

QUANTITATIVE AND EXPERIMENTAL STUDIES OF THE INTERSTITIAL FAUNA IN FOUR SWEDISH SANDY BEACHES

BENGT-OWE JANSSON

Department of Zoology and Askö Laboratory, University of Stockholm, Sweden.

ABSTRACT

The distribution of the interstitial metazoans was studied quantitatively in four Swedish beaches, three in the Baltic and one in the Skagerrak. As many as 1.5×10^6 individuals per m^2 were found (Askö beach, south of Stockholm). Temperature, salinity, oxygen concentration and availability, grain size, water contents and organic material were measured in connection with the sampling.

The oligochaetes, turbellarians and harpacticoids showed different degrees of submergence landwards in the beaches with the oligochaetes near the sand surface, followed by the turbellarians and – deepest down – the harpacticoids. This may be explained by a difference in dependence on water-saturation: the oligochaetes are more or less terrestrial, and the turbellarians can move in a thinner water film than can the harpacticoids.

A correlation between the distribution of oxygen and certain species was found in several cases. The microbial film on the sand grains is pointed out as an important food-source and the utilization of dissolved (or precipitated) organic material in the interstitial water is discussed.

Of the other abiotic factors temperature and salinity had the greatest influence on the major part of the fauna. Tolerance and preference experiments with these parameters were carried out with the most common species in the beaches, 2 turbellarians, 4 oligochaetes and 6 harpacticoids. Tolerance to high temperature was tested at 30°C. Most tolerant was the harpacticoid *Parastenocaris phyllura* with an LD 50 of 5-6 days, while the turbellarian *Haplovejdovskya subterranea* was very sensitive (LD 50 = 16 h). These animals also inhabit the two margins of the beach – the former the backshore and the latter the water's edge. Winter samples of totally frozen sand contained live specimens of several species, e.g. *Coronhelms lutheri*, the gastrotrichs *Turbanella hyalina* and *T. cornuta*, many nematodes, the oligochaetes *Marionina southerni* and *Aktedrilus monospermatecus*, *Parastenocaris phyllura*, and the halacarid *Halacarellus capuzinus*. The body fluids of these animals may not have been frozen as the temperature in the frozen layers seldom falls more than a few degrees below zero.

According to their salinity tolerances the experimental animals were divided into three classes. The first, most euryhaline, class comprises the turbellarian *Coronhelms lutheri* and the harpacticoids *Schizopera baltica* and *Nitochra fallaciosa f. baltica*. The second class is represented by the oligochaetes *Marionina southerni* and *Aktedrilus monospermatecus* and the harpacticoid *Nitochra fallaciosa*. The most stenohaline class comprises *Haplovejdovskya subterranea*, *Marionina preclitellochaeta* and the harpacticoids *Paraleptastacus spinicauda*, *Parastenocaris vicesima* and *P. phyllura*. The salinity tolerance tests clearly showed the importance of mucus secretion as a protective mechanism in the first phase of adjusting to a higher salinity.

The optimum zones found through the preference tests with the different species generally appeared to agree well with the field distributions.

INTRODUCTION

In previous papers I have discussed the dynamics of the chief parameters in marine sandy beaches, viz. oxygen (1968), grain size and pore water (1967b), temperature and salinity (1967c). I have also described the distribution and reactions of single interstitial species in relation to several abiotic factors in some sandy beaches: *Derocheilocaris remanei* (1966b) and *Parastenocaris vicesima* (1967a). In the present paper the whole meiofauna and its distribution will be treated and related to the major parameters on the basis of laboratory experiments with the dominating species.

Though numerous studies on the interstitial sand fauna have been published, very few are quantitative. Pennak (1940) and Neel (1948) studied the mesopsammon in North American lakes. Pennak (1942) described the zonation of intertidal copepods near Woods Hole and Wieser (1960) studied the meiofauna of a benthic community in the same area. Wieser & Kanwisher (1961) investigated the ecology and physiology of marine nematodes from a small salt marsh. At Indian beaches Ganapati & Rao (1962) and Govindankutty & Nair (1966) carried out quantitative sampling and measurements of the more important environmental factors. In France and in the Bahamas, Renaud-Debyser (1963) analyzed the faunal spectrum, demonstrated an annual variation in the distribution of the animals and pointed out the great effects of the tidal water movements on the dispersal and concentration of the animals. At several stations along the French Atlantic coast Renaud-Debyser & Salvat (1963) measured the biomass of the whole fauna in tidal beaches and described food chains for two types of beaches. In Portugal, Wells & Clark (1956) studied the intertidal distribution of interstitial crustaceans, and at Miami, Florida, Bush (1966) demonstrated an irregular distribution of the fauna in several beaches. Quantitative sampling of the sand microfauna and meiofauna has also been carried out by Fenchel & Jansson (1966) who studied the vertical distribution of the animals in relation to distribution of oxygen, pH and redox potential. Jansson (1967a) explained the distribution of the harpacticoid copepod *Parastenocaris vicesima* on the basis of laboratory experiments and field measurements. Fenchel, Jansson & v. Thun (1967) sampled the metazoan interstitial fauna, including nematodes, in a Danish beach and discussed the distribution of the different species. Fenchel (1967) studied the quantitative relations between the protozoans – especially the ciliates – and the micro-metazoans in Scandinavian waters.

The present study has been supported by grants from "Anslaget för främjandet av ograduerade forskares vetenskapliga verksamhet", Hierta-Retzus stipendiefond and Lars Hiertas minne. I am greatly indebted to my teacher, Professor Lars Silén, Stockholm, for his positive criticism and for valuable discussions. I also thank Professor Karl Lang, Stockholm, for kind and generous help with the identification of the harpacticoids, and Professor Tor G. Karling, Stockholm, for

valuable discussions, concerning the turbellarians. Professor Bent Christensen, Copenhagen, kindly checked the determinations of some of the enchytraeids. I am also in great debt to Dr. Carl-Cedric Coulianos, Stockholm, for lively and inspiring ecological discussions and to my wife, Dr. Ann-Mari Jansson for valuable advice on many ecological questions. Miss Lena Fernbrink skilfully sorted the samples and made the diagrams.

MATERIAL AND METHODS

The quantitative studies were carried out at the same four localities as those studied in Jansson (1967b, c, 1968), viz. Askö in the Baltic, about 60 km south of Stockholm; Tofta, 20 km south of Visby, Gotland; Simrishamn on the Scanian east coast; and Tylösand on the west coast of Sweden, 10 km north of Halmstad. A description of the beaches and the climatic conditions of the respective areas is presented in Jansson (1967c). These characteristics can be summarized as follows. Askö beach is rather steep and composed of heterogeneous sand, Md ϕ : 550 μ . The ground-water pressure is great, and freshwater often occurs at a few metres distance from the sea which has a salinity of about 6.5‰. The oxygen supply is quite considerable and the organic material seldom occurs in amounts causing black layers of decaying material or iron sulphides. Tofta beach is composed of homogeneous sand, Md ϕ : 400 μ . The slope is medium and the exposure softened by a shallow sublittoral. The salinity gradient in the beach is steep, the oxygen contents often depleted to zero at depths below 10–15 cm, and the amount of detritus small. Simrishamn beach is very exposed to the sea with a steep slope and a coarse, very homogeneous sand, Md ϕ : 1200 μ . The availability of oxygen is high, owing to the great permeability and turbulence, and the flow of ground water from the land is considerable, causing a rather steep salinity gradient of the interstitial water. The amount of organic material is rather large, but due to the rich oxygen supply black layers seldom occur. Tylösand beach has a flat slope, exposed to the sea and bordered landwards by tall dunes, which causes a high ground-water pressure. The salinity consequently shows great fluctuations. The sand is rather homogeneous and fine, Md ϕ : 300 μ . The oxygen supply is rather limited, and irregular occurrences of organic material sometimes give rise to black layers.

FIELD MEASUREMENTS

The slopes of the beaches were measured as done by Emery (1961). In other cases the ground-water level was used as basis line in the diagrams. The difference between the results deriving from these two methods is probably small. Temperature was measured with 0.1°C mercury thermometers, inserted in the walls of holes dug in the sand, except for the winter studies, when the values were obtained from

TABLE 1. Numbers of specimens obtained after successive washings of 10 cm³ samples from Tofta. *Marionina* anaesthetized in 10 % alcohol, *Coelogygnopora* afterwards preserved in 80 % alcohol.

Washing no.	<i>Marionina subterranea</i>				<i>Coelogygnopora schulzii</i>			
	n	%	n'	%	n	%	n'	%
1	131							
2	62							
3	29							
4	27	92	225	94	120	100	114	100
5	8							
6	9							
7	4	100	14	100	—	—	—	—
10	—		—		—	—	—	—
Total	270		239		120		114	

a multi-colour dotted-line recorder with platinum thermometers. Samples for salinity determinations were obtained from various depths in the sand with a 1 ml hypodermic syringe, and the specific conductivity was determined with a Wheatstone bridge. In the first studies, viz. at Tofta and Tylösand, the oxygen content was determined by the Winkler method on samples obtained with a 30 ml hypodermic syringe. On the other localities the availability of oxygen was measured with a stationary platinum micro-electrode. The contents of pore water was determined by a carbide method and expressed as percentage of wet weight of the sand. The grain size of the samples, from which the animals were picked quantitatively, was analyzed according to Morgans (1956). The amount of visible organic material was only estimated and classified from the no visible amounts (—), to more than 20 % of the sample consisting of detritus (+++). Further information concerning the measurements of the separate parameters can be found in Jansson, 1968 (oxygen), 1967b (grain size and pore water) and 1967c (temperature and salinity).

SAMPLING THE FAUNA

The qualitative sampling was made as done by Chappuis (1946). A hole, 1 metre in diameter, was dug to the ground-water level, the water intermittently stirred, and the suspended animals collected by means of a net with 100 μ meshes. Temperature and salinity were measured and the abundance of animals estimated. The quantitative samples were obtained with a core sampler, giving successive samples of 10 or 20 cm³. Each core represents an area of 10 cm². The sampler and the mode of operation is described in Jansson (1967b). The animals, transferred from the sampler to small glass jars, were either studied alive, as in the samples from Tofta and Askö locality B, or they were preserved in 70 % alcohol. In both

TABLE 2. Numbers of specimens obtained after successive washings of samples filled to 5 times their own volume with 10 % alcohol. The stations represent Askö, locality B, 29 July 1965.

Station	Washing no.	Turbellaria	Nematoda	Oligochaeta	Harpacticoida	Halacarida
A	1-4	3	104	76	22	4
	5	—	9	3	3	—
	6	—	—	—	—	—
B	1-6	6	72	99	18	5
	7	—	2	—	3	—
C	1-6	3	48	99	17	3
	7	—	—	2	3	—
D	1-6	—	127	33	5	1
	7	7	6	—	—	—

cases the animals were first anaesthetized with 10 % alcohol which was poured into the sample after supernatant water had been removed by sucking through a piece of plankton gauze. For preservation all free liquid was then sucked off and 80 % alcohol added. The animals were removed by gently shaking the sample with sea-water or alcohol before pouring out the suspension, and this was repeated four times. The efficiency of this method is shown in Table 1. *Marionina subterranea* and *Coelogygnopora schulzii* were chosen as representatives of forms with numerous adhesive glands, and which therefore are most difficult to separate from the sand. The oligochaetes were washed in an anaesthetized state, the turbellarians were preserved. After 4 washings 92 % of the oligochaetes were obtained, and the remainder appeared after 3 additional washings. All the turbellarians appeared after 4 washings.

At Askö, locality B, where only the horizontal distribution of the fauna was studied, whole cores were taken. The largest sample which amounted to 760 cm³ was treated in two parts. Each sample was washed 7 times with 10 % alcohol to five times its own volume, and the animals secured were then transferred to water from the habitat. The efficiency of this method is shown in Table 2. Nearly all animals were obtained after 6 washings and when the sand was examined after the 7th treatment no further specimens could be found. Anaesthetized animals recovered rapidly when transferred to habitat water and there were no complications with the identifications.

A quantitative sampling was always accompanied by qualitative samples from which a picture of the faunal composition was first obtained. The live specimens from the qualitative samples were identified and afterwards fixed just as the quantitative samples. The appearance of the preserved and already determined specimens was then noted and a simple "key" to preserved species of the separate

groups was made. With this key to the dominating species even so delicate animals as turbellarians could in most cases be identified to species.

In order to obtain samples in winter, when the ground was frozen, lumps of sand from different depths were broken off, brought to the laboratory and carefully thawed. Their volume and water content were roughly determined and, when possible, also the salinity. The animals were then washed out, identified and counted.

In all samples the whole meiofauna was collected except for Collembola, which were regarded as terrestrial. They very seldomly occurred in the quantitative samples but were sometimes found in great numbers on the ground-water surface in holes dug for qualitative sampling.

LABORATORY EXPERIMENTS

The animals chosen for laboratory experiments were usually collected in the field in connection with the quantitative sampling. They were kept in the laboratory under controlled conditions, in water from the habitat, with natural food, in darkness and at a temperature close to that of the field. The specimens for the separate experiments (adults or large juveniles – for harpacticoids males as well as females) were mostly picked out a day in advance and kept in habitat water over night to reveal the presence of any weak individuals, which were then replaced. No food was offered during the experiments.

For the tolerance tests the various salinity concentrations were obtained by diluting aged sea-water with distilled water. Small dishes were furnished with 5 ml of each concentration and the specimens were put directly into the water without previous adaptation. The water was not changed during the experiment but solid waste products were removed together with the dead animals. A specimen was regarded as dead when it did not react to the touch of a needle. The results were plotted as LD 50-curves and statistically treated with rank-sum test according to Dixon & Massey (1957 p. 289ff.). All the curves in the diagrams are eye-fitted.

The preference experiments were carried out according to the methods used by Jansson (1962). The chambers were kept in darkness at the same temperature as during the pretreatment of the animals. The number of animals in each experiment – “n” in the diagrams – refers to the number of living specimens after the experiment. Very few individuals died during the experiments. The results were treated with the χ^2 -test to show whether the obtained values differed significantly from each other.

RESULTS

FIELD STUDIES

Askö

LOCALITY A. – For studies of the seasonal variation of the fauna in the Askö beach qualitative samples were taken on 5 June, 9 August, 5 November, and 28 March 1963. The composition of the fauna in June, August and November is shown in Table 3. The abundance of the animals was only estimated and grouped in four classes from very few (+) to very numerous (+++ +). As the collecting time was rather long and the amount of sand worked through correspondingly large the animals must have been caught in proportion to their abundance, be-

TABLE 3. The abundance of interstitial animals in Askö beach 1963.

	June	August	November
TURBELLARIA			
<i>Macrostomum curvatura</i>		+++	
<i>Provortex pallidus</i>		+	
<i>Haplovedjovskya subterranea</i>		+++	+
<i>Coronhelms multispinosus</i>		++	
<i>Coronhelms lutheri</i>	++		
<i>Prognathorhynchus canaliculatus</i>		+	
GASTROTRICHA			
<i>Turbanella hyalina</i>	+		
<i>Turbanella lutheri</i>		++	
NEMATODA			
	++++	+++	+++
OLIGOCHAETA			
<i>Nais elinguis</i>	+		
<i>Marionina southerni</i>	+++	+++	+
<i>Marionina subterranea</i>		+	
<i>Lumbricillus lineatus</i>	+++		
<i>Akteredilus monospermatecus</i>	++	++	+
HARPACTICOIDA			
<i>Parastenocaris phyllura</i>	+++	++++	+
<i>Huntemannia jadensis</i>			+
HALACARIDA			
<i>Halacarellus capuzinus</i>	++		
ENVIRONMENT			
Distance from water's edge, metres ..	1	2	1
Temperature, C°	15.1	18.3	4.5
Salinity, ‰ S	3.7	0.1	0.4

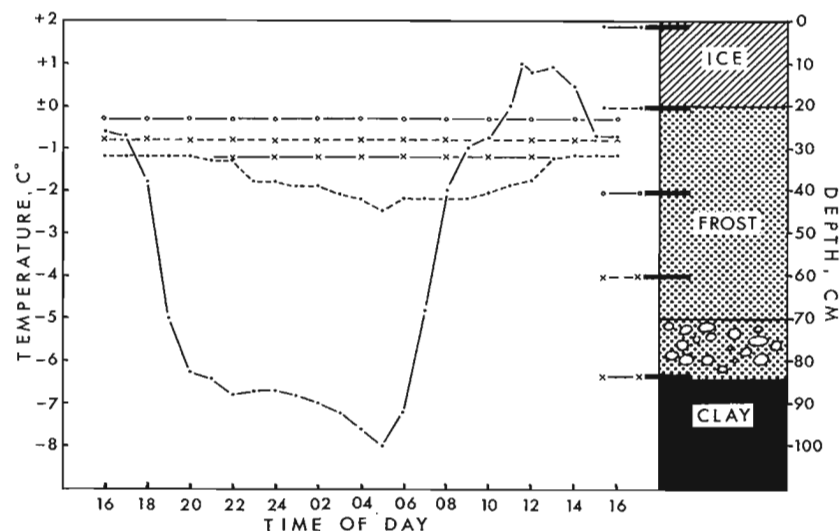


FIG. 1. Vertical section of the upper metre of the beach at Askö, 28 March 1963, with temperature variations at different depths. The distribution and abundance of the animals are shown in Table 4.

cause the differences due to patchy distribution of some species have been equalized. On basis of experience from previous samplings in the same areas the stations were placed in the most densely populated zone and the separate samples are therefore well comparable. The same station was sampled every time, the longer distance to the water line in August being caused by an exceptionally low sea level which also caused low salinities. The most outstanding feature is the scarcity of animals in November, which was also apparent in samples from the same area two weeks later. The fauna showed a maximum in August and especially the turbellarians were more numerous than in June. *Marionina southerni* and *Parastenocaris phyllura*, so numerous in the summer months, were this year very rare in late autumn.

The winter conditions of the beach are seen in Fig. 1. Below an ice cover of 20 cm the sand was frozen down to the underlying bed of blue clay. No unfrozen water could be detected as also indicated by the solidity of the sand. The temperatures were very uniform: at 40-85 cm, -0.4 to -1.2°C ; at 20 cm, -1.2 to -2.3°C ; and at 0 cm, $+1.0$ to -8.0°C . The number of animals in each sample from each 10 cm interval is shown in Table 4. The depth figures indicate the distance from the ice surface, and each sample comprises 700 cm^3 sand. The salinity at 50-60 cm depth, where the amount of water was sufficient for a determination, was 0.7‰ . The station is the same as that of June-November, but the water line

TABLE 4. The numbers of animals in 700 cm^3 frozen sand at various depths. The state of the animals after thawing of the sample are indicated by L = living and D = dead. Askö beach 28 March 1963, same station as in Table 3. The environmental conditions are shown in Figure 1. The nematode figures are approximate.

	Depth cm.											
	30-40		40-50		50-60		60-70		70-80		80-84	
	L	D	L	D	L	D	L	D	L	D	L	D
TURBELLARIA												
<i>Coronhelms lutheri</i>				1								
GASTROTRICHA												
<i>Turbanella hyalina</i>		2				2						
<i>Turbanella cornuta</i>		2										
NEMATODA												
	100	100	100	50	100	50	75	50	40	15	500	15
OLIGOCHAETA												
<i>Marionina southerni</i>	1	2	29	16		5	18		8			
<i>Marionina</i> sp.									3	16	3	4
<i>Akteredilus monospermatus</i>												
HARPACTICOIDA												
<i>Parastenocaris phyllura</i>	4	14	5	5								1
Other species						4	10		3		1	
HALACARIDA												
<i>Halacarellus capuzinus</i>			3	1	2	1	11	11	6	7	4	
EGGS												
Unidentified, olive green	28		60		24		43		12		12	

was now situated 4 m further seawards. The nematodes were dominating among the living animals. The oligochaetes were well represented, especially by *Marionina southerni*. Two thirds of the few gastrotrichs were alive. Among the harpacticoids several specimens of *Parastenocaris phyllura* were alive. *Halacarellus capuzinus* was quite common and most specimens were alive. Only one turbellarian was found, a live specimen of *Coronhelms lutheri*.

Quantitative samples were also taken on 7 August 1963. The weather had been steady and sunny with weak winds during the preceding two weeks. Measurements of the chief environmental factors are shown in Fig. 2. The salinity gradient was very steep - freshwater was found already 2 m landwards. Two days earlier, however, the water line was situated 0.5 m further landwards and the salinity at St. B was 3.8‰ (Jansson, 1967c, fig. 14). The lowering of the sea level took place during the preceding night. The distribution of pore water is irregular. Low values in rather deep layers were measured at St. C at 25 cm depth and at St. D at 35 cm

samples, taken a few decimetres apart. Corresponding environmental data are presented in Figure 2.

									Total n + n'	ind/ 10 cm³								
14 n n'		16 n n'		18 n n'		20 n n'		22 n n'		24 n n'		26 n n'		28 n n'		30 n n'		
																	18	
																	33	
																	12	
																	29	
																	325	
																	6	
																	34	
																	62	
																	76	
																	116	
																	58	
																	4	
																	9	
																	782	39
																	67	
																	50	
																	79	
																	1	
																	8	
																	693	
																	245	
																	6	
																	51	
																	5	
																	182	
																	3	
																	1657	
																	2	
																	4	
																	1	
																	1	
																	305	109
																	7	
																	4	
																	10	
																	14	
																	557	
																	14	
																	1	
																	313	
																	772	
																	2	
																	164	43
																	1	
																	1	
																	3	
																	831	
																	3	
																	339	
																	638	
																	2	
																	1818	30

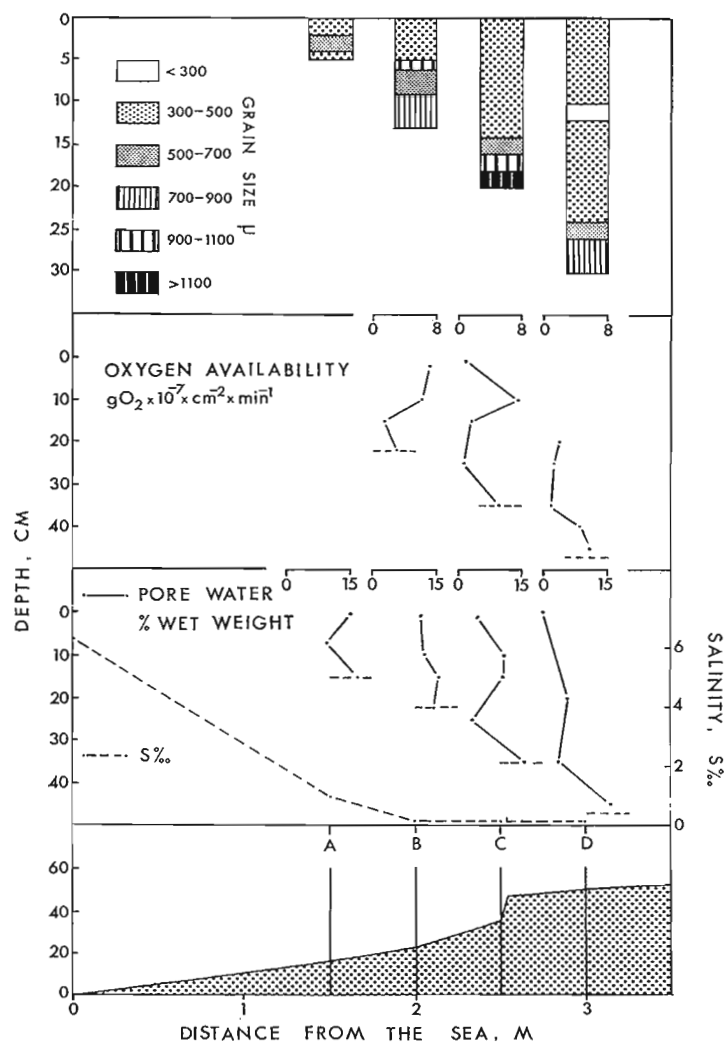


FIG. 2. The distribution of some environmental factors at Askö, locality A, 7 August 1963. The dashed, horizontal lines indicate the ground-water levels.

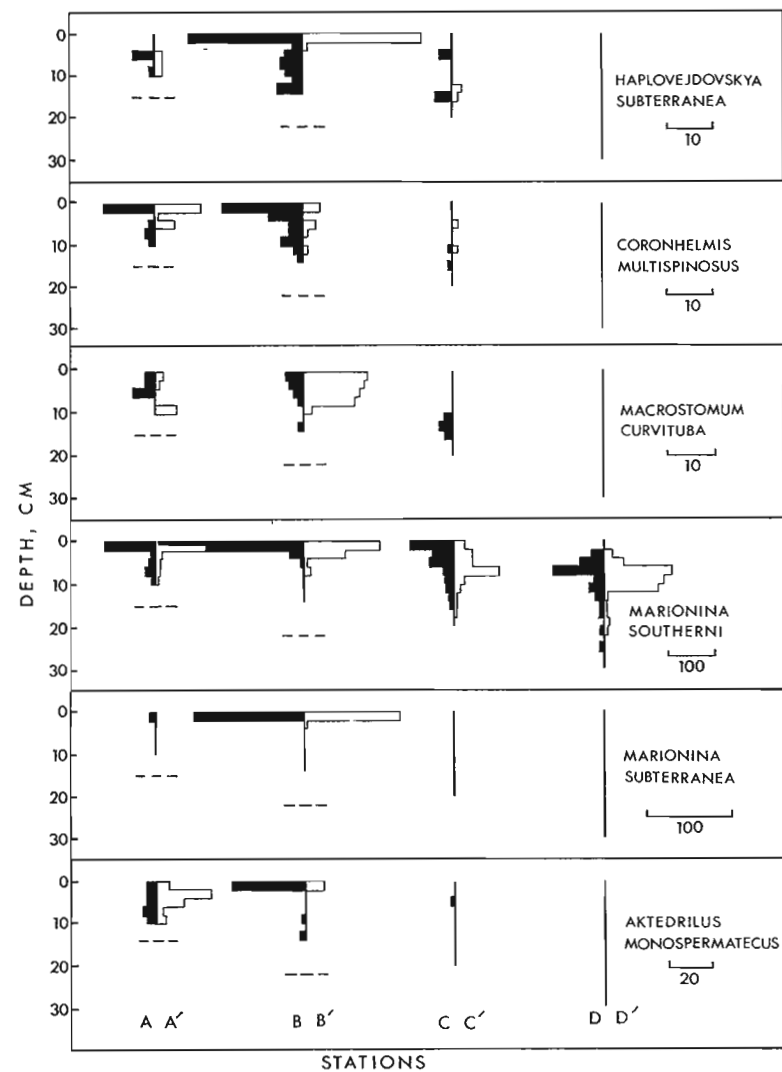


FIG. 3. The distribution of animals at Askö, locality A, 7 August 1963. The figures represent specimens per 20 cm². Corresponding environmental data are presented in Fig. 2. The total fauna is listed in Table 6.

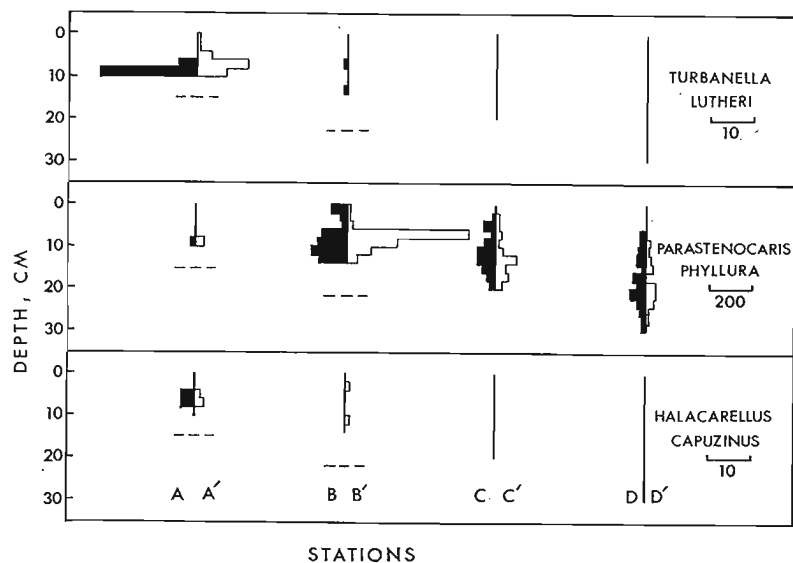


FIG. 4. The distribution of animals at Askö, locality A, 7 August 1963.
Further explanation in Fig. 3.

and upwards. The oxygen availability also shows an irregular distribution. St. B (and probably also St. A) has the greatest availability. In St. C only the areas around 10 cm depth offers good oxygen conditions for the animals. The grain size is dominated by the 300-500 μ fraction, but in the vicinity of the ground-water level coarser fractions occur. The distribution of temperature is shown in Table 6. The amount of organic material is moderate except for St. A, 8-10 cm depth and St. D, 12-14 cm depth (Table 5).

For the quantitative studies two core samples were taken at each station, 20-30 cm apart and at equal distances from the sea. In order to show the variation of the fauna laterally in the beach both of them are presented in the diagrams. Figs. 3-4 clearly show that there may be considerable differences in the numbers of specimens at corresponding depths, but that the positions of maxima, both vertically within the separate cores and horizontally in the beach, correspond well. A list of all the animals found in the separate samples is presented in Table 6. St. B has the largest number of animals with an average of 109 ind/10 cm³. Corresponding figures for the other stations are St. A, 39; St. C, 43; and St. D, 30 ind/10 cm³. Transformed to individuals per cm³ the maximum is not quite so dominating, viz. from station A landwards: 39.1, 152.7, 84.7, and 90.9.

The turbellarians are represented by three equally abundant species: *Macro-*

TABLE 6. The distribution of temperature (°C) in Askö beach, locality A, 7 August 1963.

Depth cm	Stations			
	A	B	C	D
0	19.2	28.2	22.0	21.3
5	19.7	25.6	21.6	21.2
10	19.5	—	20.6	—
15	19.3	19.2	—	—
20	—	18.5	18.0	19.6
30	—	—	—	18.4
35	—	—	17.5	—
50	—	—	—	17.3

stomum curvituba, *Coronhelmis multispinosus* and *Haplovejdovskya subterranea*. All of them occur in the upper 10 to 12 cm, with a horizontal maximum at St. B. *H. subterranea* is most abundant in the uppermost cm of the sand.

The gastrotrichs, represented by *Turbanella lutheri*, were found nearly exclusively at St. A, 4-6 cm depth.

Akteredrilus monospermatecus showed a maximum at the water line and was also common at St. B, but further landwards only 2 specimens were found. *Marionina subterranea* was concentrated in the uppermost cm at St. B with more than 170 individuals per 10 cm³. *Marionina southerni* was found at all stations. The greatest density was found at the surface of St. B, but it occurred in large numbers also at St. C and D where hardly any other oligochaetes were present.

The harpacticoids were, except for a few, unidentified specimens, represented only by *Parastenocaris phyllura*. It was the most abundant animal in the whole beach with a maximum at St. B but found abundantly also at St. C and D. The greatest density was 288 individuals per 10 cm³ at 6-8 cm depth in St. B. The distribution was very extended vertically at St. C and D.

The only halacarid, *Halacarellus capuzinus*, was concentrated in St. A.

LOCALITY B. — This is situated about 400 metres further south on the beach (Jansson, 1967c, fig. 1). Here whole cores were taken to the ground-water level on 30 July 1965. The weather had been steady for several weeks and the salinity constant for at least 17 days. The gradient was rather flat — 5 m landwards the salinity was still as high as 5.1‰ (Fig. 5). The temperature was high in the upper layers, but below 5 cm depth and downwards moderate values were found. The substrate was very heterogeneous, but mostly very coarse. Distinct layers of different grain sizes often traversed strata of more homogeneous sand. At St. D and E fresh rootlets from the sparse dune vegetation of *Elymus arenarius* pierced the sand. The amount of organic material was moderate, except at St. E which had great amounts of half-decomposed algae (Table 7). Though neither oxygen nor pore-water content were

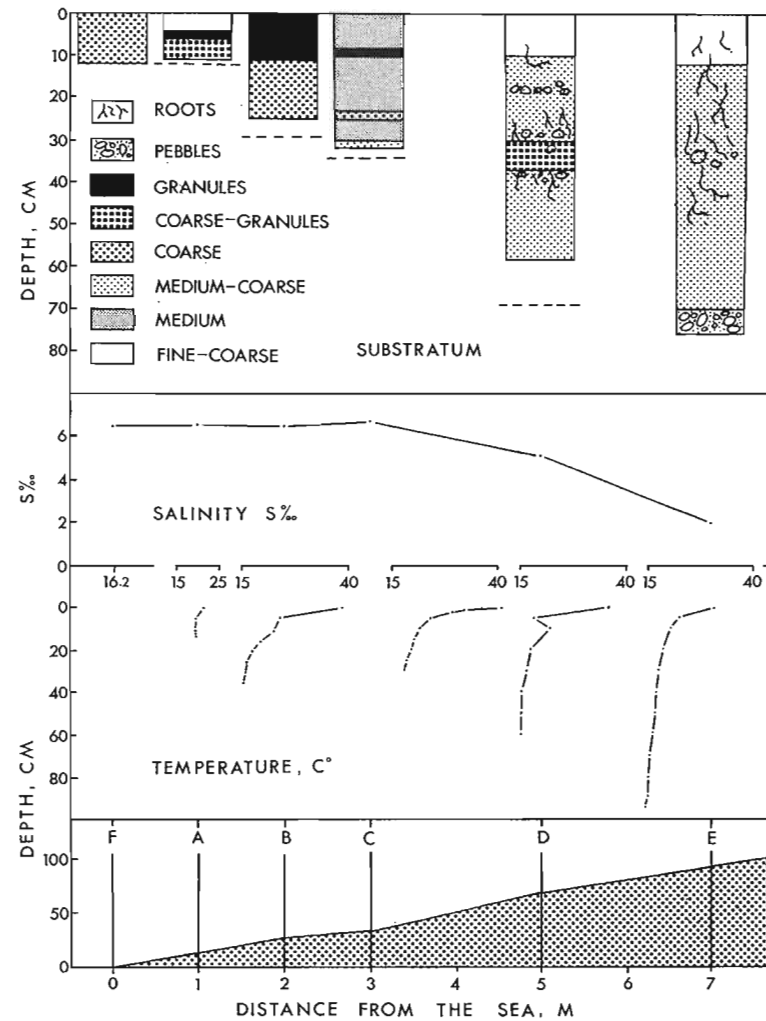


FIG. 5. The distribution of some environmental factors at Askö, locality B, 30 July 1965. The dashed lines in the grain-size diagrams indicate the ground-water levels, which at F and E were situated at 0 and 95 cm depth, respectively.

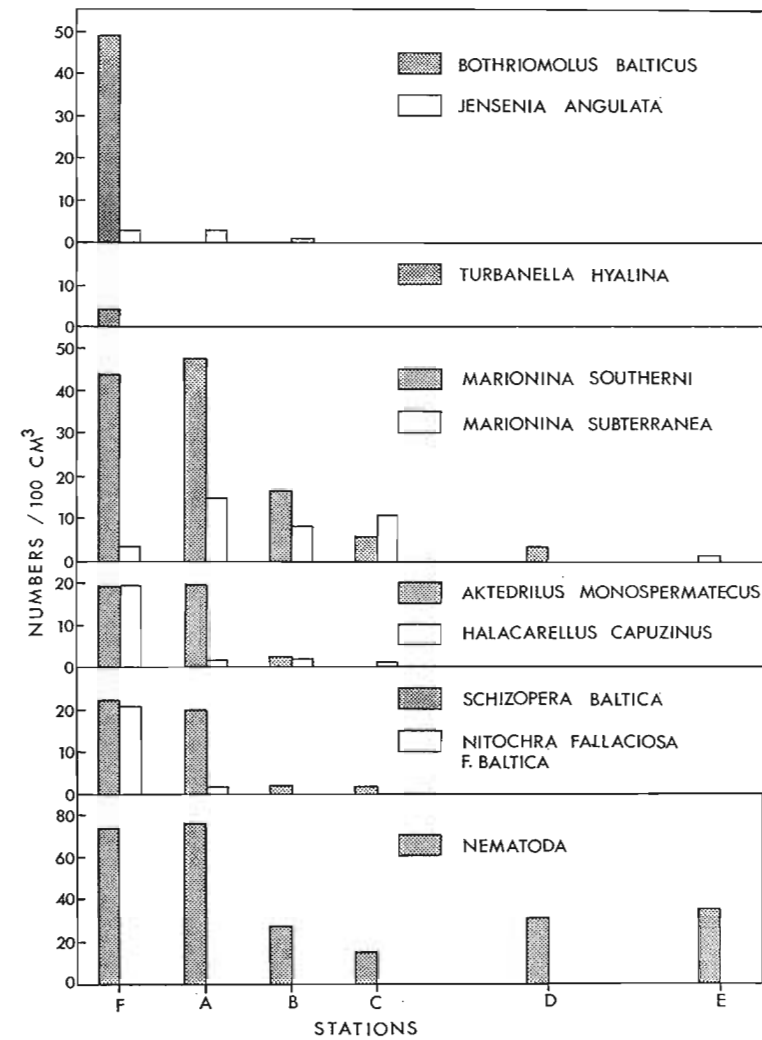


FIG. 6. The distribution of animals at Askö, locality B, 30 July 1965. The corresponding environmental data are presented in Fig. 3.

TABLE 7. The interstitial fauna at Askö, locality B, 30 July 1965. Corresponding environmental data are presented in Figure 5. The figures to the left in each column represent the actual number of specimens, the figures to the right express ind/100 cm³.

	Stations						
	F	A	B	C	D	E	
DETRITUS	—	++	+	++	+	+++	
<i>Macrostomum curvatura</i> ...	3	2.5	.	.	1	0.3	.
<i>Bothriomolus balticus</i> ...	59	49
<i>Haplovejdovskya subt.</i>	1	0.9
<i>Jensenia angulata</i> ...	3	2.5	3	2.7	1	0.4	.
<i>Pseudocirrus subterranea</i>	3	2.7
<i>Coronhelms multispinosus</i>	2	0.8	.	.	.
<i>Provortex karlingi</i>	1	0.3	.	.
<i>Carcharodorhynchus subt.</i>	1	0.3	1	0.2
<i>Promesostoma nyaesiensis</i>	1	0.4	.	.	.
<i>Turbellaria</i> ...	1	0.8	1	0.9	2	0.8	.
<i>Turbanella hyalina</i> ...	4	3.3
<i>Nematoda</i> ...	88	73	83	75.5	74	26.6	48
<i>Nais elinguis</i>	1	0.9
<i>Marionina southerni</i> ...	57	43.2	52	47.3	41	16.4	18
<i>Marionina subterranea</i> ...	4	3.3	16	14.6	20	8.0	34
<i>Enchytraeidae</i> ...	9	7.5	18	16.4	32	12.8	43
<i>Enchytraeid cocoons</i>	1	0.9
<i>Akteredilus monospermatecus</i> ...	22	18.3	21	19.1	6	2.4	.
<i>Schizopera baltica</i> ...	27	22.4	22	20	5	2.0	6
<i>Nitochra fallaciosa f. baltica</i> ...	25	20.8	2	1.8	.	.	.
<i>Paraleptastacus spinicauda</i> ...	16	13.3	8	7.3	12	3.6	11
<i>Parastenocaris vicesima</i>	2	0.8	2	0.6	18
<i>Calanoida</i>	1	0.9	1	0.9	.	.
<i>Cyclopoida</i> ...	54	44.8	.	2	0.8	1	0.3
<i>Nauplii</i> ...	7	5.8	.	5	2.0	4	0.9
<i>Halacarellus capuzinus</i> ...	23	19.1	2	1.8	5	2.0	3
Total	402	333.6	237	234.8	211	84.4	173

measured the smell and appearance of the substrate at the separate stations did not indicate anaerobic conditions, especially not at St. F-B.

The horizontal distribution of the most numerous animals is shown in Fig. 6. The turbellarians were concentrated at the most seaward stations; *Bothriomolus balticus* was restricted to St. F, but in large numbers, and *Jensenia angulata* occurred sparingly from St. F to B.

The gastrotrichs were represented by *Turbanella hyalina*, which was found only at the most seaward station.

The oligochaetes dominated at this locality, with the same species as at Locality A. *Akteredilus monospermatecus* was again found in largest numbers near the

TABLE 8. The interstitial fauna at Tofta beach, 21 July 1959. Corresponding environmental data are shown in Figure 7.

Station	Depth cm															Total ind/10 cm ³
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
DETRITUS	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Turbellaria</i> ...	1	4	4	4	5	.	4	1	5	8	36
A <i>Xenotrichula velox</i> ...	174	97	28	27	17	30	35	169	133	272	983
<i>Nematoda</i> ...	7	1	8
<i>Marionina subterranea</i>	1	.	1	2	6	12	22
																1048 104.8
DETRITUS	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Turbellaria</i>	6	7	2	6	1	2	.	2	26
B <i>Trichocerca</i> sp. ...	41	23	14	.	2	80
<i>Xenotrichula velox</i> ...	16	12	15	10	32	11	3	3	7	109
<i>Marionina subterranea</i>	1	1	4	4	1	2	4	17
																232 23.2
DETRITUS	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Turbellaria</i> ...	1	8	9
C <i>Trichocerca</i> sp. ...	1	1	.	1	.	1	.	1	.	1	.	1	.	1	.	9
<i>Xenotrichula velox</i> ...	1	26	.	4	1	3	3	1	6	2	8	.	4	8	14	81
<i>Nematoda</i> ...	13	1	14
<i>Marionina subterranea</i> ...	84	28	112
																225 15.0

water line, while *Marionina subterranea* showed a maximum further landwards. *Marionina southerni* occurred in large numbers at St. F and A, but was also found at the other stations except St. D.

The harpacticoids were rather abundant. *Paraleptastacus spinicauda* and *Parastenocaris vicesima* have already been treated by Jansson (1966a). The former species showed a maximum at St. F, but was also well represented in A-C. The latter species occurred in small numbers at St. C and D. *Schizopera baltica* had a similar distribution to that of *Paraleptastacus spinicauda* and was equally numerous. *Nitochra fallaciosa f. baltica* was concentrated at the water's edge.

Nematoda were numerous at all stations, but showed a minimum at St. B-C.

In total the fauna was very rich at the two most seaward stations with 334-235 individuals per 100 cm³. From St. A to B there is a sudden drop in the abundance, which then successively decreases landwards. At the two most landward stations there were hardly any animals, except for nematodes.

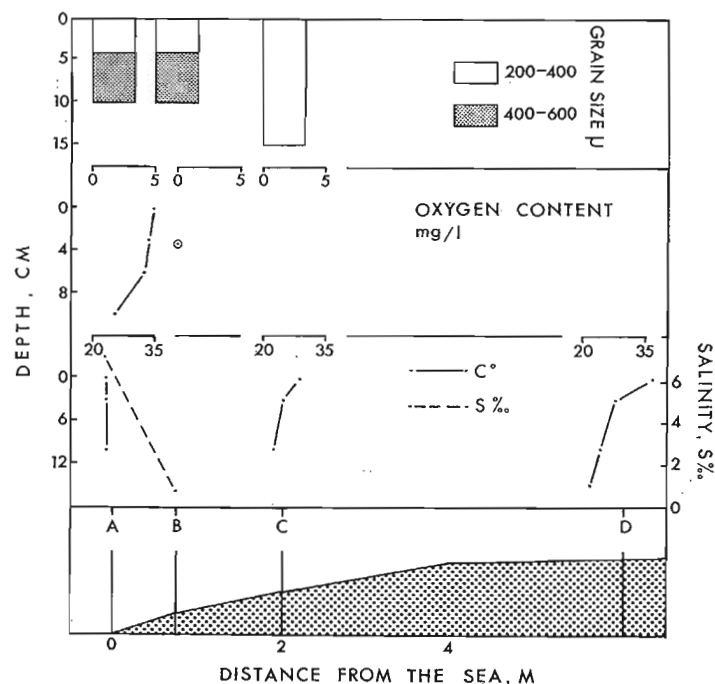


FIG. 7. The distribution of some environmental factors at Tofta, 21 July 1959. The sand was anaerobic below 4 cm depth at St. B, and below 29 cm at St. C.

Tofta

Some of the abiotic factors of the habitat were measured in connection with the quantitative sampling on 21 July 1959. The weather during the preceding week had been dry and steady. The salinity gradient was very steep; already at 80 cm distance from the sea the interstitial water was fresh (Fig. 7). Four days earlier, salinities between 7 and 11‰ were measured at 1 m distance from the sea (Jansson 1967c, fig. 10). The temperatures at the three stations where samples were taken were moderate at the time of collection, but had surpassed 29°C at the surface of St. C about three hours before sampling. The oxygen content decreased rapidly with depth, reaching zero at 4 cm depth at St. B and below 10 cm at St. A. At St. C water could not be obtained until a depth of 27 cm, where no trace of oxygen could be found. The sand was rather homogeneous, especially at St. C, where all the samples had mean grain sizes between 200 and 400 μ. Visible organic material was nearly absent. (Table 8). Though the content of pore water was not measured, the two seaward stations could be regarded as saturated to the surface. St. C. ap-

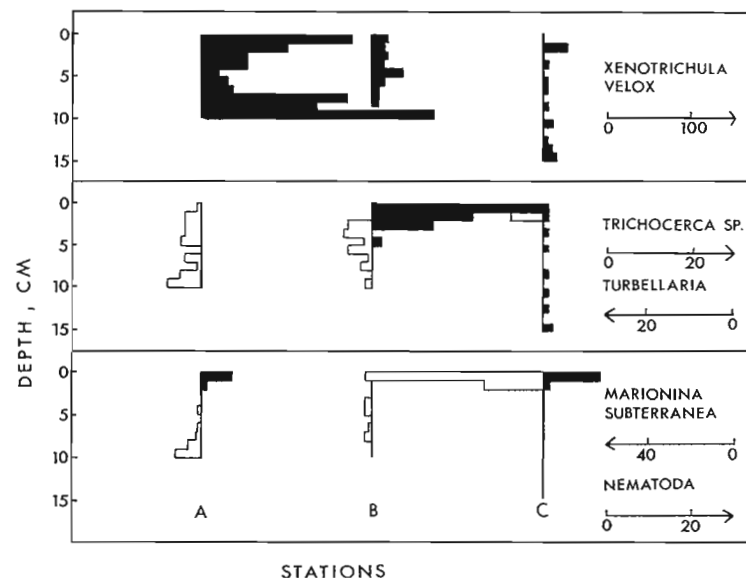


FIG. 8. The distribution of animals at Tofta beach, 21 July 1959. The figures represent specimens per 10 cm³. Corresponding environmental data are presented in Fig. 7.

parently had high percentages of water below 10 cm depth. All the animals found in the samples are listed in Table 8. The fauna is apparently very poor. *Coelognopora* spp. were the dominating turbellarians. The distribution of the animals is illustrated in Fig. 8. The dominating animals are the gastrotrichs, represented by *Xenotrichula velox*, found in large numbers at St. A and more sparingly at B and C. The vertical distribution shows a pronounced minimum at 5 cm depth, St. A. The rotatorian *Trichocerca* sp. was abundant in the upper cm at St. B, but decreased markedly landwards. *Marionina subterranea* was found at all stations, but showed a maximum at the surface of St. C. The nematodes were remarkably few and were totally absent at St. B. The number of animals at St. A was more than 4 times as large as at St. B, where the number was slightly larger than at St. C.

Simrishamn

The investigation was carried out on 4-5 December 1963. The weather before the sampling had been rainy with moderate winds, but the intervening night was steady with no precipitation. The data from St. C and D – which are based on collections made on the second day – are therefore comparable with those from St. A and B. Data on environmental factors are shown in Fig. 9. The salinity gradient was

TABLE 9. The interstitial fauna at Simrishamn beach, 4-5 December 1963.

Station		Depth cm																
		2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34
A	DETRITUS	+	+	+	+	+	+	+	+	+	+	+	+	+	+			
	<i>Pseudocyrtis subt.</i>	2	.	.	7	7	.	3			
	<i>Macrostomum curv.</i>	2	.	.	.	1	.			
	<i>Kalyptorhynchia</i>	1	.			
	<i>Turbellaria</i>	2			
	<i>Lumbricillus knoell.</i>	2	1	1	.		
	<i>Lumbricillus sp.</i>	2	2	2	.	2			
	<i>Enchytraeidae</i>	1			
	<i>Akteredilus monosp.</i>	1	2			
<i>Nitochra fallaciosa</i>	2			
<i>Halacarellus cap.</i>	6			
B	DETRITUS	—	—	—	—	—	+	+	+	+	—	—	+	+	—	—	—	—
	<i>Pseudocyrtis subt.</i>	2	.	1	3	2	3	3	3	2	16	4
	<i>Macrostomum curv.</i>	3	6	1	1
	<i>Kalyptorhynchia</i>	1
	<i>Turbellaria</i>	1	1
	<i>Lumbricillus knoell.</i>	5	5	14	1	8	14	4	10	7	2	.	9
	<i>Lumbricillus sp.</i>	3	1	1	.	1	1
	<i>Enchytraeidae</i>	3
	<i>Akteredilus monosp.</i>
	<i>Nitochra fallaciosa</i>	1	1	1	2	2	3
	<i>Paraleptastacus spin.</i>
<i>Cyclopoidea</i>	
<i>Halacarellus cap.</i>	1	
C	DETRITUS	—	+	+	+	+	—	+	+	+	+	+	+	++	++	+	+	+
	<i>Pseudocyrtis subt.</i>	3	.	.	.	1	6	2
	<i>Macrostomum curv.</i>	1	.	.	.	1	4	.	.	3
	<i>Turbellaria</i>
	<i>Lumbricillus knoell.</i>	.	.	.	2	1	4	1	.	.	2	1	7	9	8	5	.	3
	<i>Lumbricillus sp.</i>	.	.	.	1	.	1	.	.	1	2	.	12	5	2	.	1	
	<i>Enchytraeidae</i>	1
	<i>Akteredilus monosp.</i>	.	1	2	.	2	.	.	3	.	.	.	1	.	.	1	.	.
	<i>Nitochra fallaciosa</i>	1	1	.
	<i>Paraleptastacus spin.</i>	1	.
	<i>Itunella muelleri</i>
<i>Halacarellus cap.</i>	
D	DETRITUS	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	<i>Macrostomum curv.</i>	4	1	.	.	.
	<i>Nematoda</i>	1
	<i>Lumbricillus knoell.</i>	5	8	4	11	4	9	9	.	2	2	.	.	1	3	4	5	1
	<i>Lumbricillus sp.</i>	1	.	.	.	4	4	11	.	2	.	.	1
	<i>Enchytraeidae</i>	.	1	1	.
	<i>Akteredilus monosp.</i>
	<i>Nitochra fallaciosa</i>
	<i>Itunella muelleri</i>
	<i>Schizopera inorn.</i>	6
<i>Halacarellus cap.</i>	

Corresponding environmental data are presented in Figure 9.

																			Total	ind/ 10 cm ³	
36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	70	72			
																			19 3 1 2 4 8 1 3 2 6		
																			49	1.8	
+	+	+	—	—	—	—	—	—	—											83 37 3 3 112 13 4 7 39 4 2 11	
11	12	13	6	6	20	.	2	1	.											318	5.9
.	.	1	1											27 24 1	
.	102 43 1		
3	4	2	3	.	.	3	7	8	3											14 18 1	
.	1	2	.	2	.	.	1	2 27		
.	1			
1	1	2	4	5	.	3	3	4	6	3	4	6	1	3			
.	1	3			
.	2	8			
																			318	5.9	
+	—	—	+	—	+	—	—	+	+	+	++	++	++	++	++	++	++	++			
2	4	.	.	.	4	1	1	.	3	.	27 24 1		
.	5	.	4	102 43 1		
3	4	15	5	1	3	6	7	7	5	2	14 18 1		
5	2	1	1	.	.	2	1	.	1	.	.	2	.	.	2	.	.	1	2 27		
.	1	1	.	6			
.	.	.	1	.	1	2	2	2	.	.	1	1	1			
.	1			
.	1			
.	12			
.	2	.	.	1	2	2	.	6	.	1	1	.	.	.			
																			260	3.6	
+	+	++	+++	+++	+++	+++	+++	+++	++	++	+	+	+	+	+	+	+				
.	1	1	7 1		
10	8	7	1	1	97 40		
1	2	2	1	5	.	.	.	2	.	.	1	1	1	.	.	1	1	.	3 9		
.	2	.	3	1	2	.	1	.	4 1		
.	9 2		
.	1	1	.	1	.	.	173	2.5	

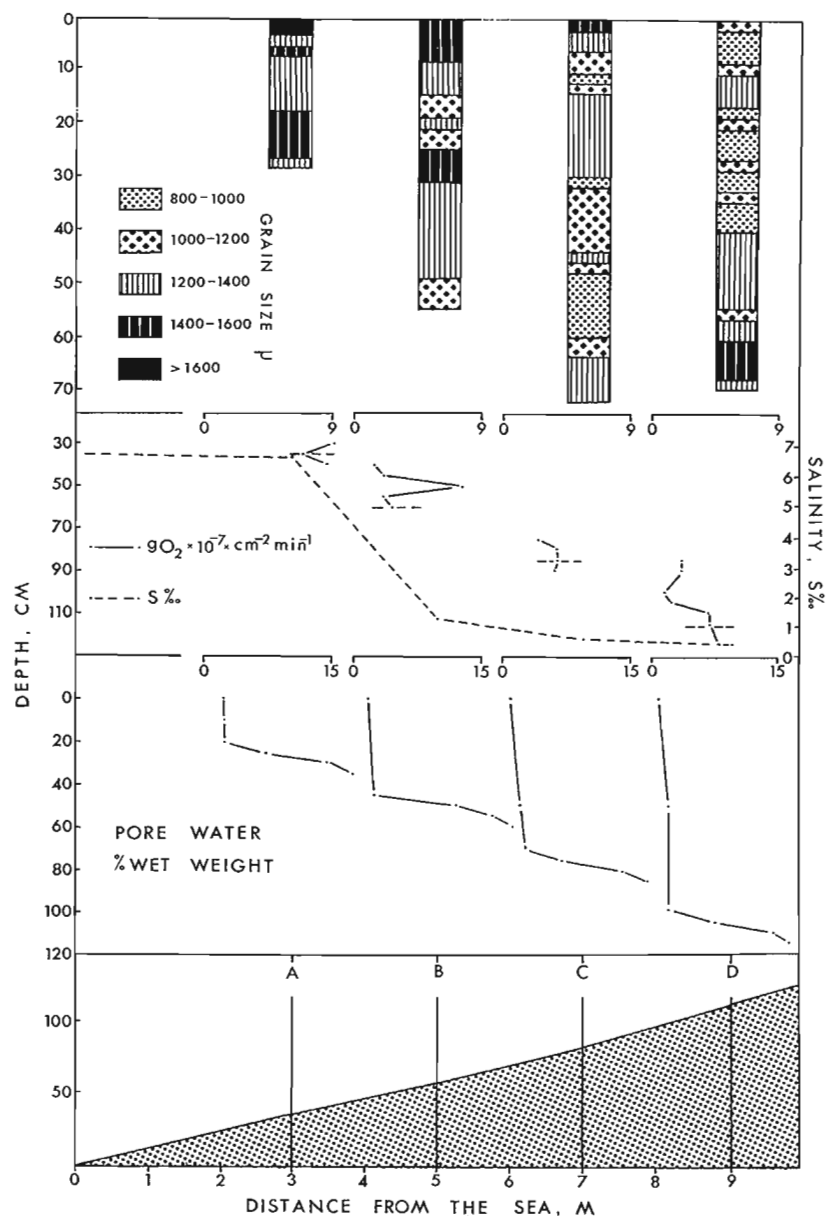


FIG. 9. The distribution of some environmental factors at Simrishamn, 4-5 December 1963. The dashed, horizontal lines in the oxygen diagram indicate the ground-water levels, which at St. D were situated at 84 and 114 cm depth, respectively.

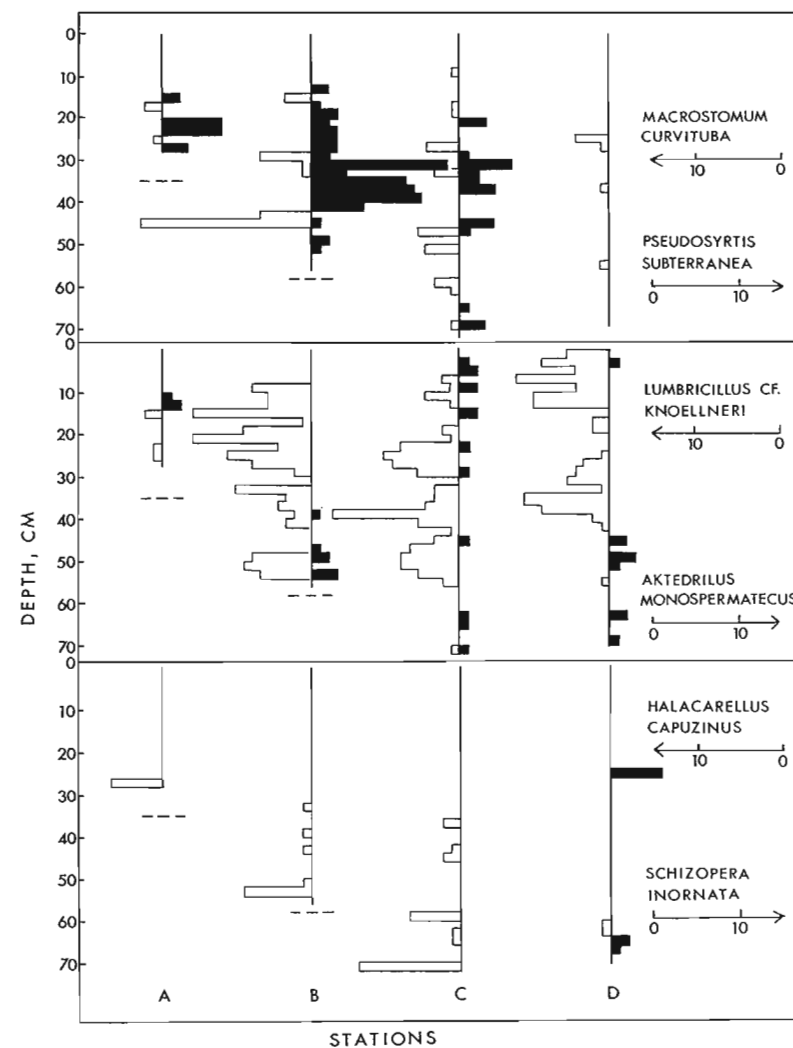


FIG. 10. The distribution of animals at Simrishamn, 4-5 December 1963. The figures represent specimens per 20 cm³. Corresponding environmental data are presented in Fig. 9.

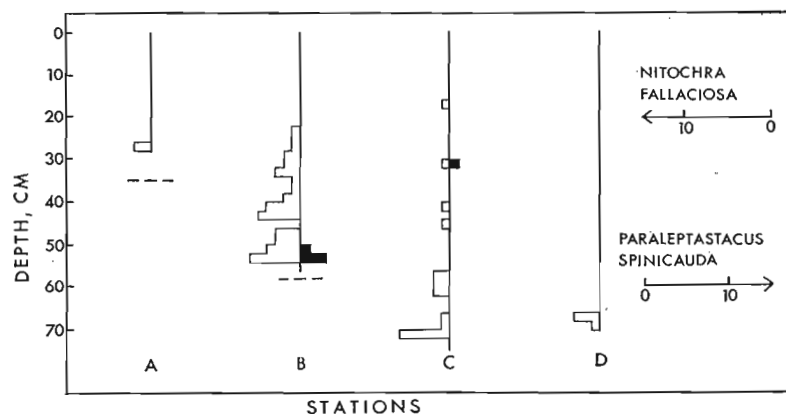


FIG. 11. The distribution of animals at Simrishamn, 4-5 December 1963. Further explanations in Fig. 10.

very steep between St. A and B, and landwards from St. C freshwater filled the interstitial spaces. The oxygen content of the beach was high. Because of the great permeability, the circulation of pore water must have been considerable. Especially at the two seaward stations the movements of the seawater caused high, but fluctuating, values of oxygen availability (Jansson, 1968). Because of the low capillarity in the coarse sand, the contents of pore water in the beach were restricted to a level a little above the ground-water level. This is a very characteristic feature of the Simrishamn beach compared to other beaches (Jansson, 1967b). The temperatures measured at various depths in the beach are presented in Table 10. The range was very small with values of 1-3°C in the surface layers and 5-6°C at about 1 m depth in the landward stations. The sand was very coarse and homogeneous especially at the two innermost stations. Visible organic material was found in great amounts at 40 to 58 cm depth at St. C, but also the deeper parts of St. C had rather large amounts (Table 9).

All the animals found in the quantitative samples are listed in Table 9, and the distribution of the more common forms is shown in Fig. 10-11. The dominating turbellarians were *Macrostomum curvituba* and *Pseudocyrtilis subterranea*. The former was found at all stations with a maximum at St. B at 44-46 cm depth. The latter shows a more continuous distribution from St. A to C, but most of the animals were concentrated at St. B at 32-42 cm depth. Both species were found only at depths below 10 cm.

Among the oligochaetes the enchytraeids were the most numerous. Several species of *Lumbricillus* were found, one of which could be identified as *L. knoellneri*, though with some uncertainty as the animals were not quite mature. It was

TABLE 10. The distribution of temperature (°C) at Simrishamn beach 4-5 December 1963.

Depth cm	Stations			
	A	B	C	D
0	2.3	2.5	1.0	1.4
5	3.0			
10	3.0			
15		2.7		
20	3.1		2.2	
30	3.5			
40		3.3	3.3	
50				3.3
60		4.3	4.5	
80			5.4	
100				6.1
115				6.5

common at all stations except at St. A and had a wide vertical distribution. Landwards the maximum of distribution within each station occurred closer to the surface. *Akteredilus monospermatecus* was less abundant, though present at each station.

Halacarellus capuzinus, which was the only halacarid found, occurred at all stations. The separate maxima were always situated in the vicinity of the ground-water level.

Only few harpacticoids were found. *Nitochra fallaciosa* was the most abundant, occurring at all stations below 16 cm depth with a maximum at St. B. There was a tendency to accumulation of animals near the ground-water level at all stations. A few specimens of *Paraleptastacus spinicauda* were found at the two middle stations.

Thus, the fauna is most numerous at St. B, but also St. C and D have fairly large numbers, mostly because of the large number of enchytraeids.

Tylösand

The period before the sampling day (20 September 1959) had been sunny with some wind, and the sea never reached St. D. Data on abiotic factors at the time of sampling are shown in Fig. 12. The salinity gradient was rather flat with 6‰ S 13.4 m from the sea. The oxygen content was only measured at St. A, C, and D and values from the same area at other times of the same day are presented in Jansson (1968, table 4). They all indicated fairly large amounts of oxygen in the foreshore. The grain size successively decreased landwards. It was rather heterogeneous at St. C but became more homogeneous landwards with a very good

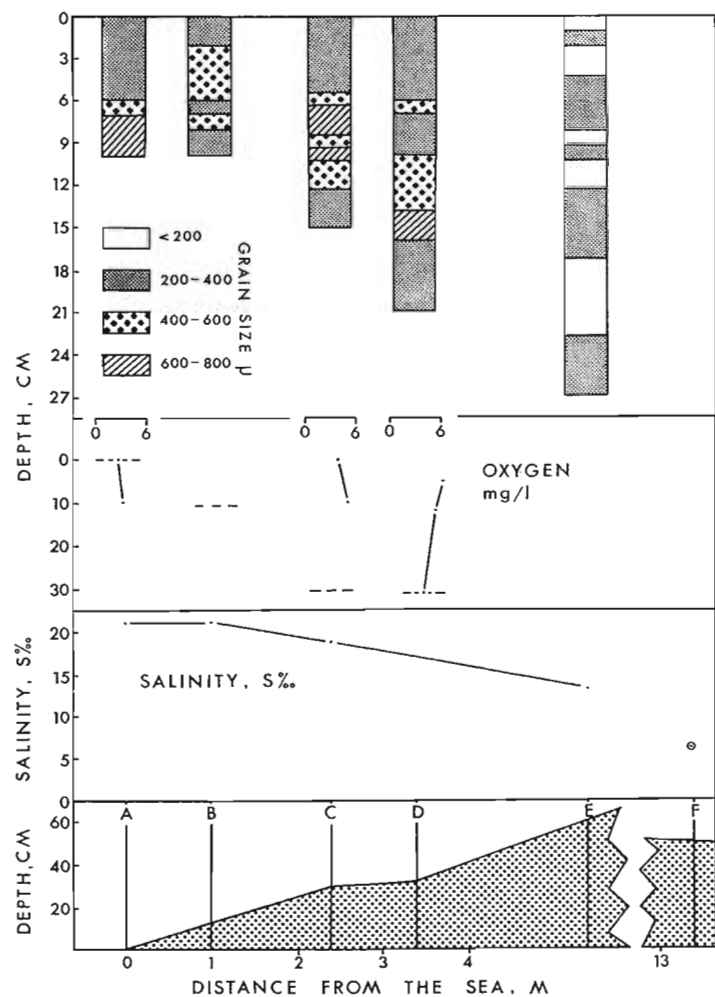


FIG. 12. The distribution of some environmental factors at Tylösand, 20 September 1959. The dashed lines indicate the ground-water levels, at St. E and F situated at 60 and 44 cm depth, respectively.

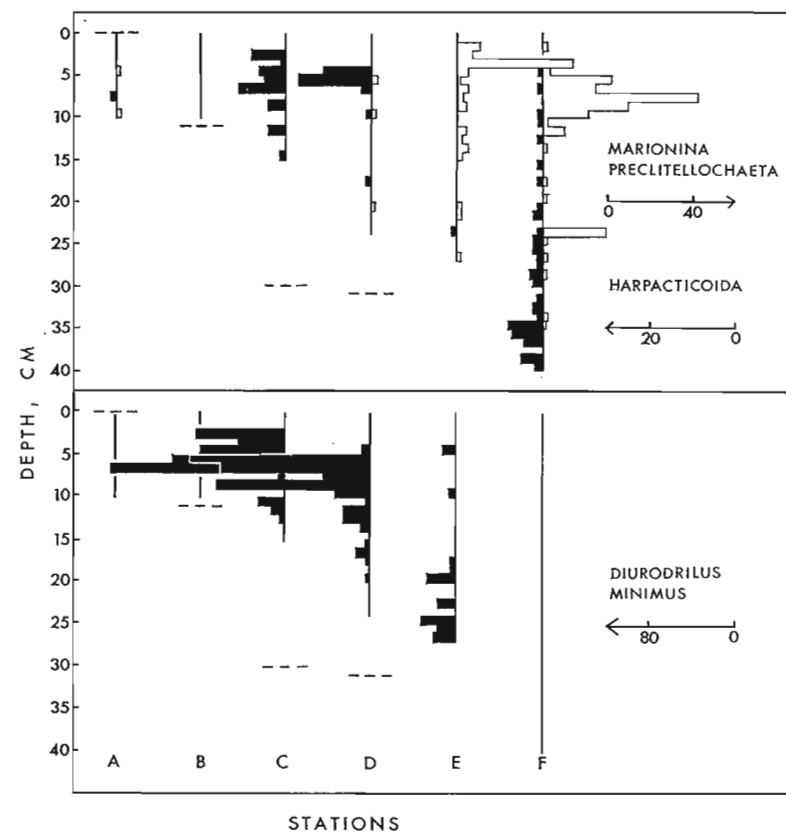


FIG. 13. The distribution of animals at Tylösand beach, 20 September 1959. The figures represent specimens per 10 cm³. Corresponding environmental data are presented in Fig. 12.

TABLE 12. The distribution of temperature (°C) at Tylösand, 20 September 1959.

Depth cm	Stations			
	A	B	C	E
0	15.4	15.3	14.8	15.3
5	15.0	15.0	15.4	14.0
15		16.0		14.4

sorting at St. E. The sand further landwards apparently had the same properties as at St. E, but this were not measured. The physical aspect of the grain-size distribution at Tylösand is discussed in Jansson (1967b). Large amounts of detritus were found between 6 and 10 cm depth at St. A and B (Table 11). All other samples contained small or, in a few cases, moderate amounts. The temperatures in the beach are shown in Table 12. They ranged from 14.0 to 16.0°C.

All the animals found in the samples are listed in Table 11 and the most important species in Fig. 13. The turbellarians were all small, unidentifiable forms. There were rather few except at St. C at 3 and 15 cm depth. The number of nematodes increased successively landwards to a maximum at St. D, but decreased rapidly further landwards. The most abundant animal in the beach was the archiannelid *Diurodrilus minimus*. It was found only at St. C-E where it sometimes reached considerable abundance. The most densely populated layers in these sta-

TABLE 13. The origin and pretreatment of the animals used in the laboratory experiments.

Species	Experiment	Habitat	Pretreatment
<i>Haplovejdovskya subterranea</i>	Sal.-tolerance	Askö, 6.6 ‰ S, 6.5°C	6.6 ‰ S, 10°C, 4 days
	Temp.-tolerance	Askö, 6.6 ‰ S, 6.5°C	6.6 ‰ S, 10°C, 23 days
<i>Coronhelmis lutheri</i>	Sal.-tolerance	Askö, 6.2 ‰ S, 20°C	6.2 ‰ S, 5°C, 12 days
	Temp.-tolerance	Askö, 6.2 ‰ S, 20°C	6.2 ‰ S, 5°C, 12 days
<i>Marionina subterranea</i>	Sal.-tolerance	Tofta, 7.5 ‰ S, 19°C	7.5 ‰ S, 16-18°C, 1 day
	Temp.-tolerance	Tofta, 2 ‰ S, 16°C	2 ‰ S, 20-22°C, 2 days
<i>Marionina southerni</i>	Sal.-tolerance	Askö, 8.2 ‰ S, 16°C	8.2 ‰ S, 15°C, 2 days
	Sal.-preference	Askö, 6.5 ‰ S, 17°C	6.5 ‰ S, 15°C, 4-10 days
<i>Akteredrilus monospermatecus</i>	Temp.-tolerance	Tofta, 6.2 ‰ S, 18°C	6.2 ‰ S, 13-17°C, 17 days
<i>Schizopera baltica</i>	Sal.-tolerance	Askö, 5.8 ‰ S, 15°C	5.8 ‰ S, 4°C, 1 day
	Sal.-preference	Askö, 5.8 ‰ S, 15°C	5.8 ‰ S, 4-7°C, 1-5 days
<i>Nitochra fallaciosa</i> f. <i>baltica</i>	Sal.-tolerance	Askö, 6.6 ‰ S, 6.5°C	6.6 ‰ S, 10°C, 22 days
	Sal.-preference	Askö, 6.8 ‰ S, 16°C	6.8 ‰ S, 15°C, 5-7 days
	Temp.-tolerance	Askö, 6.6 ‰ S, 6.5°C	6.6 ‰ S, 10°C, 22 days
<i>Nitochra fallaciosa</i>	Sal.-tolerance	Simris-hamn, 6.3 ‰ S, 5°C	6.3 ‰ S, 5°C, 40 days
	Sal.-preference	Simris-hamn, 6.3 ‰ S, 5°C	6.3 ‰ S, 5°C, 38-39 days
<i>Paraleptastacus spinicauda</i>	Sal.-tolerance	Askö, 6.6 ‰ S, 6.5°C	6.6 ‰ S, 10°C, 3 days
	Sal.-preference	Askö, 4-6 ‰ S, 8°C	6-7 ‰ S, 15°C, 1 day
	Temp.-tolerance	Askö, 6.6 ‰ S, 6.5°C	6.6 ‰ S, 10°C, 12 days
<i>Parastenocaris phyllura</i>	Sal.-tolerance	Askö, 0.1 ‰ S, 8.6°C	0.1 ‰ S, 10°C, 3 days
	Temp.-tolerance	Askö, 0.1 ‰ S, 8.6°C	0.1 ‰ S, 10°C, 11 days

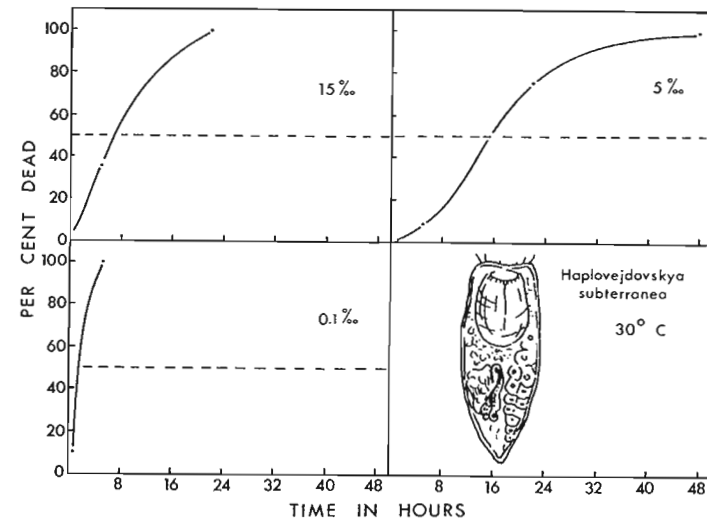


FIG. 14. Tolerance of *Haplovejdovskya subterranea* to 30°C in different salinities (n = 25). 19-21 November 1964.

tions were situated between 6 and 10 cm depth. Landwards a displacement towards deeper strata could be seen. *Marionina preclitellochaeta* was the other dominating species in the beach. With the exception of 6 specimens at St. A and D, all the animals were found at St. E and F, with a maximum at the latter station. Vertically the layers from the sand surface down to 10 cm depth were the most densely populated. The harpacticoids occurred in moderate numbers and were concentrated at St. C-D and F. While most animals at the seaward stations were distributed within the upper layers, they showed a maximum at 35-40 cm depth at the most landward station.

Taken as a whole the abundance of the interstitial fauna at Tylösand had a very definite maximum at St. C-D, and a minimum at St. A.

LABORATORY EXPERIMENTS

Only experiments on the significance of salinity and temperature were carried out, as I believe that these parameters are the most important ones in the beaches studied. As the effects of these two factors upon the organisms are almost impossible to separate they are here treated together and the results are presented with the experimental animal as a unit.

The origin and pretreatment of the animals are summarized in Table 13. In some cases further pretreatment was undertaken and this will be noted for each case.

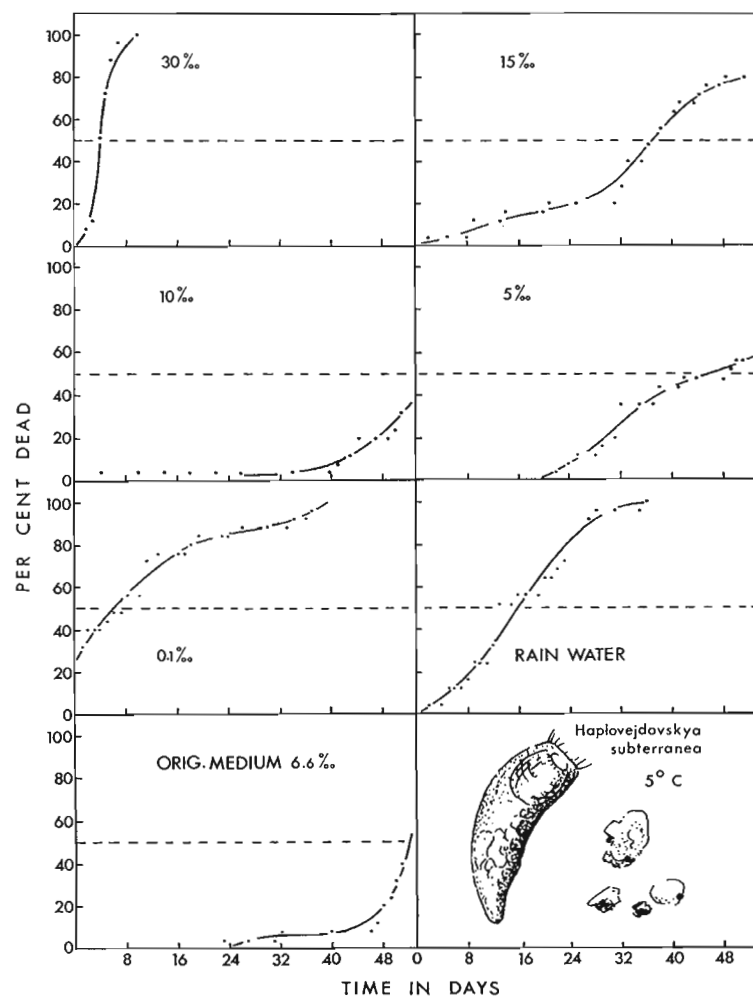


FIG. 15. Tolerance of *Haplovejdovskya subterranea* to different salinities at 5°C (n = 25). 30 October to 20 December 1964.

Haplovejdovskya subterranea

The results of the salinity tolerance tests are shown in Fig. 15. Five hours after the animals were transferred to the test concentrations, all the specimens in 30‰ S were imbedded in a thick mantle of mucus and were more or less motionless.

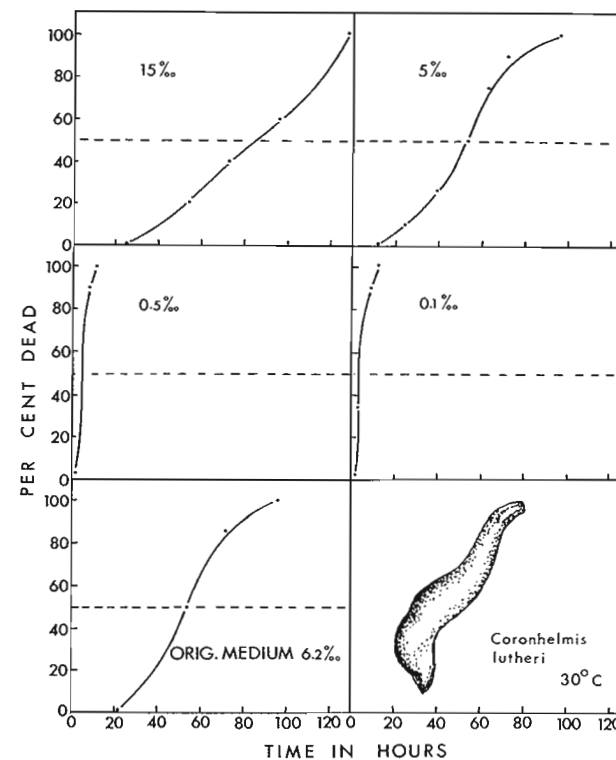


FIG. 16. Tolerance of *Coronelmis lutheri* to 30°C in different salinities (n = 20). 5 July-10 August 1966.

In 15‰ S they were clearly smaller and more sluggish than normal, and a slower locomotion was also typical of the specimens in the concentrations of 5‰ S or less. The greatest activity was shown by animals in 10‰ S and in the habitat water, and this lasted during the whole experiment. The secretion of a mucus mantle was typical of all the specimens kept in extreme salinities but after five to ten hours the animals left the mucus envelope and started creeping around. As clearly shown in the diagram the survival rate was significantly higher in 5 to 10‰ S and in water from the habitat than in the other salinities. Rain-water was endured better than water of 0.1‰ S.

The tolerance to a temperature of 30°C is shown in Fig. 14. All specimens died within 48 hours at all three salinities, but they survived longest in 5‰.

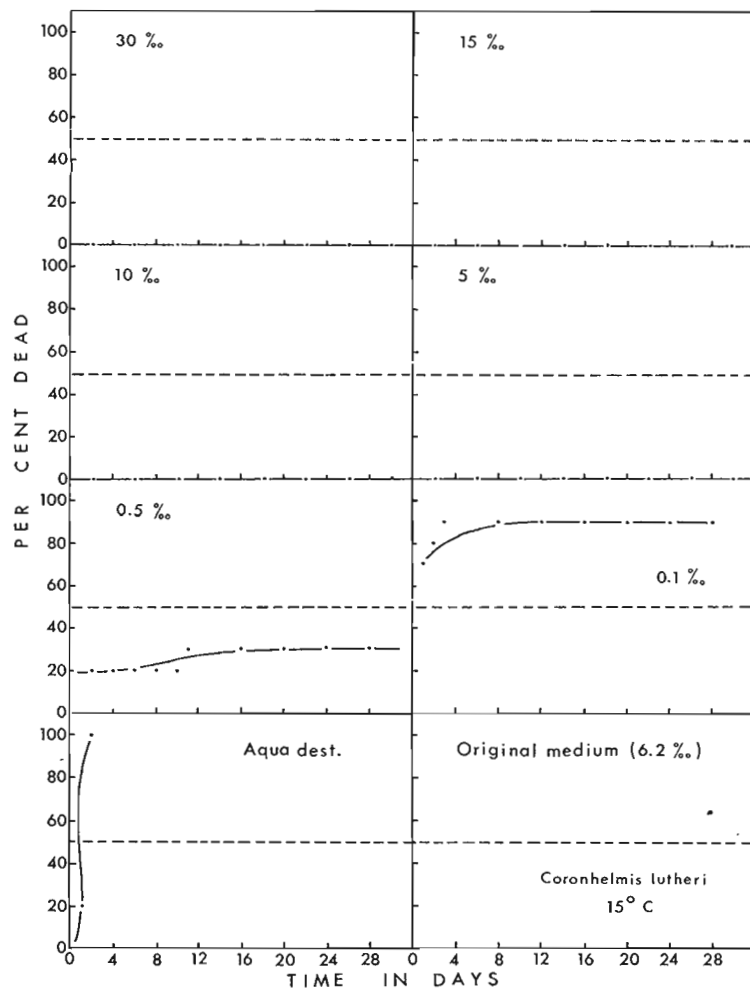


FIG. 17. Tolerance of *Coronhelmis lutheri* ($n = 10$) to different salinities at 15°C .
30 June-29 July 1966.

Coronhelmis lutheri

Twenty-four hours before the start of the salinity tolerance experiments the animals were transferred from the storing temperature, 5°C , to the experimental temperature, 15°C .

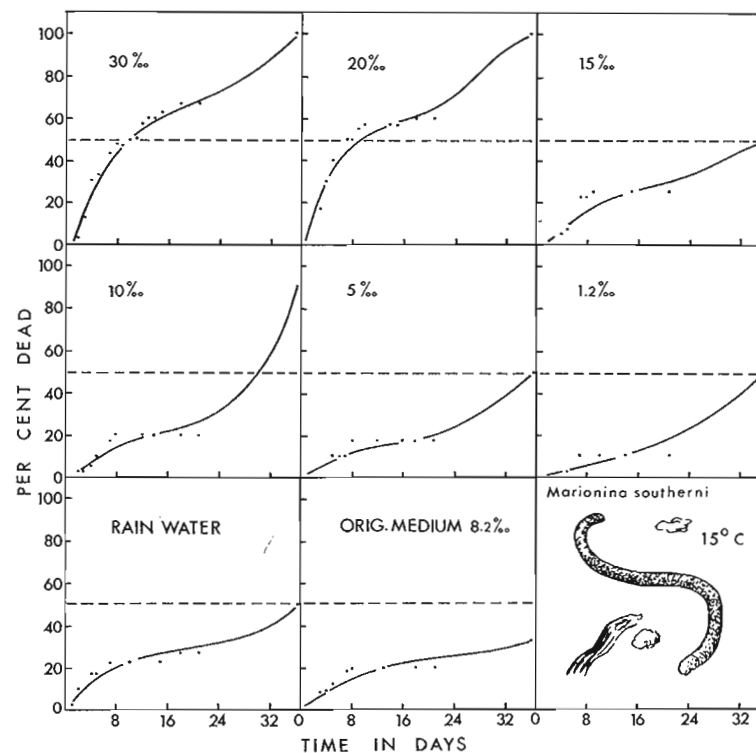


FIG. 18. Tolerance of *Marionina southerni* to different salinities at 15°C ($n = 40$).
31 August-6 October 1963.

The results of the tests are shown in Fig. 17. After 8 hours the specimens in distilled water were very swollen, those in 0.1‰ S sluggish, some of them adhering to one another, animals in 0.5‰ S were nearly normal and those in 5‰ S quite normal. The animals in $10\text{--}15\text{‰}$ S were rather thin but crept lively around, while those in 30‰ S were more sluggish. After 24 hours all the animals in $0.5\text{--}15\text{‰}$ S were very active, those in 15‰ S being thinner than the others. All specimens in 30‰ S were lively. After 45 hours the conditions remained nearly unchanged for 30 days, whereafter the experiment was terminated.

The rate of survival at high temperature, 30°C , is presented in Fig. 16. Whereas the animals in $0.1\text{--}0.5\text{‰}$ S died within the first 12 hours, there was a significantly better survival in 5‰ S and in habitat water (6.2‰ S) and still better in 15‰ S.

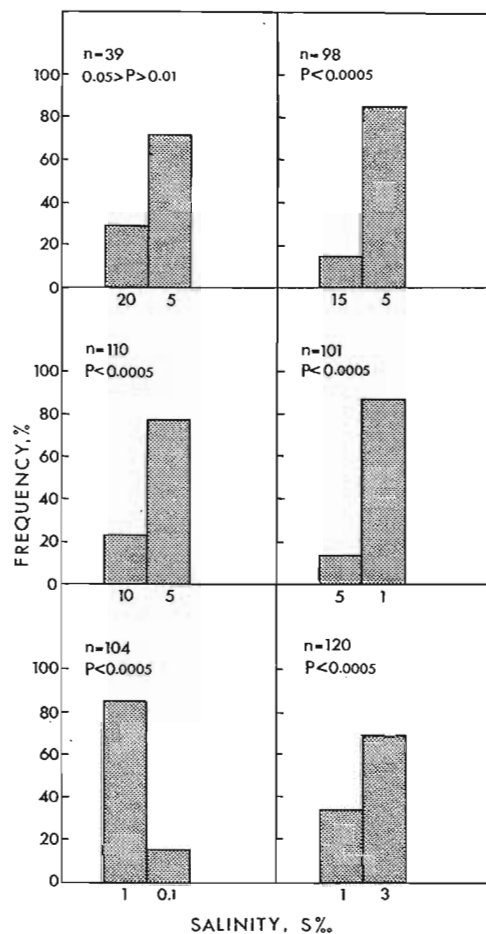


FIG. 19. Salinity preference of *Marionina southerni* at 15°C. 3-9 July 1965.

Marionina southerni

Owing to the great tolerance of this species, the salinity experiments had to be terminated before total LD 50-curves had been obtained for all of the test concentrations (Fig. 18). The survival was high in rain-water to 15‰ S and a significant difference was not found until between 15 and 20‰ S. In 20 and 30‰ S 50% of the animals lived for more than a week. A clear optimum was therefore not

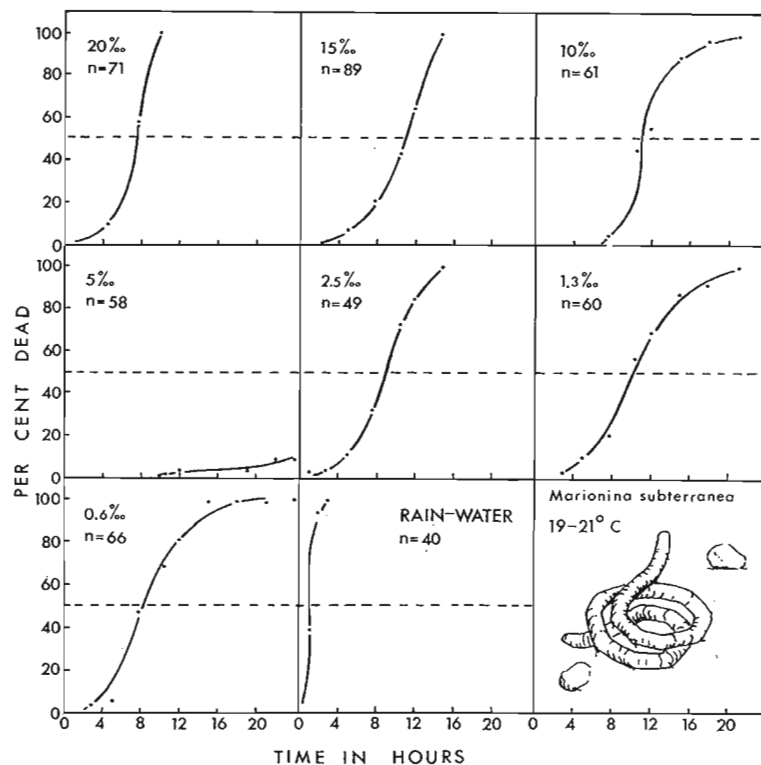


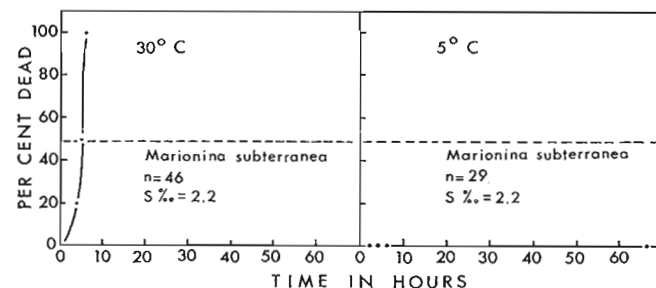
FIG. 20. Tolerance of *Marionina subterranea* to different salinities at 19-21°C. 7-9 August 1960.

obtained but the specimens used apparently thrived well in salinities from fresh-water to 15‰ S.

The preference experiments were carried out in collaboration with Mr. Ragnar Elmgren, Stockholm, as an introduction to his experimental studies on the significance of adaptation for the salinity preference of this species (Fig. 19). The animals clearly reacted in the different salinity gradients and were in good condition after the separate experiments. Of the concentrations offered, *M. southerni* significantly preferred 3‰ S.

Marionina subterranea

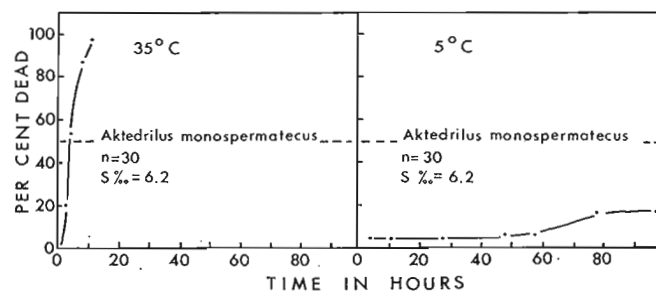
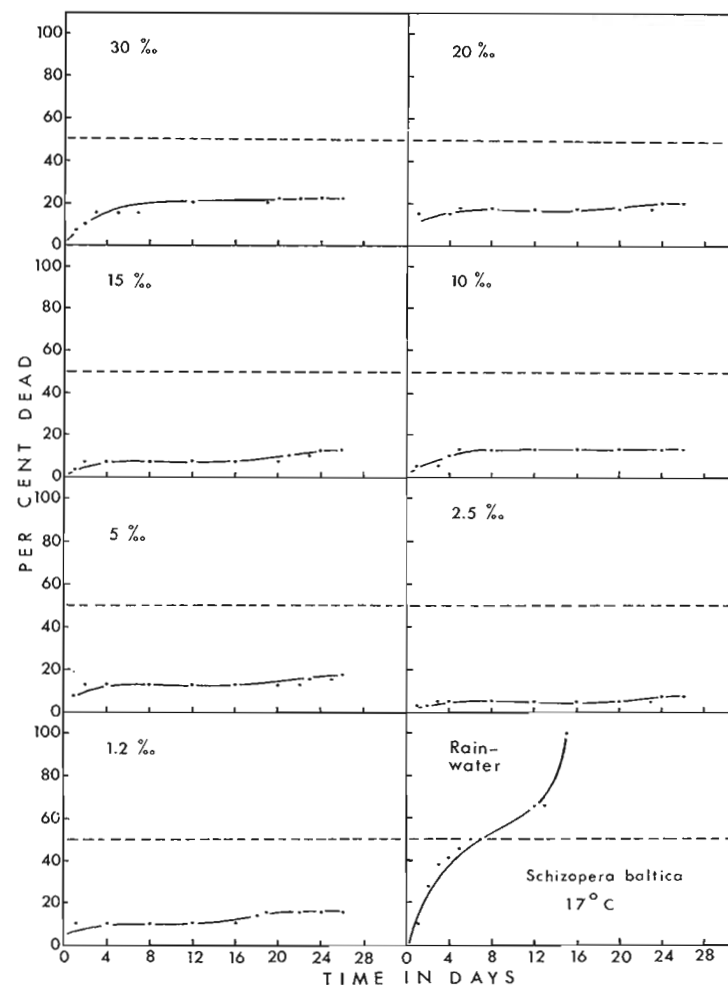
This species survived for a surprisingly short time in the salinity tests (Fig. 20), except in 5‰ S, where only 50% of the animals were dead after 50 hours. The tolerance was significantly lower both to higher and to lower salinities, and the animals only survived for 2-3 hours in rainwater.

FIG. 21. Temperature tolerance of *Marionina subterranea*, 4-7 August 1960.

The temperature tolerance was tested at two temperatures with the animals in water from the habitat (2‰ S) (Fig. 21). While all the animals lived during the whole experiment at 5°, about 50% were dead at 30°C already after 5 hours. The animals at 5° were very contracted, many of them fastened to the bottom of the dish. The low temperature had apparently induced secretion from the large, dorsal, setal glands in the posterior part of the body. At 30° the specimens became sluggish already after a few hours and after 4 hours the mortality increased rapidly.

Akteredilus monospermatecus

Two days before the start of the temperature-tolerance experiments (Fig. 22) the animals were transferred from the storing temperature of 13-17° to 22-23°C. At 5°C the specimens lay tightly rolled up, but they became active at the increase of temperature during examination. At 35°C they soon became sluggish and about 50% were dead after 4 hours. Though no controlled tolerance experiment was carried out at room temperature *Akteredilus monospermatecus* has shown a

FIG. 22. Temperature tolerance of *Akteredilus monospermatecus*, 6-10 October 1960.FIG. 23. Tolerance of *Schizopera baltica* to different salinities (n = 40). 24 August-19 September 1962.

high tolerance to intermediate temperatures. It has been kept in water and some sand from the habitat in ordinary Petri dishes at 21-24°C for more than two months without noticeable mortality in the population.

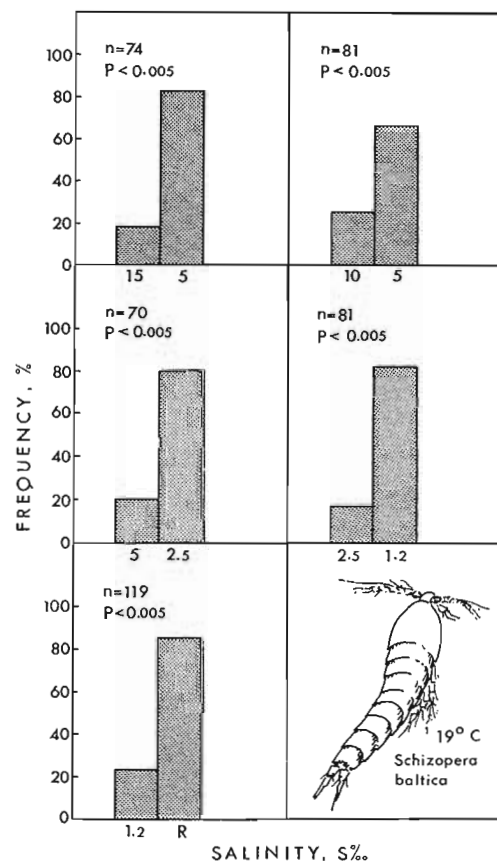


FIG. 24. Salinity preference of *Schizopera baltica* at 19°C.
R - rain-water. 24-29 August 1962.

Schizopera baltica

Two hours before the start of the salinity-tolerance experiment the animals were acclimatized to the experimental temperature, 17°C. Data on the experiment were taken once a day during 26 days. The animals showed a very high tolerance in all salinities offered except in rainwater where LD-50 was reached after 7 days (Fig. 23). The most natural behaviour was shown by the specimens in 1.2-2.5‰ S. In 30‰ S they were less active, mostly due to secretion of mucus which totally imbedded 3-4 specimens, which had to be carefully disentangled. This also occurred to some individuals in 5 and 10‰ S, though the mucus here was limited to a few

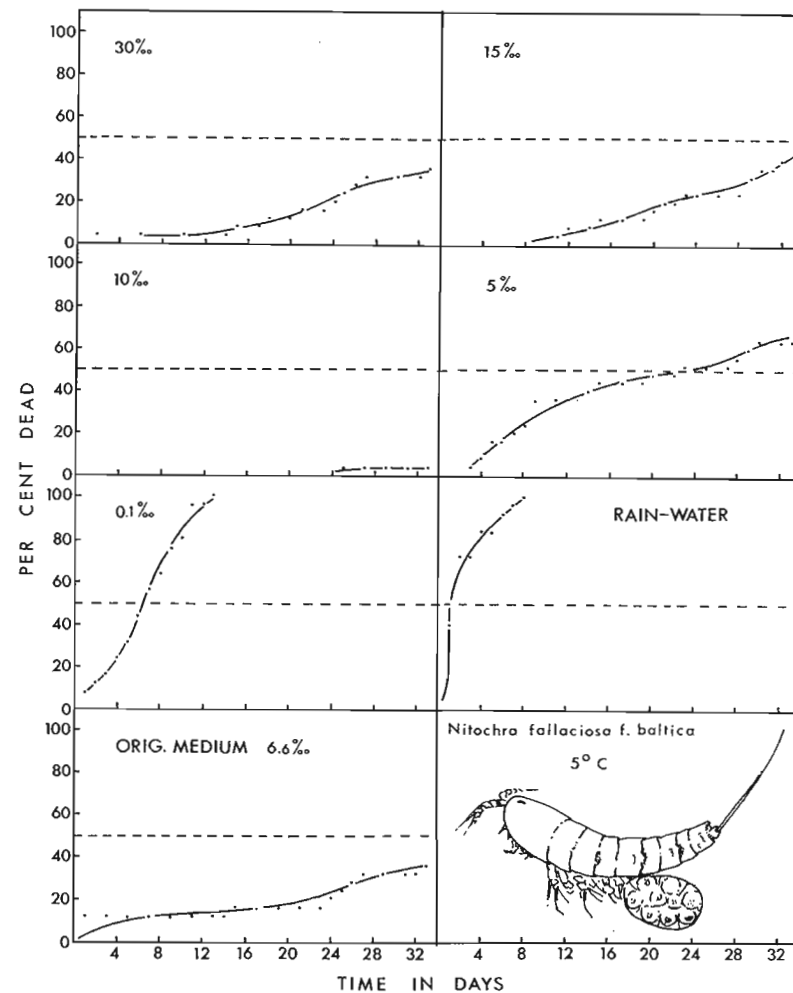


FIG. 25. Tolerance of *Nitochra fallaciosa f. baltica* to different salinities at 5°C (n = 25).
17 November-20 December 1964.

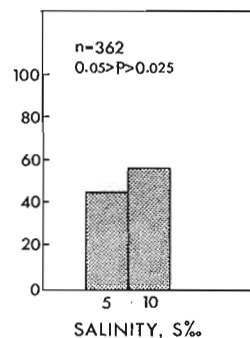


FIG. 26. Salinity preference of *Nitochra fallaciosa f. baltica* at 15°C. 23-25 July 1965.

small strands from the hind and ventral part of the abdomen. On the 19th day several nauplii were released in the 20‰ S experiment, and already after 4 days they resembled the adults, though the number of segments was less. On the 23rd day nauplii were found also in the 5‰ S experiment. Several moultings were noted during the experiment.

The results of the preference experiments are shown in Fig. 24. The animals were acclimatized overnight to the experimental temperature, 19°C. As the preference for rain-water is rather unexpected, the experiments were repeated several times with other alternative chambers, different ways of washing out of the separate sides after the end of the experiment etc., but always with the same strong preference for the lower concentration (see discussion, p. 61).

Nitochra fallaciosa f. baltica

This species is apparently very sensitive to rain-water (Fig. 25). Though one ecdysis was noted in this concentration, the animals rapidly became inactive and died. The survival in 0.1‰ S was somewhat better but significantly lower than in the higher salinities. There is thus a distinct increase in the survival rate between 0.1 and 5‰ S. The tolerance is lower to 5‰ than to 10-30‰ S. During the whole experiment only one specimen died in 10‰, and the animals kept at this salinity showed a slightly greater activity than those kept in 15-30‰ S. Eggs were hatched in salinities from 5 to 15‰ and in habitat water. After two weeks only the nauplii kept in 10 and 15‰ S were living, though some mortality had occurred.

To study the salinity optimum of *N. fallaciosa f. baltica*, which in the tolerance experiments seemed to be situated above 5‰ S, preference experiments were made, the results of which are shown in Fig. 26. Five separate experiments were

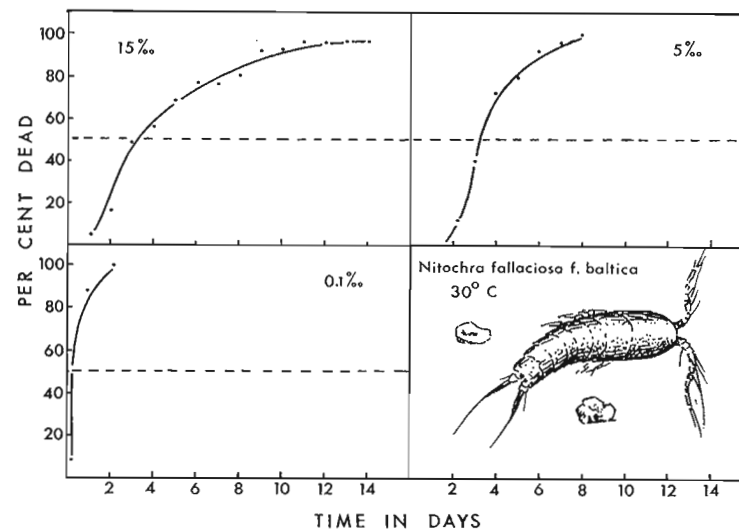


FIG. 27. Tolerance of *Nitochra fallaciosa f. baltica* to high temperature (30°C) in different salinities (n = 25). 17 November-1 December 1964.

made with the same alternatives, the results of which are pooled. The animals significantly preferred 10‰ S.

The tolerance to 30°C is shown in Fig. 27. The survival period in 0.1‰ S was very short – 88% were dead after 24 hours. Though the Ld 50-values in 5 and 15‰ S are of the same magnitude the second half of the 15‰ S-population lived longer.

Nitochra fallaciosa

The tolerance to rain-water was very low – 88% of the specimens were dead after 13 hours (Fig. 28). The survival rate in 0.5‰ S was much greater, but also here the animals soon became weak. On the third day they lay on their backs motionless, reacting only to a touch of the preparation needle. The range of salinities tolerated by this animal is apparently very broad, i.e. from somewhere between 0.5 and 5‰ to at least 20‰ S.

The results of the salinity-preference experiments are rather surprising. (Fig. 29). The successive tests pointed to a highly significant preference for 1‰ S, but towards the still lower salinities there was apparently no clear limit – the animals made no clear choice between 1‰ S and rain-water.

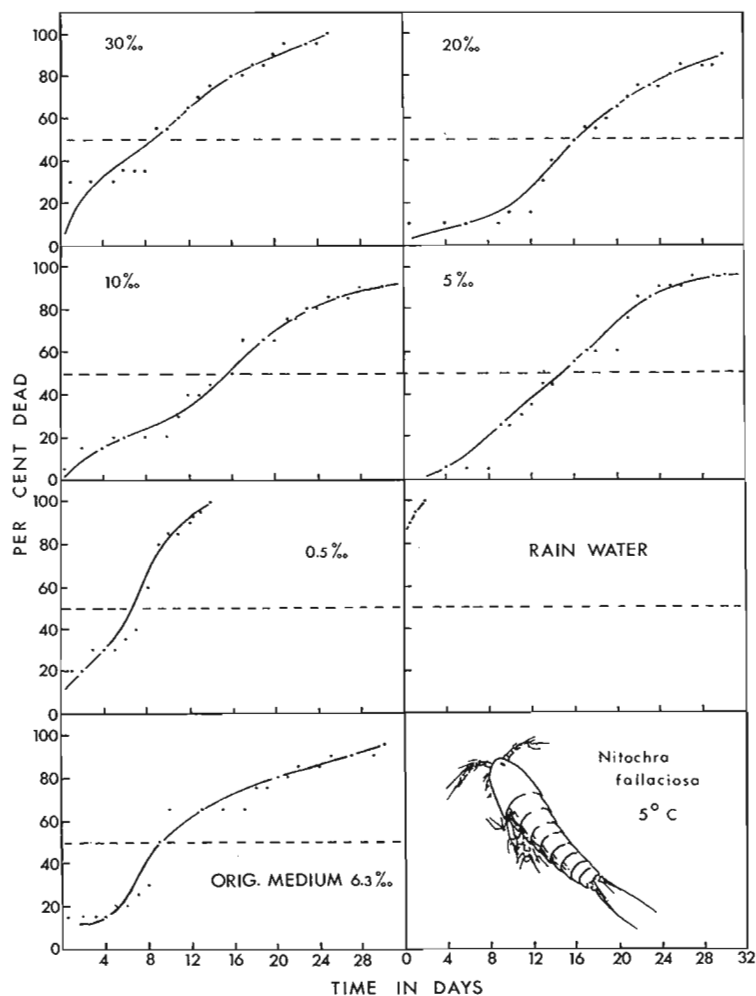


FIG. 28. Tolerance of *Nitochra fallaciosa* to different salinities at 5°C (n = 20).
16 January-15 February 1964.

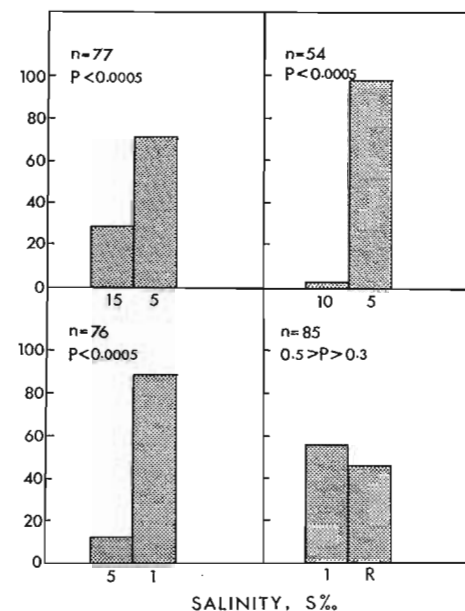


FIG. 29. Salinity preference of *Nitochra fallaciosa* at 20°C.
R = rain-water. 14-15 January 1964.

Paraleptastacus spinicauda

The results of the salinity-tolerance tests are shown in Fig. 30. The tolerance to freshwater is low and in 0.1‰ S Ld 50 was reached after less than 5 hours. Optimal conditions appeared to exist between 10 and 15‰ S. Secretion of mucus was noted both in rain-water and in 30‰ S.

The results of the salinity-preference experiments are shown in Fig. 31. The animals preferred 10 rather than 1‰ S, but hardly discriminated between 5 and 15‰ or 5 and 10‰ S. The activity in the alternative chambers was very high – the animals skilfully crawled in the thin layers of sand on the bottom.

While 50% of the population lived for 12-13 days at 5°C at optimal salinity concentrations, the corresponding figure for the tolerance at 30°C was 3-4 days (Fig. 32). When the animals kept in 0.1‰ S were taken from 30°C to room temperature (23°C) for examination they at first lay immobile, but they soon recovered and after 10 minutes they crept lively around. In the higher concentrations the animals constantly showed an abnormally high activity. The tolerance in 15‰ is greater than in 5‰ S.

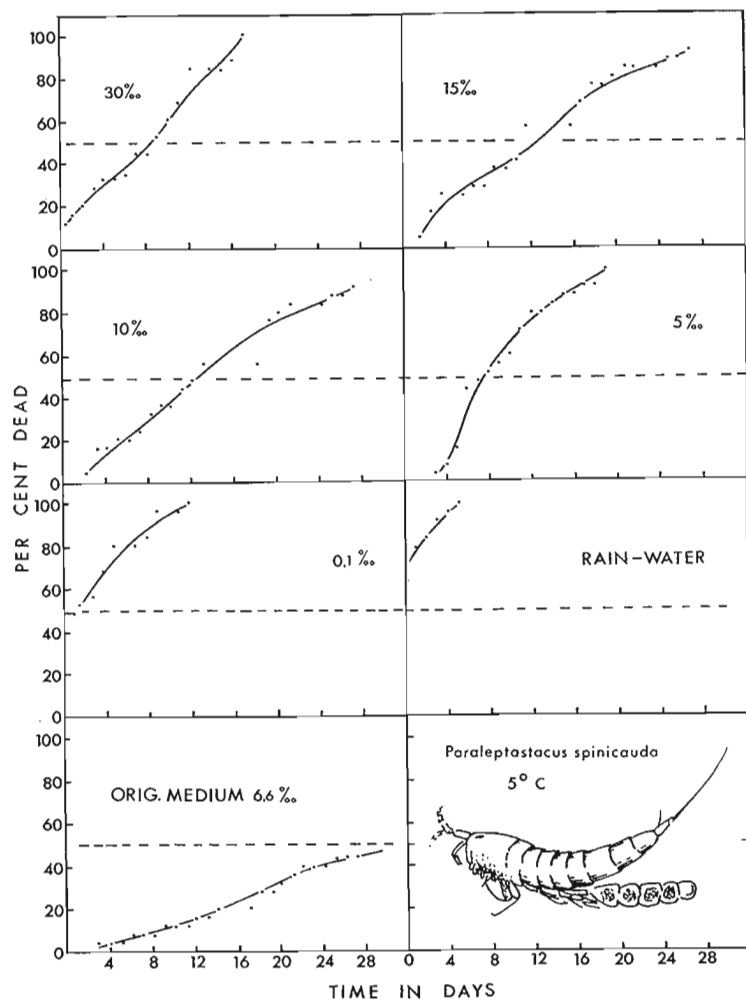


FIG. 30. Tolerance of *Paraleptastacus spinicauda* to different salinities at 5°C (n = 25). 29 October-25 November 1964.

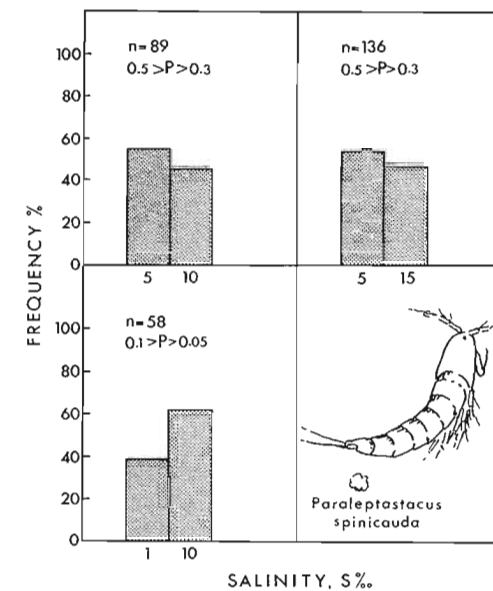


FIG. 31. Salinity preference of *Paraleptastacus spinicauda* at 15°C. 14-15 October 1964.

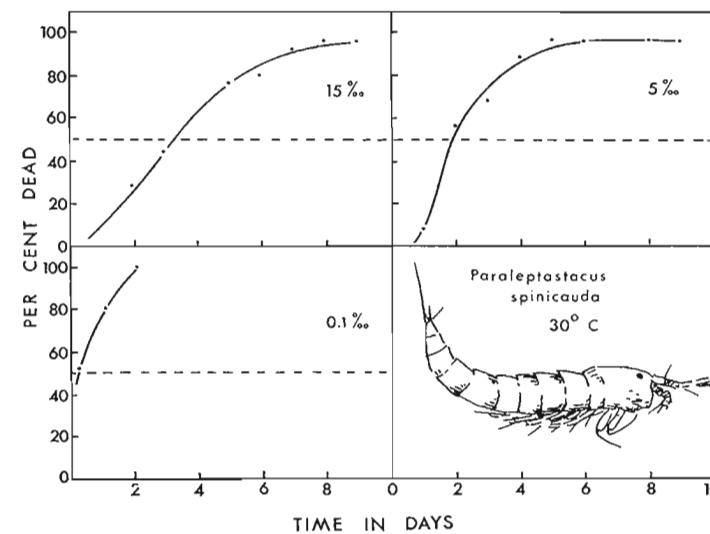


FIG. 32. Tolerance of *Paraleptastacus spinicauda* to high temperature (30°C) in different salinities (n = 25). 7-16 November 1964.

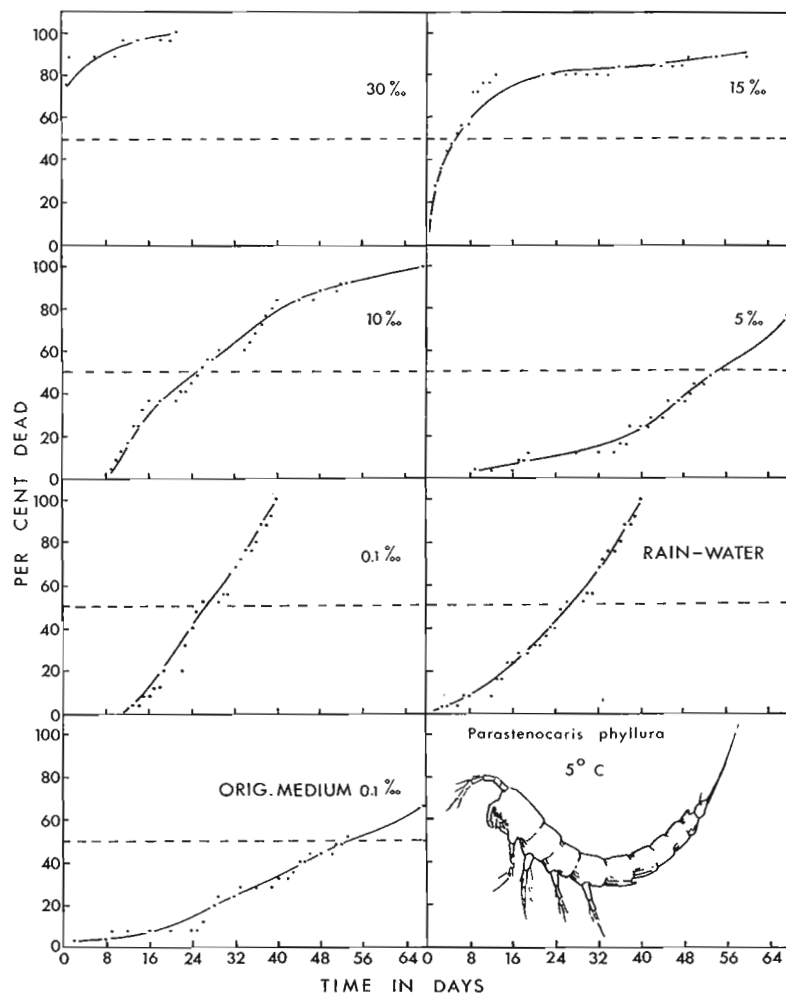


FIG. 33. Tolerance of *Parastenocaris phyllura* to different salinities ($n = 25$) at 5°C .
28 October-22 December 1964.

Parastenocaris phyllura

This species is very tolerant to rain-water (Fig. 33) in which LD 50 was reached after 25 days. In 30‰ S, 88% of the animals were dead after 16 hours. The intervening curves show that the optimum is around 5‰ S. In this concentra-

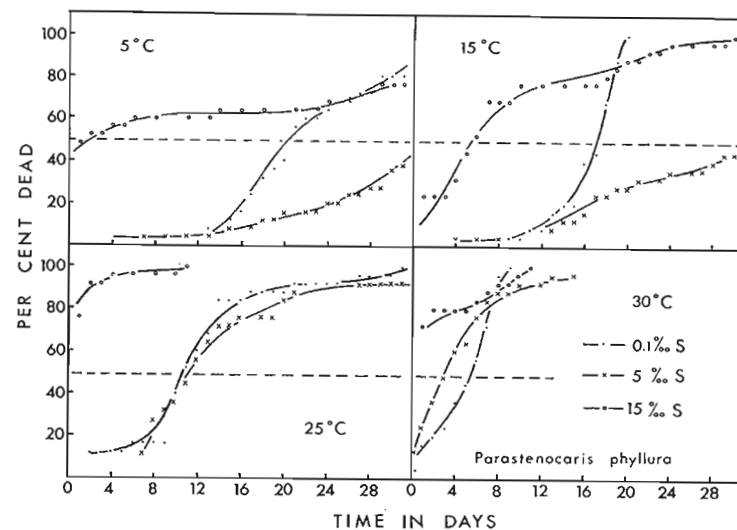


FIG. 34. Tolerance of *Parastenocaris phyllura* to high temperature (30°C) in different salinities ($n = 25$). 5 November-20 December 1964.

tion the animals also showed the most normal activity during the whole experiment.

The temperature tolerance was tested at 4 different temperatures: 5, 15, 25 and 30°C (Fig. 34). The greatest differences in the survival rates in the three salinities were found at the low temperatures. The survival rate was for all temperatures lowest in 15‰ S. At 5 and 15°C the survival rate was clearly highest in 5‰, but at 30°C the animals live longest in 0.1‰ S. There was a great difference in survival rate between 25 and 30°C . For 0.1 and 5‰ the LD 50-values are about 11 days at 25°C and 3-5 days at 30°C . At the latter temperature the animals were paralyzed, lying immobile on the bottom of the dishes, but they soon became active when transferred to a temperature of $20-23^{\circ}\text{C}$.

DISCUSSION

As shown by the quantitative investigations of the fauna, many animals are distributed in characteristic patterns in the beach. When trying to explain this we have to look for correlations between the distributions of the animals and the environmental factors. These differ mostly in two directions, vertically and perpendicular to the shore, while the conditions are more homogeneous in directions parallel to

the shore line. This has been proved for oxygen content and grain size by Jansson (1968, 1967b). The amount of organic material, however, often shows patchiness, and this may be one of the reasons why the interstitial fauna laterally sometimes shows an irregular distribution. The problem of patchiness within microhabitats has been discussed e.g. by Nielsen (1945) and Lackey (1961), both of whom stress the importance of the microclimatic conditions. Nielsen took his samples within areas as homogeneous as possible and he therefore assumed that the aggregations of the enchytraeids might be due to differences in mortality, natality and local oviposition. As the chief environmental factors were investigated in my studies and were nearly identical in most of the parallel samples, the major differences in the distribution of the animals might be due to characteristics in the life history or in the distribution of food. As the extent and composition of the organic film around the sand grains were not measured in this investigation, nothing can be said about the distribution of this food fraction. The role of bacteria as food for the interstitial fauna has been stressed by several authors and this may have a definite significance, especially when other environmental conditions are optimal.

WATER CONTENT

Of the several parameters on which the distribution of the interstitial animals depends, the content of pore water certainly is the most important one (Jansson, 1967b). Many animals were found deeper down landwards due to the decreasing amounts of water in the surface layers. At Askö St. C, the turbellarians (Fig. 3) were restricted to layers below 4 cm depth, where the amount of water was above 7-8% wet weight (Fig. 2). *Parastenocaris phyllura* was found successively deeper from St. B with a maximum at St. B at 5-10 cm depth to 18-24 cm at St. D (Fig. 4). The same is true for *Marionina southerni* (Fig. 3), though to a less conspicuous extent. In Simrishamn beach the distribution of pore water was very conspicuous as the pore-water content above the ground-water table rapidly decreased to a few per cent (Fig. 9). Several species were totally absent from the upper 10-18 cm (Figs. 10-11): *Macrostomum curvituba*, *Pseudocyrus subterranea*, and *Nitochra fallaciosa*. *Halacarellus capuzinus* was not found above 28 cm depth (St. A). Both the harpacticoids and the halacarids clearly submerged landwards. The water content was not measured at Tylösand but since the sand of the landward stations was dry at the surface a vertical gradient must have existed. The fine sand and the comparatively deep ground-water level suggest the presence of a successively decreasing water content upwards with reasonable amounts even near the surface at the most landward station. *Diurodrilus minimus* (Fig. 13) with a maximum at 5-7 cm depth at St. C and D was found mainly at 25-28 cm depth at St. E. Also here the harpacticoids (Fig. 13) show a successive submergence from the uppermost 7 cm at C and D to 35-40 cm depth at St. F. *Marionina preclitellochaeta* submerges only slightly landwards (Fig. 13).

Of the major taxonomical groups the harpacticoids are the most sensitive ones to decreasing amounts of pore water. The turbellarians are less sensitive and the oligochaetes are almost indifferent. This causes a stratification in the landward stations with harpacticoids at the bottom, turbellarians in the middle and oligochaetes near the surface. Concerning the harpacticoids this general scheme is supported by the findings of Pennak (1942), who found the largest populations at the low tide mark in the uppermost 4 cm of sand, and near the high tide mark at 12-16 cm depth. If his values of the average horizontal and vertical distribution of Copepoda at the stations 6.0, 7.5 and 9.0 (- high tide) metres landwards from the low tide line (op. cit., table II) are compared with the amounts of water, expressed as per cent saturation at corresponding layers (op. cit., table IV), we find an approximate lower limit at saturation values around 45%. For the Askö beach (Fig. 2) this corresponds to about 7% water of the wet weight, the saturated sand at the ground-water level having an average of 16% water. Areas with a water content of 7% of the wet weight or more are at St. B found through the whole core, at St. C at 5-20 cm depth and at St. D below 40 cm depth. As Pennak's values are average values of the distribution of several species (different from those found in Askö beach) we cannot expect a complete correspondence. *Parastenocaris phyllura* (Fig. 4) occurs in the whole core at St. B and between 5 and 20 cm depth at St. C, but at St. D we do not know the lower limit of distribution since this species still occurred at 30 cm depth where the core ended. At this station the highest pore-water content above the ground-water level was measured at 20 cm depth (5.7%) and *Parastenocaris* showed a weak maximum at this depth. At Simrishamn beach (Fig. 9) the upper limit for the distribution of the harpacticoids ought to be situated in St. A at 26 cm, in St. B at 48 cm, in St. C at 78 cm, and in St. D at 108 cm depth. Due to the length of the cores this can only be tested for St. A and B where the agreement is rather good (Fig. 11). The reason for this submergence may be that the harpacticoids can only migrate in water and are therefore readily stopped by the air-filled spaces between the still water-filled pore necks.

The dominance of the oligochaetes in the upper layers clearly reveals their terrestrial origin. Their morphology enables the animals to move and thrive even in far from fully saturated pore spaces. Landwards the fauna therefore shows increasingly terrestrial features, and the oligochaetes, especially the enchytraeids are dominating. The sandy beach successively passes into a soil habitat with increasing amounts of fine particles and organic material. The sand fauna is replaced by a soil fauna. Already the backshore shows some terrestrial features. Instead of measuring the water content of the substrate, pF-curves (Nielsen, 1959) must be obtained at the extreme landward limits of the beach. A coarse, sandy soil with a water content of 3% of dry weight corresponds to a pF of 2.7 and at these low values the enchytraeids cannot move - the limit of locomotion being about pF-3.9 (Nielsen, 1959). According to the same author these animals are incapable of

reacting to a moisture gradient as they quickly accumulate in small areas which have larger contents of water, e.g. around roots and debris, and become isolated when the surrounding substrate dries (op. cit., p. 167). This will probably only happen occasionally in sandy beaches as the substrate is more homogeneous.

The importance of water content as a limiting factor for the distribution of interstitial animals has further been stressed by de Zio & Grimaldi (1964, 1966) who showed that the tardigrade *Batillipes pennaki* was more abundant in deeper layers with increasing distance from the water line. Pennak (1940) found very few animals in freshwater beaches in layers with less than 10% saturation. Ganapati & Rao (1962) found a poor fauna both in the fully saturated and in the nearly dry layers.

The abundance of animals generally decreases towards the ground-water table. This is in contrast to the findings of Renaud-Debyser (1963, p. 142), but in her beaches the tidal movements certainly prevent the establishment of a stable ground-water level, typical of non-tidal beaches and often characterized by poor oxygenation.

OXYGEN

Though no areas with extremely poor oxygen conditions with formation of black layers were found, some areas showed low values: Askö, St. B at 15 cm depth, St. C at 15-30 cm depth and St. D at 35 cm depth (Fig. 2). At Tofta no oxygen was recorded below 10, 4 and 29 cm depth at St. A, B and D respectively (Fig. 7). At Simrishamn the availability was very low at St. D at 95 cm depth (Fig. 9). The distribution of several species is influenced by these oxygen minima. Since the values from Tofta are concentration values and the figures from Askö and Simrishamn values of the oxygen availability, correlations between the beaches cannot be carried out. At Askö most species showed a maximum occurrence at the surface layers of St. B (Figs. 3-4), probably due to the concurrent maximum oxygen content. At St. C the aggregations of *Haplovedovskya subterranea*, *Macrostromum curvituba* and *Parastenocaris phyllura* at 10-15 cm depth corresponded to a maximum in the availability of oxygen. The high frequency of air-filled pores and the small amounts of organic material at St. C point to favourable oxygen conditions, though actual oxygen measurements could not be carried out. *Mariolina southerni* is very abundant in these layers (Fig. 3). At Tofta (Fig. 8) *Trichocerca* sp. is restricted to the upper oxygenated layers at St. B. At St. A the oxygen concentration measured in connection with the sampling, was 1.88 mg/l at 10 cm depth. On that occasion weak waves passed the station. One hour earlier when wave action was much less, as it had been all the morning, the corresponding value was only 0.38 mg/l. The distribution of *Xenotrichula velox* with a large maximum immediately above 10 cm depth may have been a result of this poor oxygenation. At Simrishamn St. B (Fig. 9) the low oxygen availability values at and above 45 cm depth might have been caused by a water content so low that the whole elec-

trode surface was not moistened. If so it is not surprising that aggregations of *Pseudocyrstis subterranea* and *Macrostromum curvituba* were found in these layers (Fig. 10). At Tylösand St. C the oxygen concentration increased from the surface almost down to 10 cm depth (Fig. 12). The maxima of *Diurodrilus minimus* and the harpacticoids lie in this region (Fig. 13).

Pennak (1940) interpreted the distribution of the majority of the rotifers in freshwater beaches as a response to the different oxygen concentrations. Jansson (1966b) correlated the vertical distribution of mystacocarids in a Mediterranean beach with differences in oxygen availability. The harpacticoid *Parastenocaris vicesima* was restricted to layers with an oxygen availability surpassing $1 \times 10^{-7} \text{ g O}_2 \times \text{cm}^{-2} \times \text{min}^{-1}$ (Jansson, 1967a). He also found the distribution of the turbellarians and nematodes in a brackish-water beach to correspond to the distribution of the oxygen concentrations (1968). Fenchel & Jansson (1966) correlated the vertical extension of the microfauna, especially the ciliates, with the oxygen availability and the redox-potential of the sediments of a brackish-water beach. Fenchel, Jansson & von Thun (1967) made a complete analysis of the interstitial metazoan fauna in a sandy beach in the northern Øresund and correlated the distribution of the different species with the distribution of salinity, temperature, grain size, water content and oxygen availability. Gray (1966, 1967) found that *Protodrilus symbioticus* and *P. rubropharyngeus* preferred the higher oxygen concentrations in experiments with oxygen gradients. That oxygen is an important factor for the distribution of interstitial animals is thus a well established fact, but the lower tolerance limits for interstitial animals have not been established. Ivleva (1960) found that 45% of a sample of *Enchytraeus albidus* were still alive after 18.5 hours in an oxygen-free medium. Wieser and Kanwisher (1961) measured the respiration of marine nematodes from a soft-bottom community and showed that several species could survive anaerobic conditions. Nielsen (1961) measured the respiration of soil nematodes and enchytraeids and found a higher respiration rate for the nematodes. There are few data on the tolerance of substrate-living microfauna to low oxygen tensions. Even if the respiratory rate is known, we know little of how the animals can withstand periods of poor oxygen supply. Newell & Northcroft (1967) showed that a variety of intertidal macroanimals have two rates of oxygen uptake, a high one which is temperature dependent and corresponds to activity ("active metabolism") and a slow, temperature independent one, corresponding to quiescence ("maintenance metabolism"). In the latter state the animals are therefore well suited to survive in surroundings with a high temperature and a low oxygen content. Furthermore, Teal & Carey (1967) demonstrated that marsh crabs (*Uca* and *Sesarma*) under anaerobic conditions show a metabolism which is only $1/4$ of that found during aerobic conditions. Such capabilities of adjusting to adverse oxygen conditions may also exist among interstitial animals, but this aspect has not been studied. Nor have any studies on the relation between oxygen availability and the distribution of marine animals, except

those by Jansson (1967a), been carried out. The only relevant data on the significance of the oxygen supply for the distribution of the fauna in the beach is the lower tolerance limit of *Parastenocaris vicesima* which is around $1 \times 10^{-7} \text{ g O}_2 \times \text{cm}^{-2} \times \text{min}^{-1}$. As this animal is very small, about 0.3 mm long, we may assume that this value is comparatively high. Zeuthen (1947, p. 157) has shown, however, that the proportionate decrease of respiration, following an increase of body volume is smaller the smaller the animals. This value was therefore used as a reference value when classifying the layers poor in oxygen.

GRAIN SIZE

The grain size may sometimes vary within very small distances and animals with sliding locomotion have been shown to be distributed according to these variations (Jansson, 1967b with discussion of the literature). Thus, *Marionina subterranea* showed a preference for sand of 125-500 μ and *Parastenocaris vicesima* for 125-250 μ grain diameter. However, the effect of grain size upon the fauna is mostly exerted through other factors, e.g. water content, water circulation and oxygen availability. Since the animals thus seem to be unable to distinguish differences in grain size smaller than about 200 μ , the grain size is given with intervals of this size in the diagrams. Comparing the grain-size diagram for Askö (Fig. 2) to the distribution of the animals (Figs. 3-4) the only apparent correlation is seen at St. B, 5-6 cm depth, where *Parastenocaris phyllura* has a distinct minimum in a layer of coarse sand. The worm-like body and wriggling mode of locomotion of this animal indicate that this correlation is not fortuitous. Tofta beach is very homogeneous (Fig. 7) and an affinity for one of the two plotted grain sizes cannot be traced in the distribution of the animals (Fig. 8). For Simrishamn the grain-size diagram shows a patchy distribution (Fig. 9) as does the animal distribution (Figs. 10-11), but because of lack of laboratory experiments the interdependency is uncertain. Nematodes were totally absent except for one specimen, perhaps because the coarse substrate is unsuitable for a sliding locomotion. Tylösand has a rather homogeneous sand (Fig. 12), and the distributions of the meiofauna species cannot be correlated with the variations in the grain size (Fig. 13). Only the distribution of *Parastenocaris phyllura* at Askö seems thus to be dependent on the grain size. The mode of locomotion of the nematodes indicates that their distribution may be dependent on the grain size, but as they were not determined to species or size this could not be investigated. Besides the nematodes, *Marionina subterranea* could be expected to be distributed within layers of defined grain sizes and at both localities where it was found, Askö and Tofta, this was in fact the case. (Figs. 3, 8). The question of grain-size dependence of the sampled animals may therefore have two answers. Either the animals do not really react to differences in the grain-size composition or the stress of the other environmental factors overshadows these.

DETRITUS

Besides the valuable work of Perkins (1958) little work has been done on the food and feeding of the interstitial fauna of sandy beaches. Diatoms – an important food source for the sublittoral sand-microfauna – are mostly absent, except in the superficial layers. Detritus has therefore been regarded as a major source of food for many interstitial groups by several authors, e.g. Remane & Schultz (1935), Remane (1952) and Renaud-Debyser & Salvat (1963). In his comprehensive studies along the German coasts, Noodt (1957) observed ingestion of detritus by most of the harpacticoids. Muus (1967) found detritus to be necessary for the rearing of some harpacticoids. Nevertheless, some authors have found a very rich interstitial fauna including harpacticoids in beaches with very small amounts of detritus (Pennak, 1942; Renaud-Debyser, 1963). Ganapati & Rao (1962) found no correlation between amounts of detritus and the distribution of the fauna. This indicates the utilization of another source of food – the microbes. Jansson (1966b) suggests that the amount of bacteria on the surfaces of the sand grains does not necessarily follow the distribution and concentration of visible organic matter in the beach. Wood (1967) stressed the importance of the finest particles of estuarine sediments – mostly consisting of a large number of microbes, including bacteria – as food for many bottom-feeding species. The harpacticoids are supposed to feed largely on bacteria (Mare, 1942; ZoBell, 1946; Smidt, 1952). The amount of bacteria in the beach, supplemented with suspended microbes in the seawater, is increased if the sand of the beach is fine and the salinity concentration of the sea high (Wagner & Schwartz, 1963). Meadows & Anderson (1966) studied the distribution of various microbes on the surfaces of the sand grains of some beaches. The distribution of bacteria showed a maximum at the sand surface between mid-tide level and low water. Dissolved organic material is found in greater concentrations in the interstitial water of the beach than in the water outside (Stangenberg, 1934; Pennak, 1940). As dissolved organic material has a tendency to aggregate in seawater, forming “marine snow” (for a short review see Riley, 1963) this may constitute a food source for the interstitial fauna. Baylor & Sutcliffe (1963) clearly showed that this material had a nutritive value in feeding experiments with *Artemia salina*. Sutcliffe, Baylor & Mentzel (1963) showed that dissolved organic matter aggregates around small air bubbles, and electrostatic forces combined with high water circulation may substitute the air bubbles in producing organic aggregates in the sand. If so, these aggregates are likely to adhere to the surface of the sand grains, thus forming part of the organic film, which by Gray (1966, 1967) and others has been shown to constitute the attractive factor for sand-living animals. This film must certainly be of nutritive importance.

My own studies showed that the detritus was very irregularly distributed in the beaches. The greater amounts, e.g. at Simrishamn St. C (24-28 cm depth) and Askö, locality A, St. A (6-10 cm depth), were not correlated with the maximum

density of the fauna. In the laboratory, however, detritus concentrations in the culture dishes sometimes attracted certain species. A half-decomposed piece of *Zostera*, initially free from animals, was after a little while invaded by 30 *Marionina southerni*, 6 *Akteredilus monospermatecus* and 10 nematodes. Other animals, known to prefer accumulated debris, are *Marionina subterranea* and *Lumbricillus knoellneri* (Nielsen & Christensen, 1959). This was not demonstrated in my quantitative samples, however.

Another feeding-type which must be considered is the predator. According to Remane (1952) predators occur among turbellarians, nematodes and ciliates. The scarce investigations on food and feeding of the benthic meiofauna give poor data for a discussion, but from the few existing facts "it becomes increasingly clear that many of the marine benthic animals that have been called "predators" actually behave as deposit feeders most of the time" (Wieser, 1960, p. 135). The thorough investigation of Perkins (1958), for instance, hardly revealed any metazoan prey in the gut of representatives of the meiofauna. The present investigation deals only with few animals known or suspected to be predators. *Macrostomum curvita* is known to be a very voracious species and has been found to contain both oligochaetes and turbellarians (Karling, in Luther, 1960) as well as rotatorians, diatoms and flagellates. I have seen animals filled with diatoms probably originating from freshly deposited detritus. *Pseudocyrtilis subterranea* may be a predator as it has a rapid locomotion as well as a comparatively large size.

Most of the collected animals no doubt feed on what is usually called "detritus" in the widest sense of the word, including all kinds of organic debris as well as living microorganisms such as bacteria, which, thus, offers a large number of food niches to the animals.

SALINITY AND TEMPERATURE

The results of the laboratory experiments with salinity and temperature show that many species exhibit a physiological ability to withstand strong fluctuations of these factors. An interpretation of the role of these two parameters for the distribution of the animals is only possible when the responses of the species are known. In Fig. 35 the optimum salinity zones found in experiments with 12 different species, are plotted. These zones have, of course, no sharp limits but they represent the salinities where the survival rate at the temperature listed was highest. The zones may be divided into three classes with successively narrower ranges of salinity tolerance: 1) 25-30‰-range represented by *Coronhelmis lutheri*, *Schizopera baltica* and *Nitochra fallaciosa f. baltica*. 2) 15-19‰-range: *Nitochra fallaciosa*, *Akteredilus monospermatecus*, *Marionina southerni*. 3) 5-7.5‰-range: *Marionina preclitellochaeta*, *Haplovejdovskya subterranea*, *Paraleptastacus spinicauda*, *Parastenocaris phyllura*, *P. vicesima* and *Marionina subterranea*.

Coronhelmis lutheri was remarkably tolerant (Fig. 17). This animal is regarded

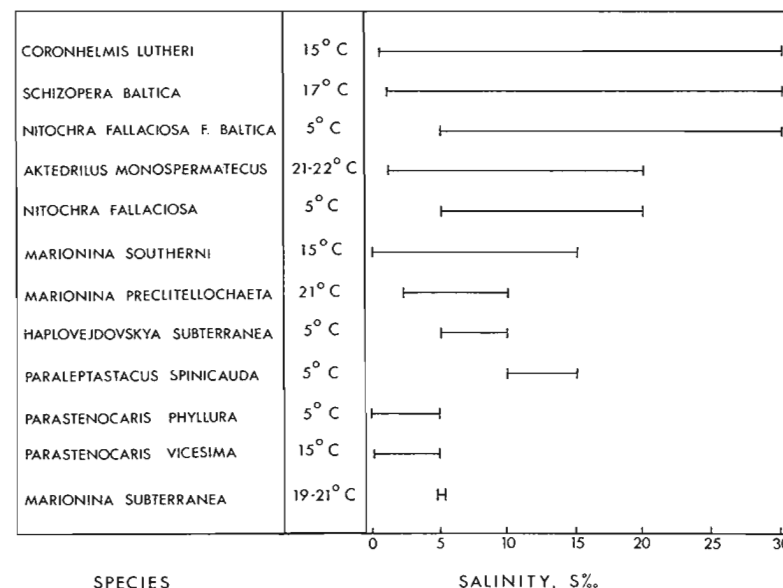


FIG. 35. Salinity optima, based on the tolerance experiments with the different species.

as a brackish water species on the basis of its geographical distribution (Ax, 1956), but it is very interesting to find such a high tolerance within the same population. Reuter (1961) demonstrated how three isolated populations of the holeuryhaline turbellarian *Gyratrix hermaphrodites* showed different salinity tolerances. The specimens from a forest pond had a much narrower tolerance zone than the specimens from a coastal pond and from brackish water, and each of the groups had a different number of chromosomes. Other tolerance experiments with turbellarians are few: Rees (1941) studied the temperature and salinity tolerance of *Mono-coelis fusca* and found good correspondance between the tolerance ranges observed in the laboratory and in the field. Schmitt (1955) found high survival for *Planaria gonocephala* and *P. lugubris* at 3 and 5‰ S, respectively.

Schizopera baltica and *Nitochra fallaciosa f. baltica* are described from Askö by Lang (1965), and have so far not been found elsewhere. Both species produced nauplii in my experiments. Those of *Schizopera baltica* survived and grew rapidly at 17°C both in 20 and 5‰ S, but of the *Nitochra* nauplii released at 5°C in 5 to 15‰ S, only those in 10 and 15‰ survived. This also points to a difference in tolerance to lower salinity concentrations between these two species as shown in Fig. 35.

Of the second group *Nitochra fallaciosa* is a euryhaline and eurytopic species, which in the Baltic is often found in coastal ground-water (Noodt, 1955). Both

Marionina southerni and *Aktedrilus monospermatecus* are known from a wide salinity range (Hagen, 1951, in Remane, 1958).

Of the species with a narrow salinity optimum (group 3) *Marionina preclitellochaeta* is very little known. It has been recorded from Sweden (Jansson, 1966), Denmark (Nielsen & Christensen, 1963; Fenchel, Jansson & v. Thun, 1967) and France (Lasserre, 1966). The French specimens occurred in 18 to 33‰ S, but at Tylösand I have collected this species in salinities from 0 to 7.4‰. Studies on the salinity response of different geographical populations therefore seem necessary. *Marionina subterranea* is a well-known enchytraeid from the coastal ground water, and is regarded as very euryhaline (Nielsen & Christensen, 1959). The remarkably limited optimum around 5‰ S in the tolerance tests (Fig. 20) is not representative for the Baltic population of the species. More typical is surely the similar survival in salinities from 1.3 to 15‰. Nevertheless, *M. subterranea* was always found within 1 metre from the water's edge at Tofta beach, the locality of the "experimental" population, where the salinity mostly is about the same as that of the sea (7‰ S). *Haplovejdovskya subterranea*, described by Ax (1954) from Finland, is mostly found in coastal ground water (Luther, 1962) and is regarded as a typical brackish-water species (Ax, 1956). This is further stressed by the narrow salinity optimum at 5-10‰. The remaining species in the class with the narrow salinity range, the harpacticoids, comprises both marine and limnetic species. *Paraleptastacus spinicauda* is an euryhaline, marine species, bound to sandy areas and often found in coastal ground water (Noodt, 1953). Its lower salinity limit is 8-3(2)‰ (Noodt, 1957). This is in agreement with both the tolerance and preference results (Figs. 30, 31). *Parastenocaris vicesima* and *P. phyllura* are both freshwater species and characteristic members of the subterranean fauna of the continents, but both also thrive in brackish water of low salinity. *P. vicesima* with an upper tolerance limit of around 8‰ S (Noodt, 1957) is the characteristic species of the coastal ground water in brackish-water beaches. It is often found together with the more oligohaline freshwater species *P. phyllura* (Noodt, 1957). The results of the tolerance tests with *P. vicesima* (see Jansson, 1967a) as well as with *P. phyllura* agree well with these field results. The tolerance to 10‰ S is clearly higher for *P. vicesima*.

The preference for a certain salinity is certainly a less fixed characteristic of an animal than the tolerance. For that reason the tolerance zones, not the preferences, are plotted in Fig. 35. In spite of the different temperature conditions during the experiments the optimum zones are well comparable as the temperatures – by no means extreme – are not likely to exert a greatly differing influence upon the animals (Fig. 34).

The results of the salinity-tolerance experiments can easily be compared to the distribution of the animals in the field in relation to the salinity distribution. If the field conditions, after a period of great fluctuations, have been stable for a long time, the animals initially living outside their tolerance area, will either have

died or have escaped to favourable areas (this has been shown for the mystacocarid *Derocheilocaris remanei* by Jansson (1966b)). This immigration from unfavourable areas implies firstly that the animals can perceive and migrate in a gradient, and secondly, that a gradient exists in the field for a sufficiently long time. That many animals migrate in a salinity gradient has already been shown, e.g. in the experiments reported on here. That very steep salinity gradients often occur in sandy beaches is a well-established fact. The stability of the gradient must be discussed in relation to the locomotory abilities of the animals. For the interstitial oligochaetes the rate of movement in a thin layer of fine sand has been measured to 3 cm per minute (Jansson, 1962), which may be taken as an average value as for instance the harpacticoids are much faster. Most animals therefore have ample opportunities to reach a preference zone in a steep gradient in the beach, as also shown for *Derocheilocaris remanei* (Jansson, 1966b) and *Parastenocaris vicesima* (Jansson, 1967a). The stability of a preference for a narrow salinity range has been discussed by Jansson (1962). In these experiments *Aktedrilus monospermatecus* showed an unaltered preference for 2.5‰ S even after 8 days in 20‰ S.

As many stimuli may influence the animals moving in a gradient, the aggregations may sometimes not be due to a preference for a certain salinity concentration. In the present experiments two species were found aggregated in salinities outside the tolerance zones. *Schizopera baltica* chose rain-water in spite of a rather low tolerance to that medium, and *Nitochra fallaciosa* did not distinguish between rain-water and 1‰ S, although it proved to be very sensitive to rain-water. Therefore, it seems that the specimens deposited in the freshwater side of the alternative chamber were either unable to detect a gradient or they were so weak, that they could not return to the more optimal side. The last explanation seems less probable as the animals were able to crawl after the experiment. Probably the animals showed a change in reaction similar to that of *Gammarus oceanicus*, which reacted negatively to sea-water after treatment with a weak salt solution (Zubov, 1964). The discrepancy between the tolerance and preference experiments with *Marionina preclitellochaeta* is only an apparent one as different populations were used for the two types of experiments. In fact the results agree well with the corresponding field distribution (Jansson, 1962).

The secretion of mucus by *Haplovejdovskya subterranea*, *Schizopera baltica* and *Paraleptastacus spinicauda* was apparently caused by the abrupt transfer of the animals to the test concentrations. The behaviour of *H. subterranea* points to an important protective function of the mucus. It is well known that many animals secrete mucus under salinity stress (Kinne, 1964a) and that this mucus greatly reduces the permeability of the integument (Potts & Parry, 1964). Another response to increased salinity stress was the reduction of volume of the turbellarians, especially of *H. subterranea*, e.g. in 15‰ S. Their bodies never fully regained the volume they had in habitat water but a certain compensation was observed, indi-

cating an active osmoregulation. Similar reactions of *Procerodes ulvae*, described by Pantin (1931), are by Potts & Parry (1964, p. 157) regarded as analogous to the osmoregulatory behaviour of *Nereis diversicolor*. Within the thick coat of mucus, which reduces the rate of outflux of water from the body, *Haplovejdovskya subterranea* could slowly begin to counterbalance the loss of water, when the difference of concentration between the animal and the medium became sufficiently low. The animal then left the used mantle of mucus and moved around, though weak and with a reduced body volume. There was much less mucus secretion from the harpacticoids, and a "coma" like that seen in the turbellarians was not observed. Crustaceans have a protective integument – the cuticula – which is not so permeable as the body wall of the turbellarians, especially of the marine forms (Steinbach, 1962).

The species investigated by me showed different resistency to high temperature (30°C). Most species showed LD 50-values from 3 to 4 days in the optimal salinity concentrations – *Parastenocaris phyllura* being the most tolerant one with 5–6 days – but *Haplovejdovskya subterranea* and *Marionina subterranea* were very sensitive and 50% of the specimens were dead after 16 and 5 hours, respectively. The better survival rate in 5‰ S for *H. subterranea* further stresses that it is a typical brackish-water species. Similarly *Parastenocaris phyllura* survived best at 30°C in 0.1‰ S, which also indicates that the species is of limnetic origin. Of the other species tested at 30°C in several salinities, *Coronhelms lutheri* and *Paraleptastacus spinicauda* survived significantly better in the highest concentration (15‰) while *Nitochra fallaciosa* f. *baltica* was as resistant in 5 as in 15‰ S. All specimens used in the temperature-salinity tests were kept at 10°C during the period before the experiments, except for *Coronhelms lutheri* which was kept at 5°C. As Matutani (1961) has shown that acclimatization, both at a high and a low temperature, increases the heat resistance of *Tigriopus japonicus*, the tolerance of *C. lutheri* may be somewhat too high compared with that shown by the other species.

The abnormally high activity at 30°C of *Paraleptastacus spinicauda* may be interpreted as a shock-response, an overshoot, caused by the transfer to the high temperature (Kinne, 1964b). A similar phenomenon was observed by Jansson (1966b) for *Derocheilocaris remanei* at 27–30°C.

A temperature of 5°C is easily endured by the interstitial animals. The activity is usually much lower than at higher temperatures and for instance the turbellarians often lie slightly contracted and passive, but they become active after a few minutes at room temperature. Death from low temperatures above zero has not been noted. Some preference experiments at 5°C with *Nitochra fallaciosa* gave totally randomized results – the animals did not prefer any of the concentrations from 1 to 15‰ S, whereas preference experiments with animals from the same sampling kept at 15°C rendered a distinct preference (Fig. 29). This might be due either to the low activity of the animals or to a suppression of the ability to distinguish between the different concentrations in the lower temperature.

In the field the abundance of the total fauna follows the seasonal fluctuations of temperature (Table 3) with a maximum in the autumn. In more temperate beaches the fauna is abundant during the whole year but submerges during the cold period as beautifully shown by Renaud-Debyser (1963). During winter the animals are subject to often very low temperatures. Animals may readily withstand negative temperatures without ice formation as was shown by Gray (1965) for *Protodrilus symbioticus* and Muus (1967, p. 232) for harpacticoids. Some groups also survive a frozen state: Aoki & Konno (1962) reported a high survival rate for nematodes, rotifers and tardigrades from frozen freshwater algae in the Antarctic region. Less well known is the survival in frozen sand of turbellarians, gastrotrichs and oligochaetes (Table 4). It is impossible to judge, however, whether the animals have actually been frozen or not. According to Kinne (1963) the freezing points of body fluids from marine and brackish-water animals are generally "similar to, or lower than that of the external medium". Certain mechanisms exist, however, that may lower the freezing point. Lowering of temperature may, thus, induce formation of glycerol in the body (Asahina, 1961). Chock-effects from short periods of low temperature may increase the cold-resistance (Schlieper, 1966). The dehydration concentrates the body fluids, lowering the freezing-point. As has also been shown by Jansson (1967c), the temperature in the frozen sand is seldom much below zero (Fig. 1). With a slight increase of the internal concentration the animals may therefore totally avoid freezing and survive during the cold months of the year, captured – but also thermally protected – in the frozen sand.

The possible correlations between the salinity and temperature and the distribution of the separate species in the field will now be discussed.

Macrostomum curvatura is known to be a typical brackish-water species, preferring sandy beaches (Ax, 1954) and to be common both in the coastal ground water and in the sublittoral (Luther, 1960). Though it has been found in freshwater (Remane, 1958, p. 126), it apparently prefers the seaward part of the beach both at Askö and Simrishamn. According to Ax (1954) it inhabits "in erster Linie die ufernahen Sandbiotope".

Bothriomolus balticus is regarded as a typical member of the *Otoplana*-zone – Sterrer (1965) showed a maximum occurrence 40 cm seawards from the water line. At Askö, locality B, it was also found only at the most seaward station.

Pseudocirrus subterranea is regarded as a typical member of the coastal groundwater fauna (Luther, 1960). This view is in accordance with the maximal distribution found at Simrishamn St. B.

Haplovejdovskya subterranea was most abundant at Askö, locality A, St. B. In numerous quantitative samplings, not accounted for here, this species has always been found in salinities between 6 and 7‰. It has already been mentioned that the sea level suddenly fell the night before the sampling at Askö, locality A, and that this caused a salinity decrease from about 4‰ to 0.1‰. This low salinity

must have ruled for about 12 hours. Considering the low locomotion ability of the animals, this period is too short for an escape, and the animals were therefore probably "caught" in water of a non-optimal salinity. Thus, the animals may usually occur in salinities within the optimum zone found in the experiments (5-10‰ S, Fig. 15).

Jensenia angulata is a purely marine species according to Remane (1958, p. 72). Nevertheless it was found at Askö in the foreshore (Fig. 6).

Coronhelms multispinosus is a typical brackish-water species (Ax, 1956), often found in the interstitial habitat. Like other authors (e.g. Luther, 1962) I have mostly found this species in late summer or autumn samples (Table 3). As for *Macrostomum curvifurca* and *Haplovelodovskya subterranea* there is a sharp limit in the horizontal distribution in Askö beach (Fig. 3) between St. B and C. Maybe this is caused by the above mentioned decrease in salinity which must have influenced the more landward station first, forcing the animals seawards. All these species showed a maximum at St. B in the surface layers, where the temperature at the time of the sampling was 25-28°C. Especially *H. subterranea* lived here near the limit of its temperature tolerance range. Because of the evaporation, however, the salinity in the uppermost cm may be significantly higher than that of the ground water, which suppressed the stress of the high temperature.

Coronhelms lutheri has been found in salinities down to 0.05‰ (Luther, 1962). This is in accordance with the great euryhalinity shown in the salinity tolerance experiments. At high temperatures it has an optimum at higher salinity concentrations (Fig. 17). This may be the reason why I mostly found this species during winter and early summer when the animals can still tolerate low salinities because of the low temperature.

Carcharodorhynchus subterraneus was only found in 4 specimens at Askö (locality B, St. C-D, Table 7). This distribution, restricted to the backshore, is similar to that found at Julebæk beach, Denmark, by Fenchel, Jansson & v. Thun (1967). All previous findings have also been restricted to coastal ground water or moist sand, except for one case (Karling, 1963).

The nematodes were less dominating than expected. The greatest abundance was recorded at Askö, localities A (Table 5) and B (Fig. 6). The great abundance both close to the sea and far landwards at locality B points to a dominance of marine and terrestrial species, respectively, as has been shown for German beaches by Gerlach (1954). The scarcity of nematodes in the Swedish beaches is apparent, compared to the abundance of these animals in Julebæk beach, where more than 50% of all sampled animals were nematodes (Fenchel, Jansson & v. Thun, 1967).

Xenotrichula velox shows a maximum occurrence at the water's edge and this is certainly correlated with the salinity gradient (Fig. 8). This is the second record from the Northern Baltic; Karling (1954) found 1 specimen at 1 m depth off Gothland.

Turbanella lutheri, *T. hyalina* and *T. cornuta* were all found at the most sea-

ward stations at Askö (Figs. 4, 6 and Tables 3, 4), probably at their lower salinity tolerance limit. Both *T. hyalina* and *T. cornuta* survive in a freezing state. Karling (1954) has found all three species in the Northern Baltic as far as Nynäshamn-Nämndö, slightly north of Askö.

Marionina southerni, *M. subterranea* and *M. preclitellochaeta* occupy three different zones in the beaches. *M. southerni* has the widest distribution, with a maximum in the fore shore it extends landwards till the water is almost fresh (Figs. 3, 6). This agrees well with the results from the salinity experiments. The preference for salinities about 1‰ will keep most of the animals near the water line but the great tolerance to freshwater enables them to endure the nearly fresh interstitial water of the backshore. *M. subterranea* (Figs. 3, 6, 8) is more restricted to the fore shore which may be due, partly to the low resistance to rain-water, partly to the low tolerance to high temperatures. *M. preclitellochaeta* shows a maximum in the backshore (Fig. 13) which is in agreement with its optimum salinity zone (for discussion see Jansson, 1962).

Lumbricillus knoellneri is a sand-living enchytraeid with preference for decaying seaweed (Nielsen & Christensen, 1951). It is an euryhaline species and this is also obvious from the wide distribution in the beach (Fig. 10). It is identical to the "*Fridericia ?bulbosa*" found at Simrishamn by Brinck, Dahl & Wieser (1955).

Aktedrilus monospermatecus is a well known species of sandy beaches, sometimes found in nearly fresh water (Hagen, 1951, in Remane, 1958). It showed a maximum in the fore shore but was present landwards, sometimes far into the backshore (Figs. 3, 6, 10). Jansson (1962) showed that the salinity optimum zone of a Baltic population was 1.3 to 20‰ with a preference for 2.5 to 5‰, and this is in accordance with the distribution at Askö and Simrishamn. It also agrees rather well with the findings of Fenchel, Jansson & v. Thun (1967).

Diurodrilus minimus (Fig. 13) shows a distribution which is very similar to that found in Julebæk beach by Fenchel, Jansson & v. Thun (1967) with a maximum in the middle part of the beach. The landward limit is certainly due to low salinity while the absence from the seaward station must be due to another factor, probably turbulence.

Schizopera baltica shows the greatest abundance in the seaward part of the beach, but extends to zones, where the salinity may often reach low values (Fig. 6). This euryhalinity, which is also shown in the tolerance and preference experiments (Figs. 23, 24), is typical of species inhabiting the coastal ground water.

Schizopera inornata (Fig. 10) was found in nine specimens at Simrishamn St. D. According to Brinck, Dahl & Wieser (1955) it was common in the beach still 9 m landwards where the salinity was 1.1‰.

Nitochra fallaciosa has a distribution in the Simrishamn beach (Fig. 11) which is in agreement with the results obtained in the experiments. The tolerance to very low salinities allows the animals to extend far landwards. The preference for sali-

nities about 1‰ corresponds to the maximum occurrence in the field at St. B (1.2‰ S).

Nitochra fallaciosa f. *baltica* has always been found in salinities above 6‰ and its distribution in the quantitative samples is restricted to the two seaward stations (Fig. 6). Both the salinity tolerance and preference experiments point to an optimum zone around or above 10‰. The low tolerance to rain-water will effectively keep the animals away from the backshore, while the high temperature tolerance enables them to inhabit the outer portions of the beach.

Paraleptastacus spinicauda is by Noodt (1957) regarded as a characteristic species of the coastal ground water of marine habitats. Similarly, Renaud-Debyser (1963) regarded it as a typical species of the high beach. The distribution at Askö, locality B, was concentrated in the seaward part of the shore, agreeing well with the salinity optimum (Jansson, 1966a). The results of the preference experiments also showed an affinity to higher salinities. The better survival rate at higher temperatures in higher salinities also indicates that the fore shore is the most favourable part of the beach for this species.

Parastenocaris vicesima was the subject of a previous study (Jansson, 1967a), where the main parameters for the distribution of this species in the field were found to be grain size, salinity and oxygen availability. The abundance of the animals in the quantitative studies at Askö, locality B, has already been published (Jansson, 1966a). The distribution at Askö with a maximum inside the fore shore is in agreement with the findings of Noodt (1953) in Finnish beaches.

Parastenocaris phyllura is, contrary to *P. vicesima*, a common member of the subterranean fauna of the land (Husmann, 1966). Together with *Marionina southerni* it is the dominating species in the backshore at Askö. At high temperature it shows a lower salinity optimum than *P. vicesima*, which further explains the difference in their horizontal distribution in the field. According to Husmann (op. cit., p. 258) both *P. phyllura* and *P. vicesima* move to deeper layers towards winter.

Halacarellus capuzinus is an euryhaline halacarid with a main distribution in the sandy sublittoral. At Askö it is usually found in the vicinity of the water line, but in the more permeable – and therefore more saline – Simrishamn beach it was still abundant 7 m inside the water's edge.

CONCLUSIONS

If the separate core samples, corresponding to 10 cm² surface, are converted to individuals per m², we find the highest abundance at Askö beach, St. B, where the total number of metazoans was 1.5×10^6 . The figures for the separate samples in the beaches are of about the same order as those presented by Fenchel (1967) for Scandinavian waters.

A close correlation between the responses of the animals in the laboratory and in the field cannot be expected *per se*. Furthermore, the present studies do not include experiments where all the chief parameters have been varied. Such experiments are necessary for a full understanding of the dynamics of an ecosystem and will follow the more simple experiments presented here. The tolerances observed in the laboratory do not always agree with the tolerance limits shown by the field distribution, as shown for instance by Schlieper & Bläsing (1952). They demonstrated that the ecological temperature zone of *Planaria alpina* was more restricted than the physiological zone observed in laboratory experiments. The more restricted distribution of the animals in the field was explained by the fact that the long periods of medium temperature, not the short maxima or minima, limit the spawning and distributions. However, in a sandy beach characterized by strong gradients within short areas, the animals may have time enough to respond to maxima and minima of rather short duration by migration. The reported rapid lowering of the sea level at Askö, causing a sudden drop in the interstitial salinities, gives a typical example of a situation, where the animals have not yet had time to react on the change in the environment by migrating.

The present investigation, however, has given several examples of an agreement between the physiological and ecological tolerances of the animals. The chief limiting factor is the amount of pore water, which constitutes the first qualification for an interstitial life. Oxygen availability may sometimes be limiting, especially where large amounts of detritus create anaerobic conditions or where the flow of interstitial water is small, owing to low permeability and low ground-water pressure. The grain size proper constitutes a limiting factor only when it is extreme, offering pores either too small or too large for interstitial animals. At moderate grain sizes other parameters are more important. Though the food factor has been very little studied, especially regarding the microbial fraction, I have generally found the largest populations of animals in beaches containing medium amounts of visible detritus, provided that the permeability is good. Except for pore-water content, however, the most important parameters of the non-tidal beach for the horizontal and vertical distribution of the animals have proved to be temperature and salinity. This is in agreement with the conditions in estuaries as Muus (1967, p. 229) stresses that temperature is the most important factor for animals adapted to a habitat characterized by fluctuating temperatures and salinities. In a sandy beach, however, the animals may easily avoid the extremes by migrating.

APPENDIX

List of the animals which were identified to species

Turbellaria

- Macrostomum curvatura* Luther
Bothriomolus balticus Meixner
Pseudocystis subterranea Ax
Coelogyropora schulzii Meixner
Provortex pallidus Luther
P. karlingi Ax
Haplovedjovskya subterranea Ax
Jensenia angulata (Jensen)
Coronhelms multispinosus Luther
C. lutheri Ax
Promesostoma nynaesiensis Karling
Prognathorhynchus canaliculatus Karling
Carcharodorhynchus subterraneus Meixner
- Gastrotricha
Xenotrichula velox Remane
Turbanella hyalina Schultze
T. cornuta Remane
T. lutheri Remane
- Polychaeta
Diurodrilus minimus Remane

Oligochaeta

- Nais elinguis* Müller
Lumbricillus lineatus (Müller)
L. knoellneri Nielsen & Christensen
Marionina subterranea Knöllner
M. southerni Cernovsikov
M. preclitellochaeta Jansson
Aktedrilus monospermatecus Knöllner
- Harpacticoida
Schizopera inornata Noodt
S. baltica Lang
Nitochra fallaciosa Klie
N. fallaciosa f. baltica Lang
Itunella muelleri Gagnon
Paraleptastacus spinicauda T & A. Scott
Parastenocaris vicesima Klie
P. phyllura Kiefer
Huntemannia jadensis Poppe
- Halacarida
Halacarellus capuzinus Lohmann

REFERENCES

- AOKI, K. & H. KONNO. 1961. Frost-resistance of the rotifer in Antarctic region. Bull. biol. Stn Asamushi, 10: 247-250.
- ASAHINA, E. 1961. Some notes on the mechanism of frost resistance in living animal and plant at climatic low temperatures. Bull. biol. Stn Asamushi, 10: 251-256.
- AX, P. 1954. Die Turbellarienfauna des Küstengrundwassers am Finnischen Meerbusen. Acta zool. fenn., 81: 1-54.
- 1956. Das ökologische Verhalten der Turbellarien in Brackwassergebieten. Int. Congr. Zool., Copenhagen 1953, pp. 462-464.
- BAYLOR, E. R. & W. H. SUTCLIFFE, Jr. 1963. Dissolved organic matter in seawater as a source of particulate food. Limnol. Oceanogr., 8: 369-381.
- BRINCK, P., E. DAHL & W. WIESER. 1955. On the littoral subsoil fauna of the Simrishamn beach in eastern Scania. K. fysiogr. Sällsk. Lund Förh., 25: 1-21.
- BUSH, L. F. 1966. Distribution of sand fauna in beaches at Miami, Florida. Bull. Mar. Sci., 16: 58-75.
- CHAPPUIS, P. A. 1946. Un nouveau biotope de la faune souterraine aquatique. Bull. Sect. Acad. scient. roum., 29: 21.
- DIXON, W. J. & F. J. MASSEY, Jr. 1957. Introduction to statistical analysis. 2nd ed. McGraw-Hill, New York, 488 pp.
- EMERY, K. O. 1961. A simple method of measuring beach profiles. Limnol. Oceanogr., 6: 90-93.
- FENCHEL, T. 1967. The ecology of marine microbenthos I. The quantitative importance of ciliates as compared with metazoans in various types of sediments. Ophelia, 4: 121-137.

- FENCHEL, T. & B.-O. JANSSON. 1966. On the vertical distribution of the microfauna in the sediments of a brackish-water beach. Ibid., 3: 161-177.
- FENCHEL, T., B.-O. JANSSON & W. VON THUN. 1967. Vertical and horizontal distribution of the metazoan microfauna and of some physical factors in a sandy beach in the northern part of the Øresund. Ibid., 4: 227-243.
- GANAPATI, P. N. & G. CHANDRASEKHARA RAO. 1962. Ecology of the interstitial fauna inhabiting the sandy beach of Waltair coast. J. mar. biol. Ass. India, 4: 44-57.
- GERLACH, S. A. 1954. Das Supralitoral der sandigen Meeresküsten als Lebensraum einer Mikrofauna. Kieler Meeresforsch., 10: 121-129.
- GOVINDANKUTTY, A. G. & N. B. BALAKRISHNAN NAIR. 1966. Preliminary observations on the interstitial fauna of South-West coast of India. Hydrobiologia, 28: 101-122.
- GRAY, J. S. 1965. The behaviour of *Protodrilus symbioticus* Giard in temperature gradients. J. Anim. Ecol., 34: 455-461.
- 1966. Factors controlling the localisation of populations of *Protodrilus symbioticus* Giard. Ibid., 35: 435-442.
- 1967. Substrate selection by the archiannelid *Protodrilus rubropharyngeus*. Helgoländer wiss. Meeresunters., 15: 253-269.
- HUSMANN, S. 1966. Versuch einer ökologischen Gliederung des interstitiellen Grundwassers in Lebensbereiche eigener Prägung. Arch. Hydrobiol., 62: 231-268.
- IVLEVA, I. V. 1960. Respiration of the white enchytrae (*Enchytraeus albidus* Henle). Zool. Zh., 39: 165-175.
- JANSSON, B.-O. 1962. Salinity resistance and salinity preference of two oligochaetes *Aktedrilus monospermatecus* Knöllner and *Marionina preclitellochaeta* n. sp. from the interstitial fauna of marine sandy beaches. Oikos, 13: 293-305.
- 1966a. Microdistribution of factors and fauna in marine sandy beaches. Veröff. Inst. Meeresforsch. Bremerh., Sonderbd. 2: 77-86.
- 1966b. On the ecology of *Derocheilocaris remanei* Delmare & Chappuis (Crustacea, Mystacocarida). Vie Milieu, 17: 143-186.
- 1967a. The importance of tolerance and preference experiments for the interpretation of mesopsammon field distributions. Helgoländer wiss. Meeresunters., 15: 41-58.
- 1967b. The significance of grain size and pore water content for the interstitial fauna of sandy beaches. Oikos, 18: 311-322.
- 1967c. Diurnal and annual variations of temperature and salinity of interstitial water in sandy beaches. Ophelia, 4: 173-201.
- 1968. The availability of oxygen for the interstitial fauna of sandy beaches. J. exp. mar. Biol. Ecol., 1: 123-143.
- KARLING, T. G. 1954. Über einige Kleintiere des Meeressandes des Nordsee-Ostsee-Gebietes. Ark. Zool., 2. Ser., 7: 241-249.
- 1963. Die Turbellarien des Ostfennoskandians. V. Neorhabdocoela. 3. Kalyptorhynchia. Fauna fenn., 17: 1-59.
- KINNE, O. 1963. The effects of temperature and salinity on marine and brackish water animals. I. Temperature. Oceanogr. mar. Biol. Ann. Rev., 1: 301-340.
- 1964a. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature salinity combinations. Ibid., 2: 281-339.
- 1964b. Non-genetic adaptation to temperature and salinity. Helgoländer wiss. Meeresunters., 9: 433-458.
- LACKEY, J. B. 1961. Bottom sampling and environmental niches. Limnol. Oceanogr., 6: 271-279.
- LANG, K. 1965. Copepoda Harpacticoida aus dem Küstengrundwasser dicht bei dem Askö-laboratorium. Ark. Zool., 2. Ser., 18: 73-83.
- LESSERRE, P. 1966. Oligochètes marins des côtes de France. I. Bassin d'Arcachon: Systématique. Cah. Biol. mar., 7: 295-317.

- LUTHER, A. 1960. Die Turbellarien Ostfennoskandiens. I. Acoela, Catenulida, Macrostomida, Lecithoepitheliata, Prolethophora, und Proseriata. Fauna fenn., 7: 1-155.
- 1962. Die Turbellarien Ostfennoskandiens III. Neorhabdocoela 1. Daliyellioidea, Typhloplanoida: Byrsophlebiidae und Trigonostomidae. Ibid., 12: 1-71.
- MARE, M.F. 1942. A study of marine benthic community with special reference to the micro-organisms. J. mar. biol. Ass. U.K., 25: 517-554.
- MATUTANI, K. 1961. Studies on the heat resistance of *Tigriopus japonicus*. Publ. Seto mar. biol. Lab., 9: 379-411.
- MEADOWS, P.S. & J.G. ANDERSON. 1966. Micro-organisms attached to marine and freshwater sand grains. Nature, 212: 1059-1060.
- MORGAN, J.F.C. 1956. Notes on the analysis of shallow-water soft substrata. J. anim. Ecol., 25: 367-387.
- MUUS, B.J. The fauna of Danish estuaries and lagoons. Meddr. Danm. Fisk.- og Havunders., 5: 1-316.
- NEEL, J.K. 1948. A limnological investigation of the psammon in Douglas Lake, Michigan, with especial reference to shoal and shoreline dynamics. Trans. Amer. micr. Soc., 67: 1-53.
- NEWELL, R.C. & H.R. NORTHCROFT. 1967. A re-interpretation of the effect of temperature on the metabolism of certain marine invertebrates (*Actinia equina*, *Nephtys hombergi*, *Littorina littorea*, *Cardium edule*). J. Zool., 151: 277-298.
- NIELSEN, C. OVERGAARD. 1954. Studies on Enchytraeidae 3. The micro-distribution of Enchytraeidae. Oikos, 5: 167-178.
- 1959. Soil fauna and the moisture regime of its environment. Int. Congr. Zool., London 1958, pp. 349-351.
- 1961. Respiratory metabolism of some populations of enchytraeid worms and freeliving nematodes. Oikos, 12: 17-35.
- NIELSEN, C. OVERGAARD & B. CHRISTENSEN. 1959. The Enchytraeidae. Critical revision and taxonomy of European species. Natura Jutl., 8-9: 1-160.
- 1963. The Enchytraeidae. Critical revision and taxonomy of European species. Ibid., 10, Suppl., 2: 1-19.
- NOODT, W. 1953. Entomotracer aus dem Litoral und dem Küstengrundwasser des finnischen Meerbusens. Acta zool. fenn., 72: 1-12.
- 1954. Sandstrand-Copepoden von der schwedischen Ostküste. K. fysiogr. Sällsk. Lund Förh., 24: 1-8.
- 1957. Zur Ökologie der Harpacticoida (Crust. Cop.) des Eulitorals der deutschen Meeresküste und der angrenzenden Brackgewässer. Z. Morph. Ökol. Tiere, 46: 149-242.
- PANTIN, C.F.A. 1931. The adaptation of *Gunda ulvae* to salinity. III. The electrolyte exchange. J. exp. Biol., 8: 82-94.
- PENNAK, R.W. 1940. Ecology of the microscopic Metazoa inhabiting sandy beaches of some Wisconsin lakes. Ecol. Monogr., 12: 537-615.
- 1942. Ecology of some copepods inhabiting intertidal beaches near Woods Hole, Massachusetts. Ecology, 23: 446-456.
- PERKINS, E.J. 1958. The food relationships of the microbenthos, with particular reference to that found at Whitstable, Kent. Ann. Mag. nat. Hist., 13. Ser., 1: 64-77.
- POTTS, W.T.W. & G. PARRY. 1964. Osmotic regulation in Animals. Pergamon Press Ltd., London, 423 pp.
- REES, G. 1941. The resistance of the flatworm *Monocoelis fusca* to changes in temperature and salinity under natural and experimental conditions. J. anim. Ecol., 10: 121-145.
- REMANE, A. 1951. Die Besiedlung des Sandbodens im Meere und die Bedeutung der Lebensformtypen für die Ökologie. Verh. dt. zool. Ges., 1951: 327-359.
- 1958. Ökologie des Brackwassers. Binnengewässer, 22: 1-216.

- REMANE, A. & E. SCHULZ. 1934. Das Küstengrundwasser als Lebensraum. Schr. naturw. Ver. Schlesw.-Holst., 20: 399-408.
- RENAUD-DEBYSER, J. 1963. Recherches écologiques sur la faune interstitielle des sables (Bassin d'Arcachon, île de Bimini, Bahamas). Vie Milieu, Suppl., 15: 1-157.
- RENAUD-DEBYSER, J. & B. SALVAT. 1963. Eléments de prospérité des biotopes des sédiments meubles intertidaux et écologie de leurs populations en microfaune et macrofaune. Ibid., 14: 463-550.
- REUTER, M. 1961. Untersuchungen über Rassenbildung bei *Gyatrix hermaphrodites* (Turbellaria Neorhabdocoela). Acta zool. fenn., 100: 1-32.
- RILEY, G.A. 1963. Organic aggregates in seawater and the dynamics of their formation and utilization. Limnol. Oceanogr., 8: 372-381.
- SCHLIEPER, C. 1966. Physiologie écologique cellulaire des invertébrés marins. Rev. roumaine Biol., Ser. Zool., 11: 51-58.
- SCHLIEPER, C. & J. BLÄSING. 1952. Über Unterschiede in dem individuellen und ökologischen Temperaturbereich von *Planaria alpina* Dana. Arch. Hydrobiol., 47: 288-294.
- SCHMITT, E. 1955. Über das Verhalten von Süßwasserplanarien (*Planaria goniocephala* Dugès und *P. lugubris* O. Schmidt) in Brackwasser. Kieler Meeresforsch., 11: 48-58.
- SMIDT, E. 1951. Animal production in the Danish wadden sea. Meddr. Komm. Danm. Fisk.- og Havunders., Fiskeri, 11: 1-151.
- STANGENBERG, M. 1934. Psammolitoral, ein extrem eutrophes Wassermedium. Arch. Hydrobiol. Ichtyol., 8: 273-284.
- STEIBACH, H.B. Ionic and water balance of Planarians. Biol. Bull. mar. biol. Lab., Woods Hole 122: 310-319.
- STERRER, W. 1965. Zur Ökologie der Turbellarien eines südfinnischen Sandstrandes. Botanica gothoburg., 3: 211-219.
- SUTCLIFF, W.H., Jr., E. R. BAYLOR & D.W. MENZEL. 1963. Sea surface chemistry and Langmuir circulation. Deep-Sea Res., 10: 233-243.
- TEAL, J.M. & F.G. CAREY. 1967. The metabolism of marsh crabs under conditions of reduced oxygen pressure. Physiol. Zool., 40: 83-91.
- WAGNER, M. & W. SCHWARTZ. 1963. Behaviour of a suspension of microbes, migrating through sediments under marine and limnic conditions. In C. H. Oppenheimer (Ed.): Symposium on limnic conditions. C. C. Thomas, Springfield, Illinois, pp. 179-186.
- WELLS, J.B.J. & M.E. CLARK. 1965. The interstitial Crustacea of two beaches in Portugal. Revista Biol., 5: 87-108.
- WIESER, W. 1960. Benthic studies in Buzzards Bay. II. The meiofauna. Limnol. Oceanogr., 5: 121-137.
- WIESER, W. & J. KANWISHER. 1961. Ecological and physiological studies on marine nematodes from a small salt marsh near Woods Hole, Massachusetts. Ibid., 6: 262-270.
- WOOD, E.J. 1967. Microbiology of oceans and estuaries. Elsevier Publishing Company, Amsterdam, 319 pp.
- ZEUTHEN, E. 1947. Body size and metabolic rate in the animal kingdom. C.r. Trav. Lab. Carlsberg, Ser. chim., 26: 20-165.
- DE ZIO, S. & P. GRIMALDI. 1964. Analisi comparative del mesopsammon del due spiagge Pugliesi in Rapporto ad alcuni fattori ecologici. Arch. Bot. Biogr. Ital., 40: 357-367.
- 1966. Ecological aspects of Tardigrada distribution in South Adriatic beaches. Veröff. Inst. Meeresforsch. Bremerh., Sonderbd., 2: 105-116.
- ZOBELL, C.E. 1946. Marine microbiology. Chronica Botanica, Waltham, Mass. 240 pp.
- ZUBOV, A.N. 1964. Chemoreception in crustaceans. 3. Effect of salt adaptation on the analysis of chemical stimulants in *Gammarus oceanicus*. Trudy murmansk. biol. Inst., 59: 186-193.