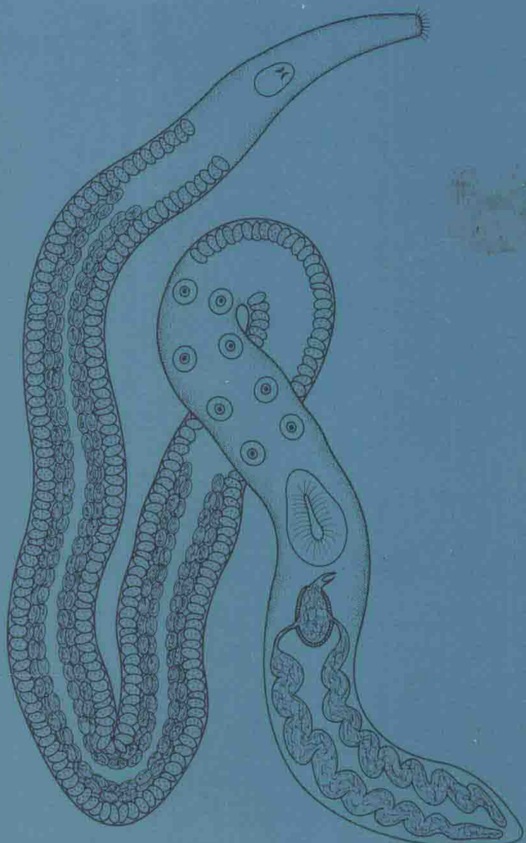
Microfauna Marina

Editor: Peter Ax



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Vorwort des Herausgebers

Die mikrobenthische Meeresfauna – eine Welt mikroskopischer Organismen in den Sedimenten des Meeresbodens – gehört zu den arten- und individuenreichsten Tiergemeinschaften der Erde. Aufgrund unterschiedlicher Körperdimensionen oft in Microfauna und Meiofauna eingeteilt, oder, im Hinblick auf die Siedlung in den Lückenräumen von Sedimenten, als interstitielle Fauna bezeichnet, repräsentiert das marine Mikrobenthos ein Paradebeispiel für die engen Beziehungen zwischen dem abiotischen Gefüge von Lebensräumen sowie der Organisation und Lebensweise ihrer Bewohner.

Über eine Fülle spezifischer Anpassungen an das Milieu hat diese Fauna selbst die extremsten Habitate der Meeresküste erobert. Das interstitielle Mikrobenthos besiedelt die Brandungsufer von Sandstränden, in denen Sediment und Organismen mit jedem Wellenschlag umhergewirbelt werden, gleichermaßen wie die lebensfeindliche Sulfidschicht des Wattbodens, wo es entlang der sauerstofführenden Wohnröhren großer Polychaeten wie Arenicola marina in lichtlose Tiefen eindringt.

Nahezu alle großen Einheiten der Tiere sind im Mikrohöhlensystem mariner Sedimente vertreten. Die stammesgeschichtliche Entwicklung verschiedener artenreicher Taxa wie der Gnathostomulida, Schizorhynchia (Plathelminthes), Macrodasyoidea (Gastrotricha) oder Arthrotardigrada hat sich fast vollständig in diesem Lebensraum vollzogen. Nur ein Teil des Artenbestandes ist bisher wissenschaftlich beschrieben worden. Weite Meeresregionen sind noch gänzlich unbearbeitet.

Die Vielfalt evolutiver Adaptationen reicht von der Gestalt bis in die Feinstruktur von Geweben und Zellen. Die Einpassungen in das abiotische Milieu erstrekken sich auf die gezeiten- und jahresperiodischen Wanderungen ganzer Populationen von Arten im Sandstrand und erfassen selbst minutiöse Details des Fortpflanzungsverhaltens mit einzigartigen Mechanismen der Übertragung von Spermien sowie der Abgabe der Eier in das instabile Substrat. In den Meeressänden leben auf engstem Raum sehr viele Arten miteinander. Fragen zur Spezialisierung und zu den Wechselbeziehungen innerhalb der Lebensgemeinschaften sind noch weitgehend offen.

„Microfauna Marina" will das Spektrum unterschiedlichster Aspekte der Ökologie, Systematik und Evolution, der Morphologie und Ultrastruktur ebenso wie der Lebensweise dieser Faunenkomponente des Meeres erschließen. Die Zeitschrift dient in erster Linie der Publikation von Untersuchungen der Kommission für Zoologie der Akademie der Wissenschaften und der Literatur

Mainz. Darüber hinaus soll in jedem Band auf internationaler Ebene ein Wissenschaftler mit einem Übersichtsreferat aus seinem Arbeitsgebiet zu Wort kommen.

Die Zeitschrift „Microfauna Marina" bildet die Fortsetzung der Schriftenreihe „Mikrofauna des Meeresbodens" (1–90, 1970–1983) der Akademie Mainz. In der kostensenkenden Zusammenfassung mehrerer Beiträge soll sie jährlich mit einem Band im Umfang des vorliegenden Vol. 1 erscheinen. Verlag und Herausgeber möchten den Bezug der „Microfauna Marina" mit dieser Maßnahme für die Abonnenten kalkulierbar machen.

Peter Ax

Foreword of the Editor

The marine microbenthic fauna, defined as animals of microscopic size living in the sediments of the sea, is one of the earth's animal communities of highest species richness and individual abundance. Because of different body dimensions it is frequently separated into microfauna and meiofauna, and it is also called the interstitial fauna with respect to those dwelling in the small spaces between the grains of sand. This microbenthos represents a paragon for the close relationship between the abiotic regime of the environment and the organization and life styles of its inhabitants.

With a wealth of specific adaptations to its environments, this fauna even thrives in the most extreme seashore habitats. The interstitial microbenthos populates the surf zone of sandy beaches, where sediment and organisms are stirred up with each breaker. It similarly colonizes the inhospitable sulfide layer of tidal flats, where the animals penetrate alongside oxic burrows of polychaetes, such as the lugworms, down to lightless depth.

Almost all larger groups of animals are represented in the interstitial system of marine sediments. The phylogenetic development of various diverse taxa such as Gnathostomulida, Schizorhynchia (Plathelminthes), Macrodasyoidea (Gastrotricha) or the Arthrotardigrada took place almost exclusively in this habitat. Merely some part of the total stock of species has been described scientifically. Wide regions of the sea are still completely uninvestigated.

The diversity of evolutionary adaptations includes body shape as well as ultrastructures of tissues and cells. Adjustments to the abiotic regime extend from tidal and seasonal migrations of entire populations within the sandy beach to even minute details of reproductive behaviour with unique mechanisms of sperm transfer or egg deposition in this unstable substrate. A high number of species coexists in the narrow spaces of these marine sands. Most questions to niche refinements and interactions within this animal community still await their answers.

"Microfauna Marina" intends to cover the spectrum of all aspects of ecology, systematics and evolution, of morphology and ultrastructure, just as the natural history of this faunal component of the sea. Primarily the journal serves to publish research of the commission of zoology of the Mainz Academy of Science and Literature. Furthermore on an international level, each volume will give a scientist the opportunity to review her or his field of investigation.

The journal "Microfauna Marina" is an continuation of the series "Mikrofauna des Meeresbodens" (1–90, 1970–1983) of the Academy of Mainz. In the cost reducing condensation of several contributions, the publication will be annually with one volume in the size of the present Vol. 1. With this step the publisher and editor want to make the purchase of "Microfauna Marina" calculable to subscribers.

Peter Ax

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Free-Living Platyhelminthes (Turbellaria) of a Marine Sand Flat: An Ecological Study

by KARSTEN REISE

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Abstract

In a 10 × 10 m area of a sheltered, sandy flat in the lower intertidal at the island of Sylt (North Sea), free-living Platyhelminthes (Turbellaria) were investigated with respect to species composition, diversity, abundance, size distribution, trophic categories, spatial and temporal patterns of species coexistence. Burrows of the lugworm *Arenicola marina* are the dominant biogenic structures in this coarse grained sediment. Every fourth months from June 1980 to June 1981, 260 samples of 2 cm^3 were taken from 26 micro-sites (18 from burrows and 8 from depth intervals of the normal sediment).

The average below 10 cm^2 is 111 individuals (11% of all Metazoa), 24 species, and a biomass of $2.6 \cdot 10^{-4}$ g dry organic weight of Turbellaria. The total number of species is 83. Sizes range from $2 \cdot 10^{-4}$ to 1 mm^3. Predators are larger than grazers, comprise 53% of abundance, 65% of all species, and 88% of biomass. The order Proseriata dominates in biomass, while the Kalyptorhynchia are more abundant and richer in species.

Turbellaria perceive the sand flat sediment as a structurally complex and variable environment. Horizontal distribution is patchy. Populations differ significantly in vertical positions on gradients from the oxic sediment surface to anaerobic depth. Lugworm burrows exhibit high individuality and provide 5 distinct habitats which seasonally change their hospitality. Burrows include refuges, centers of population growth, alternatives when other habitats deteriorate, and also attract tourist species.

Populations confined to the sediment surface are less predictable than those dwelling below. Large size of spatial niches is correlated with low population variability. Assemblage structures seem to mirror the spatio-temporal patterning of the environment. High species richness is probably caused by habitat complexity at a scale where the small sized Turbellaria are most responsive.

A. Introduction

Intertidal sand flats in the Wadden Sea at the island of Sylt are subject to harsh physical conditions: semi-diurnal exposure with high temperatures in summer, ice cover in winter, occasionally anaerobic conditions, and sediment disturbances during gales. In such an environment, a benthic community of simple structure is to be expected, where few generalist species of variable population size partition the available resources. However, the small Turbellaria, 0.2 to 8 mm in length, feeding on bacteria, microalgae or small zoobenthos, are exceptionally rich in species, have different reproductive seasons, and require rather specific habitat conditions (Ax 1977; Reise & Ax 1979).

In this study, the role of small-scale habitat heterogeneity on species composition and other assemblage characteristics of the Turbellaria is explored. All data were collected from a 10 × 10 m plot. First, overall parameters of the assemblage are presented, and then the micro-spatial habitat partitioning among species is analyzed. Special attention is payed to burrows of lugworms as habitats to Turbellaria. It is concluded that the sand flat constitutes a structurally very complex, ever changing environment where many similar species of Turbellaria can coexist without displacing each other, and this causes a very high species diversity.

This ecological study would have been impossible without the diligent care and effort devoted to the taxonomy of Turbellaria at the island of Sylt (AX 1956, 1971; AX & HELLER 1970; DÖRJES 1968; EHLERS 1972, 1974; FAUBEL 1974 a, b; SCHILKE 1970; SOPOTT 1972).

This research was supported by the Deutsche Forschungsgemeinschaft (DFG). I thank Prof. Dr. Otto KINNE and the staff at the Litoralstation List, Biologische Anstalt Helgoland, who generously provided superb laboratory facilities. The greatest debt of gratitude I have to Prof. Dr. Peter AX for his stimulating introduction into the diversity of Turbellaria. My thanks also go to many friends and colleagues who helped with taxonomic advice, observations and keen questions: Werner ARMONIES, Dr. Ragnhild ASMUS and Dr. Harald ASMUS, Sabine DITTMANN, Dr. Beate EHLERS and Dr. Ulrich EHLERS, Dr. Anno FAUBEL, Monika HELLWIG, Silke RIEBENSAHM, Prof. Dr. Reinhard RIEGER, Bernd SCHERER, Christian WEHRENBERG, Prof. Dr. Wilfried WESTHEIDE, Willy XYLANDER and Marianne ZOCHER. Thanks are due to Bernd BAUMGART who skillfully prepared the art work.

B. Material and Methods

Sampling Turbellaria

Samples were taken from a 100-m^2 plot, from June 1980 to August 1981. During low tide, sediment cores were obtained with a transparent tube of 2 cm^2 cross area and 10 cm in length. Immediately after withdrawing the closed tube, I let the sediment core slide on a plate and dissected it into 1-cm intervals down to 8 cm, thus obtaining 8 samples of 2 cm^3 each. In the laboratory, each 2-cm^3 sample was diluted with sea-water, repeatedly shaken and decanted into petri dishes, including the residual sand. Neither sieves, narcotics nor stains were used. Individuals were measured under the binocular or microscope, identified to species level, and the gut content was recorded.

Samples were taken from the normal sediment and from burrows of the lugworm *Arenicola marina* (L.) which constitute the major biogenic habitat to Turbellaria in the subsurface layer. From a total of 26 micro-sites, 8 were located along the gradient from the oxic sediment surface to the anaerobic subsurface, and 18 were located at lugworm burrows (Fig. 1). In each of 4 months (June and October 1980, February and June 1981) each micro-site was sampled 10 times. Thus, the total set comprised 4 × 26 × 10 = 1040 samples equal to 2080 cm^3 of

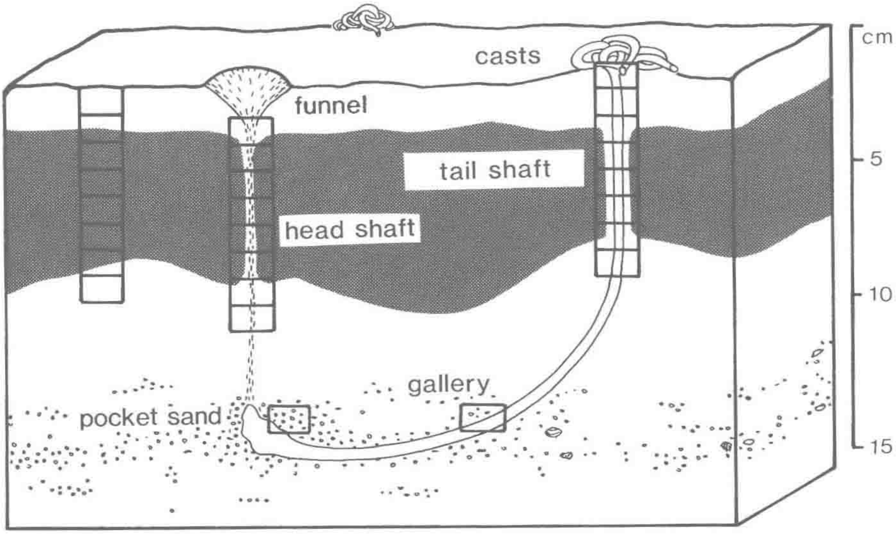

Fig. 1. Sampling design at the sand flat with burrows of *Arenicola marina*. Each of the 26 squares marks the position of a 2-cm^3 sample (diameter 1.6 cm, height 1 cm). Dark shading: monosulfide-horizon. Dotted region: coarse grained material in the bisulfide-horizon.

sediment. Additional samples have been taken during experiments in September 1980 and July and August 1981.

Estimating Abundance and Biomass

To estimate overall abundance of Turbellaria per area, the 26 micro-sites are multiplied by the frequency and the size of the habitat structures they represent (Table 1). For simplicity, micro-sites are grouped into 8 major habitat structures. This decision is based on an analysis of faunal similarity. The normal sediment is divided into a surface layer and a subsurface layer. Lugworm burrows comprise 6 major habitat structures: funnels and casts in the surface layer; head and tail shafts, feeding pockets and galleries in the subsurface layer. The size of burrow structures is variable, and so is the number of burrows. In this study, standard sizes and a constant number of burrows are taken to calculate overall abundance of Turbellaria. Instead of actual diameters of vertical shafts of the burrows, a 2-cm^2 cross section is assumed to include Turbellaria of the immediate vicinity.

Biomass of Turbellaria was not weighted but is calculated from individual volumes. Estimates of volumes are based on length measurements obtained from crawling individuals. Width was measured for every length class of a species. Shapes are assumed to be cylinders; in Acoela and Coelogynoporidae half-cylinders. Biovolume per area is calculated the same way as abundance (Table 1).

Table 1: Estimating abundance of Turbellaria for 1 m^2 of sand flat with 60 burrows of *Arenicola marina*. Individuals counted in the monthly sum of samples taken from each habitat structure are multiplied by an appropriate conversion factor. The sum of these products is the estimate of abundance $\cdot m^{-2}$. The total of 26 micro-sites is grouped into 8 habitat structures on the basis of faunal similarity. LB = lugworm burrows.

Habitat structure	dimensions and frequency of structure	volume of structure ($cm^3 \cdot m^{-2}$)	volume sampled (cm^3)	conversion factor
surface layer	upper 1 cm, excluding casts and funnels	8 800	20	440
funnels of LB	($10\ cm^2$/0–1 cm) × 60	600	20	30
casts of LB	($10\ cm^2$/0–1 cm) × 60	600	20	30
subsurface layer	1–8 cm depth, excluding LB	68 320	140	488
head shafts of LB	($2\ cm^2$/1–15 cm) × 60	1 680	140	12
tail shafts of LB	($2\ cm^2$/1–15 cm) × 60	1 680	140	12
pocket sand of LB	($10\ cm^3$) × 60	600	20	30
galleries of LB	($10\ cm^3$) × 60	600	20	30

Biomass is obtained by multiplying volume with 0.22. This factor is inferred from a specific gravity of 1.1 and a dry weight: wet weight ratio of 0.2 (see McINTYRE 1969; HANSEN 1978). These estimates compare well with measurements on the dry weight of 3 length classes of Turbellaria given by FAUBEL (1982).

Statistical Analysis

Temporal and spatial variability in abundance is expressed as $v = s/\bar{x}$, with s and $\bar{x}$ being standard deviation and mean respectively. Patchiness is evaluated by plotting $\bar{x}$ versus $s^2/\bar{x}$ on logarithmic scales. Significance is obtained by reference to the appropriate chi square (at $P = 0.05$ and $n = 10$ observations $\chi^2 = 16.92$, to be divided by $n - 1$). Thus, ratios of $s^2/\bar{x}$ exceeding 1.88 indicate significant deviation from random expectation (see GAGE & GEEKIE 1973).

In comparisons between microhabitats the nonparametric U-test (WILCOXON, MANN & WHITNEY) and H-Test (KRUSKAL & WALLIS) are applied (SACHS 1974: 230 and 238). Because equality of ranks occurs frequently in the data, RAATZ's method of rank partitioning is used (LIENERT 1973: 233). In pairwise comparisons of distributions along vertical gradients in the sediment, the test is on significant differences in location (sum of ranks test for grouped observations developed by RAATZ in LIENERT (1973: 233)). Grouped observations are the number of individuals in a 1-cm interval of the gradient. To supplement this test, an index is used: sum of coexisting individuals of a pair of species divided by all individuals. Spatial correlations between pairs of species are calculated over all 26 micro-sites. Significance is evaluated with SPEARMAN's rank correlation coefficient, corrected when equality of ranks occurs (SACHS 1974: 309).

Affinities between microhabitats are expressed with RENKONEN's index ($R = \sum p_s$, with p_s being the proportion of individuals in the microhabitat where the species s is less abundant) and SØRENSEN's index ($S = 2j/(a+b)$, with j being the joint number of species, and a and b are the number of species in the two microhabitats (RENKONEN 1938, SØRENSEN 1948).

Species diversity is characterized by 4 indices which give different weight to species richness and the sequence of dominance. (1) SHANNON's entropy $H' = -\sum p_i \, ln \, p_i$, where p_i is the importance value (proportion of individuals or biomass) of the i-th species with i = 1,2,3... S. Figuratively, H' may be taken as the logarithmic number of the abundant species within the sequence. (2) A modification of SIMPSON's measure of concentration: $D = 1 - \sum p_i^2$. This gives the mean probability that an individual will as a next random encounter meet one of a different species (HURLBERT 1971). (3) HILL's ratio modified by ALATALO (1981) is used as a measure of evenness: $E = ((1/\sum p_i^2) - 1)/((exp H') - 1)$, where *exp*H' denotes the antilogarithmic SHANNON's entropy. This measure may be interpreted as the number of very abundant species divided by the number of abundant ones. Rare species are neglected and thus E should be reasonably independent of species richness (ALATALO 1981). (4) A measure of dominance (d) is the ratio of the most dominant species versus the total. In the form of 1 – d, this measure may be viewed as an index of diversity.

C. The Sand Flat Environment

Physical Conditions

The sand flat is located in Königshafen, a sheltered bay in the Northfrisian Wadden Sea, east to the island of Sylt (55° 02' N, 8° 06' W) (Fig. 2). Tidal range is 1.7 m. Salinity remains close to 31. The annual mean water temperature is 10° C. In summer the average is 15.1 and in winter 4.5. Extreme temperatures (30° C) occur sporadically in summer during low tides in small residual water

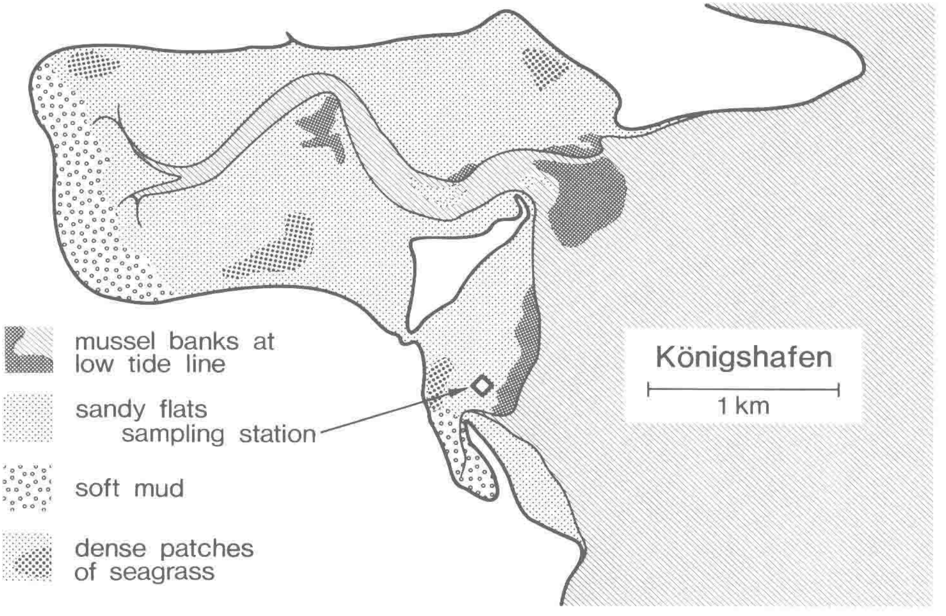

Fig. 2. Intertidal Königshafen at northern end of Sylt. Arrow points to sampling station.

Fig. 3. Sand flat investigated. The small mounds are casts of *Arenicola marina*, and there are several low tide puddles.

bodies. Severe winters with prolonged ice cover occur every 6 to 10 years. This happened prior to this study early in 1979. A detailed description of the Königshafen, its sediments and the macrofauna, is given by WOHLENBERG (1937).

The sand flat is positioned close to low tide line and exposed to air for about 2 hours per semi-lunar tidal cycle. Depth at high tide is 1.6 m (– 0.75 m NN). The sediment remains water saturated throughout and always some puddles persist until the tide comes back (Fig. 3). In spite of the sheltered position, the sediment is relatively coarse grained. Dry sieving gives a median of 0.456 mm (phi = 1.14) and a sorting coefficient of 1.5. Measuring particle size of minerals with a microscope, a median diameter of 0.485 mm (705 particles) is obtained. Sand grains between 0.25 and 1.00 mm diameter contribute 85% to the sediment dry weight. Abundance of coarse grains is not the result of strong currents but is caused by sand dunes. In the past, they migrated from an exposed high energy beach into the bay (PRIESMEIER 1970). Weight of dry organic substance in the sediment is 0.44%, determined as weight loss at 600°C.

On the average, the upper 2 cm of the sand flat sediment are brownish. Below, the colour changes abruptly to black which in turn gives way to grey at about 7 cm depth. This tricolor is caused by chemical reactions with iron compounds (van STRAATEN 1954; LITTLE-GADOW 1978). As in other marine sediments, oxy-

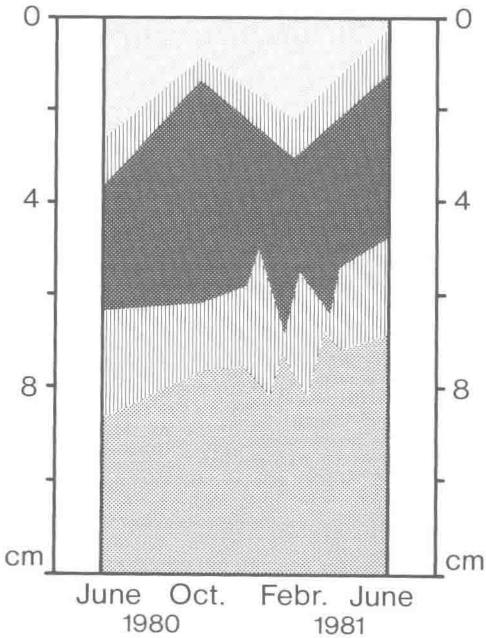

Fig. 4. Vertical extension of 3 coloured horizons (brown–black–grey) in the sand flat sediment from June 1980 to June 1981. Zones of transition are vertically shaded and refer to standard deviations of 10 measurements at a time. In winter black and grey horizons are indistinctly delimited.