1977). The species also avoids decaying plant material (e. g. old wrack

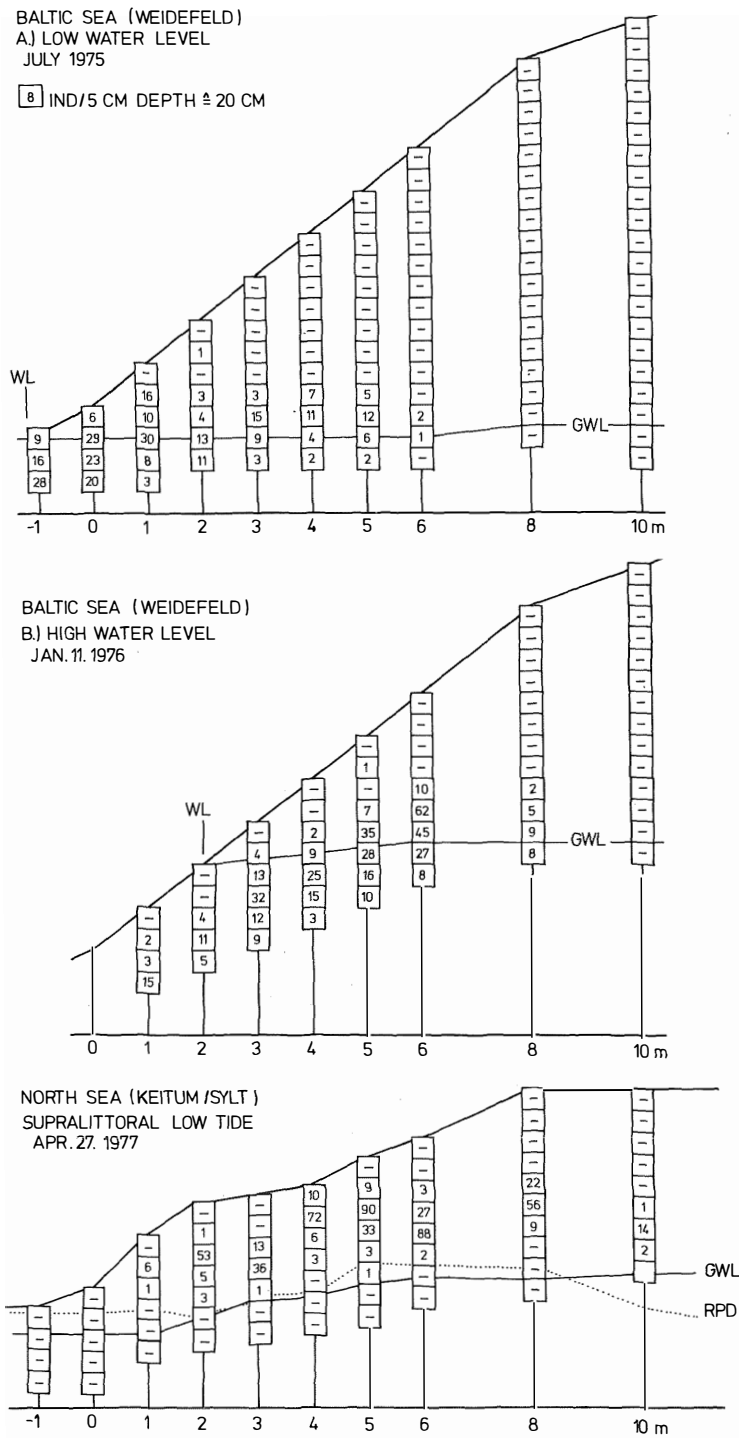


Figure 3
 Field distribution of *Ph. monospermathecus*
 (WL. = water line; GWL. = Ground water line; RPD. = redox potential discontinuity)

beds) which at Keitum beach are to be found embedded in the sand (GIERE, 1970). Hence, here it is mainly the RPD-layer which indicates the lower level of the species' occurrence. The low oxygen content (Eh-recordings not higher than + 50 mV) and adverse debris-horizons force the animals to live above the GWL which is in contrast to their occurrence in the well oxidized Baltic sediments. Occurrence of *Ph. monospermathecus* is also prohibited in the lower parts of the shore, i. e. the upper edge of the wadden flats, by unfavourable sediment and oxygen conditions (silty sand to mud, oxygen deficiency already at about 0.5 cm depth).

The question remains, however, which ecofactors prevent this species from populating also the upper horizons and the back shore both in the Baltic and the North Sea. Underneath the extremely astatic surface layer, life conditions are not unfavourable for marine oligochaetes in general which is proved by the occurrence of rich populations of interstitial enchytraeids (GIERE, 1970, 1973; PFANNKUCHE, 1977). However, first preference experiments in moisture gradients clearly confirmed the strong binding of *Ph. monospermathecus* to rich water supply indicated already by the species' occurrence near the GWL. It chose regularly the areas almost or fully saturated with water and was only scarcely to be found beyond 80 % water saturation.

Since the upper horizons of the higher beach and the back shore were far from being saturated (water content often less than 5%, Fig. 3), it can be concluded that also in the field the population decrease in the higher beaches is caused by lack of moisture. Especially in the Baltic, this negative effect was enhanced by very low salinities (5‰ S).

In contrast to this, the Bermuda supralittoral beach contained sufficient water, salinity and oxygen throughout (12–16% water; 36‰ S; + 400 to 430 mV redoxpot.). Despite these favourable conditions, the upper beaches were only scarcely inhabited by *Ph. monospermathecus*, populations of which were found to be aggregated at the lower end of the slope slightly below HW-line where decaying organic matter had accumulated. Thus, here the distributional pattern of *Ph. monospermathecus* was probably modified by attraction to food and not determined by exclusion through adverse edaphic factors as in the other stations.

Discussion

The extreme physiological tolerance of *Ph. monospermathecus*, resulting already from the Bermuda experiments (GIERE, 1977 a) and from Baltic studies (Gotland; JANSSON, 1962), is fully confirmed by our tests with populations from the North Sea and the Baltic: If other ecologically significant abiotic parameters stay in their "normal" range, the worms are not restricted by temperatures or salinities usually occurring in their habitat. However, it must remain open whether the considerably narrower tolerance range both at 0‰ S, 10‰ S and 25‰ S, found by JANSSON (1962), can be referred to the somewhat more stable salinity conditions in the eastern Baltic compared to those in the extremely astatic Belt Sea area.

A clear difference in tolerance capacity was also to be revealed between the boreal and subtropical populations investigated here: The specimens both from the mesohaline Baltic shores and the polyhaline North Sea coast suffered from temperatures above 30°C, whereas survival of the Bermuda animals was only limited beyond 35°C.

On the other hand, both climatically different groups showed no restriction to very low temperatures. Under these conditions, apparently, the metabolism is so much

decelerated that even additional stress factors like extreme salinity show an only slightly adverse effect, at least in short-term experiments. This ability of the Bermuda animals not only to tolerate unnaturally low temperatures but within this extreme range even to survive unfavourable factor combinations, apparently, is not a general feature for warm-water invertebrates, since from several species a severe impairment in cool temperatures has been reported (BHATTACHARYA and KEWALRAMANI, 1972, 1973, 1975, 1976).

The resistance against extreme salinity disappeared, however, at higher temperatures. Then, tolerance was clearly restricted, but restriction was diversified in all three populations according to their differently saline biotopes (Fig. 2): Optimal survival was always recorded at the respective "habitat salinity", invariably at which temperature survival was tested. This is evident especially in the populations from the Baltic (in JANSSON's studies, 1962, too) and from Bermuda, but was noticeable also in the North Sea worms which had intermediate survival times (e.g. 7 h at 30‰ S and 30°C as compared with 1 h 30' in the Baltic and more than 12 h on Bermuda). Maximal temperature tolerance at salinities close to the habitat water was also reported by BHATTACHARYA and KEWALRAMANI, op. cit.) for planktonic species.

Comparing the fields of corresponding LT 50-values in salinity/temperature-diagrams (Fig. 4), the Baltic population is striking due to its relatively large area of massive restriction (LT 50 less than 1 h). The asymmetrical shape of this area with its wide extension towards high salinities characterizes the adaptation of these animals to low salinities where they can survive relatively well even adversely high temperatures. In high salinities, however, survival of the brackish-water population is aggravated even if temperatures are favourably low.

This is principally different in the Bermuda worms (Fig. 4), at ebb-tide regularly exposed to very high salinities. Thus, their lower mortality in the high-salinity tests, especially at the high temperatures typical for the subtropics, is illustrated by the narrow upper field for short survival. This field expands, however, approaching towards low salinities, rarely to be encountered in the habitat.

Although the Baltic populations in the experiments exhibit a larger overall-area of heavily reduced viability (high salinity + high temperature) than populations from Bermuda, it can be concluded that short-term extremes of the abiotic milieu do not define the microdistribution of the boreal specimens (with exception of anoxia and desiccation as indicated above). Viability in low-low conditions is always rendered, and on the other hand, the tolerance for high-high factor combinations exceeds the natural climatic range. Even extreme pH-values, a severe factor in the subtropical Bermudian flats (GIERE, 1977a; GNAIGER et al., 1978), have no significant effect on the oligochaetes from temperate climate, since they restrict viability only in high experimental salinities and temperatures.

It can be stated that in boreal climate the short-term tolerance range of *Ph. monospermathecus* is extended beyond the natural range of edaphic parameters, whereas in subtropical (and tropical) beaches the upper tolerance capacity is enclosed in the field of climatical conditions close to the upper edge of their amplitude (GIERE, 1977 a).

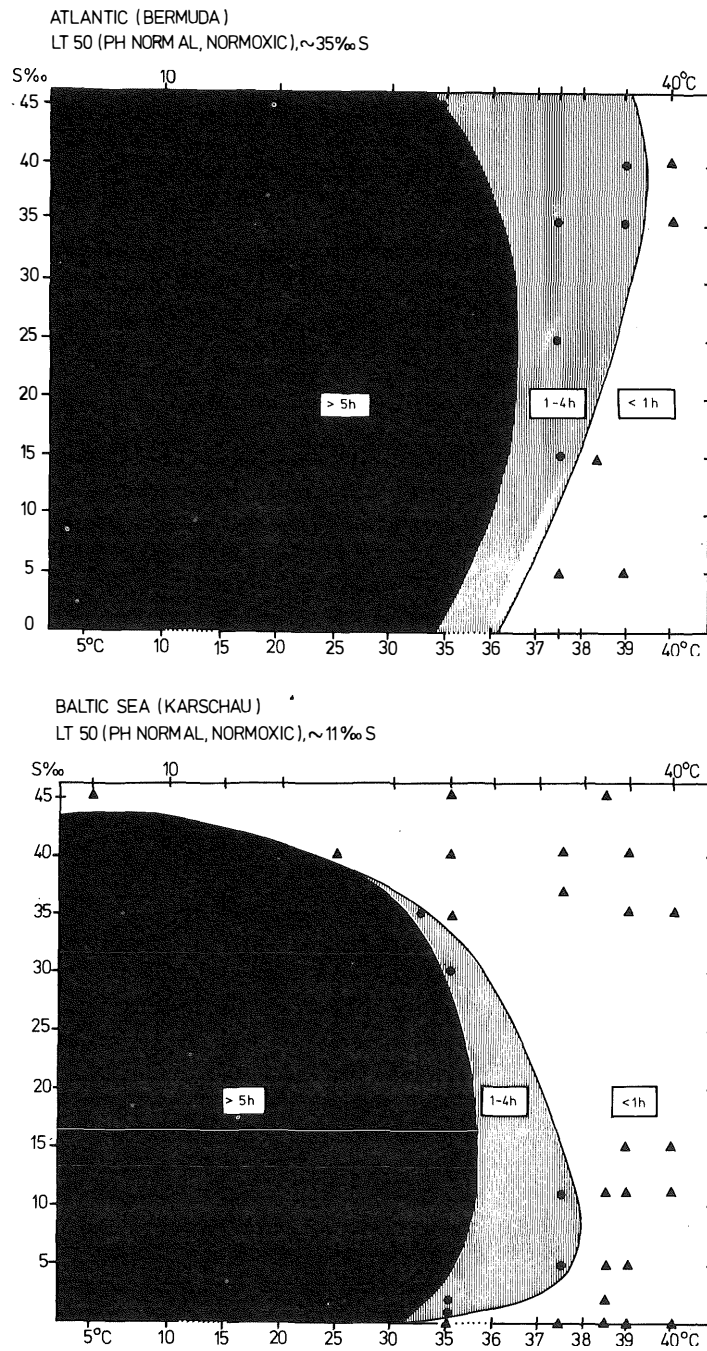


Figure 4

Salinity/temperature tolerance of *Ph. monospermathecus*: Comparison of "survival fields" in Baltic Sea and Bermuda populations

Thus, one can derive that despite local modifications due to some biotic factors (like food, see above), in the warm-water populations the general distributional pattern is in principal physically controlled, evident already in short-term experiments. In corresponding boreal populations, however, sublethal long-term effects and preference reactions beside biotic regulations gain considerable distributional importance: BRINKHURST, CHUA and KAUSHIK (1972); CHUA and BRINKHURST (1973) and GIÈRE (1975) underlined the food specificity of oligochaetes and the role food availability can attain in population structure and occurrence. Distributional relevance of preference reactions is evident from first choice experiments with *Ph. monospermathecus* and various other oligochaetes which showed the preference range for salinity, temperature and moisture to be strikingly narrower and more directly bound to habitat conditions than the resp. tolerance was (BACKLUND, 1945; JANSSON, 1962, 1968; GIÈRE, 1977b; TYNEN, 1969), certainly a principle of general validity (DORGELO, 1975). Hence, preference can be expected to express the differences in adaptation of disjunct conspecific populations from various climatical regions and their variance in field distribution much sharper than tolerance would do. Further experiments on salinity and temperature preferences are in progress.

It is perhaps possible to extend the different distributional principles, discussed above for interstitial oligochaetes, to conspecific disjunct populations of eulittoral meiofauna in general, since a close adjustment of metabolic tolerance capacities and micro-environment in the subtropics was found also for nematodes and other meiofauna groups by WIESER et al., 1974; WIESER (1975) and WIESER and SCHIEMER (1977). On the other hand, the same author (WIESER, 1964) stressed the importance of biotic factors and competition for the microdistribution of nematodes from temperate beaches. The distributional relevance both of long-term (seasonal) fluctuations, food availability and competition have also been pointed out by DÖRJES (1968), HUMMON (1968), POLLOCK (1970) and especially by WESTHEIDE (1972) for other meiofauna groups from temperate (Woods Hole) and boreal (Isle of Sylt) areas.

The more a clearly diversified pattern of ecophysiological reactions within disjunct populations of one species becomes apparent, the more required are explanations of the nature of these different adaptive responses. Are they only relatively stable long-term non-genetic adaptations (KINNE, 1970) or is the different physiological range already genetically fixed?

Diverging tolerance ranges of disjunct populations in climatically differing habitats have been reported occasionally for euectocous macrofauna species (KINNE, 1970, 1971, LOCKWOOD, 1976). However, for meiofauna animals, this phenomenon has rarely been investigated. Hence, the following considerations are rather speculative and need further evidence from long-term adaption experiments.

The consistently wide tolerance for low temperatures of all *Phallo-drilus* populations, regardless of their different climatical home-situation on the one hand, and their different response to high temperatures and salinities on the other hand, might indicate a uniform extremely wide genetically fixed physiological background of the species which covers even conditions never occurring in tropical environments (e.g. tolerance of less than 10°C). On the basis of exposure to different climatical conditions through long periods of time, diverse steady-state reactions (KINNE, 1970) with different preferences could have been created. This would represent a non-genetic resistance adaptation (PRECHT, 1958) as explanation for the diverging tolerances of the populations in question. This concept would also refer to the

widely dispersed occurrence of *Ph. monospermathecus* and possibly also many other interstitial animals, for which maintenance of a wide genetical background, adjustable to local physiographical conditions by long-term acclimation, certainly would be evolutionarily more favourable than any rapid fixation on the basis of natural genetical variability resulting in true racial differences.

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