EFFECT OF TEMPERATURE AND OXYGEN ON THE DISTRIBUTION OF *DIOPHRYS SCUTUM* DUJARDIN (CILIOPHORA, HYPOTRICHIDA) ON A TEMPERATE SANDY BEACH. AN ECOPHYSIOLOGICAL STUDY.

by

Eike Hartwig

Zoologlsches Institut und Zoologisches **Museum** dor Universistät,
Martin Luther-King-Platz 3, D-2000 Hamburg 13, Bundesrepublik Deutschland.

Résumé

Effets de la température et de l'oxygène sur **la** distribution des *Diophrys scutum* (Ciliophora, Hypotrichida) sur une plage sableuse tempérée.
Etude écophysiologique.

Le Cilié *Diophrys scutum,* espèce psammique à large répartition, qui habite l'estuaire sableux peu exposé de la côte Est de l'île de Sylt (Mer du Nord, allemande), est caractérisé par sa distribution horizontale et verticale en corrélation avec la température, la teneur en oxygène et le potentiel d'oxydo-réduction, la granulométrie, la teneur en matière organique, la salinité et le pH, ainsi que sa tolérance aux températures très variables (—4 à +35°C) sous des conditions de normoxie (100 p. 100 saturation) et d'oligoxie (8 p. 100 saturation).

D. scutum montre des modes de distribution différents dans l'estuaire sableux, en raison des fluctuations saisonnières et verticales de la couche de discontinuité du potentiel d'oxydoréduction. L'espèce se trouve dans la zone superficielle oxydée au-dessus de la couche réduite, en dehors des mois d'été. Pendant l'été, avec les hautes températures de la surface du sédiment, le Cilié se trouve en grande quantité dans les centimètres supérieurs de la couche réduite, formée sous la surface du sédiment. Les deux modes de distribution sont confirmés par des expériences de tolérance.

Si la tolérance à la température est comparée aux valeurs de haute pression d'oxygène par rapport aux valeurs de basse pression, on constate que le *D. scutum,* aux températures élevées, est plus ou moins insensible à la pression partielle de l'oxygène (la différence maximale des valeurs LT_{50} était seulement de 0.4°C). Aux basses températures, le Cilié est plus sensible à la température en condition d'oligoxie qu'en condition de normoxie (dans ce dernier cas, aucun effet de mortalité ne se produit à des températures allant jusqu'à —4°C).

Introduction

The marine interstitial ciliates of intertidal beaches live in a permanently fluctuating environment which is characterized by a reticular system of vertical and horizontal gradients. The heterogeneous distribution pattern of these organisms is determined by complicated interactions of ecological parameters (Fenchel, 1969; Fenchel and

CAHIERS DE BIOLOGIE MARINE
Tome XXIII - 1982 - pp. 227-242

Jansson, 1966; Hartwig, 1973 b). Ecophysiological experiments, using factorial combinations, permit a study of the survival limits of the species found in this biotope (Vernberg, 1975; Vernberg and Coull, 1975; Vernberg and Vernberg, 1975), and provide informations on the respective habitats. These experiments are to achieve an understanding of the habitat requirements for interstitial ciliates (Ax and Ax, 1960; Hartwig, Gluth and Wieser, 1977; Parker, 1976, 1978). *Diophrys scutum* has cosmopolitan distribution. It has been isolated from temperate beaches as well as from those in subtropical and tropical climates (Burkovsky, 1968; Dragesco, 1965; Hartwig, 1973 a, 1980; Hartwig and Parker, 1977; Kattar, 1970).

The subject of the present survey is the determination of the synergic effect on the thermo-oxygen-tolerance of this species in the laboratory and the attempt to apply the results of it to the relation of the two abiotic factors to the species on a sandy beach of the island of Sylt in the North Sea (see Hartwig, 1973 b). We are aware of the fact that "temperature" and "oxygen" are only two links in a chain of ecological parameters. Their evident fluctuations in the field, however, is implicated in the composition and distribution of the fauna.

Materials and methods

Study area

Between 1968 and 1971 (Hartwig, 1973 b) sampling and field measurements were carried out on a sandy beach in front of the "Litoralstation der Biologische Anstalt Helgoland" at List on the east side of the island of Sylt (North Sea). Judging by the motion of the water, the examined sand flat may be called lenitic. The mid-low-water-line (MLWL) is about 50m seawards from the *Strandknick* (the sharp, steep outwashed line of demarcation between sand flat and sand slope).

Sampling and extraction

In order to study the three-dimensional distribution of the fauna, profiles with fixed sampling marks (0, 10, 25, and 50m seawards from the *Strandknick)* were placed across the beach. With the help of a corer (cross section $2cm^2$), four sediment cores were taken at each mark (to consider the heterogeneous distribution in the biotope) with a maximal length of 30cm. These were cut into subsamples of 5cm thickness corresponding to a volume of 10ccm. Unless stated otherwise, the data on frequency refer to a sediment volume of 10ccm. To extract the ciliates from the sediments, a modified seawater-ice method (Uhlig, Thiel and Gray, 1973) was used. The animals extracted from each section were counted.

Field measurements of abiotic factors

The grain size composition in representative samples was measured with the help of sieves recommended by Hulings and Gray (1971). The respective temperatures were taken with mercury thermometers. Salinity was determined with a refractometer. Oxygen (given as the oxygen diffusion rate in $g \times 10^{-7} \times cm^{-2} \times min^{-1}$), pH and redox-potential (Eh in mV) were recorded with thin electrodes (see Giere, 1973), inserted into the different layers of the sediment. The content of organic particles (given in percentage of the loss of weight) was determined by ashing dry samples in the laboratotry.

Survival experiments

In June 1978, survival experiments were carried out with specimens which had been extracted from qualitative sediment samples and kept at 15° C in the laboratory. In two tightly closed medical "Sputum-dishes" of a diameter of 35mm, 30 specimens each were placed without sediment. The following procedures were employed:

Temperature and pO_2. After a gradually initial acclimatisation of the specimens for 12 hours to the experimental temperature (see below) they were transferred into filtered seawater (30 permil salinity) from a reservoir which was either aerated (" normoxic" conditions) or deoxygenated by flushing with nitrogen under continuous control of pH-values. This latter procedure does not remove every trace of oxygen, but an oxygen pressure of 8 percent saturation ("oligoxic" conditions), measured during the experiments, was achieved. After closing the dishes, the remaining gas bubbles were removed by means of a hypodermic syringe. The "Sputum-dishes" were put into a water-bath under light closure, where they were kept for 1, 6 or 12 hours. After the experiment, the dead specimens were separated from those still alive and the percentage of the survival rate calculated. Fixed temperatures of -4, 0, 5, 10, 15, 20, 25, 30, and 35°C were applied. The temperatures were not measured within the "Sputum-dishes" but of the surrounding water-bath only. Three different time periods were chosen: exposition for one hour to simulate a condition when highest temperatures coincide with low tide; six hours for the conditions during the period of low tide, and 12 hours exposition for the average conditions during a full day.

In order to demonstrate the relations between temperature tolerance, pO_2 and exposition time, LT_{50} values (50 percent survival rate) were used. The difference between the LT_{50} valucs under oligoxic and normoxic conditions (ΔT) were used to measure the grade of oxygen dependence of the examined species.

Diophrys scutum feeds on diatoms as reported by several authors (Borror, 1963; Fenchel, 1968 a, 1978). In order to eliminate any interfering influence of hunger or malnutrition on the tolerance of the species of abiotic factors, benthic diatoms from the area of investigation were added into the "Sputum-dishes".

RESULTS

Environmental factors

In addition to temperature, oxygen and redox potential, connected with these, further abiotic factors from the examined beach (sediment composition and grain size, content of organic particles, salinity, pH-values) will also be described.

Temperature

The temperatures of the open water vary between 21.5° C in summer and —2.6 °C in winter. Temperature in spring increases rather regularly (Hartwig, 1973 b).

The air temperature is also subject to considerable variations; it also influences the boltom and water temperature of the biotope. In December 1969 the lowest temperature was taken with —12°C, the highest in July 1969 with 29.2° C

The highest surface temperature of the sand flat was taken with more than 30°C in summer. A comparison of the temperature extremes of the bottom during the different seasons (Table 1) shows that, only during the summer season, significant greater temperature differences between the surface and deeper sediment layers exist. The heat conductivity of the sediment is not sufficient to allow an equalization of the temperature of the different sediment layers. This equalization is prevented by the quick heating of the surface, the high evaporation at the surface and the increased water retaining ability of deeper layers, caused by the medium sized grain and the content of detritus (Linke, 1939). In the winter season, the bottom temperatures drop below zero (—1.8° C ; January 1969).

In general, we may say that the fluctuation of the temperature decreases with the depth.

TABLE 1

Temperature extremes (°C) and variations in open water and sediment of a sand flat (Island of Sylt, North Sea) during the seasons (July 1968—March 1970) (from Hartwig, 1973 h)

	Spring (20.3.-20.6.) min. max. temperature	Summer (21.6.-22.9.) min. max. temperature	Autumn (23.9.-21.12.) min. max. temperature	Winter (22.12.-19.3.) min. max. temperature
	(variations put in parentheses)			
open water	+1.4 +17.8 (16.4)	+13.5 +21.5 (8.0)	—2.0 +13.3 (15.3)	—2.6 +2.5 (5.1)
flat, surface	+1.5 +23.5 (22.0)	+13.5 +30.5 (17.0)	—1.0 +14.8 (15.8)	—1.8 +5.8 (7.6)
flat, 7.5cm depth	+0.2 +21.5 (21.3)	+15.5 +27.0 (11.5)	—0.4 +13.8 (14.2)	—1.8 +3.7 (5.5)

Redox potential and oxygen

A vertical distribution of the sand flat into an oxidized and reduced environment is shown by the colour change from yellow over grey to black.

The vertical decrease of the redox potential (Table 2) is more or less distinct in the different parts of the sand flat and shows already negative values in the grey "redox potential discontinuity layer" (RPD; Fenchel and Riedl, 1970). In summer, these values may decrease in places with a thin oxydation layer immediately below the surface to —200 mV. According to Wieser (1975), values below —100 mV indicate the nonavailability of molecular oxygen for aerobic metabolism. Baas-Becking and Wood (1955) found sulphur reduction to begin at +100 mV.

TABLE 2

Vertical distribution of redox potentials at several stations of the sand flat in spring and summer (sediment colour is indicated; ——: position of RPD layer).

Depth (cm)	Eh (mV)	Sediment Colour
"Strandknick":		16.3.1971
0- 2	+160	yellow
2- 5	+125	yellow
5-15	+115	yellow-grey
		11.8.1970
0- 5	+85	yellow-brown
5-10	+15	yellow-brown
10-15	+75	light grey
10-m-station:		18.3.1970
0- 5	+125	yellow
5-10	+ 80	yellow
10-12	+ 5	dark grey-black
12-15	— 5	dark grey-black
		25.8.1970
0 - 2.5	+15	yellow-brown
2.5-10	—50	dark grey
10 -25	—90	light grey
25 -27	—70	black
25-m-station:		16.3.1971
0-3	+140	yellow (RPD layer at 7cm)
15	— 55	black
		12.8.1970
0 - 0.5	— 30	yellow-brown
0.5-10	—200	black
10 -15	— 10	black
15 -20	— 70	black

Within the range of the *Strandknick* and the inshore-part of the sand flat, the sediment does not adopt a greyish colour above a depth of 20cm; this indicates the position of the RPD layer. Increased shifting of the sand by water motion causes a satisfactory aeration.

In general, the redox potential is here placed higher than at other parts of the sand flat (Table 2).

The amount of available oxygen, given by the oxygen diffusion rate decreases from the *Strandknick* (with stronger sediment shifting) with maximal 3.63 g x 10^{-7}x cm^{-2}x min^{-1} in direction towards the water line, where it amount only to 0.12 g x 10^{-7}x cm^{-2}x min^{-1}. The quantity of oxygen is found by comparison with values in surface layers of the beach slope between 0.92 to 10.3 g x 10^{-7x} cm^{-2}x min^{-1} (Schmidt, 1968; Wcstheide, 1968).

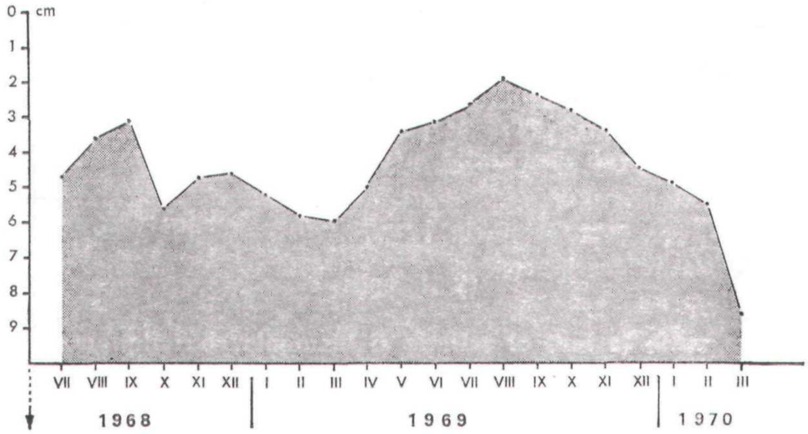

FIG. 1

Seasonal fluctuations of the RPD layer in their vertical location in the sand flat in front of "Litoralstation List" (the points significate mean values during one month; the stippled area shows the "black zone") (adapted from Hartwig, 1973 b).

The vertical position of the RPD layer is of importance for the distribution of the fauna. It is subject to seasonal variations (Fig. 1) which are caused by abiotic factors (for instance temperature, solubility of oxygen, sorting and shifting of the sediments) and biotic factors (faunistic colonization) (Perkins, 1957). During the summer months, it is highest immediately below the surface of the sand flat (only 0.1cm in September 1969), whilst during winter it is located deeper within the sediment.

Sediment composition **and** grain size

The sediment consists to 90 percent of quartz, less than 1 percent of other minerals and a moderate amount of calcareous shell particles (Pratje, 1931). Medium sized sand (250-500µm) prevails with 65.6-83.2 percent. The average grain size was found 315 and 430µm. The proportion of fine sand decreases from the low water line to the *Strandknick* from 18.8 to 3.4 percent, whilst the content of coarse sand (larger than 500µm) increases in the same direction from 4.1 to 30.6 percent. The sediment is well sorted down to a depth of 40cm with a coefficient for sorting between 1.22 and 2.45.

The pore volume is given by Schmidt (1968) as 33 to 38 percent of the total volume of a sample. Thus the interstitial fauna finds favourable conditions for colonization.

Content of detritus

The content of organic particles increases from the *Strandknick* to the low water line from 0.33 to 0.66 percent ascertained in a sediment depth to 5cm. A decrease with depth was found at all sampling points. Compared with other biotopes, these content values are low: Linke (1939) found in the sand of the Jade Bay (North Sea) an average of 1.5 percent.

Salinity

Fluctuations of the salinity in the sand flat saturated with water is caused by evaporation, rainfall and freshwater influx from the land; it is not great and affects only the surface of the sand (Callame, 1960; Johnson, 1967). The salinity of the open water varied during the period of the survey between 25.7 and 31.8 permil. It takes a direct influence on the salinity conditions of the sand flat bottom. This is to say that the interstitial water maintains the salinity of the open water.

pH-Values

Values taken at the surface of the sandy beach examined varied between 7.6 and 8.1. Vertically, the pH-values fluctuated between 7.0 and 8.2. The open water has a pH-value of 8 (water temperature: 17.5-19.6°C).

Distribution and population dynamics of *Diophrys scutum*

This species prefers lenitic and sublittoral biotopes on the island of Sylt (Hartwig, 1973 a, b). The whole area of the sand flat from

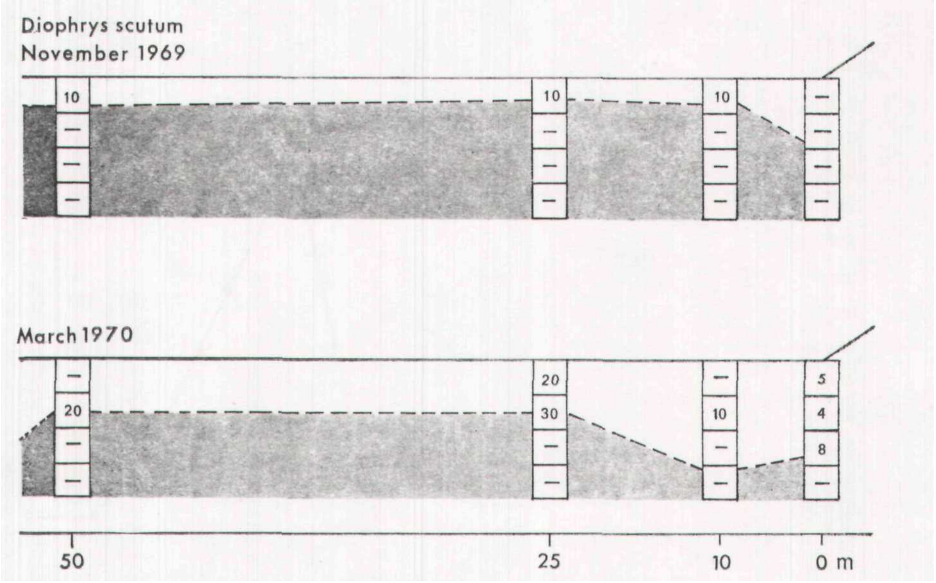

FIG. 2

Vertical distribution of *Diophrys scutum* in the sand flat in November 1960 and March 1070. All individuals are found above the reduction zone (specimen number, given per 100ccm from a sediment of H = 5cm, are average values from four samples; stippled area shows location of reduction zone; — — —: location of RPD layer, mean values from single data).

the *Strandknick* to the low water line was colonized by *Diophrys scutum*. No local concentration was found. The population density generally attained values between 10 and 30 specimens per 100ccm sediment. Many samples contained more than 100 specimens. In August 1969, the maximum with 790 specimens was found.

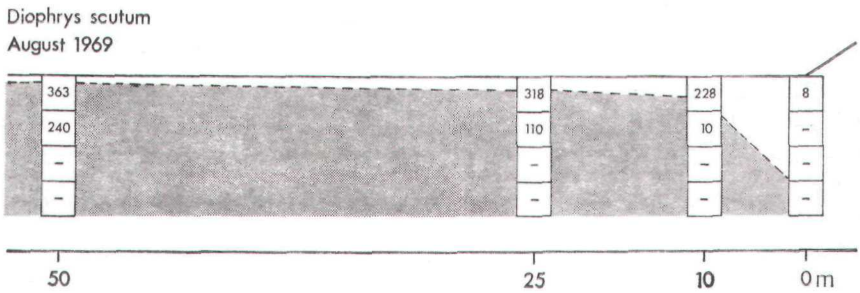

FIG. 3
Vertical distribution of *Diophrys scutum* in the sandflat in August 1969 (text, see Fig. 2).

In its vertical distribution, *Diophrys scutum* is restricted, except during the summer months, to the oxidized zone above the reduction horizon (Fig. 2). In the inshore-part of the sand flat, where the reduction zone often begins in a depth of 20cm, the species may attain this depth. During the summer months (Fig. 3), when the RPD layer, whose depth is subject to seasonal fluctuations, is formed only few centimeters below the surface of the sediment (Fig. 1), this species

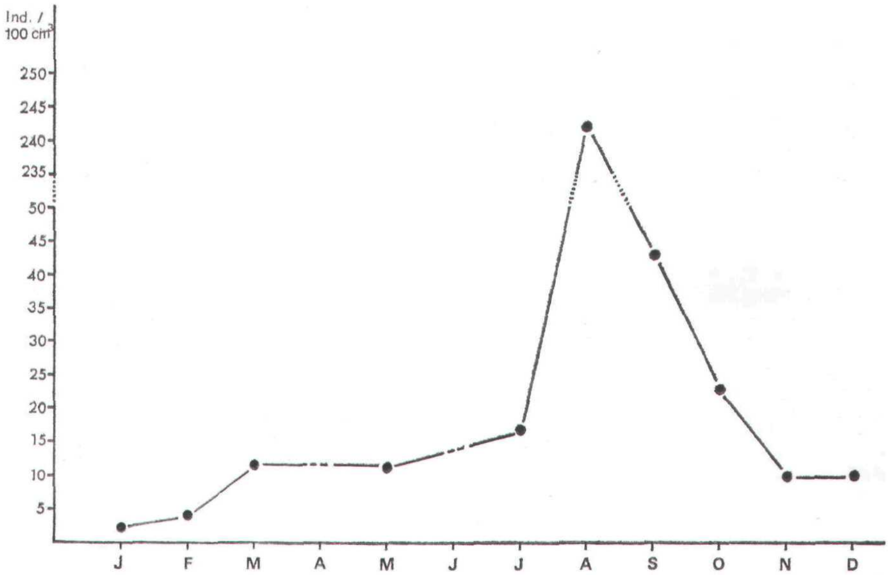

FIG. 4
Annual population dynamics of *Diophrys scutum* (time period: 1969-1970; only samples with animals were considered).

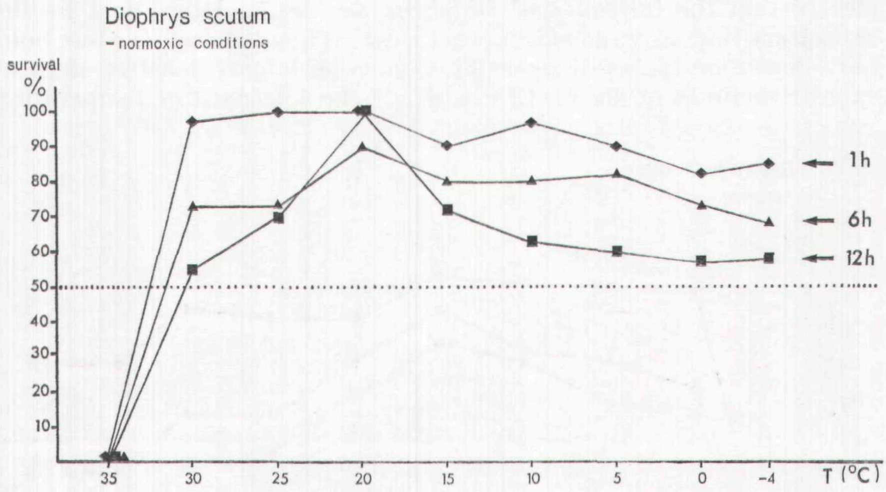

FIG. 5

Survival rate at different temperatures and three different time periods under normoxic conditions (the line of 50 percent survival, LT_{50}, is indicated).

is also found with high densities in the uppermost part of the reduction zone. In general, it is stated that the population density decreases with the vertically increasing reducing conditions and decreasing oxygen content. Similar findings are reported by Fenchel (1969) from Danish shoal biotopes. Vertical migration has not yet been found.

The maximum of the annual population dynamics (Fig. 4) is found in August with a mean population density of 242 specimens in 100cm sediment. More than 70 percent of the samples contained more than 100 specimens. In January, the minimum was found with 3 specimens in 100ccm.

Survival experiments

Temperature and oxygen

Fig. 5 and 6 demonstrate the survival rate at three different time intervals for the combination of low/high pO_2. This shows

TABLE 3

Lethal temperatures (LT_{50}) for *Diophyrus scutum* tested, at three exposure levels, under normoxic and oligoxic conditions (explanation for ΔT, see text).

	Low temperatures			High temperatures		
Time of exposure	1 h	6 h	12 h	1 h	6 h	12 h
LT_{50} (°C) under normoxic conditions	<—4.0	<—4.0	<—4.0	32.4	31.6	30.6
LT_{50} (°C) under oligoxic conditions	<—4.0	—1.6	+5.8	32.2	31.2	30.4
Δ T (°C)	?	>—2.4	>—9.8	0.2	0.4	0.2

clearly that the tolerance of *Diophrys scutum* is determined by the exposition time at various temperatures. When exposed for one hour only, lower or higher temperatures may be tolerated better than at exposition times of six or 12 hours. If the tolerance of temperature

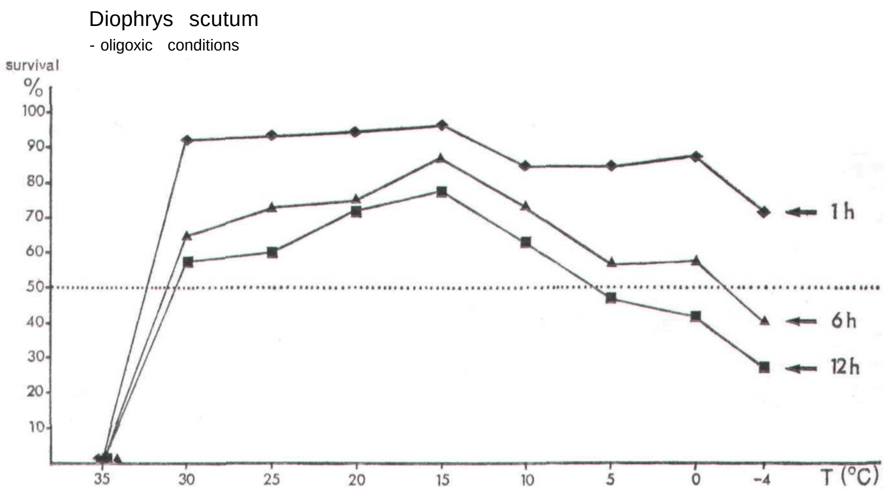

FIG. 6

Survival rate at different temperatures and three different time periods under oligoxic conditions (see Fig. 5).

at high ("normoxic") pO_2 values is compared with that of low ("oligoxic") values, it is found that *Diophrys scutum* is at high temperatures more or less unaffected by partial oxygen pressure, whilst it is at low temperatures less temperature resistant when exposed under oligoxic conditions (Table 3). AT as a measure for oxygen dependence of this species is very small at high temperatures but great at low temperatures. This explains the capability of this species to inhabit the upper part of the reduction zone in summer as well.

DISCUSSION

Temperature

During a low water period the uppermost centimeters of the sand flat surface can attain a temperatine of 30 "C (when exposed to a strong solar radiation; Table 1). The results of tolerance experiments with *Diophrys scutum* at high temperatures after an exposition of one hour gave LT_{50} values of 32.4 and 32.2°C. When exposed for six hours, the values were 31.6 and 31.2 °C and, after 12 hours exposition, decreased to only 30.6 and 30.4°C (Fig. 7). Table 3 shows that LT_{50} values differ after an exposition of six and 12 hours from those of an exposition time of one hour only between 0.8 and 1.8°C. The high-temperature-tolerance of *Diophrys scutum* is adapted to the highest temperature which may be expected in the sand flat where the distribution centre of this species is located. Furthermore, it can be concluded from the values found, that this ciliate species can tolerate relatively high temperatures for a time period of 12 hours. This may

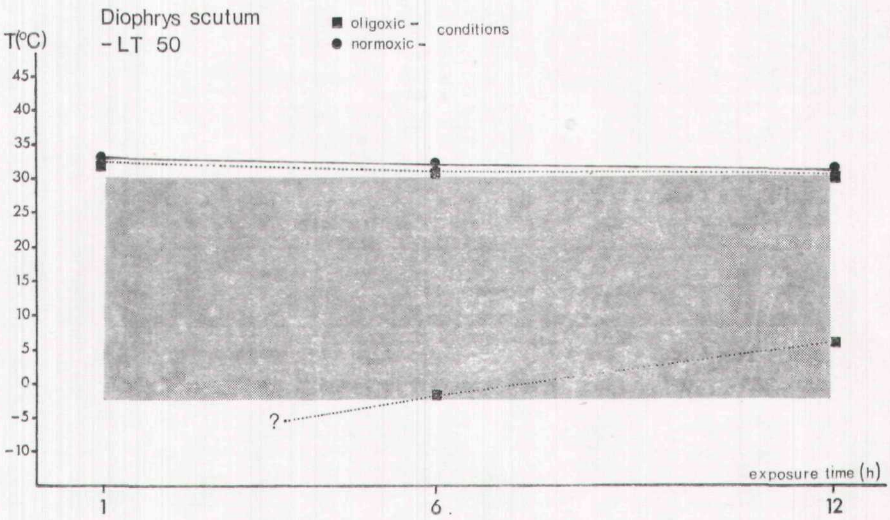

FIG. 7

Response reactions of *Dioohnis scutum* exposed to combinations of hiah and low temperatures and to pO_2 levels. LT_{50}'s under normoxic and oligoxic conditions are plotted against exposure time (the stippled area denotes the temperature range of the surface of the sand flat investigated; time period: 1968-1970).

represent the situation of a full day with strong solar irradiation. However, it may he added that this high-temperature-tolerance, found in the laboratory for a short time period, does not necessarily coincide with the ecological temperature range of the complete life cycle of the species studied; the noted reaction may be a response to an environmental extreme. Fenchel (1968 b) found the highest growth rate at 27°C; at 31-32°C almost no asexual reproduction was observed.

After an oligoxic exposure for six and 12 hours at low temperatures, the Ll_{53}values were given as —1.6 and +5.8"C. If the exposition time was limited to one hour and, after a normoxic exposition of one, six and 12 hours, the measured values dropped below —4°C (Fig. 7). During the period of this study such extreme values were not measured at the surface layer of the sand flat.

Oxygen

The redox potential decreases with depth at the various sections of the sand flat in front of the "Litoralstation" of List (Table 2). In the reduction zone below the oxydation horizon which, in summer, often measures only a few centimeters, up to —200mV may be measured. The oxygen availability in surface sediments is low and amounts only to 13-35 percent of that of the neighbouring sand slope which is well aerated.

In the light of the seasonally vertically fluctuating RPD layer *Diophrys scutum* shows at the sand flat different patterns of distribution.

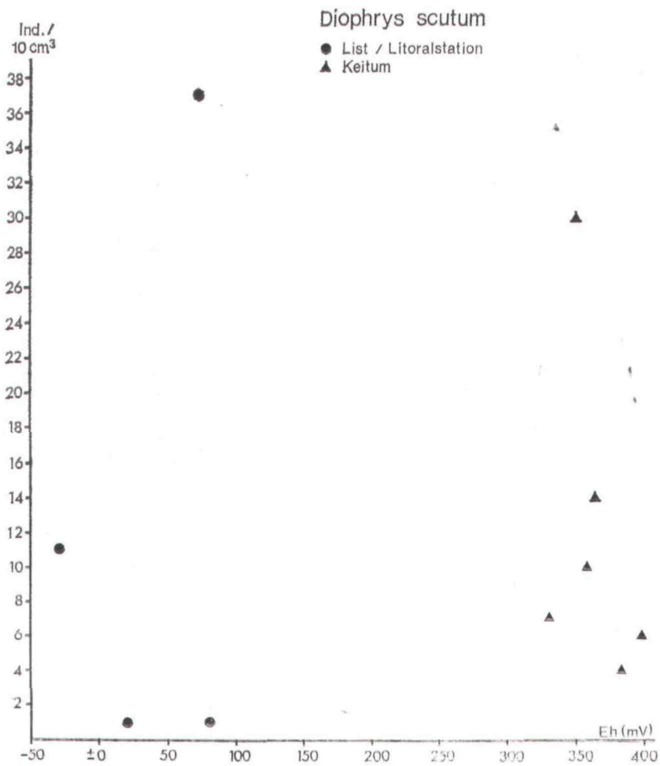

FIG. 8
The Eh-spectrum of two sandy beaches of the island of Sylt.

Except for the summer months, it lives in the oxidized surface horizon above the reduction zone (Fig. 2). The Eh-spectrum from two sandy beaches of the island of Sylt confirms this finding (Fig. 8) and often shows high mV-values predominantly in the positive range of the spectrum. The results of studies by Fenchel (1969) in Danish shallow water show a low tolerance of *Diophrys scutum* to hydrogen sulphide (up to maximum of 21mg $H_2S/1$). Such a vertical distribution shows *Diophrys scutum* to be aerophilic and a high dependence of available oxygen has to be assumed.

During summer months with high temperatures at the surface, this species is also found in the uppermost centimeters of the reduced layer (Fig. 3) with a population density of 240 specimens in 100cm. This pattern of distribution, influenced by the vertically fluctuating

RPD layer (Fig. 1), implicates a comparatively low grade of dependence of oxygen availability of this ciliate species.

Both these different patterns of distribution are ascertained by tolerance experiments carried out under different partial oxygen pressures.

The maximal difference of the lethal temperature under normoxic and oligoxic conditions at high temperatures, which were to simulate the situation during the summer months, was only 0.4°C (Table 3). The functions relating LT_{50} and exposure time was almost identical (Fig. 7) and thus indicate that *Diophrys scutum* can spend a part of its like in nature (e.g. during summer months) under conditions of low oxygen pressure.

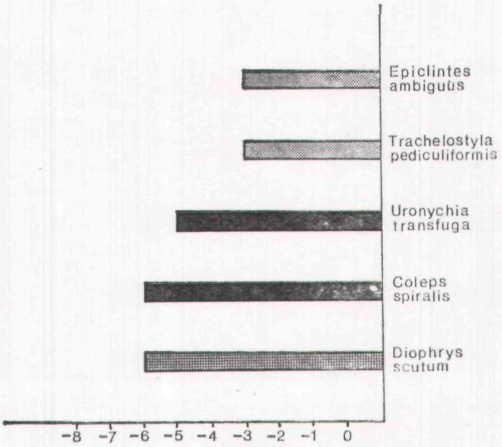

FIG. 9

Tolerance ranges of temperatures below 0°C from freezing experiments for several species from the sand flat investigated (ciliarv movement was a measure for activity; the temperatures were lowered each 24 hours for 1"C; the distribution of the species in the sand flat: *Epiclintes ambiguus* and *Trachelostyla pediculiformis* — in winter in deeper, reduced sediment layers with temperatures rarely below —3°C; *Uronychia transfugn, Coleps spiralis* and *Diophrys scutum*—in winter in oxidized surface layers) (adapted from Hartwig, 1973 b).

At low temperatures which were to simulate the conditions in the sand flat during the other months, lethal temperatures (at six and 12 hours exposure time) were only found under oligoxic conditions (Fig. 7). These, however, were still above the minimum values, in winter, found in the sand flat. No lethal effects were found at temperatures up to —4°C for all three time periods under normoxic exposure. The maximal difference of the LT is larger than —9.8°C (Table 3); this means *Diophrys scutum* is at low temperatures more resistant under normoxic conditions than under oligoxic. Hartwig (1973 b) showed the capability of this ciliate species to survive at temperatures below 0°C for several days under experimental conditions (Fig. 9). This has also been ascertained for other ciliates from temperate biotopes (epizoic *Zoothamnium hiketes* and benthic *Euplotes vannus)* (Vogel, 1966; Lee and Fenchel, 1972). That reproduction takes place at such low temperatures is doubtful, as Fenchel (1968 b) showed that even at +4°C reproduction is 10 to 20 times lower than at 20°C.

Westheide and von Basse (1978) found for two interstitial polychaetes *(Trilobodrilus axi* and *Hesionides arenaria)* from the sandy beach surveyed, supercooling resistance with no signs of mortality at —12°C after five hours exposition *(T. axi)* and —5°C after one hour exposition *(H. arenaria).*

Other factors

Sediment composition and grain size

The sand flat examined consists of well sorted sediments with 65.6 to 83.2 percent medium sand (250-500μm). The content of fine sand (125-250μm) and coarse sand (larger than 500μm) run up to maximal 18.8 and 30.6 percent respectively. The mean grain size is found between **315** and 430μm. The uniform composition of the sediment excludes any influence of the sediment composition and the grain size on the distribution of *Diophrys scutum* in the beach examined.

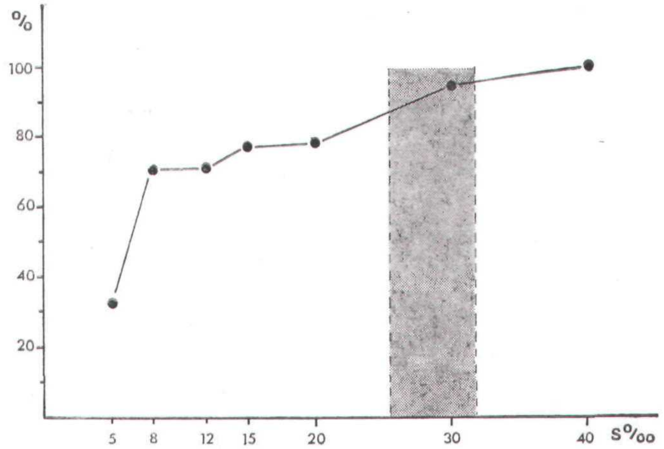

FIG. 10
Diophrys scutum
Relative population density tested at different salinities in vitro (adapted from Ax and Ax, 1960; the stippled area shows the salinity of open water at the beach investigated; time period: 1968-1970).

Content **of** detritus

The sand flat examined shows a content of detritus between 0.33 and 0.66 percent. The values decrease with depth. *D. scutum* colonizes the whole width of the sand flat. This ciliate was also found in sediment samples with a content of organic matter between 0.2 and 0.7 percent at other biotopes on the island of Sylt (Hartwig, 1973 b). The content of detritus in the sand flat in front of the "Litoralstation" does not impede the distribution of this species.

Salinity

The sand flat studied is subject to direct influence of the open water whose salinity fluctuates during the course of one year between 25.7 and 31.8 permil. Ax and Ax (1960) proved that the euryhaline species *D. scutum* evidently prefers the exclusively marine range. Experiments under laboratory conditions resulted in a decrease of specimens from an exclusively marine environment to subsaline brackish water (Fig. 10). If transfered the salinity range of the area surveyed ("stippled area") on the diagram, the relative population density is found between 84 and 95 percent.

pH-values

The pH in the sand flat examined fluctuates at the surface between 7.6 and 8.1 and between 7.0 and 8.2 in the depth. There is no evidence found that the predominant pH-values determine the distribution of *D. scutum* in this biotope.

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Summary

The cosmopolitan, interstitial ciliate species *Diophrys scutum* inhabiting a lenitic sand flat on the east side of the island of Sylt (German North Sea coast) was characterized by its horizontal and vertical distribution on the beach in correlation with temperature, oxygen and redox potential, sediment composition and grain size, content of organic particles, salinity and pH, and by its tolerance of low and high temperatures (—4 to 35°C) under normoxic (100 percent saturation) and oligoxic (8 percent saturation) conditions.

D. scutum shows different patterns of distribution at the sand flat caused by the seasonally vertically fluctuating "redox potential discontinuity" (RPD) layer. Except for the summer months, it lives in the oxidized surface zone above the reduction horizon. During summer months with high temperatures at the surface, it is also found with high densities in the uppermost centimeters of the reduced layer which is formed below the surface of the sediment. Both these patterns of distribution are ascertained by tolerance experiments.

If the tolerance of temperature at high pO_2 values is compared with that of low values, it is found that *D. scutum* is at high temperatures more or less unaffected by partial oxygen pressure (the maximal difference of the LT_{50} values was only 0.4"C), whilst it is at low temperatures less temperature resistant when exposed under oligoxic than under normoxic conditions (no lethal effects were found at temperatures up to —4°C under normoxic exposure).

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