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A STUDY OF THE ROLE OF PHYSICO-CHEMICAL FACTORS IN THE
CONTROL OF THE DISTRIBUTION OF INVERTEBRATES IN THE ALN
ESTUARY, N.E. ENGLAND

by

Sarah N. Howcroft

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A Thesis presented for the degree of
Master of Science in the University of Durham

1983

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ABSTRACT

The role of physico-chemical factors in controlling the distribution of invertebrates was investigated at Aln estuary, Alnmouth, North East England.

A general account is given of the intertidal benthic macrofauna at twelve stations along a 2.4 km tidal stretch of the Aln estuary from the open coast inland.

Species distribution was interpreted in relation to selected physico-chemical factors. Salinity was the factor to which all species had to respond to. However, it was found that not one, but several interrelated factors were operative in limiting the distribution of each species.

A detailed study was made of Corophium volutator and Haustorius arenarius. It was found that salinity and sediment characteristics were the most important factors influencing the distribution of these two species.

Although not enough time was available to quantify biological factors, the interrelationship between physico-chemical factors and biological factors was not dismissed, and the potential role of biological factors in determining the distribution of the intertidal benthic macrofauna was emphasized.

CHAPTER 1 : INTRODUCTION

This dissertation reports the results of a study of the role of physico-chemical factors in the control of the distribution of invertebrates in the Aln estuary, North East England.

Many proposals have been forwarded as to the features responsible for the distribution of benthic invertebrates found in estuaries, but as yet there is no general agreement.

The main gradient in the estuary is that of salinity (Wolff 1973) and it is considered by many authors to be the single most important factor affecting the distribution of the estuarine benthos (Gunter 1961; and Kinne 1966, in Tenore 1972). Considerable attention has also been directed towards the role of sediment characteristics in the distribution of the infaunal invertebrate distribution (Beanland 1940; Brett 1963; Davis 1925; Holme 1949; Remaine 1933; Sanders 1960; Weser 1960; Williams 1958; from Carriker 1967).

Perkins (1974) believes that factors likely to influence the distribution of estuarine animals are: (1) tidal changes; (2) physical and chemical conditions of the water; (3) degree of exposure to wave and current action; and (4) the effects of predation. However, of all these factors, he considers salinity to be the primary factor to which all estuarine animals have to respond.

Relatively little is known about the mode of action of the factors supposedly limiting the distribution of estuarine animals, but Holme (1949) suggests that they operate in one of three ways: by their influence on



the settling reactions of planktonic larvae, by their effect on migration of adults, or by affecting mortality after metamorphosis.

Caspers (1967) states that the most characteristic aspect of the estuarine environment is that it is a 'region of steep and variable gradient in environmental conditions'. The unstable conditions of estuaries determine their principal biological features and the 'poikilohaline conditions influence the whole biocenosis'.

Day (1951) pointed out that the distribution of animals in estuaries cannot be controlled by a single factor of the environment, but that a complex of periodically changing parameters limits the colonization to a restricted number of organisms with a wide range of ecological adaptations. Estuarine organisms are generally euryhaline forms which can penetrate and survive in an unpredictable ecosystem. The upper part of the estuary is characterized not by specialists but by tolerant euryhaline components of the fresh water biota capable of survival.

Thus, the environmental instability of the estuary and large number of interrelated limiting factors, together with the dominance of the euryhaline component are important points to remember when reviewing species richness and species distribution. This aspect of the study features in Chapter 5(C).

A. Objectives of the Present Study

My work had three main objectives:

- (1) To give a general account of the intertidal benthic macrofauna at twelve selected stations along a 2.4 km tidal

stretch of the Aln estuary, from the open coast inland.

2. To attempt to interpret the vertical and horizontal distribution of the fauna in relation to selected physico-chemical parameters, namely the chemical conditions of salinity (interstitial salinity and salinity of the overlying water), pH, % carbon content of the sediment, oxygen penetration in the interstitial environment (depth of redox potential discontinuity, R.P.D.) and the physical characteristics of sediment, depth of the water table at low tide and transect gradient.

(Vertical distribution, zonation up the shore, was investigated by taking samples at low-water (L.W.), mid-water (M.W.) and high-water (H.W.). Horizontal distribution, penetration of species up river, was surveyed at twelve sampling stations positioned 200 m apart.)

3. To carry out a more intensive study of factors controlling the distribution of two species: Corophium volutator and Haustorius arenarius. These two amphipod crustaceans were chosen for further study because they are both relatively abundant, easy to collect and handle, and are representative of a typical mud-dweller and sand-dweller respectively.

It was not possible to measure all the potentially important factors influencing the distribution of species. Factors which could not be measured within the time scale of this study include the physico-chemical factors of seasonal fluctuations in salinity, water temperature, light and oxygen saturation, current velocity, turbidity and wave action, and the biological factors of availability of optimal conditions for reproduction and settlement of

larvae and juveniles, competition, predation and parasitism. Undoubtedly the biological factors combine and interrelate with physico-chemical factors in influencing the distribution of estuarine species. But, it was only possible to quantify the most significant of the physico-chemical variables while at the same time not dismissing the potential role of the biological factors in determining the distribution of species.

B. Definition and Characteristics of the Estuary

An estuary is primarily a hydrographical phenomenon. It has been defined by Pritchard (1967) as: 'a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage.' according to Pritchard's classification, the Aln estuary may be considered as a 'positive estuary', in other words an estuary 'having a free connection with the open sea, within which runoff plus direct precipitation exceeds evaporation, and hence within which sea water is diluted by fresh water'.

In defining an estuary it is also useful to determine the boundaries of the estuarine region. Caspers (1967) considers that the upper limit of the estuary is determined not by salinity, but by tidal forces (as the place at which tidal rise and fall disappeared). In other words it is determined hydrodynamically rather than hydrochemically.

The geomorphological characteristics of estuaries and their modes of formation are varied and these conditions form the basis of the four primary subdivisions of estuaries (Pritchard 1967): (1) drowned river valleys, (2) fjord-type

estuaries, (3) bar-built estuaries, and (4) estuaries produced by tectonic processes. Aln estuary may be considered as lying somewhere between a drowned river valley and bar-built estuary. Drowned river valleys (or 'coastal plain estuaries') have been formed by marine transgression resulting from the release of ice-held water at the end of the last glaciation. Bar-built estuaries (or 'semi-enclosed bays') are typified by a sand bar forming parallel to the coastline which limits the water exchange with the sea. The sand bar at Alnmouth can be seen by referring to grid square 240 090 of the map in Figure 1.

Bowden (1967) recognised various types of estuarine circulation and salinity patterns, and thence derived a further classification of estuaries based on their internal physical conditions: water movements, mixing processes, and salinity pattern. The basic factor in determining the type of circulation is the role played by tidal currents relative to that of river flow. The interaction between these two factors is further influenced by physical dimensions of the estuary and the effect of the earth's rotation represented by the Coriolis force. The latter factor is negligible if the estuary is relatively narrow, as at Alnmouth.

The Aln estuary falls into the category of the partially mixed Type B estuary of Bowden's classification. This estuarine type is characterized by vertical mixing between the low-salinity seaward-flowing upper layer, and mixing prevents the formation of a distinct boundary. The volume of fresh water inflow is small compared with the total

volumes engaged in the net circulation pattern.

The following table (Table 1) gives a brief resume of Bowden's classification, and Figures 3 and 4 indicate the circulation and salinity patterns of a typical partially mixed Type B estuary.

C. Study Area

The Aln estuary is situated 34 miles north east of Newcastle on the Northumbrian coast (Figures 1 and 2). This estuary was chosen because it exhibits a range of substrate types (from fine sand, through silt to mud) over a relatively short distance, and pollution was known to be negligible.

The estuary is 0.25 km at its widest and narrows upstream to approximately 10 m. It is fed by the River Aln which has its origin at the confluence of Titlington Burn, Eglingham Burn and Shipley Burn, and flows south west through Alnwick and into Alnmouth Bay on the North Sea coast. The area of estuary sampled lies well below 15 m (50 ft) O.D. The mean tidal range at spring and neap tides is 4.3 m and 2.1 m respectively.

Figure 1 Location map of Alnmouth.

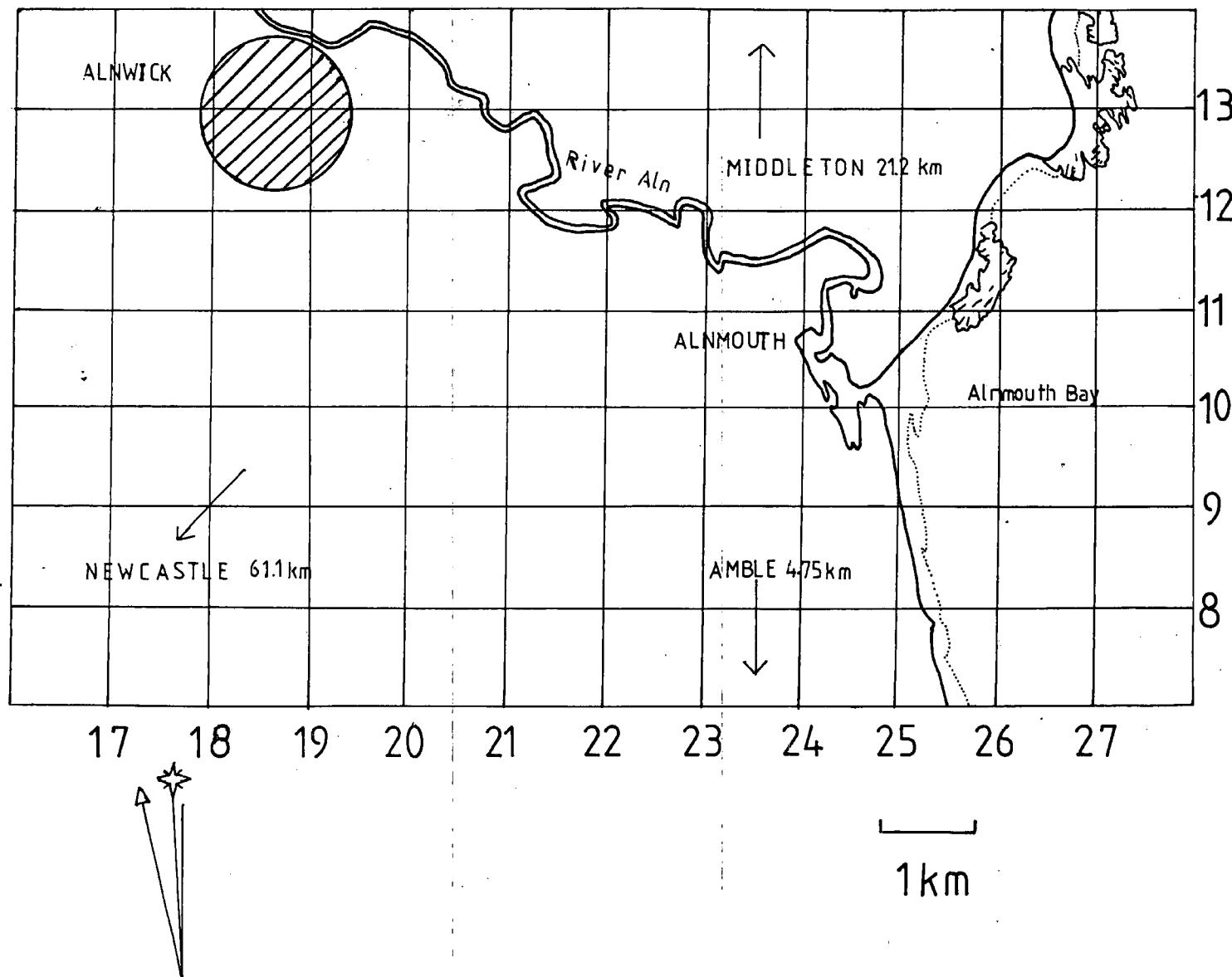


Figure 2 Location map of Aln Estuary.

(1 - 12 = Station numbers)

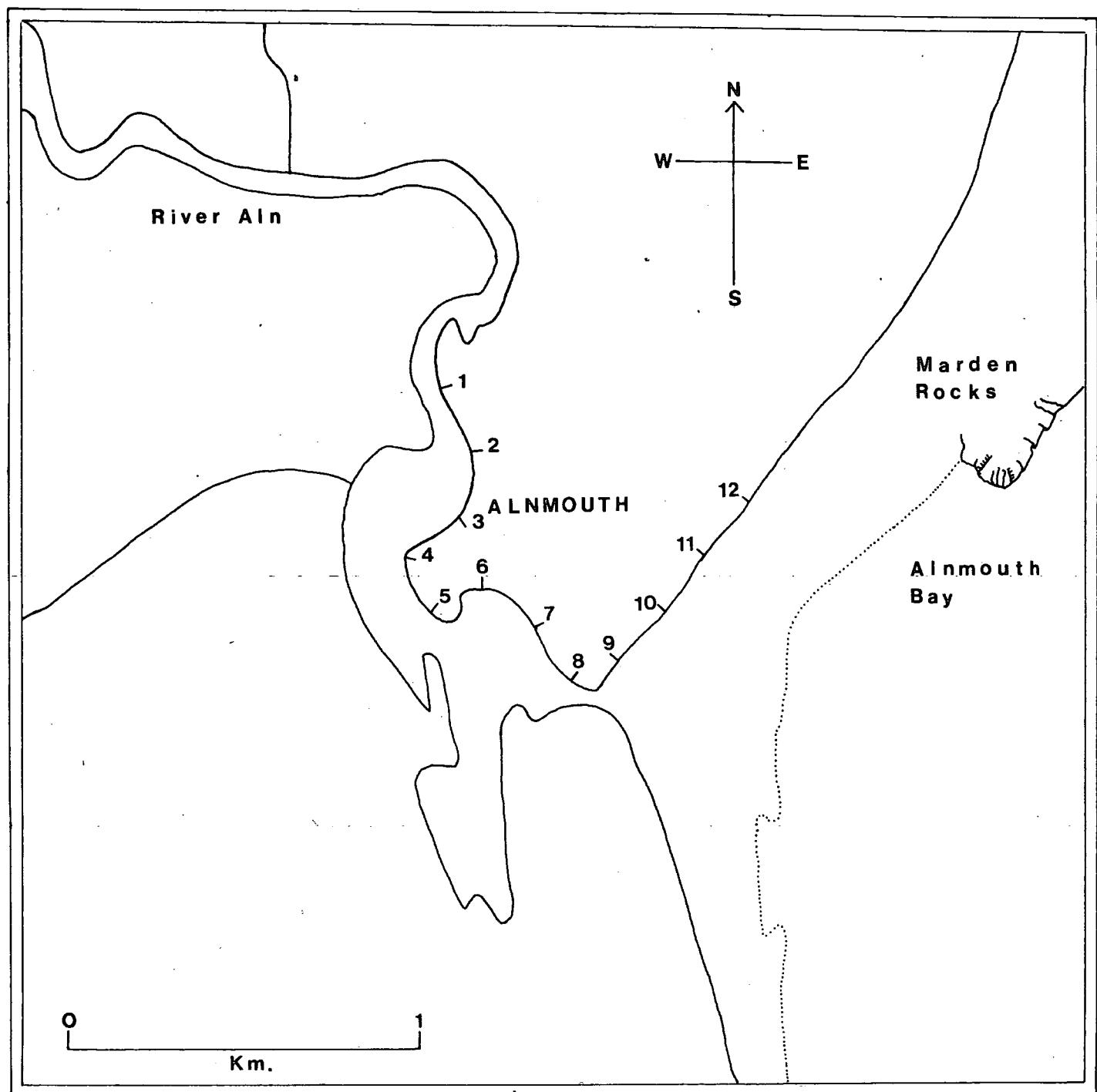


Figure 3 Partially mixed Type B Estuary (Bowden)

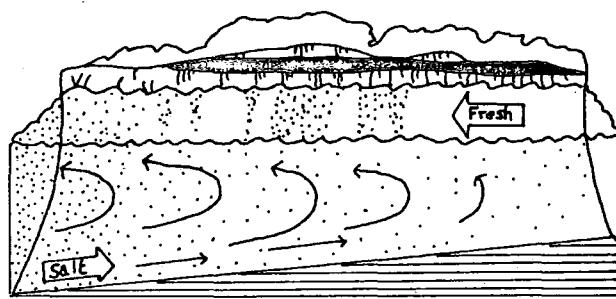


Figure 4 Distribution of isohalines in a partially-mixed estuary. (Barnes)

Vertical profile through A-B

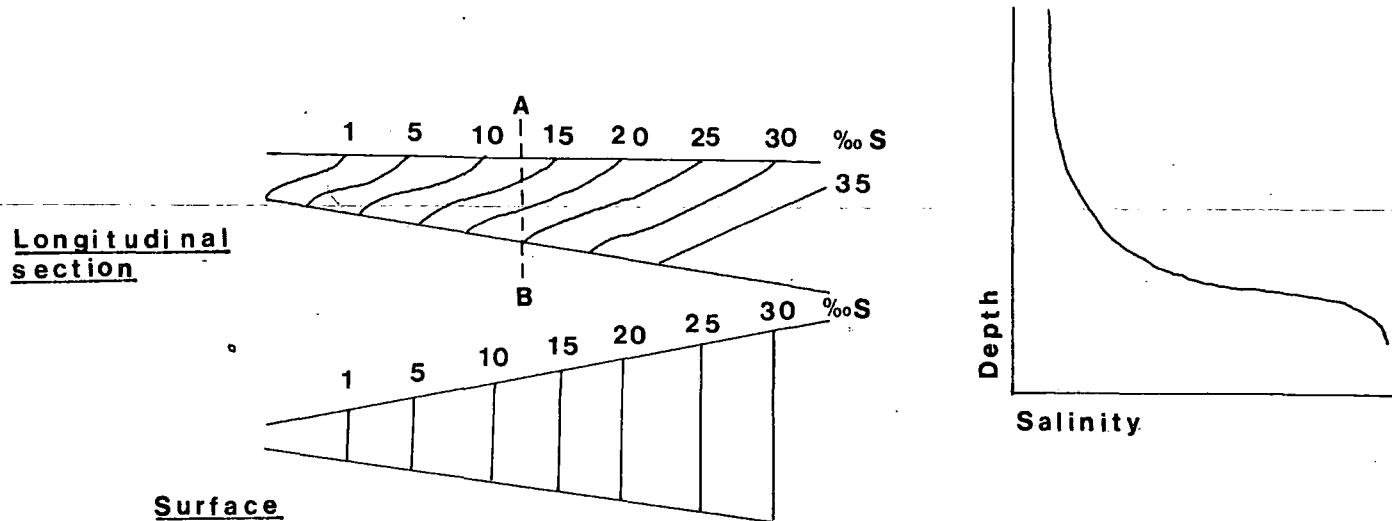


Table 1Types of estuarine circulation (after Bowden, 1967)

Type	Physical Processes	Forces
1. Salt wedge	River-flow dominant	Pressure gradients, field accelerations, Coriolis effect, interfacial friction
2. Two-layer flow with entrainment, including fjords	River-flow, modified by tidal currents	Pressure gradients, field accelerations, Coriolis effect, entrainment
3. Two-layer flow with vertical mixing	River-flow and tidal mixing	Pressure gradients, field accelerations, Coriolis effect, turbulent shear stresses
4. Vertically homogeneous (a) with lateral variation (b) laterally homogeneous	Tidal currents predominating	Pressure gradients, field accelerations, turbulent shear stresses, Coriolis effect in (a)
5. Exceptional cases: intensive mixing in restricted sections, tributary estuaries, sounds, straits etc.	-	-

CHAPTER 2 : MATERIALS AND METHOD

Samples of the intertidal benthic macroinvertebrates were taken every 200 m from the open coast at Station 12 to Station 1 2400 m up river. At each station samples were taken at LW, MW and HW using a sampling jar with an approximate volume of 400 cc, surface area of 74 cm² and depth of 8 cm. Since most intertidal benthic macroinvertebrates occur within the top few cm of substrate, it was not thought necessary to sample below 8 cm. However, Arienicola marina is known to occur down to 30 cm, so presence/absence was recorded by its surface casts. The animals contained in the sample jar were turned out onto an 8 inch diameter sieve of mesh size 20 (1 mm) and washed in sea water to remove all sediment. The animals remaining were carefully removed and placed in small sample jars containing sea water. Animals were sorted in the laboratory and number of species and individuals recorded. Four replicates were taken at each of the three tidal levels at each station. Results are expressed as numbers per m².

Substrate samples of 400 cc were taken at Stations 1, 3, 5, 7, 9 and 11, for determination of interstitial salinity, sediment analysis and carbon content.

The salinity of the overlying water at each station was determined from a sample taken at low tide. In the laboratory the salinity was measured using an E.I.L. conductivity recorder model MCI MKV. The cell constant K = 0.1 with a sample volume of 25 ml was used and the results read off the 1-10⁴ μ s/cm range. The electrolytic conductivity was converted to a salinity value (% S) after

calibration with sea water of 35‰ S, subsequent dilution and construction of a calibration graph.

Interstitial salinity readings were taken from sediment collected from Stations 1, 3, 5, 7, 9 and 11. The interstitial water was extracted using a vacuum pump and the salinity was recorded.

The pH of the overlying water was measured using a pH meter model E.L.I. 7020. Samples of the overlying water were taken from each station at the same low tide.

An indication of the depth of oxygen penetration was determined by measuring the depth of the R.P.D. at LW, MW and HW at each of the 12 stations.

The organic matter within the substrate was investigated at Stations 1, 3, 5, 7, 9 and 11 by using the ashing technique. The percentage organic content was measured by incineration of samples of approximately 2 g of oven-dried sediment (dried at 105°C for 3 days) at 500°C for 24 hours. Incineration also decomposes inorganic carbonates and this source of error was rectified by flooding the sample with ammonium carbonate solution and then heating in the oven at 110°C for 2 hrs. If the sample was then weighed (y grams) and its original dry weight was x grams, then the weight of the contained organic matter was calculated by $x-y$, expressed as a percentage of the total dry weight (x) (Barnes, 1974). The incineration method was chosen because it is straightforward and gives relative values for the 6 stations, adequate for correlation with invertebrate distribution. The titration method outlined by Morgans (1956) would also have provided relative values for the 6 stations, but since it was more time consuming

yet would have resulted in the same relative accuracy with respect to inter-station comparisons, the incineration technique was preferred.

Sediment particle sizes were measured for the Stations 1, 3, 5, 7, 9 and 11. Approximately 100 g of sediment was taken from LW, MW and HW at each of the 6 stations and oven-dried at 105°C for 3 days. The oven-dried sample was weighed and transferred to an automatic sieve-shaker for 2 mins (Wolff 1973). The sieve-shaker consisted of the following series of sieves: 10, 20, 30, 40, 60, 100, 200 meshes/inch. The amount of material retained by each sieve was then weighed. These weights were converted into percentages of the total weight of sediment retained by the bank of sieves and then into accumulated percentages. A graph of the accumulated percentage against the mean Phi (ϕ) value for each mesh size was drawn. The ϕ value = $-\log_2 D$, where D is the grain size in mm. The cumulative curve shows for any given particle size the percentage of the substratum which consists of particles greater or smaller than that size. The Phi value is used because it substitutes a logarithm for the particle diameter in mm and so translates the arithmetically unequal set of values of sieve mesh sizes into a scale of equal values.

The median grain size ($M_d \phi$) was found by reading off the ϕ size corresponding to the 50% level. Two other statistical measures based on the quartile values were also calculated. The Phi quartile deviation ($QD \phi$), or sorting coefficient, is a measure of the slope of the curve and is expressed by $QD \phi = \frac{Q3\phi - Q1\phi}{2}$, where $Q3\phi$ and $Q1\phi$ are ϕ

values for the 84% and 16% levels respectively. Perfect sorting would be represented by a vertical curve and a $QD\phi$ value of zero. For typical well-sorted sediments $QD\phi = 0.5$. The Phi quartile skewness ($Skq \phi$) indicates whether the curve is straight or curved between the quartiles and is calculated by the following equation:

$$Skq \phi = \frac{Q3\phi + Q1\phi - 2Md\phi}{2}$$

A straight line between the quartiles has $Skq \phi = 0$ and represents a perfectly symmetrical distribution where the mean equals the median. Negative values indicate that the mean of the quartile values is to the left of the median value; in other words, that the smaller particles are better sorted than the larger. Results from the sediment analysis appear in Tables 3a-b.

The depth of the water table was measured at low water on the same day for each of the stations at the three levels of LW, MW and HW. The depth was determined by digging down into the substratum until water appeared. The level of the water table is believed to be correlated with the R.P.D. and angle of the bench transect. Subsequent analysis of this appears on pages

A transect profile was drawn for each station because this gives some indication of the drainage potential of each station, which is in turn related to the R.P.D. and water table level. The profiles were constructed using a Silva inclinometer type 15T. Transect profiles of the 12 stations can be found on pages

Table 2
Salinity and pH Results

Station No.	Tidal level	Interstitial Salinity $\times 10^4 \mu\text{m}/\text{cm}$	S‰	Cl‰	Overlying Sea Water Salinity $\times 10^4 \mu\text{m}/\text{cm}$	S‰	Cl‰	pH
1	LW	30	17.49	9.85	3.9	2.28	1.28	8.00
	MW	40	23.33	13.14				
	HW	43	25.08	15.13				
2					5.7	3.30	1.86	8.60
3	LW	45	26.25	14.79	7.5	4.38	2.47	8.55
	MW	45	26.25	14.79				
	HW	55	32.08	18.07				
4					7.7	4.49	2.53	8.45
5	LW	40	23.33	13.14	8.0	4.67	2.63	8.25
	MW	55	32.08	18.07				
	HW	60	35.00	19.72				
6					10.0	5.83	3.29	7.55
7	LW	58	33.83	19.05	13.0	7.58	4.27	7.90
	MW	60	35.00	19.72				
	HW	60	35.00	19.72				
8					16.0	9.33	5.26	7.95
9	LW	55	32.08	18.07	16.5	9.63	5.42	7.90
	MW	58	33.83	19.05				
	HW	60	35.00	19.72				
10					14.5	8.46	4.77	8.00
11	LW	60	35.00	19.72	50.0	29.17	16.43	7.60
	MW	60	35.00	19.72				
	HW	60	35.00	19.72				
12					60.0	35.00	19.72	7.80

Table 3a
Results of Sediment Analysis

Station No.	Median Particle Size (mm)	Md ϕ	QD ϕ	Skq ϕ
1 LW	0.36	1.48	1.34	0.37
1 MW	0.41	1.28	1.50	0.32
1 HW	0.44	1.20	1.33	0.33
3 LW	0.66	0.58	0.48	0.14
3 MW	0.47	1.08	0.47	-0.03
3 HW	0.38	1.38	1.49	0.29
5 LW	1.10	-0.06	1.07	0.17
5 MW	0.33	1.64	1.64	0.20
5 HW	0.36	1.50	2.25	0.95
7 LW	0.76	0.40	0.32	0.10
7 MW	0.29	1.76	1.66	-0.20
7 HW	0.26	1.97	1.78	0.17
9 LW	0.41	1.28	0.45	-0.17
9 MW	0.38	1.42	0.40	-0.10
9 HW	0.38	1.36	0.48	-0.10
10 LW	0.43	1.26	0.57	-0.33
10 MW	0.42	1.28	1.54	0.28
10 HW	0.44	1.24	0.34	-0.22
11 LW	0.50	0.98	0.52	-0.02
11 MW	0.66	0.60	0.47	0.13
11 HW	0.41	1.30	0.57	-0.19
12 LW	0.66	0.62	0.76	0.30
12 MW	0.53	0.94	0.61	-0.09
12 HW	0.40	1.34	0.35	-0.11

Table 3bResults of the % silt-clay content in the sediment

Station no.	% silt-clay
1 LW	16.47
1 MW	15.99
1 HW	13.19
3 LW	3.45
3 MW	0.00
3 HW	16.81
5 LW	4.33
5 MW	23.07
5 HW	33.99
7 LW	0.00
7 MW	18.67
7 HW	30.08
9 LW	0.00
9 MW	0.00
9 HW	0.00
10 LW	0.00
10 MW	0.00
10 HW	0.00
11 LW	0.00
11 MW	0.00
11 HW	0.00
12 LW	0.00
12 MW	0.00
12 HW	0.00

Table 4

Results of water table depth, RPD depth, % carbon content of the sediment and angles of the transects

Station No.	Depth of Water Table (cm)	Depth of RPD (cm)	% Carbon content of sediment	Angle of Transect (°)
1 LW	19	01	05.88	18
1 MW	20	06	10.26	22
1 HW	24	05	6.13	24
2 LW	07	03	-	08
2 MW	06	03	-	06
2 HW	18	06	-	05
3 LW	04	03	03.19	12
3 MW	36	07	01.20	04
3 HW	45	17	06.98	04
4 LW	05	03	-	10
4 MW	08	04	-	13
4 HW	13	02	-	8
5 LW	04	04	03.11	6
5 MW	07	04	11.22	17
5 HW	16	06	09.61	16
6 LW	19	09	-	08
6 MW	21	08	-	24
6 HW	32	12	-	22
7 LW	04	07	02.50	07
7 MW	18	08	10.75	10
7 HW	24	05	08.70	09
8 LW	09	04	-	05
8 MW	18	07	-	08
8 HW	20	01	-	02
9 LW	11	04	01.88	04
9 MW	38	27	02.42	03
9 HW	56	32	01.48	04
10 LW	15	09	-	06
10 MW	68	43	-	04
10 HW	71	55	-	03
11 LW	33	24	01.99	04
11 MW	76	67	01.57	01
11 HW	82	73	01.99	02
12 LW	36	31	-	03
12 MW	81	74	-	02
12 HW	97	81	-	01

CHAPTER 3 : RESULTS

A. Description of Stations

For each of the 12 stations a photograph was taken, a transect profile constructed and the flora was described. The physico-chemical factors were measured and the macrofauna was sampled using the methods described in Chapter 2.

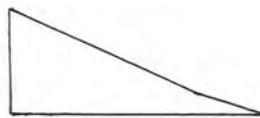
Details of the macrofauna sampling occur in Appendices 1, 3, 5, and results of the physico-chemical factors are presented in Tables 2-4.

Station 1

Figure 5a Photograph of Station 1 (2400 m. up river)



Figure 5b Transect Profile Scale for Stations 1-9: 30mm=10m.



Vegetation:

% cover = 70

LW : sparse Enteromorpha spp.

MW]: mainly Fucus ceranoides and Fucus spiralis
HW]

Station 2

Figure 6a Photograph of Station 2 (2200 m. up river)



Figure 6b Transect Profile



Vegetation:

% cover = 20

LW : Enteromorpha spp.

MW : F. ceranoides

HW : F. ceranoides and Blue-green algal mat

Station 3

Figure 7a Photograph of Station 3 (2000 m. up river)

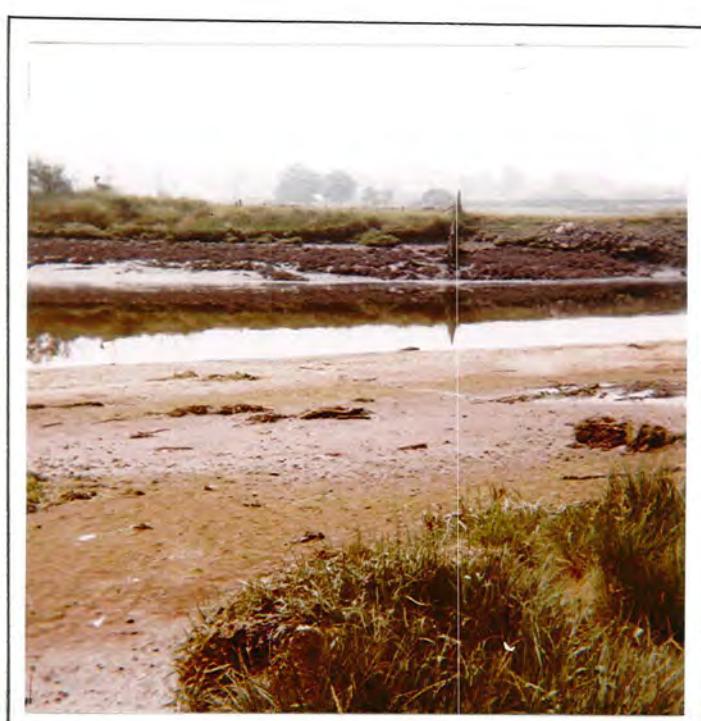


Figure 7b Transect Profile



Vegetation:

% cover = 30

LW : Enteromorpha spp.

MW : -

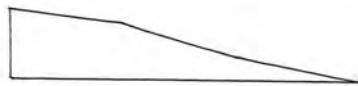
HW : Blue-green algal mat

Station 4

Figure 8a Photograph of Station 4 (1800 m. up river)



Figure 8b Transect Profile



Vegetation:

% cover = 20

LW : F. ceranoides and Enteromorpha spp.

MW : " " "

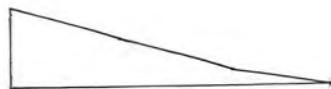
HW : Enteromorpha spp.

Station 5

Figure 9a Photograph of Station 5 (1600 m. up river)



Figure 9b Transect Profile



Vegetation :

% cover = 80

LW : F. ceranoides and Enteromorpha spp.

MW : " " "

HW : " " Blue-green algal mat

Station 6

Figure 10a Photograph of Station 6 (1400 m. up river)

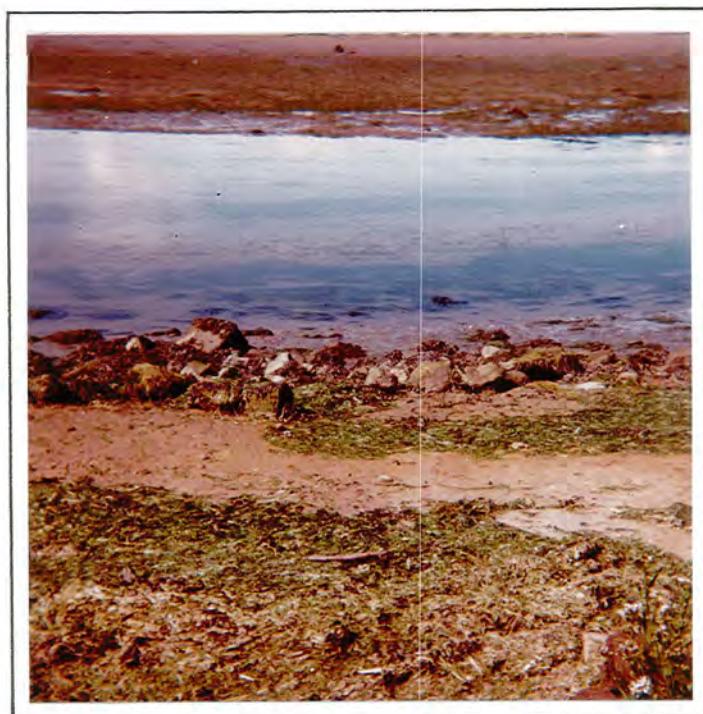
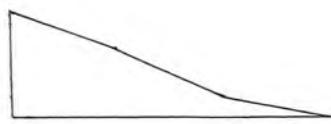


Figure 10b Transect Profile



Vegetation :

% cover = 70

LW : Enteromorpha spp.

MW : " and F. ceranoides

MW : "

Station 7

Figure 11a Photograph of Station 7 (1200 m. up river)

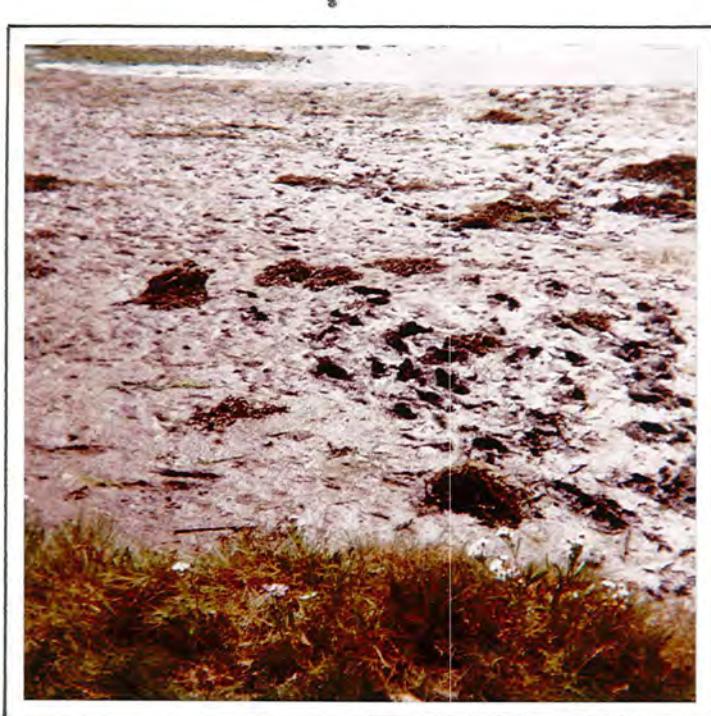


Figure 11b Transect Profile



Vegetation:

% cover = 10

LW : Enteromorpha spp. and F. ceranoides

MW : " " "

HW : " (scattered)

Station 8

Figure 12a Photograph of Station 8 (1000 m. up river)

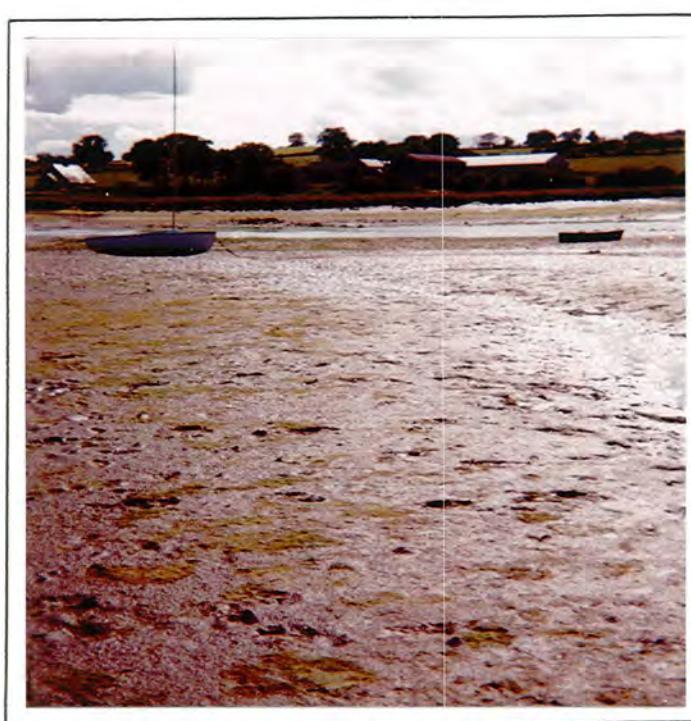


Figure 12b Transect Profile p32

Vegetation:

% cover = 10

LW : Dense Blue-green algal mat

MW : -

HW : Patches of Blue-green algal mat

Station 9

Figure 13a Photograph of Station 9 (800 m. up river)

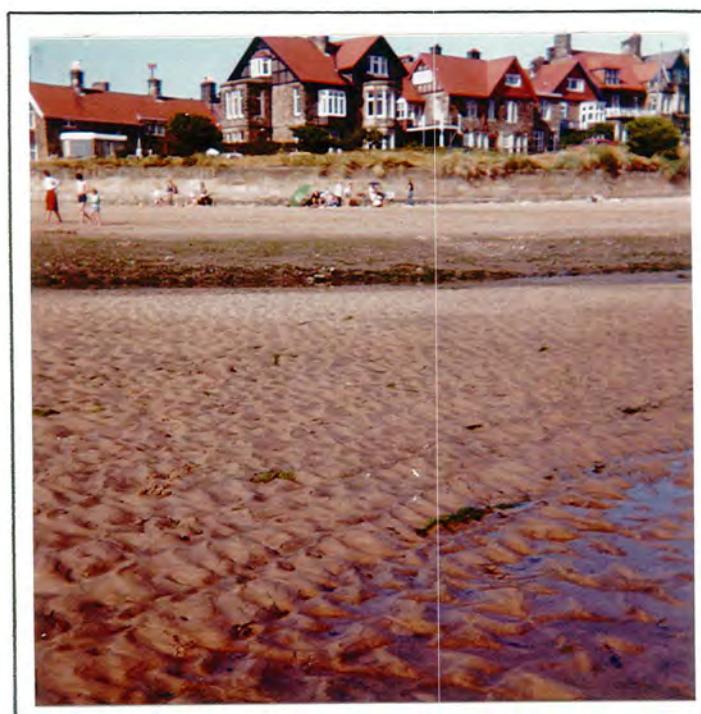


Figure 13b Transect Profile p32

Vegetation:

% cover = 10

LW : -

MW : Enteromorpha spp.

HW : -

Station 10

Figure 14a Photograph of Station 10 (600 m. up river)

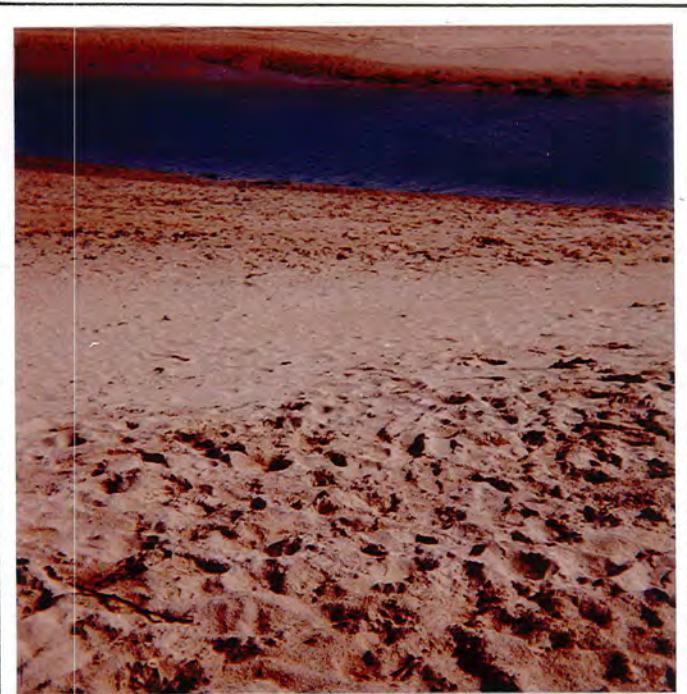


Figure 14b Transect Profile p32

Vegetation:

% cover = L5

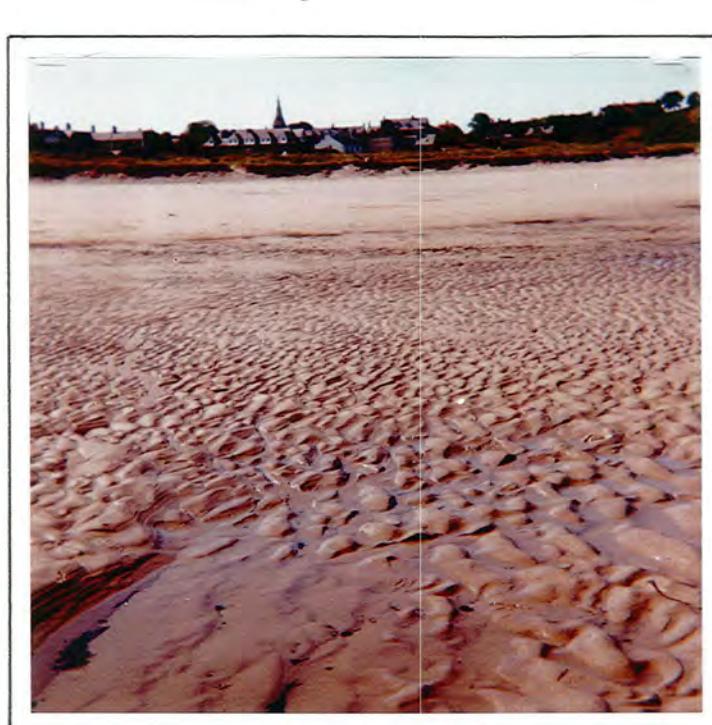
LW : Scattered and very sparse Enteromorpha spp.

MW : -

HW : Scattered sand-dune plants

Station 11

Figure 15a Photograph of Station 11 (400 m. up river)



Vegetation:

% cover = 10

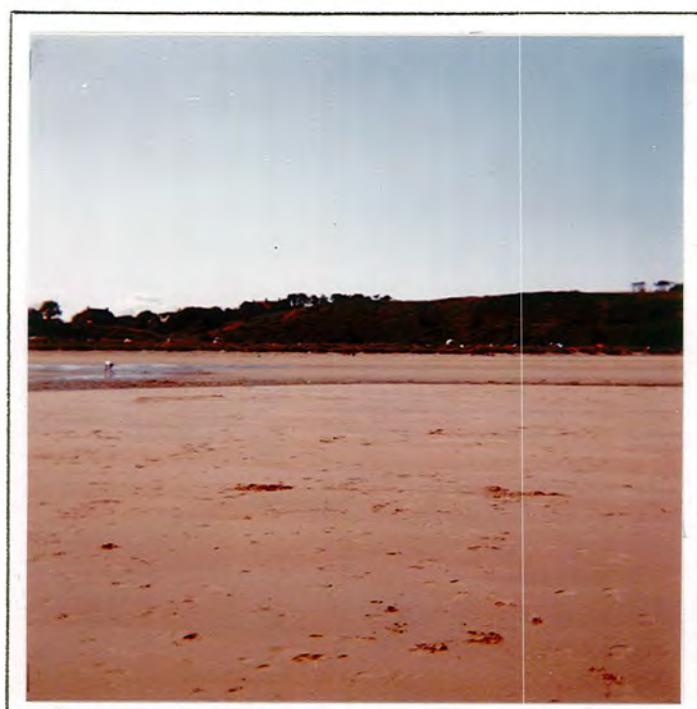
LW : -

MW : -

HW : Patches of washed-up vegetation

Station 12

Figure 16a Photograph of Station 12 (200 m. up river)



Figures 12b - 16b Stations 8 - 12. Transcet Profiles of

Figure 12b Station 8 Scale for Stations 8-9: 30mm=10m

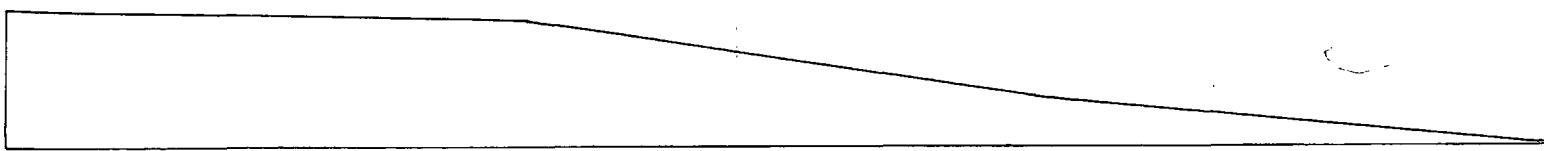
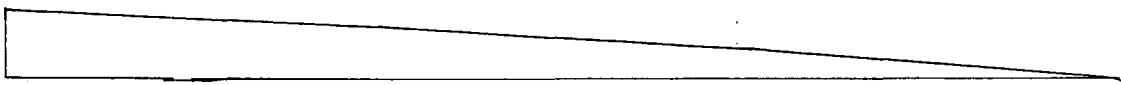


Figure 13b Station 9



Scale for Stations 10-12: 30mm= 20m.

Figure 14b Station 10

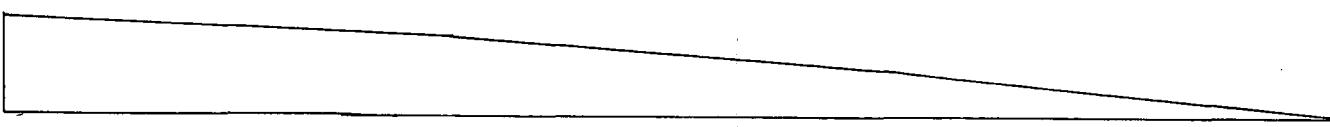


Figure 15b Station 11

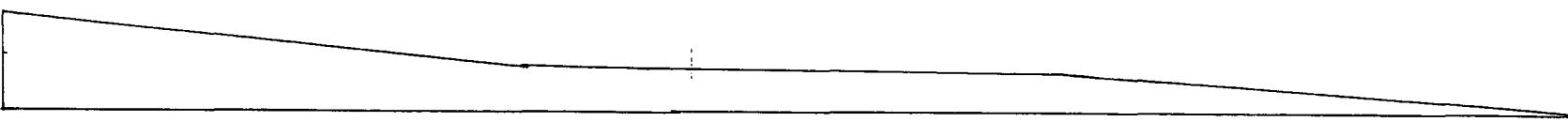


Figure 16b Station 12

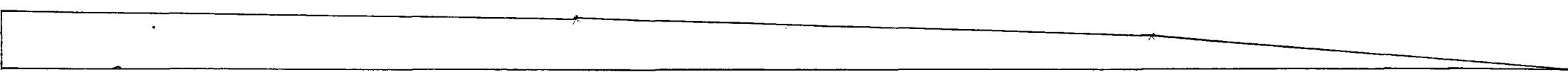


Figure 16b Transect Profile p 32

Vegetation:

% cover = 0
LW : -
MW : -
HW : Band of washed-up vegetation, 0.5 m wide.

B. Results of the Physico-Chemical Factors

Analysis of data recorded for species and physico-chemical factors was carried out using D.MTS and MIDAS programmes on the computer. A correlation matrix was first computed for all possible permutations of the variables, and any significant relationships were further investigated by constructing a scatter plot. If, after examination of the scatter plot, there was an adumbration of linearity, then a linear regression was further calculated to elucidate the relationship. Alternatively, if the scatter plot did not suggest linearity, the non-parametric rho or rs correlation coefficient was calculated.

At first sight the data collected might appear to lend itself to multivariate data analysis. However, this technique is based upon assumptions of additivity, independence, linearity, normality and homoscedasticity. An attempt to employ multivariate data analysis would cause gross violation of underlying principles and lead to inaccurate and spurious conclusions.

It must be emphasized that results of the statistics used should be interpreted with care since there are several inter-correlations between the variables. For example, the angle of the transect may appear to be correlated with % carbon content of sediment, but the relationship is not causal.

(a) Chemical factors

Results of salinity and pH are presented in Table 2.

(b) Physical factors

Results of the sediment analysis are given in Tables 3a and b. Measurements of water table and RPD depth, % carbon content of the sediment and angles of the transects appear in Table 4.

Correlation was carried out between the physico-chemical factors, and results appear in Table 5. For discussion of these results see Chapter 5, Section A and B.

C. Results of the Species Survey

The raw data of species occurrence appears in Appendix 1. Kite diagrams were constructed from the raw data in order to illustrate species occurrence and abundance visually (Figures 18a-e). The raw data was also used to calculate the order of species penetration up river (Figure 19) and to construct a graph of species number against station number (Figure 20). One important point to mention at this stage is the fact that the adults of some specimens occur below the sampling depth. This applies to Arenicola marina, Lanice conchilega, Mya arenaria, Nereis diversicolor and Scrobicularia plana, hence the abundance results for these species probably only represent the abundance of juveniles.

Figure 17LIST OF SPECIESAbbreviationNEMERTINILineus spp. L.spp.Nemertopsis flava N.f.ANNELIDAArenicola marina A.m.Lanice conchilega L.c.Nereis diversicolor N.d.Polydora spp. P.spp.Sabella pavonia Sabella p.ARTHROPODA CRUSTACEACarcinus maenas C.m.Corophium volutator C.v.Euyridice pulchra E.p.Gammarus spp. G.spp.Haustorius arenarius H.a.Talitrus saltator T.s.MOLLUSCA GASTROPODAAcmea virginia A.v.Gibbula umbilicalis G.u.Hydrobia jenkinsi H.j.Littorina littoralis L.l.Nassarius incrassatus N.i.Natica alderi N.a.LAMELLIBRANCHIADonax vittatus D.v. Tellina crassa T.c.Macoma balthica M.b. Venus ovata V.o.Mya arenaria M.a.Mytilus edulis M.e.Scrobicularia plana S.p.

Table 5Correlation matrices for station species number and the physico-chemical factorsVariable Key:

SPECIES	=	station species number
MM	=	median particle diameter
SORT	=	$Qd\phi$
SKEW	=	$Skq\phi$
IS	=	interstitial salinity
RPD	=	R.P.D. depth
C	=	% carbon content
WT	=	water table depth
DEGREE	=	angle of transect profile
OS	=	salinity of surface water

Correlation matrix:

$N = 18$, $DF = 16$, $R @ 0.0500 = 0.4683$, $R @ 0.0100 = 0.5897$

Variable

SPECIES	1.0000
MM	0.2213 1.0000
SORT	0.1487 0.3947 1.0000
SKEW	0.2400 0.0361 0.6514 1.0000
IS	0.0167 0.2650 0.1039 0.2419 1.0000
RPD	0.4599 0.0803 0.4455 0.2558 0.4828 1.0000
C	0.1924 0.4656 0.9174 0.4680 0.0647 0.4650 1.0000
WT	0.0499 0.1979 0.3185 0.2591 0.3877 0.7045 0.3950 1.0000
DEGREE	0.4066 0.1695 0.5842 0.6091 0.5039 0.3404 0.6375 0.3879 1.0000

SPECIES MM SORT SKEW IS RPD C WT DEGREE

Rank Order Correlation:

$N = 18$, RHO

Variable

SPECIES	1.0000
MM	0.1288 1.0000
SORT	0.3386 0.6542 1.0000
SKEW	0.4013 0.1371 0.5383 1.0000
IS	0.0898 0.2644 0.0353 0.4466 1.0000
RPD	0.0667 0.1036 0.2711 0.4624 0.6914 1.0000
C	0.3915 0.5459 0.8186 0.5230 0.1602 0.4342 1.0000
WT	0.2504 0.1300 0.1212 0.2336 0.4130 0.7560 0.4358 1.0000
DEGREE	0.6483 0.1300 0.5182 0.7048 0.3684 0.5029 0.6436 0.4456 1.0000

SPECIES MM SORT SKEW IS RPD C WT DEGREE

Correlation Matrix:

$N = 10$, $DF = 8$, $R @ 0.0500 = 0.6319$, $R @ 0.0100 = 0.7646$

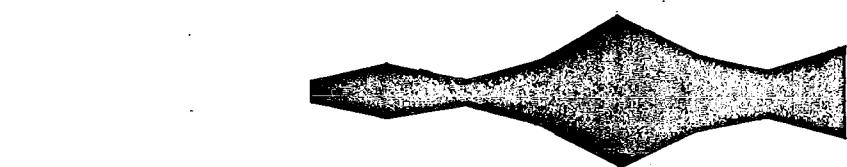
Correlation between SPECIES and OS = 0.1078.

Rank Order Correlation:

N = 10, RHO

Variable

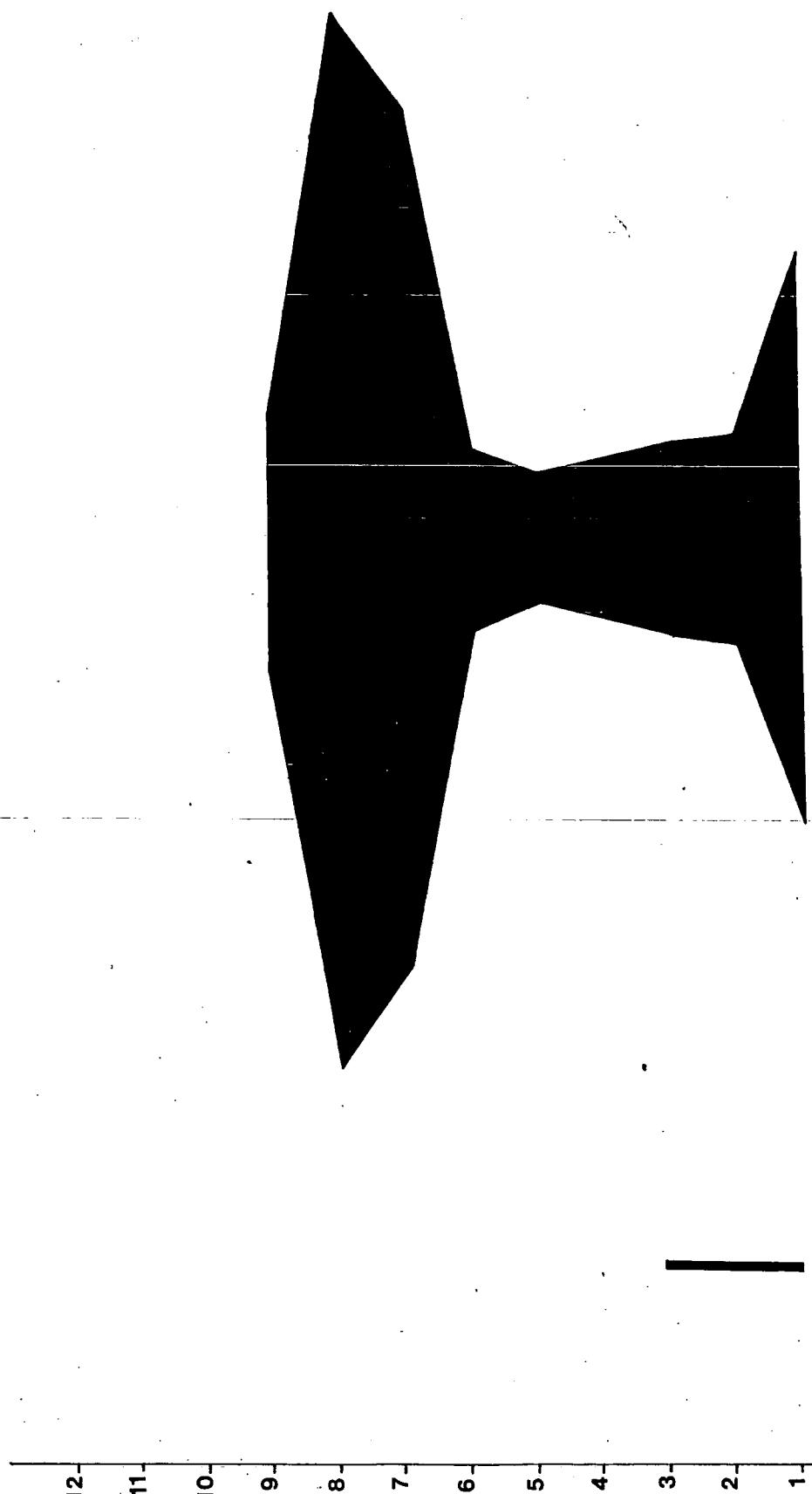
SPECIES	1.0000
OS	-0.3541
SPECIES	OS

Figure 18a0 200 (Nos. m^{-2})Nemertini*Lineus* spp.*Nemertopsis* *tilavida**Arebicola* *marina**Lanice* *conchilega**Nereis* *diversicolor**Polydora* spp.Annelida

Sabellida *pavonina*
Polychaeta spp.

Figure 18b

Arthropoda - Crustacea



Cracinius
maeonus

Corophium
volutator

Figure 18c

Arthropoda—Crustacea

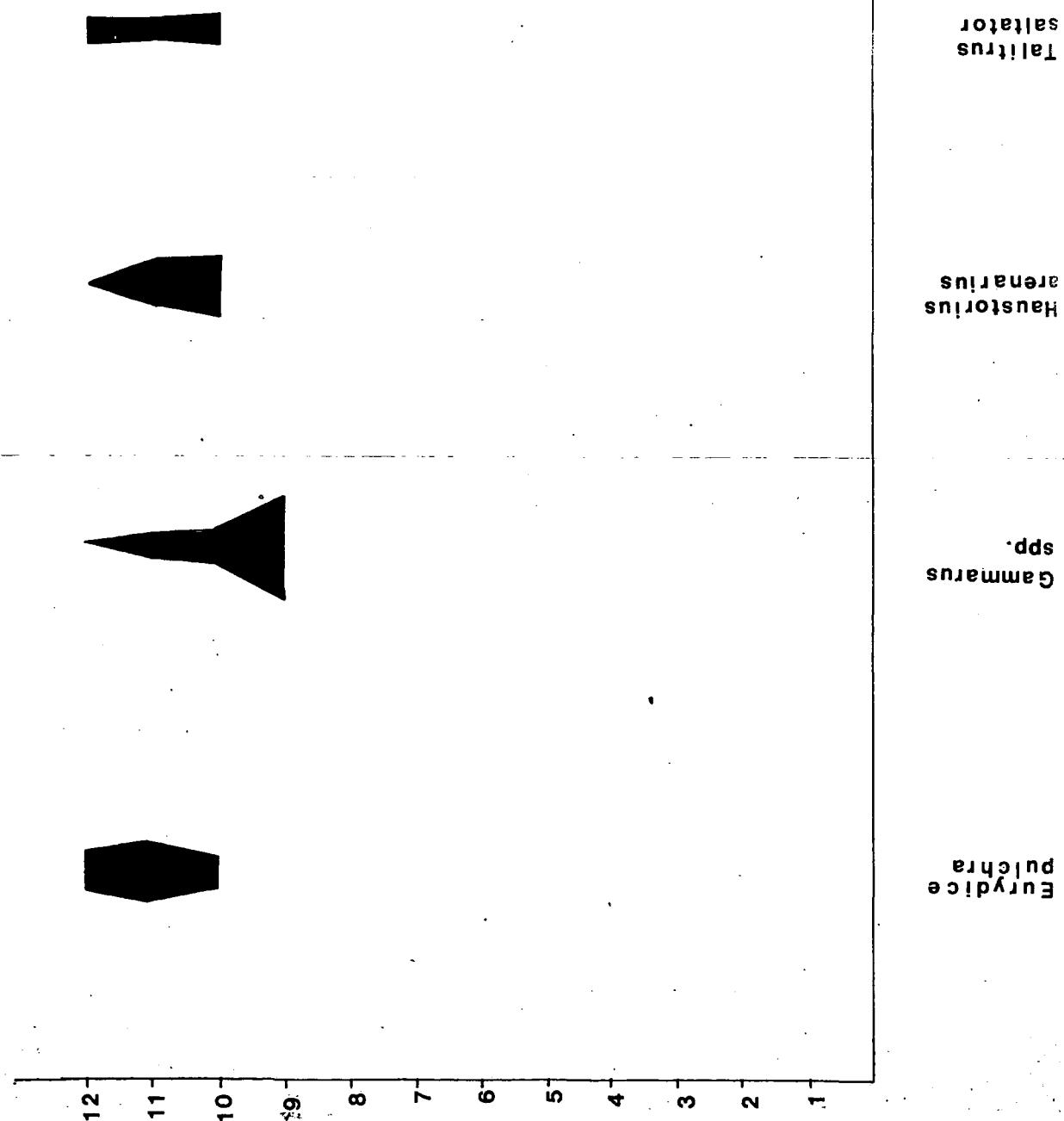
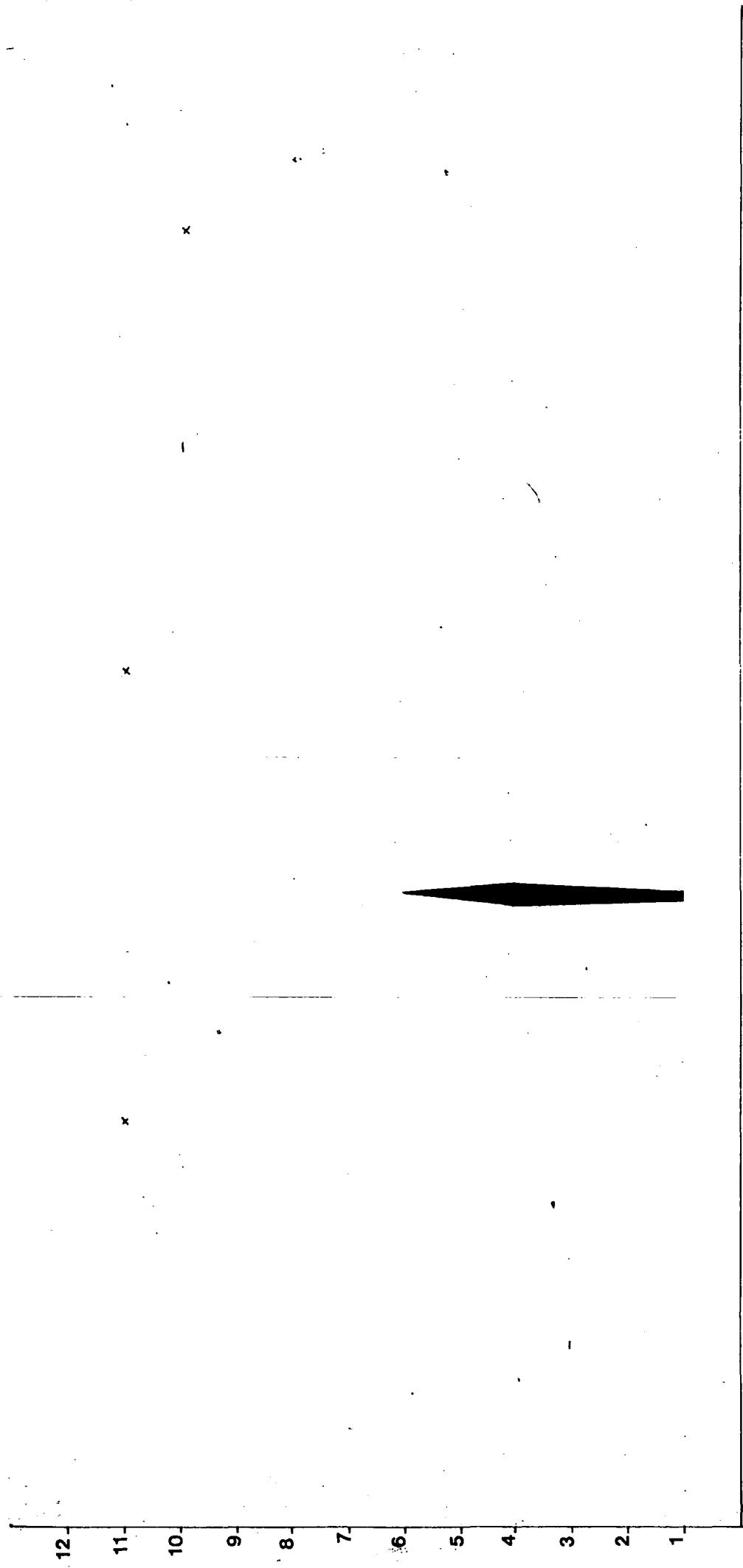


Figure 18dMollusca-Gastropoda

Venus
ovataTellina
crasseaScrobicularia
planariaMytilus
edulisMya
arenariaMacoma
balthicaDonax
vittatusMollusca - Lamellibranchia

Figure 18e

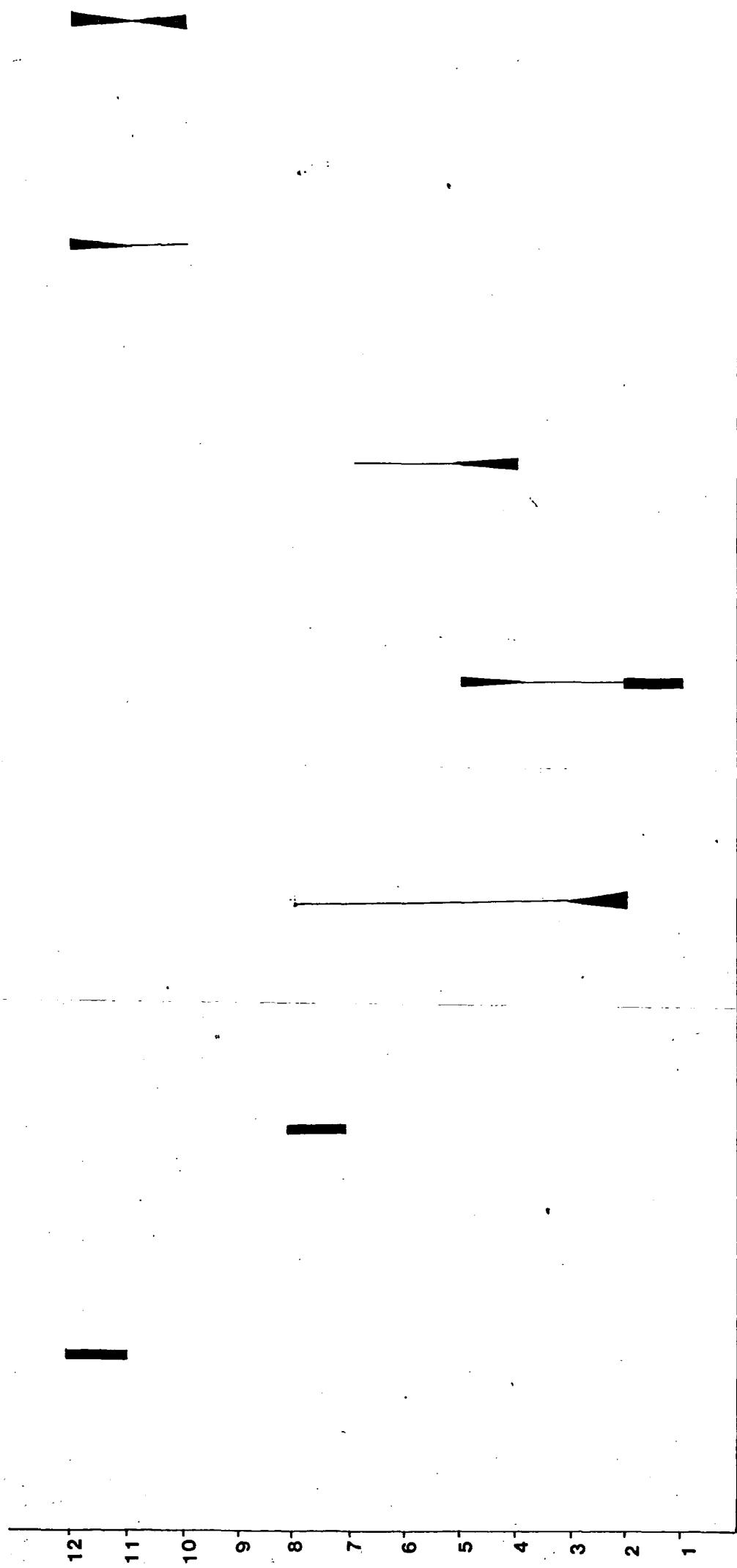
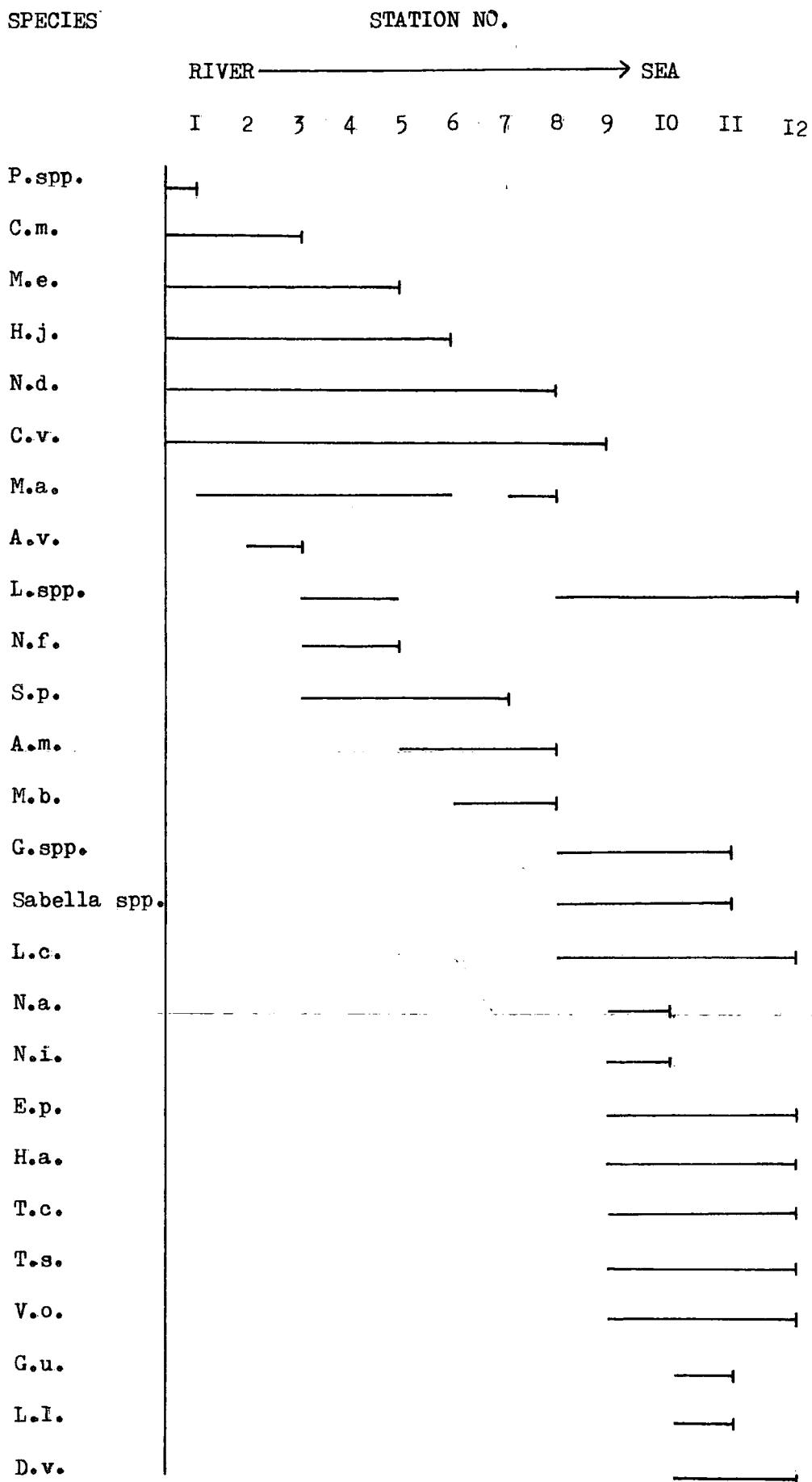


Figure 19 Horizontal Distribution Of Species - Order Of Penetration Up River.



Another feature to consider is the chances of missing clumped distributions of species. An attempt to overcome this problem was made by sampling either side of the transect at each station at LW, MW and HW. Five transects were sampled for each station. If time had permitted, more samples would have been preferable.

One other interesting point is whether I would have found the same picture of species distribution and density if I had sampled in March (before the floods), or late August after two dry months and with more 'juveniles' present. Generally, I would expect to sample a similar distribution except in the case of Carcinus which migrates seawards during the colder months. However, using the same sampling technique, I would expect to record species abundance more accurately because in the case of most species, a greater proportion of the population would be 'juveniles' which inhabit the upper few centimetres of sediment. I would anticipate recording greater densities for the deep-burrowing species, namely, Arenicola marina, Lanice conchilega, Mya arenaria, Nereis diversicolor and Scrobicularia plana.

Correlation was carried out between species number and the physico-chemical factors (correlation matrices, Table 5). Species number was not significantly related to any of the physico-chemical factors. Further discussion of this appears in Chapter 5, Section C(i).

CHAPTER 4 : DETAILED STUDY OF THE DISTRIBUTION OF COROPHIUM VOLUTATOR AND HAUSTORIUS ARENARIUS

A. Corophium Volutator

Experiment to determine substrate selection by Corophium volutator

This experiment was designed to test whether Corophium volutator prefers substrata of specific particle size when such are available.

The apparatus used consisted of a large enamel tray divided into four sections. Each section contained approximately 2560 cm^3 of fresh substrate, the substrate having been sieved in sea water to remove all previous specimens. The whole tray was flooded with sea water of 18°C to a depth of 1 cm and illuminated from above by a constant light source of 40 W. The light was used to encourage burrowing because Corophium v. is negatively phototactic out of water. Four substrates of different known particle sizes were used. Two hundred Corophium v. all approximately 7 mm in length, were collected from the estuary, transported back to the laboratory in ambient sea water and released in the centre of the tray.

The experiments were conducted for 3 hrs. This was considered to be adequate time since the majority of Corophium were observed to burrow within the first 15 mins. After 3 hrs each substrate was sieved to determine the number of Corophium which had burrowed into each.

The results (Table 7) are based on two experiments, both experiments indicating significant preference for mud. It was found that significantly more individuals preferred mud of median particle diameter (Md mm) = 0.29.

($\chi^2 = 60.84$, $v = 3$, $p = 0.001$, critical χ^2 at $p = 0.001 = 16.27$). The null hypothesis (that Corophium v. is not substrate specific) was rejected and it was concluded that the distribution of Corophium v. among the four substrate types was not due to chance but due to a preference exerted by the Corophium. The species was not significantly deceived into burrowing into sand covered by 1 cm of mud.

It is concluded that Corophium v. is substratum specific, preferring mud of particle size $Md \text{ mm} = 0.29$, and that substrate particle size plays an important role in determining the distribution of Corophium v. at Alnmouth. Provided with no alternatives, however, it is known that Corophium v. can burrow, successfully survive and grow in a wide range of particle sizes. Substrate selection by this species may depend upon the detection of the amount of organic matter present, but further research into this aspect is needed (Barnes 1974).

For calculation of χ^2 see Table 7. Table 6 below lists the mean χ^2 values.

Table 6
Corophium volutator - mean χ^2 values for the four substrate types

<u>Substrate</u>	<u>Mean χ^2 value</u>
Sand	4.84
Mud	46.24
Sand + 1 cm mud	4.00
Silt	5.76

$$\chi^2 = 60.84$$

Table 7

χ^2 calculation for the experiment to determine substrate selection by *Corophium volutator*

Total no. of specimens = 200
Mean length of specimens = 7mm

Substrate description	Mean particle size (mm)	Nos. in each substrate after 3hrs.	
		1st Expt.	2nd Expt.
Sand	0.66	12	15 (most on the surface)
Mud	0.29	65	53 (majority had burrowed)
Sand + 1cm mud	0.6 (sand) 0.29 (mud)	13	17 (most on the surface)
Silt	0.53	10	15 (a few on the surface)

$$\chi^2 = \frac{(O_i - E_i)^2}{E_i} \quad E = 25$$

Substrate	1st Expt.	χ^2	
		2nd Expt.	
Sand	6.76	4.00	
Mud	64.00	31.36	
Sand + 1cm mud	5.76	2.56	
Silt	9.00	4.00	

$$\chi^2 = 85.53 \quad \chi^2 = 41.92$$

$$v = 4 - 1$$

$v = 3$, critical value of χ^2 at $p = 0.001 = 16.27$

H_0 = no difference in the distribution of *Corophium v.* among the four substrates, i.e. the species is not substratum specific.

Calculation of χ^2 for the combined result of the first and second experiments:

Substrate description	Mean particle size (mm)	Nos. in each sediment after 3hrs.	
		(nos. = mean result of 1st & 2nd expts.)	
Sand	0.66	14	
Mud	0.29	59	
Sand + 1cm mud	0.66 (sand) 0.29 (mud)	15	
Silt	0.53	13	

$$\chi^2 = \frac{(O_i - E_i)^2}{E_i} \quad E = 25$$

Continued ...

Substrate	χ^2
Sand	4.84
Mud	46.23
Sand + 1cm mud	4.00
Silt	5.76

$$\chi^2 = 60.84$$

The χ^2 values of the first and second experiments and for the mean of the two experiments are well above the critical value of 16.27 for $p = 0.001$, $\nu = 3$. There is therefore a 99.9% probability of the inverse of H_0 (H_1) being correct, i.e. that the distribution of the species among the four substrates was not due to chance but due to some preference exerted by Corophium v. The species preferred to inhabit mud and was not deceived by sand + 1cm mud. This result was also found by Meadows (1964).

Experiment to investigate the salinity tolerance of
Corophium volutator

Two preliminary experiments were carried out whereby *Corophium* were placed in sodium chloride solutions of known salinity, ranging from 1.16-66.90 % S. Thirty animals were placed in each solution. All the animals used were approximately 7mm in length from telson to rostrum to ensure that only adult tolerance was being tested.

In the first experiment the salinity range was 1.16-66.90 % S, and in the second experiment the range was narrowed down to 27.6-36.4% S. Each experiment was carried out over a 10-day period, and at the end of every day the numbers of *Corophium* alive were counted. Dead specimens were removed to ensure that products of decay did not affect the remaining animals.

The *Corophium* used were collected from Stations 1 M.W. and 9 M.W. in order to determine whether the *Corophium* at Station 1 were more tolerant of lower salinities than animals from Station 9. The interstitial salinity measurements from Stations 1 M.W. and 9 M.W. were 23.33 % S and 33.83 % S respectively.

Results of the first and second experiment are presented in Table 8. The results represent mean values of two identical experiments. Analysis of variance showed significantly greater variance between groups than within. In other words, there was significantly greater variance between samples of different salinities than within a sample of the same salinity. The values calculated were: *Corophium* from Station 1 M.W., $F = 10.73$, $p = 0.01$ and *Corophium* from Station 9 M.W., $F = 11.71$, $p = 0.01$. Therefore

Table 8

Results of experiment to investigate the salinity tolerance
of *Corophium volutator*

Figures indicate the number of animals alive at the end of the day. All results are based on the mean of 2 identical experiments.

Corophium volutator from Station 1 M.W.

Approximate length of specimens = 7mm
30 specimens in each NaCl concentration

Corophium volutator from Station 9 M.W.

Approximate length of specimens = 7mm
30 specimens in each Na Cl concentration

salinity had a significant effect on survival of Corophium.

For calculation of the analysis of variance, see Appendix 2.

Wolff (1973) investigated the salinity tolerance of Corophium volutator in the laboratory, he found the minimum and maximum tolerance to be 2.13% S and 53.3 % S respectively. My experiment indicated a much narrower range of salinity tolerance in the laboratory than that found by Wolff. Corophium from Station 1 M.W. tolerated the range 6.96-36.4 % S, and Corophium from Station 9 M.W. tolerated the range 6.96-37.9 % S. The salinity preference was taken to be the salinity level which appeared optimal in terms of the highest numbers of Corophium surviving. In the following table, the salinity preference established in the laboratory is compared with that in the field, i.e. the interstitial salinity at Stations 1 M.W. and 9 M.W.

Table 9

Salinity preference of Corophium volutator in the laboratory and in the field

Origin of Corophium	Laboratory Salinity Preference (% S)	Field Salinity Preference (% S)
Station 1 M.W.	23.20	23.33
Station 9 M.W.	35.00	33.83

Table 9 clearly demonstrates the close similarity between field and laboratory salinity preference. The laboratory salinity preference level effectively acts as a control salinity.

Animals from Station 1 M.W. exhibited a smaller range of salinity tolerance than animals from Station 9 M.W., and

were less tolerant of the higher salinities than were Station 9 M.W. animals. Station 9 M.W. animals were less tolerant of the lower salinities than were Station 1 M.W. animals. The difference in salinity tolerance found in the laboratory is illustrated in Figure 21.

The results of this experiment suggest the possibility of the existence of two physiological races. However, further intensive research would be necessary to clarify this proposal.

Experiment to investigate the distribution of *Corophium volutator* in the field

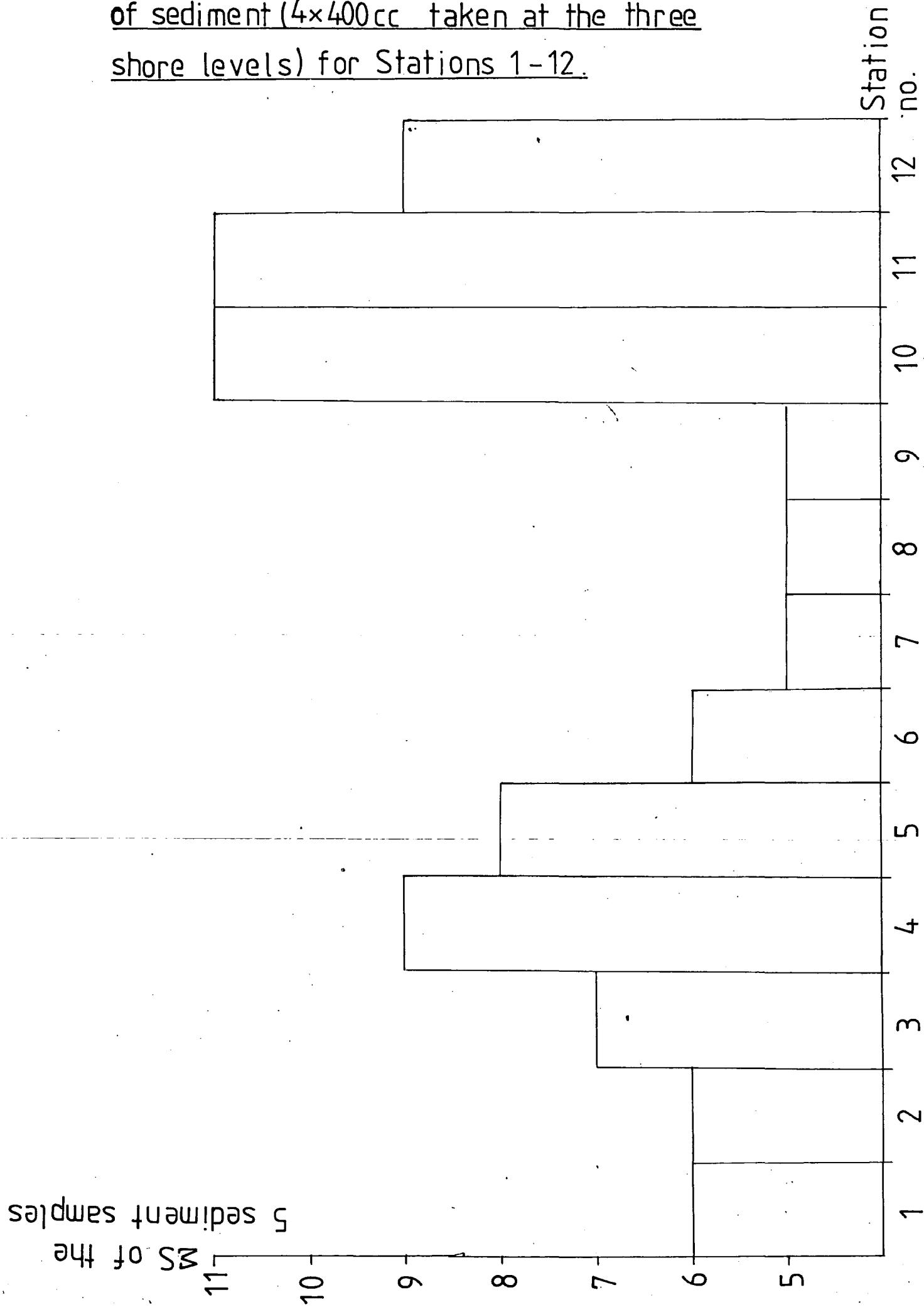
This experiment was performed as a preliminary experiment for the investigation of the microdistribution of the species, since the microdistribution study needed to be carried out in an area where Corophium occurred at a high density.

From the general survey of the distribution of species within the estuary (Appendix 5), it was found that Corophium occurred at a relatively high density at Station 9 (mean density = 760 m^{-2}). In order to establish the shore level at which the species was most numerous, a one metre square quadrat was sampled along a transect from 5m above L.W.M. to the upper shore level at 95m. A duplicate transect was sampled 2m to one side of the first transect to obtain representative results (Table 10). Corophium were found to be most abundant at 45m above L.W.M. The corresponding measurements of physical and chemical factors are tabulated below.

The distribution of Corophium within the substrate was studied by recording the number of animals present in

Figure 20 Graph to show ΣS of the 5 samples of sediment ($4 \times 400 \text{ cc}$ taken at the three shore levels) for Stations 1-12.

53



54
Figure 21 Graph showing laboratory salinity tolerance of *Corophium v.* from Stn. 1MW and Stn. 9MW.

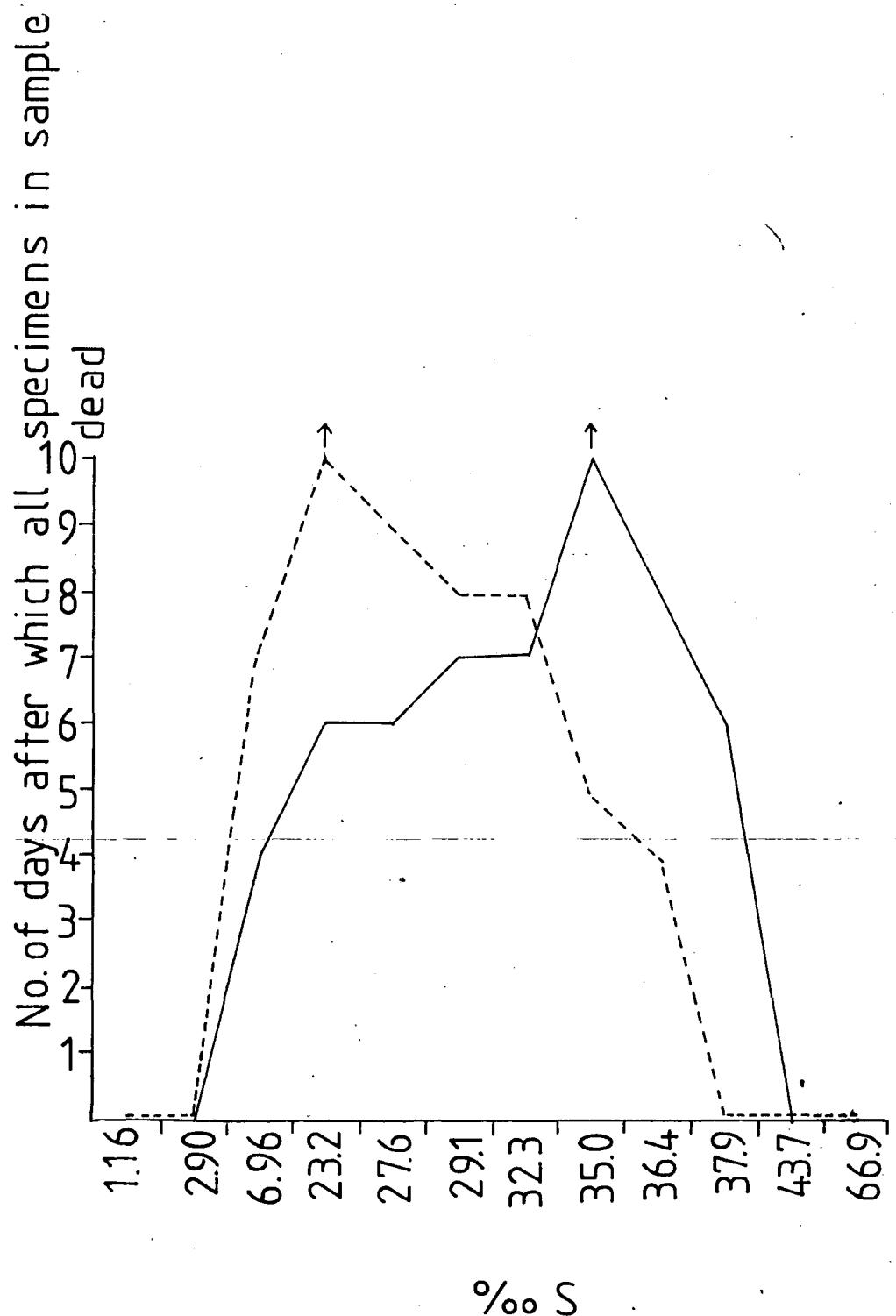


Table 10

Corophium Volutator - Results of Length and Density
 (Results are mean values from 2 transects at Station 9)

Distance from L.W.		Occurrence in depth of substrate							Nos. m^{-2} in 1-7cm of substrate
		1cm	2cm	3cm	4cm	5cm	6cm	7cm	
5m	(\bar{x} length)								
	Mean length (mm)	5.38	5.29	5.92	6.25	-	-	-	
	(\bar{x} N)								
	Mean nos. individuals	12	9	4	8	-	-	-	
	Nos. m^{-2}	96	72	32	64	-	-	-	264
10m	\bar{x} length	5.62	5.20	6.03	6.59	6.41	6.95	-	
	\bar{x} N	28	17	7	9	8	8	-	
	Nos. m^{-2}	224	136	56	72	64	64	-	556
20m	\bar{x} length	5.55	5.65	6.41	6.47	7.03	7.00	8.00	
	\bar{x} N	41	24	8	4	5	3	2	
	Nos. m^{-2}	328	192	64	32	40	24	16	1152
25m	\bar{x} length	5.69	6.03	6.37	6.43	7.26	7.25	7.50	
	\bar{x} N	48	53	31	17	6	3	2	
	Nos. m^{-2}	384	424	248	136	48	24	16	1280
30m	\bar{x} length	5.56	5.91	6.34	6.89	6.54	7.25	7.50	
	\bar{x} N	38	24	10	6	4	4	2	
	Nos. m^{-2}	304	192	80	48	32	32	16	704
35m	\bar{x} length	5.84	6.04	6.19	6.92	7.15	7.34	8.25	
	\bar{x} N	37	25	18	9	4	2	2	
	Nos. m^{-2}	296	200	144	72	32	16	16	776
40m	\bar{x} length	5.86	6.27	6.49	6.19	7.13	6.69	7.00	
	\bar{x} N	78	28	12	8	4	5	2	
	Nos. m^{-2}	624	224	96	64	32	40	16	1096
45m	\bar{x} length	5.51	5.56	6.34	7.23	6.88	6.67	-	
	\bar{x} N	133	28	20	6	3	3	-	
	Nos. m^{-2}	1064	224	160	48	24	24	-	1544

Continued ...

Table 10 (continued)

Distance from L.W.		Occurrence in depth of substrate							Nos. m^{-2} in 1-7cm of substrate
		1cm	2cm	3cm	4cm	5cm	6cm	7cm	
50m	\bar{x} length	5.44	5.80	6.29	6.30	7.19	7.34	7.00	
	\bar{x} N	64	26	21	5	6	2	3	
	Nos. m^{-2}	512	208	168	40	48	16	24	1016
55m	\bar{x} length	5.62	6.04	6.17	6.88	7.34	7.00	7.50	
	\bar{x} N	82	34	14	4	3	4	2	
	Nos. m^{-2}	656	272	112	32	24	32	16	1144
60m	\bar{x} length	5.66	5.82	6.20	6.77	6.92	7.67	7.17	
	\bar{x} N	60	29	8	7	4	3	3	
	Nos. m^{-2}	480	232	64	56	32	24	24	912
65m	\bar{x} length	5.63	5.93	5.68	6.75	7.17	7.50	7.00	
	\bar{x} N	50	29	15	8	4	2	2	
	Nos. m^{-2}	400	232	120	64	32	16	16	880
70m	\bar{x} length	5.63	6.02	6.28	6.32	7.25	7.50	6.84	
	\bar{x} N	37	23	11	5	3	4	2	
	Nos. m^{-2}	296	184	88	40	24	32	16	680
75m	\bar{x} length	5.44	6.20	6.43	6.57	6.58	7.34	7.25	
	\bar{x} N	26	19	9	6	4	2	2	
	Nos. m^{-2}	208	152	72	48	32	16	16	544
80m	\bar{x} length	5.77	5.61	6.16	6.25	6.21	6.75	6.50	
	\bar{x} N	24	21	8	12	4	2	3	
	Nos. m^{-2}	192	168	64	96	32	16	24	592
85m	\bar{x} length	5.68	5.74	5.97	5.95	6.63	6.42	5.79	
	\bar{x} N	38	22	24	11	5	4	4	
	Nos. m^{-2}	304	176	192	88	40	32	32	864
90m	\bar{x} length	5.47	5.58	6.05	5.88	6.33	6.96	7.84	
	\bar{x} N	29	19	10	7	6	4	2	
	Nos. m^{-2}	232	152	80	56	48	32	16	616
95m	\bar{x} length	5.51	5.64	5.95	6.09	6.30	6.92	7.00	
	\bar{x} N	23	19	11	7	4	5	3	
	Nos. m^{-2}	184	152	88	56	32	40	24	576

Table 11

Physical and chemical factors at Station 9 M.W.

<u>Chemical Factors</u>	<u>Value</u>
pH	7.9
Interstitial salinity	33.83 % S
<u>Physical Factors</u>	
Mdmm	0.38mm
QdØ	0.40Ø
SkqØ	-0.10Ø

the top 1cm and in every subsequent centimetre layer of sediment down to 7cm below the surface.

From Figures 22 and 23, it is apparent that at Station 9, Corophium were most abundant within the upper centimetre of substrate at a shore level of 45m above L.W.M.

A study of the microdistribution of *Corophium volutator* occurring at high density

In order to study the factor or factor-complex which controls the microdistribution of Corophium occurring at a high density (>100 animals m^{-2} , Meadows 1964b), the population was investigated 45m upshore from LWM at Station 9. The average density of Corophium at this point was $760m^{-2}$ in 1-7cm depth of substrate. This information was gained from the preliminary 'Experiment to investigate the distribution of Corophium volutator in the field'.

Measurements were taken of animal length (from telson to rostrum), maximum burrow depth (measured to the bottom of the 'U' shape), and surface distance to the nearest burrow.

A significant linear correlation was calculated between animal length and surface distance to the nearest burrow ($R = 0.4608$, $p = 0.01$: $R @ 0.0100 = 0.2565$) which indicated a direct relationship between the two variables (see Figure 24).

Figure 22 Graph of *Corophium* v. density against distance up the shore.

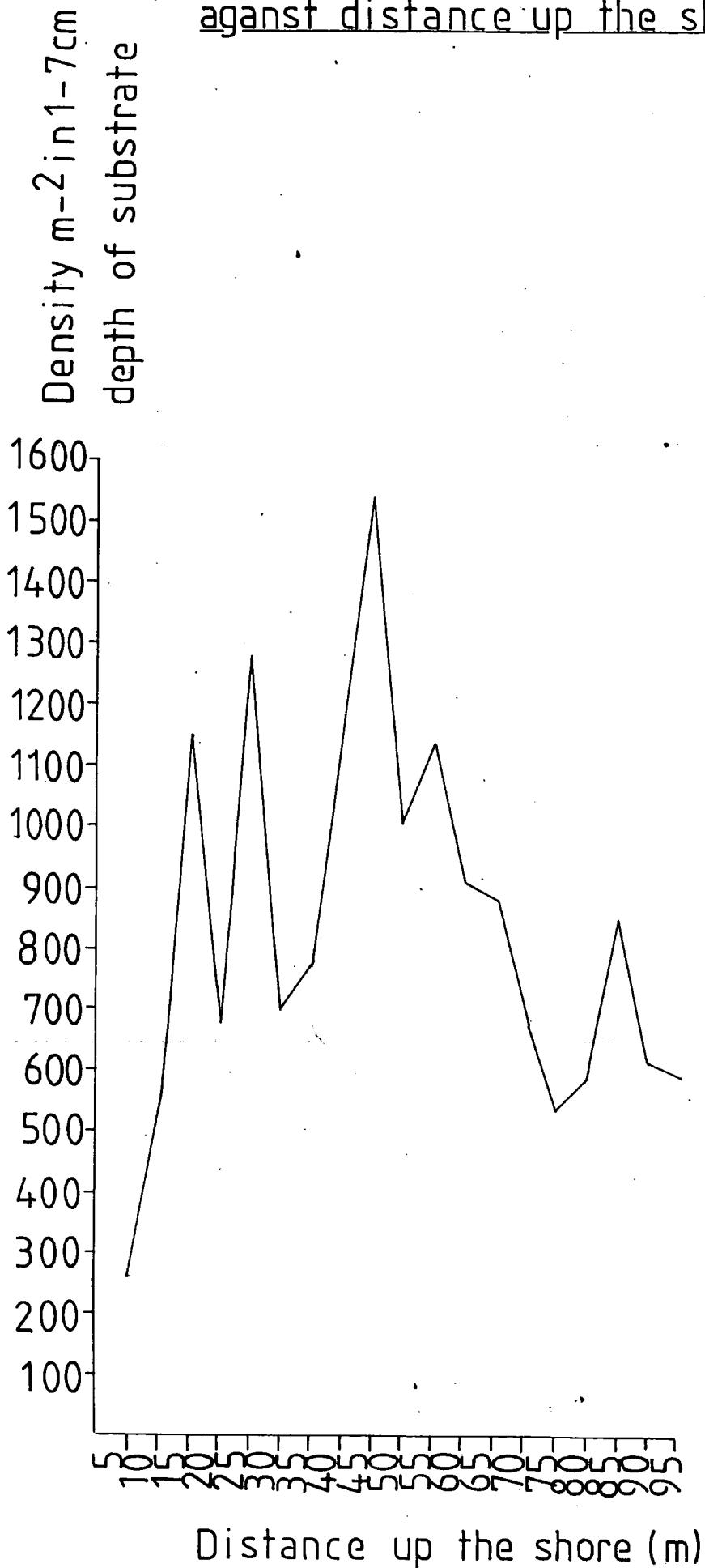


Figure 23 Histogram of *Corophium v. density* with sediment depth (1-7 cm) at Station 9.

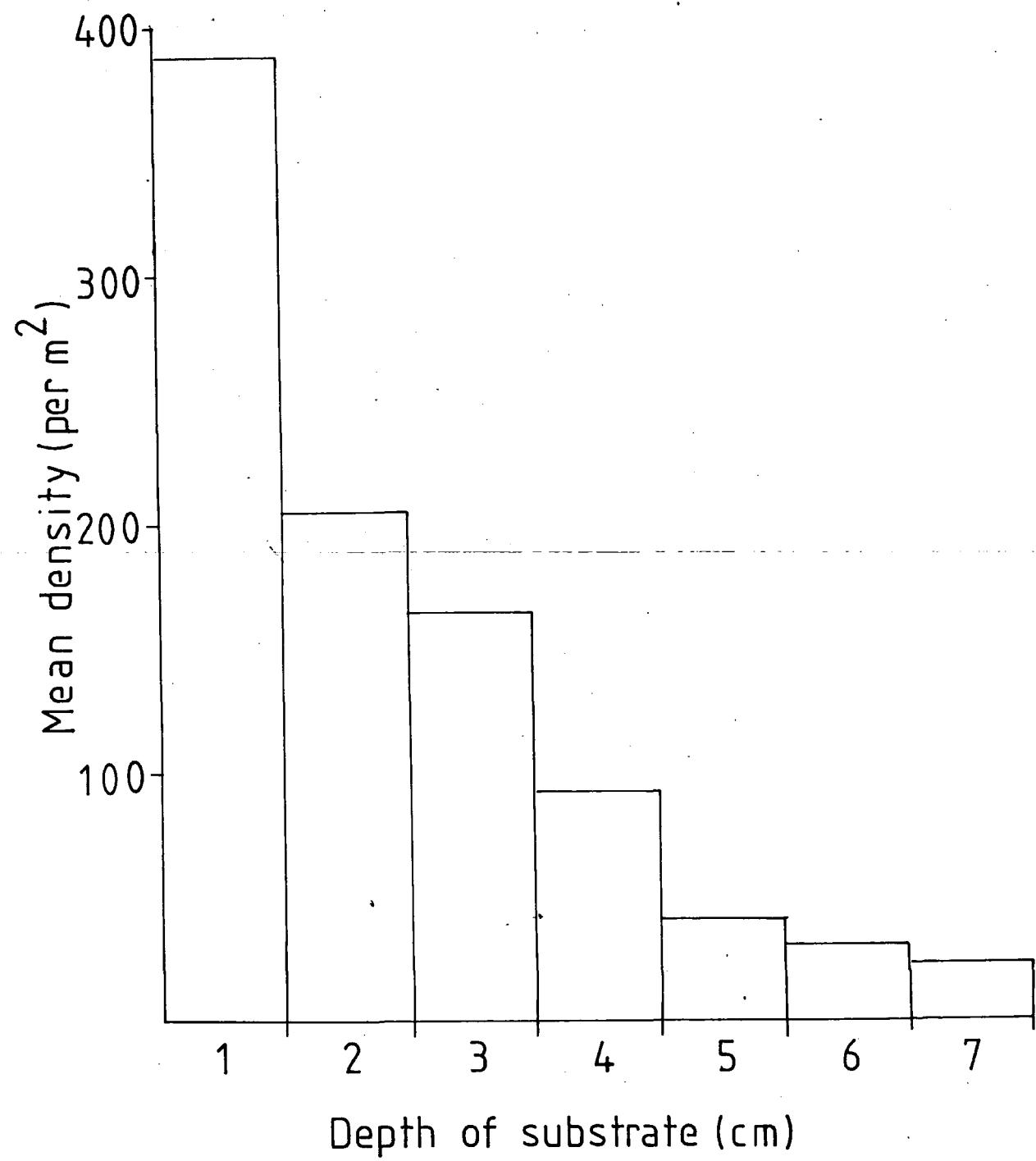
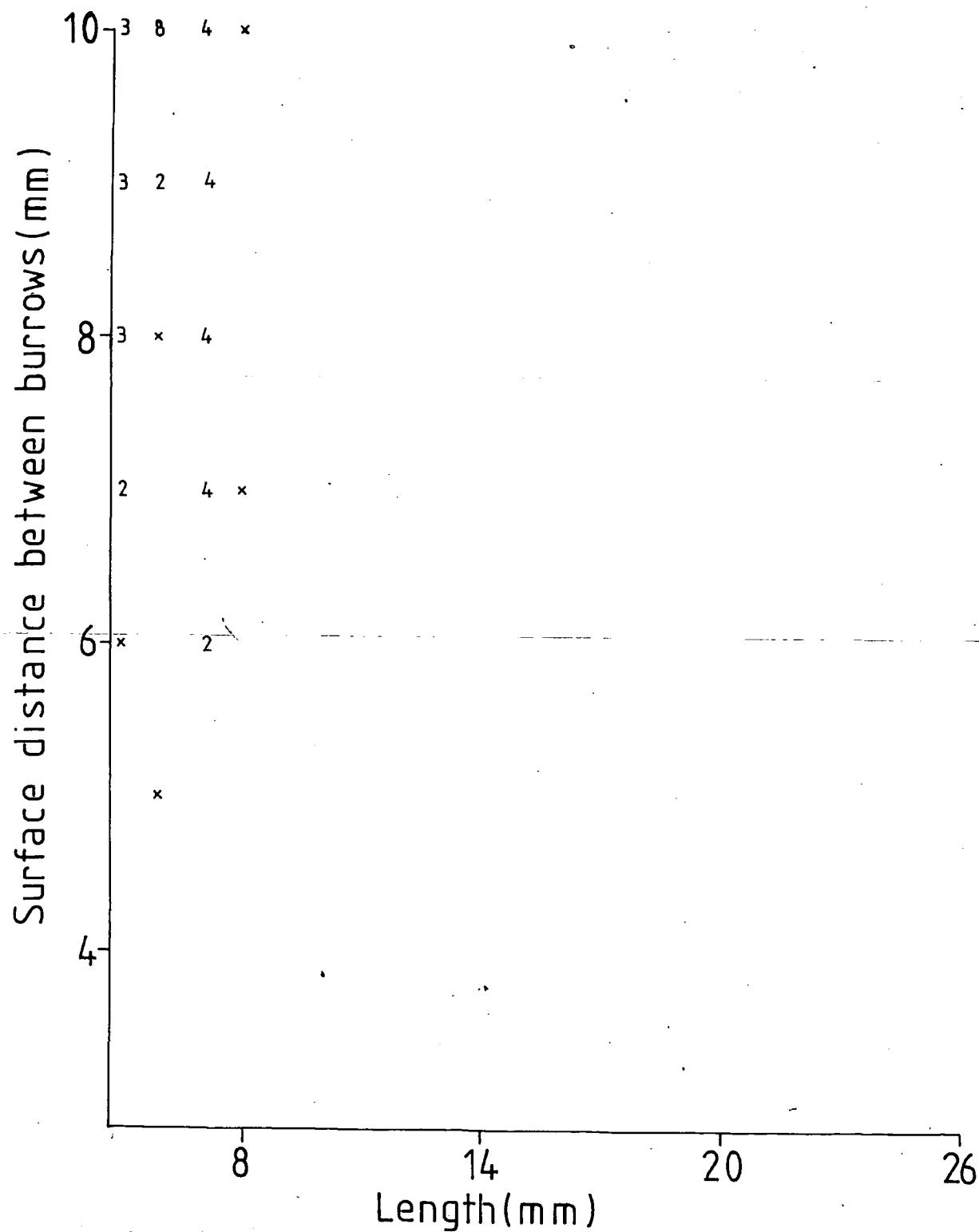


Figure 24 Scatter diagram of *Corophium v. length* against surface distance to the nearest burrow. ⁶⁰

Correlation matrix: N=100, DF=98,

R at 0.05= 0.1966, R at 0.01= 0.2565

Correlation between L and D = 0.4608



Corophium length is thought to determine burrow depth (Meadows, 1964b) and consequently larger animals require larger burrows both in length and diameter to perform the same burrowing sequence as small individuals. Larger animals burrow deeper and wider than small animals, and therefore need a greater distance between burrows than smaller animals.

The size distribution of the population may be seen as controlling the vertical distribution of Corophium within the sediment. The mean Corophium length was 7mm which was the mean length of specimens occurring down to 1cm of sediment. Larger individuals of 8-9mm in length were generally restricted to a depth of 6-7cm below the surface. This was because they required a deeper 'U'-shaped burrow than the smaller animals since they could not successfully operate or turn round in small burrows.

The deep and wide burrows of large Corophium effectively means that burrows belonging to large animals are spaced further apart than the narrower burrows of small animals. This may secondarily affect density, since fewer large than small Corophium can fit into a given area. It is therefore conceivable that, on a micro-scale, both the vertical and horizontal distribution of the species is influenced by the size frequency of the population.

Meadows (1964a) claims that at high densities, Corophium are territorial, but are gregarious at low densities. It would therefore be interesting to discover if gregariousness superimposed upon the population size frequency, significantly altered the vertical and horizontal micro-distribution of Corophium.

Investigation of *Corophium volutator* density in relation to the physico-chemical factors measured

Correlation between all variables was carried out using the computer. The correlation matrices are featured in Table 12.

Corophium density did not show a significant linear correlation with any of the physico-chemical factors. However a rank order correlation revealed that median particle size was inversely related to Corophium density ($N=5$, $Rho = -0.6000$). This implies that Corophium abundance was associated with fine sediment.

B. *Haustorius arenarius*

Experiment to determine substrate selection by *Haustorius arenarius*

This experiment was carried out in an identical fashion as the one with *Corophium volutator*. Fifty specimens of *Haustorius a.* were released in the centre of the tray. All animals used were approximately 9mm long (mean length). *Haustorius*, like *Corophium*, is negatively phototactic in air. The experiment was left for 3 hours and the number of *Haustorius* which had burrowed into the sediment types determined.

The results (Table 14) are based on two identical experiments, both experiments indicating a significant preference for sand of median particle diameter (Md_{mm}) = 0.66. ($\chi^2 = 38.52$, $v = 3$, $p = 0.001$, critical χ^2 at $p = 0.001 = 16.27$).

The null hypothesis (that *Haustorius* is not substrate-specific) was rejected and it was concluded that the distribution of *Haustorius* among the four substrate types was not due to chance but due to a preference manifest by

Table 12Correlation matrices for Corophium volutator density and physico-chemical factorsVariable key:

CV = Corophium volutator density
 IS = interstitial salinity
 MM = median particle diameter
 SC = % silt-clay content
 C = % carbon content
 OS = salinity of surface water
 WT = water table depth
 RPD = RPD depth
 DEG = angle of transect profile

Correlation matrix:

N = 5, DF = 3, R @ 0.0500 = 0.8783, R @ 0.1011 = 0.9587

Variable

CV	1.000				
IS	0.0910	1.0000			
MM	-0.4674	0.0835	1.0000		
SC	0.3117	-0.2391	0.5559	1.0000	
C	0.4349	-0.3057	0.4057	0.9848	1.0000
	CV	IS	MM	SC	C

Rank Order Correlation:

N = 5, RHO

Variable

CV	1.0000				
IS	0.3000	1.0000			
MM	-0.6000	-0.1000	1.0000		
SC	-0.1000	0.1000	0.7000	1.0000	
C	-0.2000	-0.3000	0.6000	0.9000	1.0000
	CV	IS	MM	SC	C

Correlation matrix:

N = 9, DF = 7, R @ 0.5000 = 0.6664, R @ 0.0100 = 0.7977

Variable

CV	1.0000				
OS	0.4671	1.0000			
WT	-0.0834	0.3625	1.0000		
RPD	-0.2287	0.5624	0.8499	1.0000	
DEG	-0.1271	-0.5851	-0.1065	-0.3299	1.0000
	CV	OS	WT	RPD	DEG

Table 13

Haustorius arenarius - mean χ^2 values for the four substrate types

<u>Substrate</u>	<u>Mean χ^2 value</u>
Sand	26.01
Mud	6.25
Sand + 1cm mud	0.01
Silt	6.25
	$\chi^2 = 38.52$

the species. Haustorius was not significantly deceived into burrowing into sand covered by 1cm of mud. For calculation of χ^2 see Table 14.

The conclusion of this experiment is in accordance with the remarks made by Dennell (1933), who suggests that Haustorius is limited to clean wet sand which contains relatively little debris. On this basis one would expect the occurrence of Haustorius at Alnmouth to be associated with wet sand with a relatively shallow water table.

Haustorius was most numerous at Station 10 which had a sandy sediment. Here, Haustorius only occurred at LW, where the water table was comparatively shallow (15cm). The restriction of Haustorius to relatively wet sand is exhibited by a reduction in numbers passing landwards (Table 15). Haustorius occurred at Stations 11 and 12, but at greatly reduced numbers and was restricted to LW where the water table levels were shallowest.

The sand at Station 10 LW was observed to be thixotropic, this being related to the comparatively shallow water table. This sediment property is of utmost importance for the burrowing mechanism since the burrowing power of the animal depends upon the strong current expelled by the pleopods.

Table 14

χ^2 calculation for the experiment to determine substrate selection by *Haustorius arenarius*

Total no. of specimens = 25
Mean length of specimens = 9mm

Substrate description	Mean particle size (mm)	Nos. in each substrate after 3hrs. 1st Expt.	Nos. in each substrate after 3hrs. 2nd Expt.
Sand	0.66	16	21
Mud	0.29	0	1 (dead on surface)
Sand + 1cm mud	0.66 (sand) 0.29 (mud)	8	3
Silt	0.53	1 (dead on surface)	0

$$\chi^2 = \frac{(O_i - E_i)^2}{E_i} \quad E = 6.25$$

Substrate	χ^2 1st Expt.	χ^2 2nd Expt.
Sand	15.21	34.81
Mud	6.25	4.41
Sand + 1cm mud	0.49	1.69
Silt	4.41	6.25

$$\chi^2 = 26.36 \quad \chi^2 = 47.16$$

$v = 4 - 1$
 $4 = 3$, critical value of χ^2 at $p = 0.001 = 16.27$
 H_0 = no difference in the distribution of *Haustorius a.* among the four substrates, i.e. the species is not substratum specific.

Calculation of χ^2 for the combined result of the first and second experiments:

Substrate description	Mean particle size (mm)	Nos. in each sediment after 3hrs. (Nos. = mean results of 1st & 2nd expts.)
Sand	0.66	19
Mud	0.29	0
Sand + 1cm mud	0.66 (sand) 0.29 (mud)	6
Silt	0.53	0

$$\chi^2 = \frac{(O_i - E_i)^2}{E_i} \quad E = 6.25$$

Continued ...

<u>Substrate</u>	<u>χ^2</u>
Sand	26.01
Mud	6.25
Sand + 1cm mud	0.01
Silt	6.25

$$\chi^2 = 38.52$$

The χ^2 values of the first and second experiments and for the mean of the two experiments are well above the critical value of 16.27 for $p = 0.001$, $\gamma = 3$. There is therefore a 99.9% probability of the inverse of H_0 (H_1) being correct, i.e. that the distribution of the species among the four substrates was not due to chance but due to some preference exerted by Haustorius a. The species preferred to inhabit sand.

Table 15

Distribution of Haustorius in relation to tidal level, water table depth,
R.P.D. depth and organic content of the sediment

Station No.	Tidal level	No. of specimens in sample					Water table level (cm)	R.P.D. depth (cm)	% carbon content of substrate
		1	2	3	4	5			
10	LW	2	6	7	5	8	15	9	01.36
	MW	-	-	-	-	-	68	43	00.63
	HW	-	-	-	-	-	71	55	00.34
11	LW	6	7	2	3	2	33	4	01.99
	MW	1	-	1	-	-	76	1	01.57
	HW	-	-	-	-	-	82	2	01.99
12	LW	3	-	-	1	-	36	3	00.74
	MW	-	-	-	-	-	81	2	00.52
	HW	-	-	-	-	-	97	1	00.26

Feeding also relies upon a thixotropic sediment, since as a filter-feeder, the animal dependent upon the water current produced by the maxillae (Dennell 1933).

As a consequence of filter-feeding, Dennell proposes that variation in the organic content of sediment influences Haustorius distribution. The species is most abundant at Station 10 LW which has a relatively high % carbon value of 1.36%C compared with carbon values for Stations 11 and 12.

A general synopsis of this experiment is that the distribution of Haustorius is influenced by a sandy substrate type associated with a shallow water table and high % carbon content.

Experiment to investigate the salinity tolerance of *Haustorius arenarius*

This investigation was performed in an identical way to the Corophium experiment. Ten Haustorius were placed in each solution. Animals of approximately 9mm were used since this was calculated to be the mean length. The Haustorius used were collected from Station 10 LW, which had an interstitial salinity of 31.00%S. Results of the physico-chemical factors recorded from Stations 10, 11 and 12 are summarized in Table 17.

Results of the first and second experiments are presented in Table 16. The results represent mean values of two identical experiments. Analysis of variance showed significantly greater variance between groups than within. This means that there was significantly greater variance between samples of different salinities than within a sample of the same salinity. The F value calculated was 13.77, $p = 0.01$. Therefore salinity had a significant effect on

Table 16.

Results of experiment to investigate the salinity tolerance
of *Haustorius arenarius*

Figures indicate the number of animals alive at the end of the day. All results are based on the mean of 2 identical experiments.

Haustorius arenarius from Station 10 LW

Approximate length of specimens = 9mm
10 specimens in each NaCl concentration

Figure 25 Graph showing laboratory salinity tolerance of *Haustorius a.* from Station 10 LW.

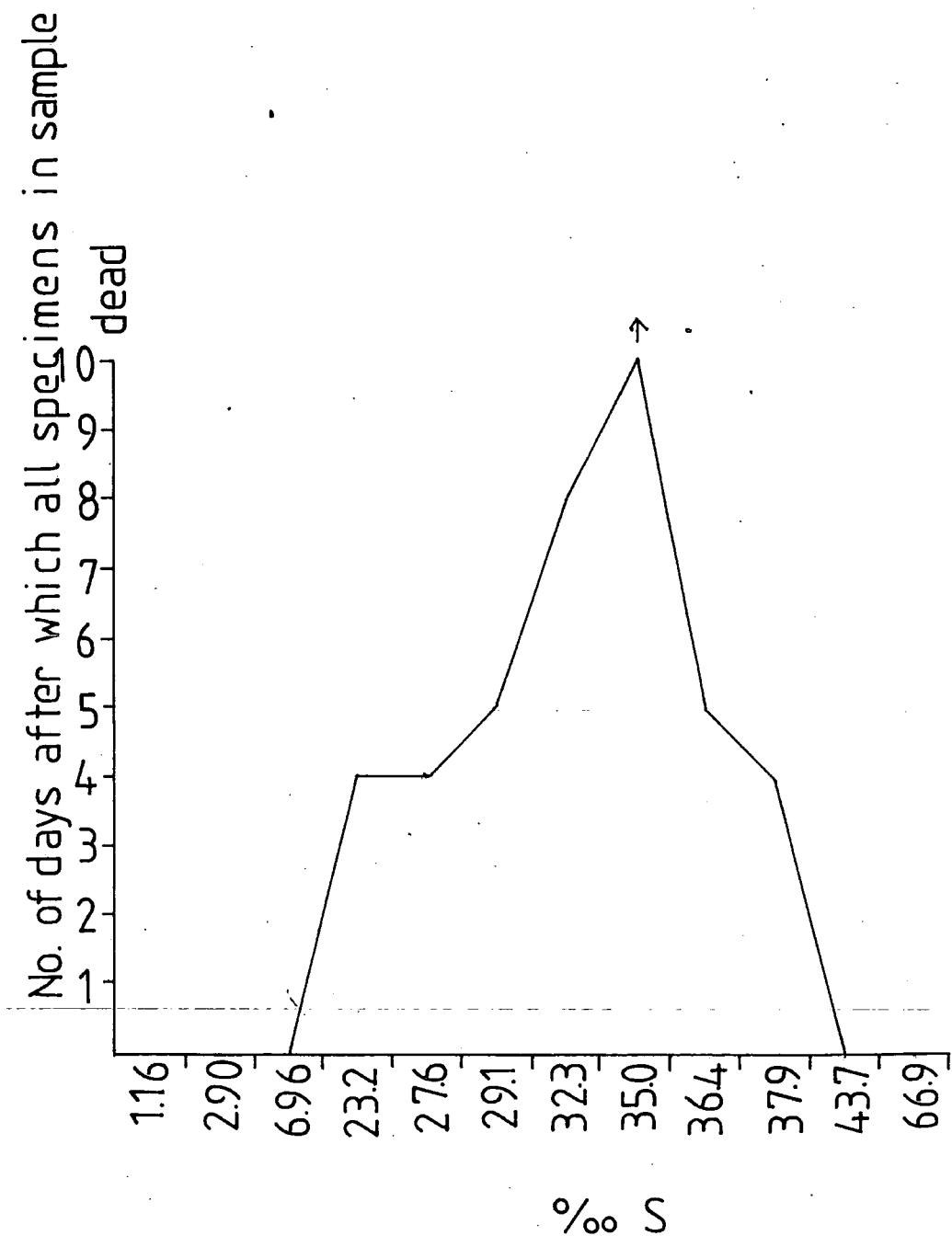


Table 17

Results of the density of *Haustorius arenarius* and the physico-chemical factors recorded for Stations 10, 11 and 12

Station No.	Density of <i>Haustorius</i> a. (m^{-2})	Salinity of surface sea water (‰ S)	Interstitial salinity (‰ S)	Mdmm	% carbon	Depth of water table (cm)	Depth of R.P.D. (cm)	Angle of transient profile (°)
10 LW	37		31.00	0.43	1.36	15	09	6
10 MW	0	8.46	34.00	0.42	0.63	68	43	4
10 HW	0		35.00	0.44	0.34	71	55	3
11 LW	27		35.00	0.50	1.99	33	24	4
11 MW	3	29.17	35.00	0.66	1.57	76	67	1
11 HW	0		35.00	0.41	1.99	82	73	2
12 LW	3		35.00	0.66	0.74	36	31	3
12 MW	0	35.00	35.00	0.53	0.52	81	74	2
12 HW	0		35.00	0.40	0.26	97	81	1

survival of Haustorius. For calculation of analysis of variance see Appendix 2.

Animal samples did not survive at salinities below 29.1 and above 36.4‰ S. In view of this, some Haustorius would be expected to occur at Stations 5, 7 and 9 where salinity ranges from 30.14 to 33.6‰ S. This was not the case in the field, one reason for their absence could be lack of the preferred sandy substrate.

Haustorius appeared to demonstrate a narrow tolerance of salinity either side of 35.00‰ S. With this regime the species is further favoured by a shallow water table with a thixotropic sandy sediment of relatively high percentage carbon content.

Investigation of *Haustorius arenarius* density in relation to the physico-chemical factors measured

A table of the data is presented in Table 17. Correlation between all variables was carried out using the computer. The correlation matrix is featured in Table 18.

Haustorius density showed a significant inverse relationship with interstitial salinity, water table and R.P.D. depth, and a significant positive correlation with the angle of transect profile.

The association between Haustorius density and R.P.D. depth is not causal, but merely a consequence of the R.P.D. being dependent upon water table depth. Similarly, the correlation between Haustorius density and the angle of the transect profile was not causal.

Haustorius density was highest at the more dilute end of the interstitial salinity range measured (31.00-35.00‰ S). High Haustorius density was associated with a shallow water

Table 18Correlation matrix for *Haustorius arenarius* density and physico-chemical factorsVariable key:

HA = *Haustorius arenarius* density
 IS = interstitial salinity
 MM = median particle diameter
 C = % carbon content
 WT = water table depth
 RPD = RPD depth

N = 9, DF = 7, R @ 0.0500 = 0.6664, R @ 0.1011 = 0.7977

HA	1.0000						
IS	-0.7298	1.0000					
MM	-0.1075	0.3025	1.0000				
C	0.4891	-0.1151	0.1166	1.0000			
WT	-0.8338	0.6236	-0.1935	-0.3583	1.0000		
RPD	-0.8019	0.6467	-0.0767	-0.2755	0.9731	1.0000	
DEG	-0.7715	-0.7865	-0.2671	0.1764	-0.8482	-0.9100	1.0000
	HA	IS	MM	C	WT	RPD	DEG

table which is in accordance with the species' need for a wet thixotropic sediment. Scatter diagrams for the relationship between Haustorius density and interstitial salinity and water table depth are drawn in Figures 26a-b.

Figure 26a Scatter diagram of *Haustorius a.* density against interstitial salinity.

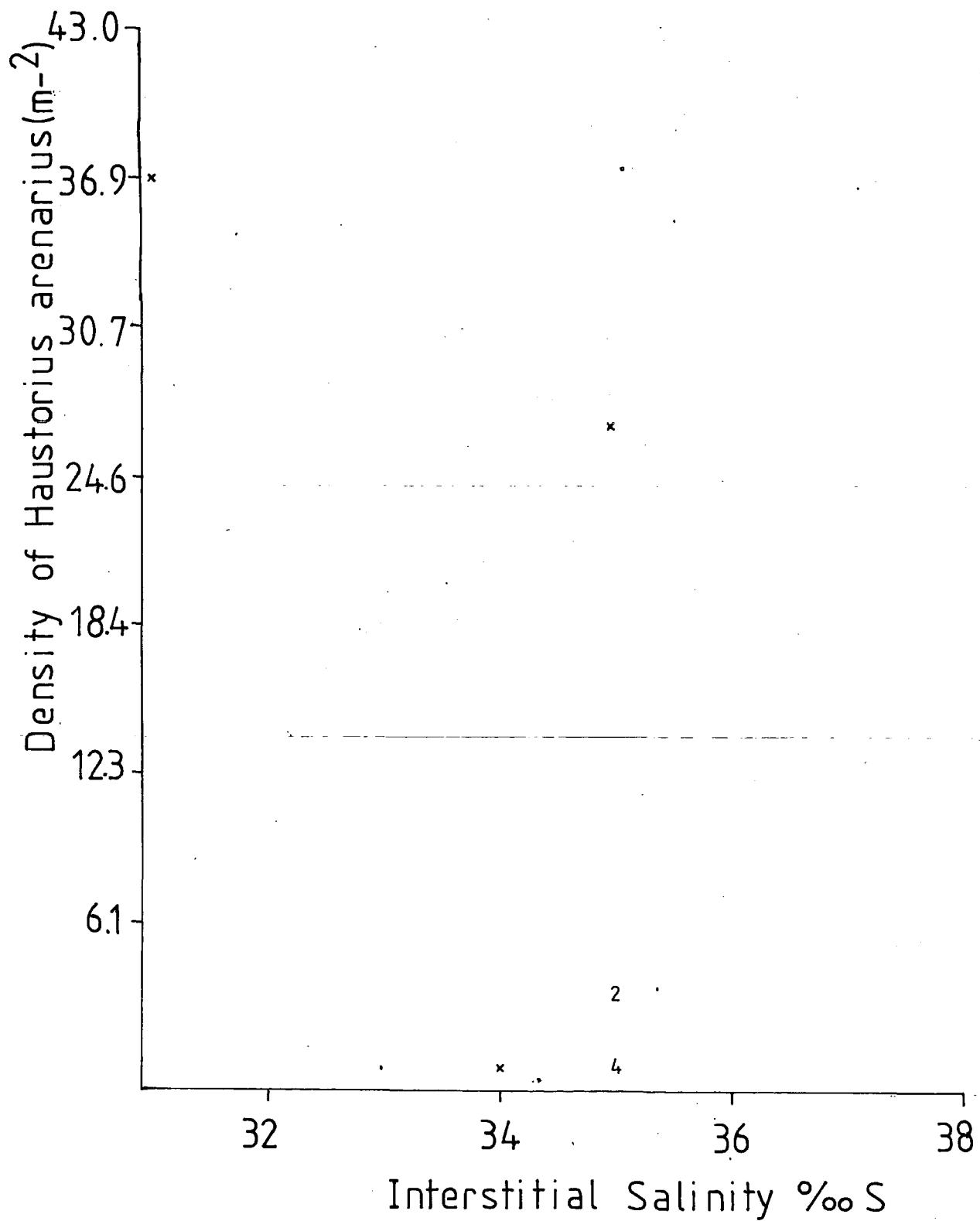
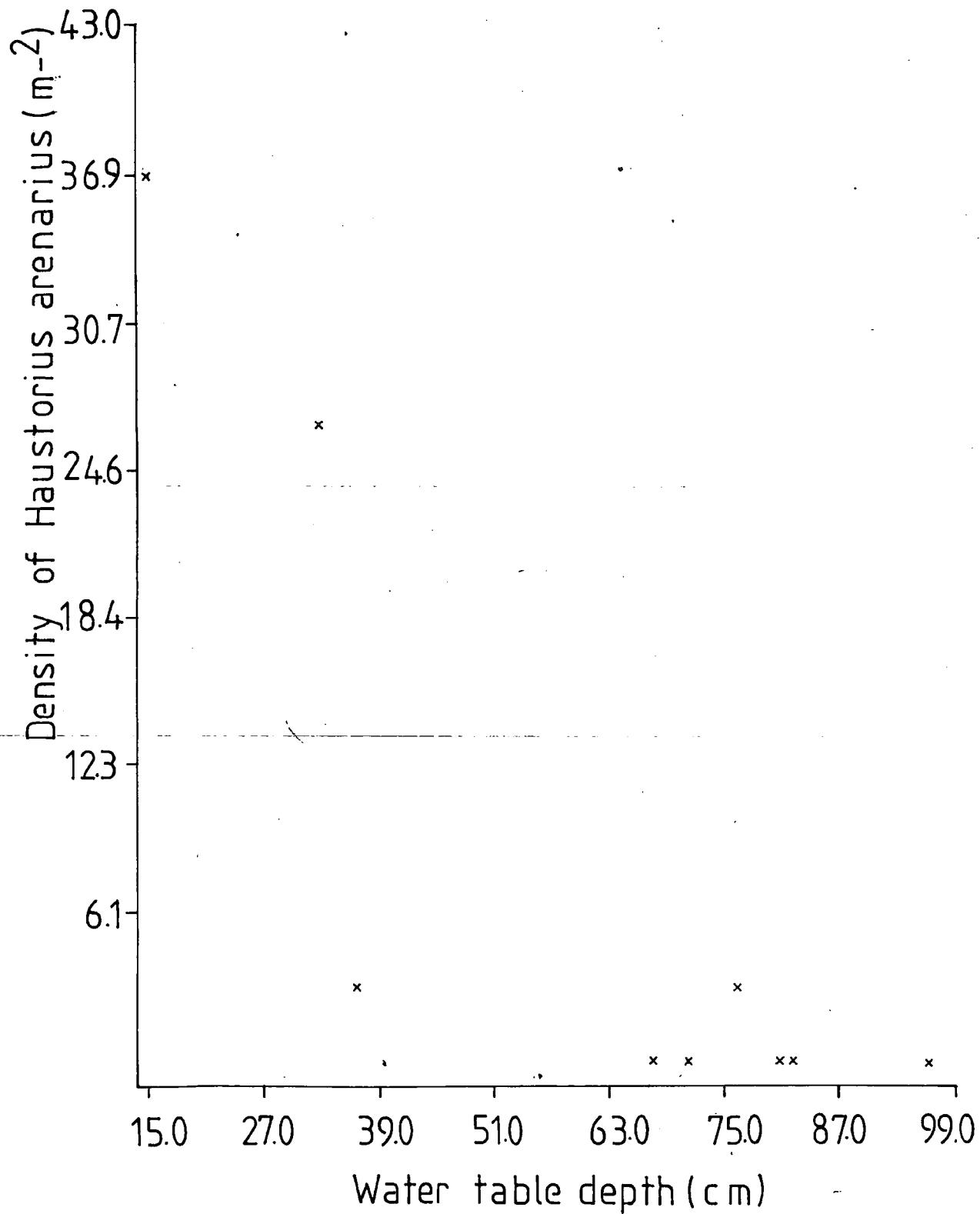


Figure 26b Scatter diagram of Haustorius a.
density against water table depth.



CHAPTER 5 : DISCUSSION

A. How chemical factors might operate to limit the distribution of benthic invertebrates in an estuary

(i) pH

Only a slight gradient along the estuary in pH of the surface water was manifest (Table 2). The mean pH of Stations 1-6 was 8.23 and for Stations 7-12 is 7.86, hence the water was slightly more alkaline up river.

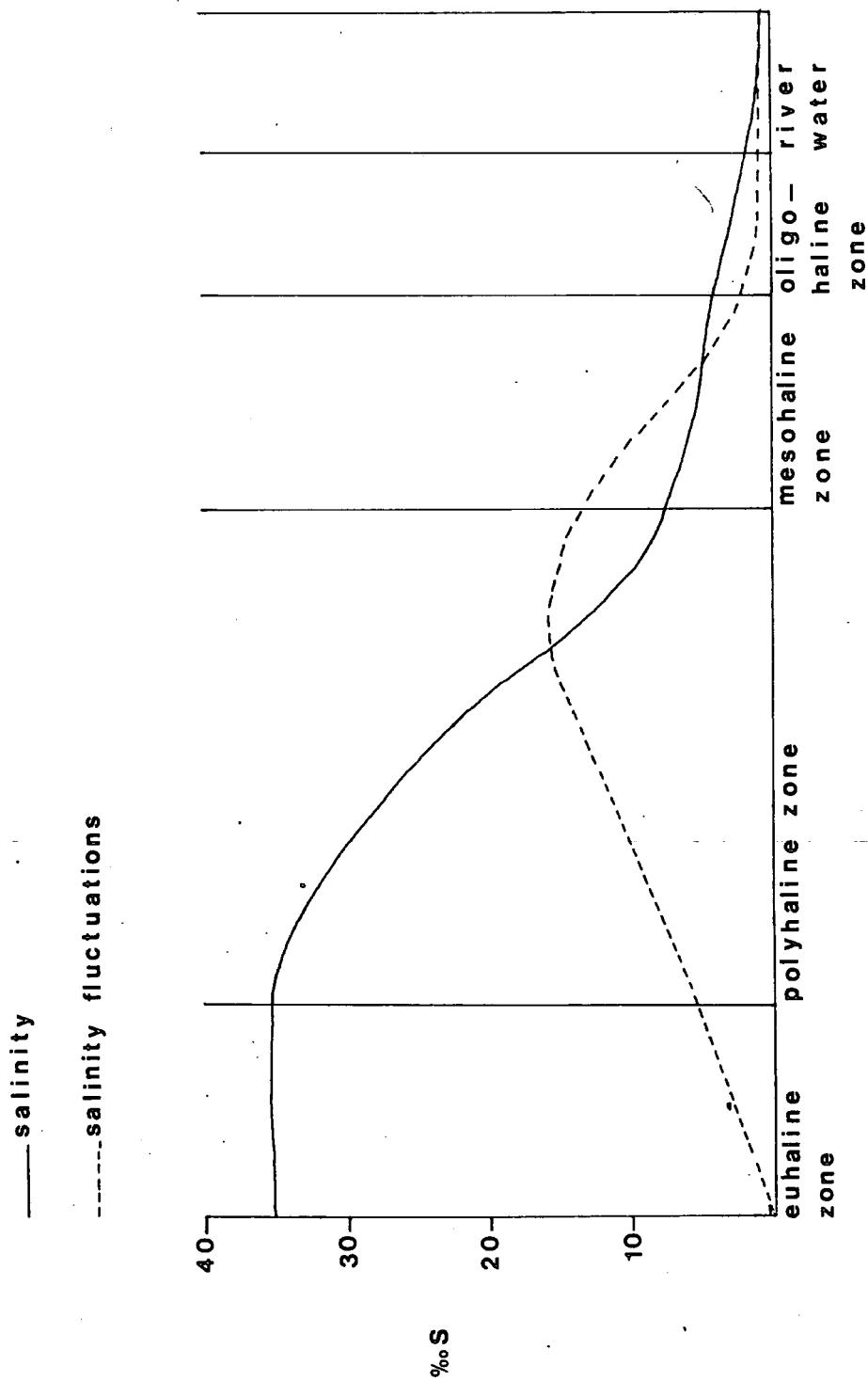
pH was not considered to be a significant parameter in the control of faunal distribution because there was no distinct variation within the estuary (Carriker in Louuff 1967; Perkins 1974). Consequently pH data was not further analysed.

(ii) Salinity

Salinity is defined by Perkins (1974) as the amount of salts dissolved in water, expressed as grams per kilogram of sea water. The salts are principally sodium and chloride ions, supplemented by potassium, calcium, magnesium and sulphate ions, plus trace amounts of many other ions. The salinity range of estuarine waters was between 0.5 and 35‰ S (McLusky 1981) (Figure 27). At the Aln estuary the salinity ranged from 2.3-35.0‰ S (Table 2).

The importance of salinity to estuarine organisms is well documented, and has been proposed to be the single most important factor affecting the distribution of benthos (Green 1968, Gunter 1961, Eltringham 1971, Kinne 1966). However, McLusky (1971) proposes that salinity determines the maximum distance to which a species is capable of penetrating, but the full potential of any species to colonize upstream

Figure 27 Schematic illustration of salinity changes at different points of an estuary. (After Kühl, 1963).



can only express itself when suitable substrata are present. Estuarine salinity presents severe problems to potential inhabitants since it fluctuates diurnally and seasonally, together with longitudinal and lateral variations.

The salinity at any particular point of an estuary depends upon the relationship between the volume of tidal water and the volume of fresh water entering, as well as the tidal amplitude, the topography of the estuary which affects the degree of mixing of the salt and fresh water and the climate of the locality. Attempts have been made to subdivide the estuary based on salinity. The most widely accepted scheme is the Venice system and is presented in Table 19. On the basis of the Venice system the Aln estuary can be similarly divided (Table 20).

The effects of salinity on estuarine organisms are complex. For example, calcium content and temperature may interact with total salinity. Higher calcium content facilitates toleration of lower salinity by most invertebrates, and some species are more tolerant of lower salinity at lower temperatures but of higher salinity at higher temperatures (Remaine and Schleiper 1971, Dorgelo 1976).

The response of an animal to salinity may vary at different stages of its life cycle. In general, animals appear to be most sensitive to extremes of salinity during the egg stage, when recently hatched, or when in adult breeding condition. For example, adults of the mussel Mytilus galloprovincialis can survive in laboratory salinities above 10% at 27.5°C, but optimal metamorphosis of the larvae only occurs above 17.5% at temperatures below 25°C (McLusky 1981).

Table 19

The Venice system for the classification of brackish waters
(From Arch. Oceanog. Limnol., Vol. 11, 1959)

<u>Zone</u>	<u>Salinity (% NaCl)</u>
Hyperhaline	>40
Euhaline	40-30
Mixohaline	(40) 30-0.5
Mixo-euhaline	>30 but < adjacent sea
-polyhaline	30-18
-mesohaline	18-5
-oligohaline	5-0.5
Limnetic (freshwater)	<0.5

Table 20

Classification of Aln estuary at low tide according to the
Vencie system

<u>Station No.</u>	<u>Zone</u>
1	Mixo-oligohaline
2	"
3	"
4	"
5	"
6	Mixo-mesohaline
7	"
8	"
9	"
10	"
11	"
12	Mixo-euhaline

Salinity may influence an animal through changes in several chemical properties of the water, namely, osmotic concentration, relative proportion of solutes, density and viscosity. Thus, when an animal responds to a change in salinity, it could be responding to a change in salt concentration, or to any of the other three factors mentioned.

Salinity stress may evoke various reactions, behavioural or physiological. Behavioural responses are common in estuarine animals, for example, when confronted by an abnormal salinity some may retreat into a burrow, or dig deeper e.g. Arenicola, while others may temporarily tolerate periods of adverse low salinity by closing their shell, such as Mytilus.

Physiological responses to abnormal salinity are either passive or active. Animals which show a passive response are unable to osmo-regulate to any significant level, are isosmotic and are known as poikilosmotic forms. Homoismotic forms are able to osmoregulate and may either maintain an internal concentration greater than that of the external environment (hyperosmotic regulation), or alternatively, maintain the body fluids at a lower concentration than that of the environment (hyposmotic regulation). Some animals, e.g. Carcinus maenas can regulate hyperosmotically at low salinities and hyposmotically at high salinities. (Figure 28). Finally, animals which osmoregulate within narrow limits, and within wide limits are said to be stenohaline and euryhaline respectively. Indication of the osmoregulatory ability of the species encountered at Alnmouth is given later in Chapter 5, Section D.

Other non-osmoregulatory physiological responses are

Figure 28 Typical patterns of osmoregulation.

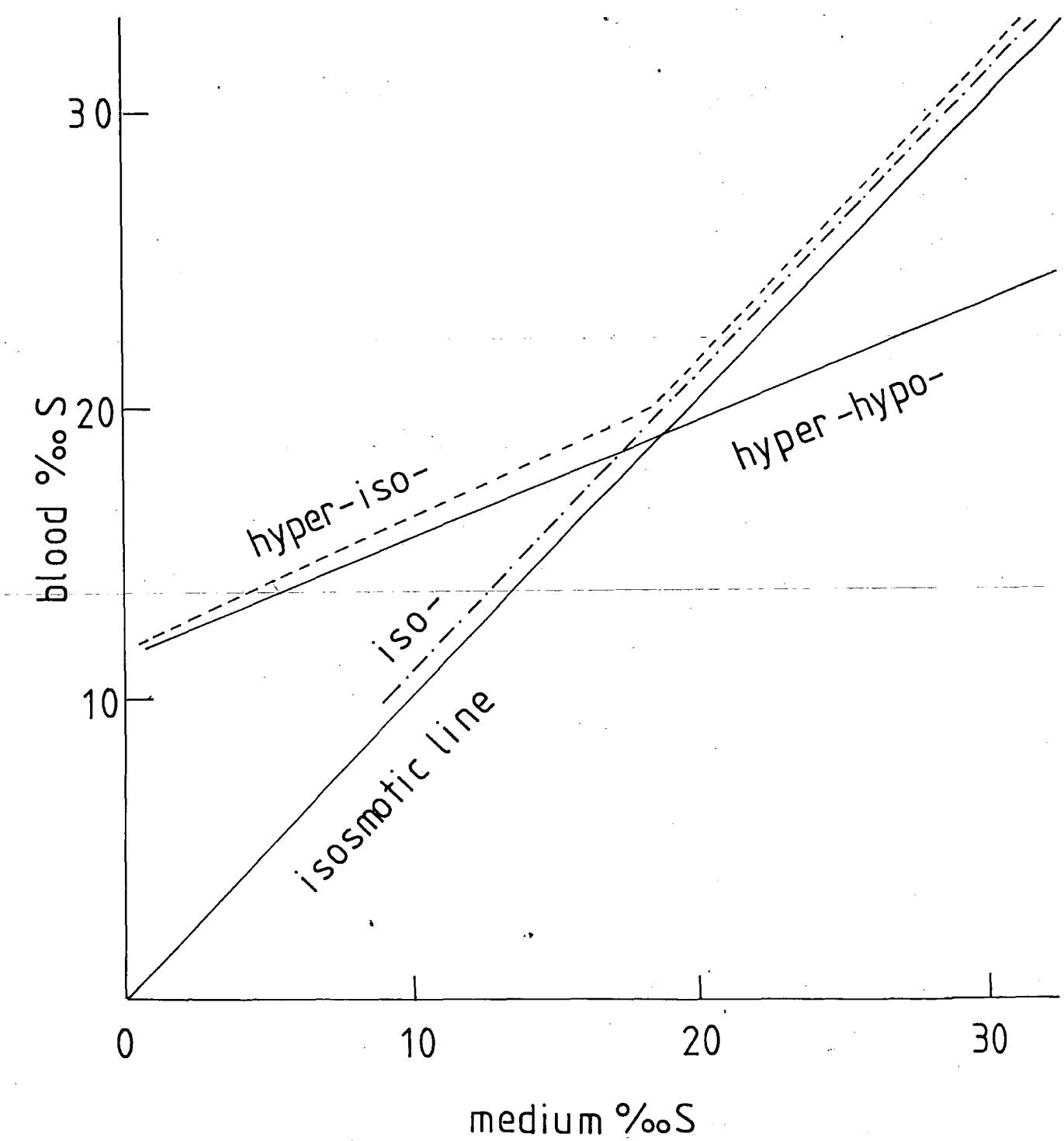
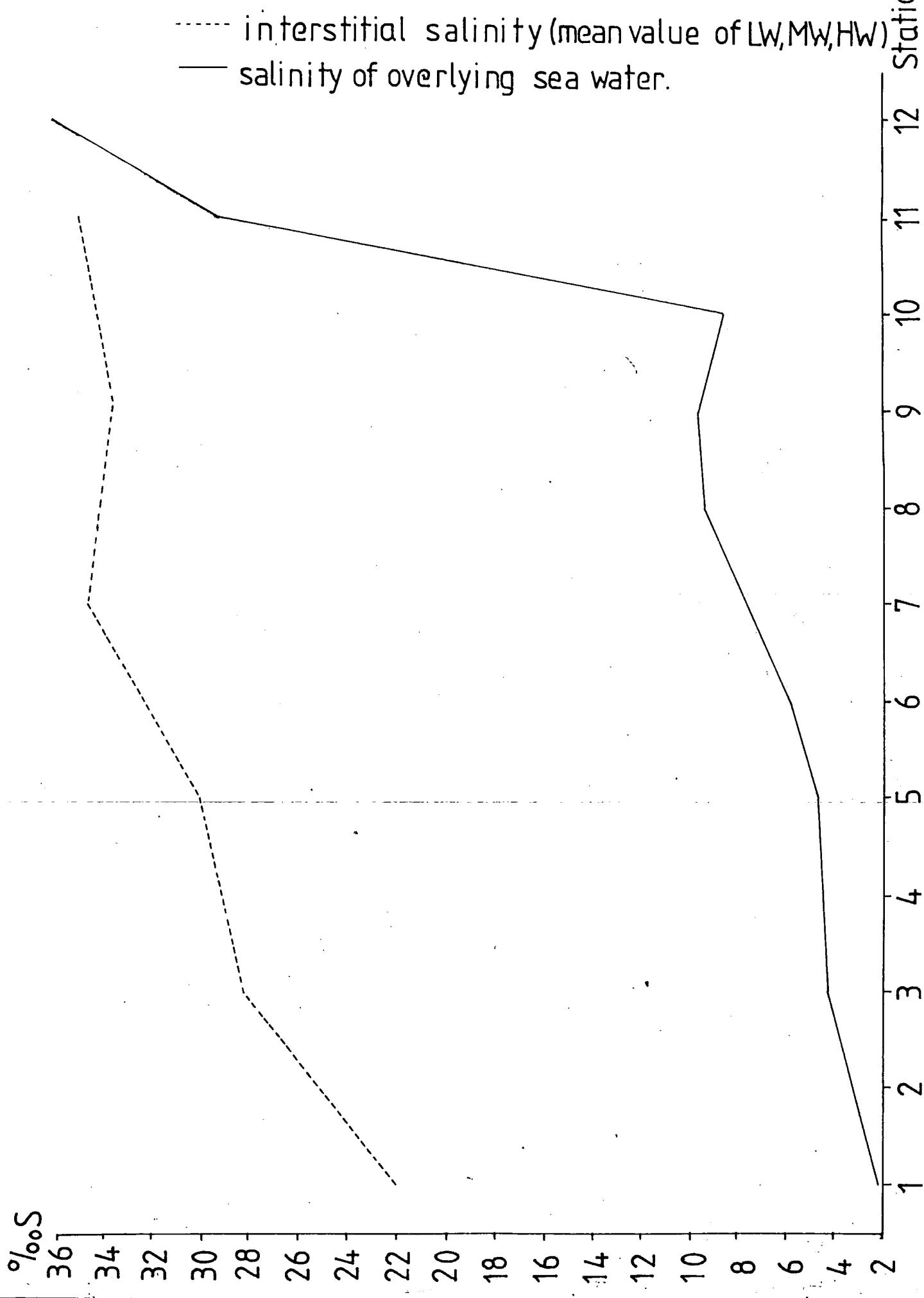


Figure 29 Interstitial salinity and salinity of overlying sea water.



shown by estuarine animals. Non-genetic adaptations include modification of metabolic rate, change in activity pattern or alteration of growth in response to salinity. Long-term genetically inherited responses may involve modified patterns of absorption and excretion of water and salts, altered ionic ratios, differential ability to store water and salts, reduced surface permeability, modified tissue tolerances and major structural alterations in response to life in different salinities. Mention of non-osmoregulatory physiological responses of Alnmouth species are similarly given later in the discussion.

Since the majority of estuarine animals live buried within the sediment, interstitial salinity is far more important than that of the surface water. Interstitial salinity is subject to less fluctuation than that of the surface water, and is likely to be appreciably higher (Spooner and Moore 1940) (Table 2).

The interstitial salinity represents an equilibrium between that of the sea water at the time of coverage and freshwater seeping out of the land ~~.....~~, but this fundamental system is subject to modification by many factors (Perkins 1974). In general, there is a salinity gradient from L.W.M. to H.W.M., which is most marked on shores of a gentle gradient. A gently sloping shore is subject to slower circulation of interstitial water than a steep shore, and the former is also more likely to retain a layer of surface water during the exposure period.

A marked vertical gradient in interstitial salinity was found for the 6 Stations (1,3,5,7,9,11) with mean L.W., M.W., and H.W. % S as presented below.

Table 21

Mean interstitial salinity values of the three tidal levels
(Mean = mean of 6 Stations)

<u>Tidal level</u>	<u>Mean interstitial salinity (% S)</u>
L.W.	27.99 \pm 0.66
M.W.	30.92 \pm 0.61
H.W.	32.86 \pm 0.58

The significant inverse correlation between interstitial salinity and angle of beach transect (Table 5) reinforces the proposal of higher salinity being associated with a gentle gradient ($r = -0.5$, $p = 0.05$). Interstitial salinity was not found to be significantly correlated with Mdmm ($\rho = -0.26$) nor with the depth of the water table ($\rho = 0.41$) (Table 5). This is contrary to expectation since a substrate of small particle size is associated with high capillarity, high water retention (i.e. shallow water table) and slow drainage (gentle transect gradient).

Interstitial salinity was associated with the R.P.D. depth ($\rho = 0.69$), but not in a causal way. The R.P.D. depth was not correlated with the median particle diameter ($\rho = 0.10$). However, one would have expected that the high water-retention properties of fine-grained sediment would be associated with a shallow R.P.D. depth due to a relatively high water table and low oxygen penetration. Interstitial salinity is reported to be causally related to median particle size and so would be expected to covary superficially with R.P.D. depth.

Neither the interstitial salinity or the salinity of the surface water was found to be correlated with the number of species ($\rho = -0.07$ and -0.35 respectively). This is in accordance with the expected relationship between the

Table 22

Vertical distribution of species and sediment characteristics

Shore level	Median particle size (mm)	Mean no. of sps.	QD ϕ	Sk $q\phi$
LW	0.632	4.3	0.69	0.098
MW	0.423	5.5	1.02	0.053
HW	0.372	3.7	1.32	1.320

numbers of species and salinity as portrayed in Figure 30. Perkins (1974) recorded these characteristic breaks in the fauna at salinities of 5 and 18‰ S, i.e. at the oligohaline-mesohaline and mesohaline-polyhaline boundaries respectively. The similar situation found at Alnmouth is illustrated in Figure 31.

A possible explanation for the reduction in species number in the middle reaches of the estuary is that this is where greatest fluctuations in salinity occurs since it is the meeting point of marine and fresh waters. Thus, only a few specialist species adapted to tolerate large salinity fluctuations, are able to inhabit the middle reaches. The importance of salinity fluctuations has also been reiterated by Bacci and Dahl (Remaine and Schleiper 1971) and Wolff (1973).

B. How physical factors might operate to limit the distribution of benthic invertebrates in an estuary

(i) Sediment analysis

Estuarine bottom sediments constitute a massive ecological complex of factors of significance to benthic organisms (Carriker 1967). Nielson (Lauff 1967) emphasizes that the complexities of estuarine sediments determine many of the subtleties of ecological relationships among the benthos; and that the major effect of the sedimentary substrate is its role in maintaining unique chemical conditions in the bottom and immediately overlying water (Lauff 1967).

Morgans (1956) proposes that factors of the substrata which affect the benthos are texture and content of dead organic matter. Sediment texture of the Alnmouth samples was

Figure 30 Expected relationship between species
number and salinity.

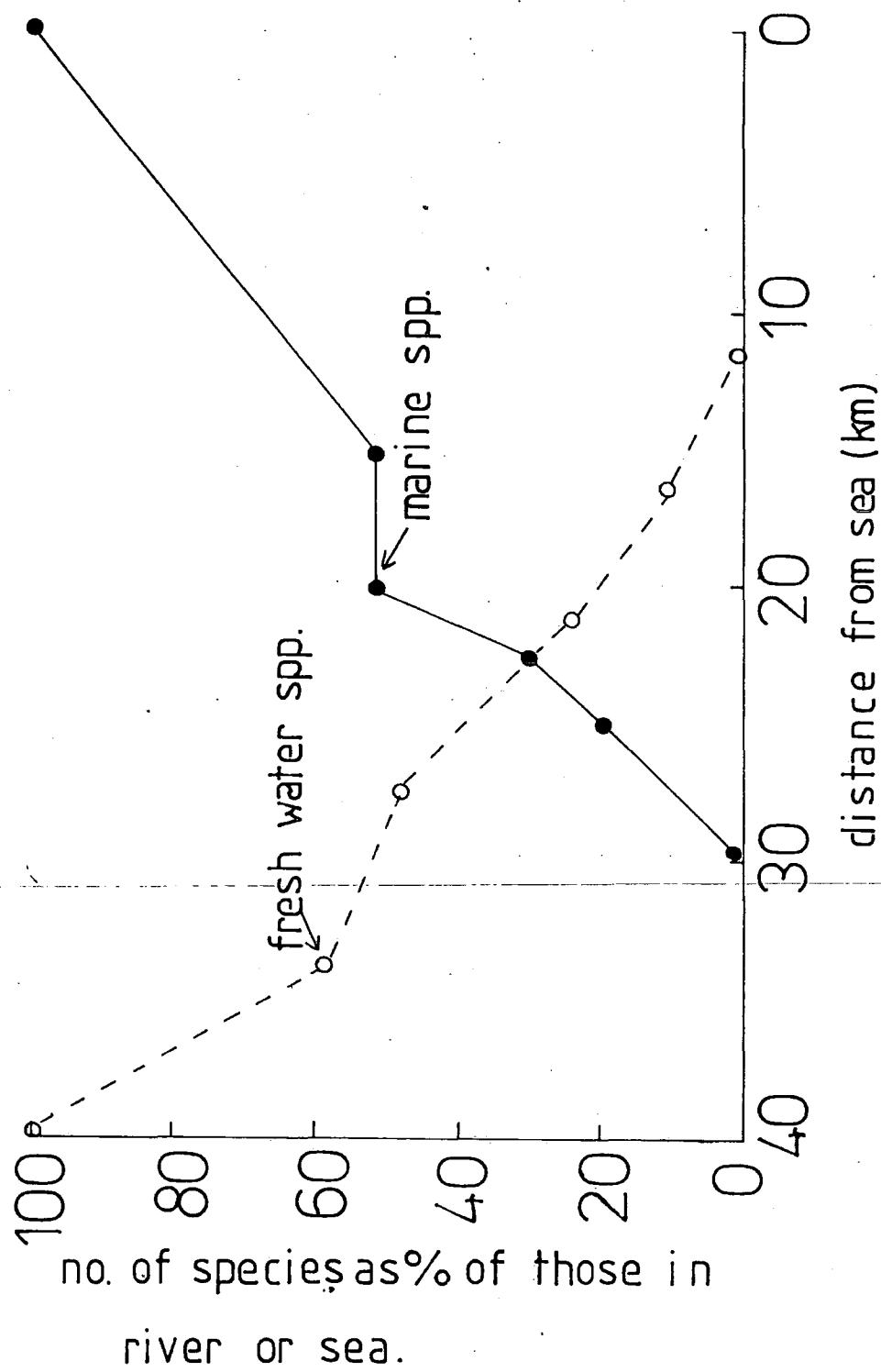
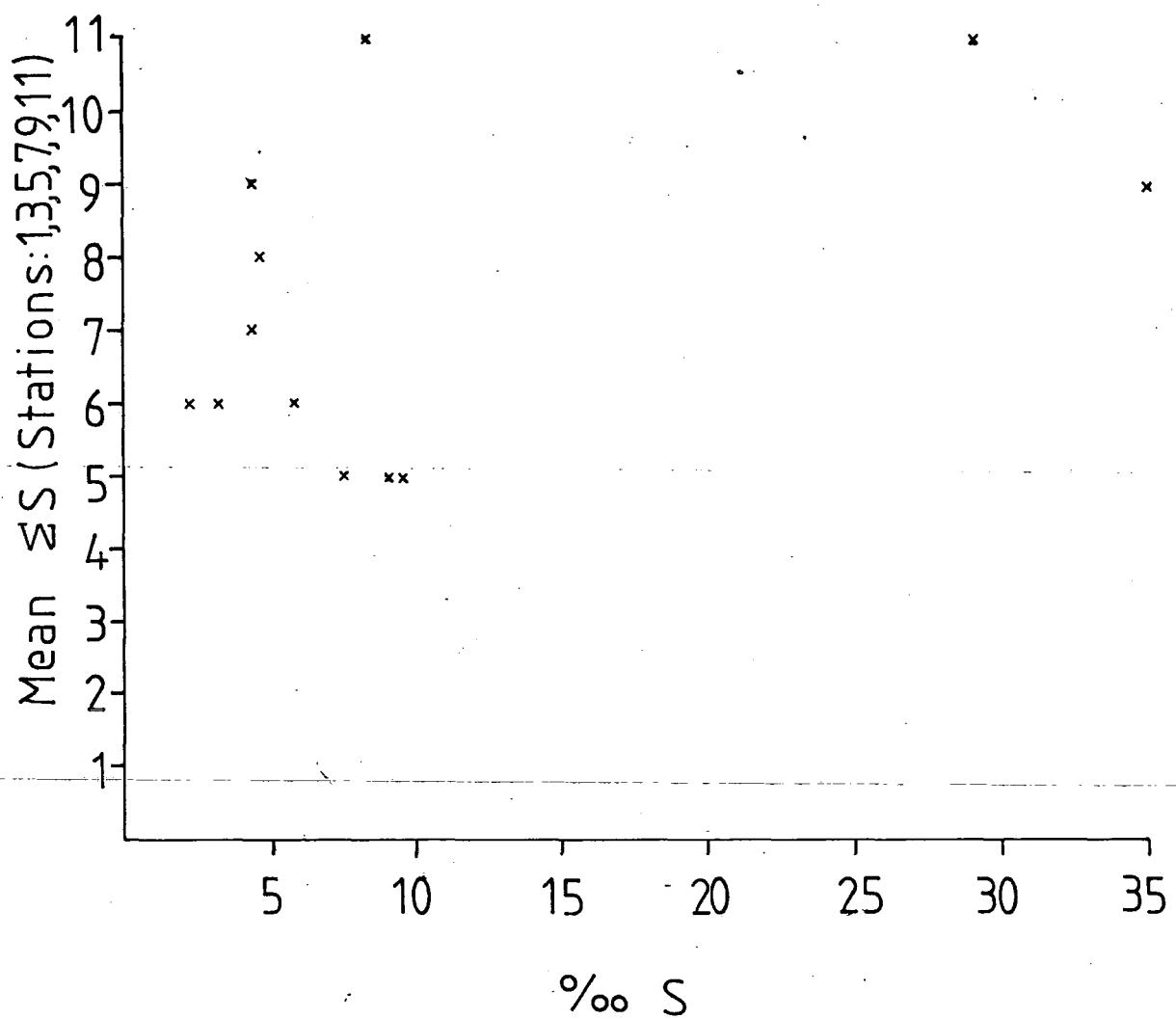


Figure 31 Graph showing mean ΣS against salinity of overlying sea water.



investigated by Mdmm (Figure 32), % silt-clay content, QDØ and SkqØ. These four variables directly influence soil water content and related porosity and permeability.

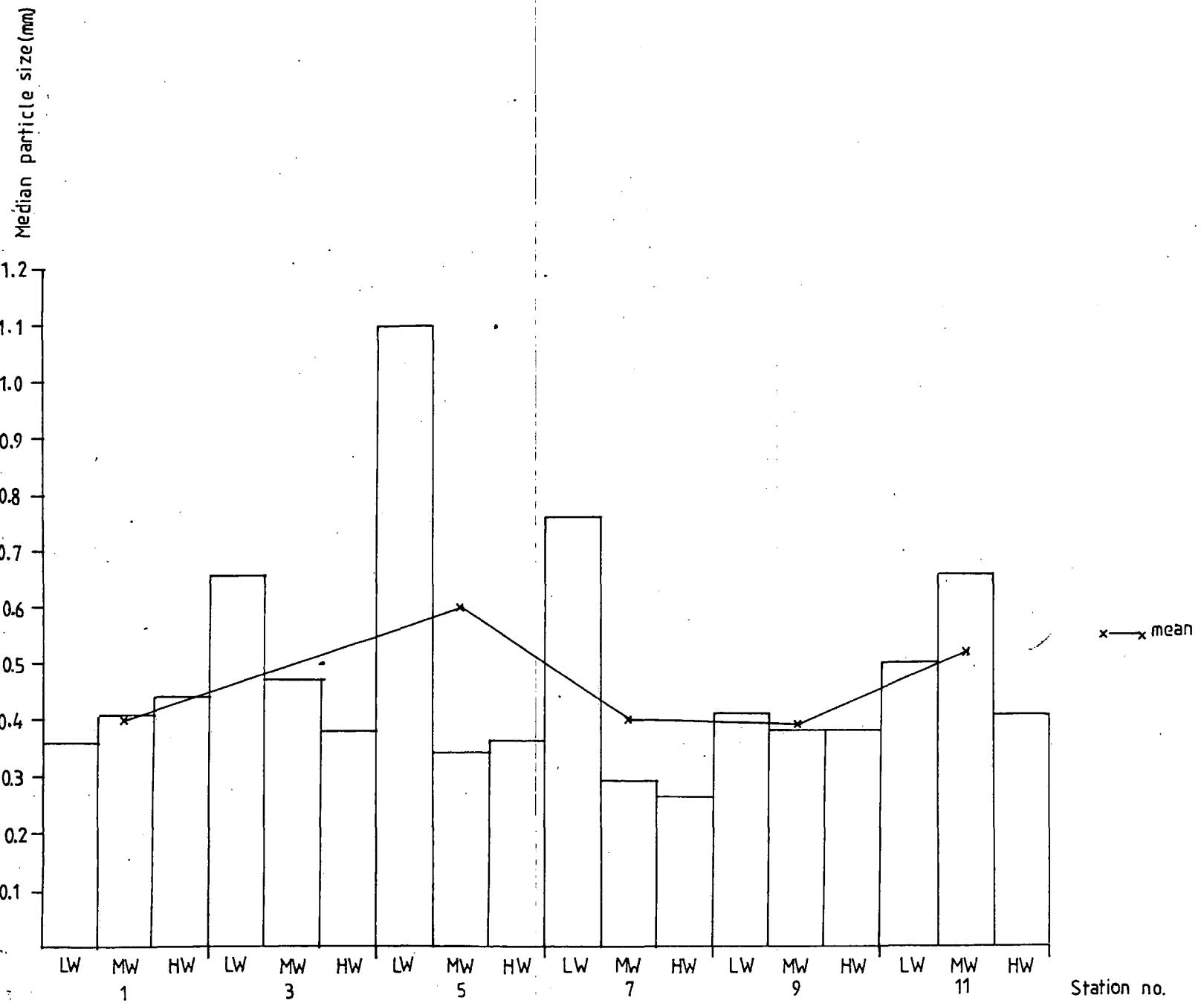
Porosity may be defined as the ratio between the volume of the voids and the total volume of the sediment; and permeability, as the rate of water flow through the sediment per unit time (Wolff 1973). Porosity is affected by complex factors which depend upon grain size, absence of uniformity in grain size, proportions of the different grain sizes, grain shapes, method of deposition and the subsequent processes of compaction solidification (Perkins 1974).

Permeability is not primarily dependent on porosity but on pore size. Permeability increases with increasing average pore size and median grain size (Wolff 1973).

Since porosity and permeability affect the water content of a soil, these factors are also related to soil hardness, which is dependent upon the amount, density and viscosity of the interstitial water. A soil may be thixotropic or dilatant, according to the soil water content. A thixotropic soil (water content $> 25\frac{1}{2}$ by weight) shows decreased resistance with increased rate of shear, e.g. quick sand, whereas a dilatant soil (water content $< 22\%$ by weight) offers increased resistance with an increased rate of shear. Thixotropic properties are important to burrowing animals such as Arenicola and Haustorius since they rely on this reduction in resistance for effective burrowing.

In the Aln estuary I found that the median particle diameter (mm) was significantly correlated only with % carbon content of the sediment ($\rho = -0.55$) and the sediment sorting coefficient ($\rho = -0.65$). However, according to

Figure 32 Histogram of median particle size of sediment samples.



the literature I would have expected significant relationships between Md_{mm} and the R.P.D. depth, water table depth and transect gradient, in addition to the % carbon content of the sediment.

Previous reports suggest that a fine-grained sediment is related to a shallow water table since associated porosity is low. A shallow water table presents a near-surface barrier to oxygen diffusion and hence results in a shallow R.P.D. depth. A gentle transect profile tends to be related to a shallow water table (and hence shallow RPD) because drainage is less than on a steeper slope. Gentle transects are associated with small particle size and efficient sorting of sediment.

No connection between interstitial or overlying water salinity and particle size was apparent (Table 5). Generally however, other researchers have found that reduced salinity is associated with finer sediments.

In order to determine the affect of sediment texture (and its associated relationships) on the benthos, the vertical and horizontal distribution of species was analysed in relation to median particle size, $QD\phi$ and $Skq\phi$. Table 22 presents this information with regards to the vertical distribution of species. It appears that as one moved up the shore the median particle size decreases, sediment was less well sorted and the $Skq\phi$ value rose indicating a skewed distribution. Since the $Skq\phi$ value for H.W. was positive this means that the particles larger than the median are better sorted than the smaller.

Because species richness was highest at M.W. (Figure 37) one may speculate that values of median particle diameter,

QDØ and SkqØ intermediate between those experienced at H.W. and L.W. are the most favourable for species colonisation.

The distribution of species along the river relative to sediment texture was evaluated by correlating the total number of species (ϵ_S) against median particle diameter (mm) (see Table 5). A significant relationship was not apparent ($\rho = 0.13$). I would have conjectured however that more species should have been associated with sandy sediments since sand provides opportunities for generalized as well as the more specialized modes of feeding (such as suspension feeding in interstitial water by Haustorius arenarius). Mud restricts water circulation and thus oxygenation within the sediment, and therefore reduces the number of possible modes of feeding.

The negative correlation that I obtained between median particle size, and carbon content ($\rho = -0.55$) is in accordance with reports by Millard (1976) and Newell (196). The sediment particle size therefore gives some indication of the potential food available. Indeed, Morgans (1956) had proposed that the associations of various animal feeding groups with soil texture is not so much influenced by texture as by the food available of which median particle size is a convenient index. To investigate this I calculated the correlation between silt/clay content of sediment and number of deposit feeders (Appendix 6). The r_s value of 0.637, significant at $p = 0.01$ supports Morgan's proposal.

One other important way in which sediment might effect distribution is that larval settlement is affect by particle size. Larval of several benthic species are very discriminating in their choice of a substratum, and, in the case

of sedentary species, this will be reflected in the distribution of adults. Corophium volutator and Haustorius arenarius are substrate-specific to mud and sand respectively. Other species however are reported to be not so limited and live in a range of sediment grades, but they do exhibit an optimum abundance in one or two specific grades of sediment (Wolff 1973).

(ii) % carbon content of the sediment

The organic matter within estuaries may consist either of live organisms, or of detritus, such as material resulting from excretion and decomposition, augmented by organic particles and dissolved organic matter carried into the estuary. Within the estuary the organic matter may be cycled and transformed as in Figure 33. Dissolved organic matter is derived from the material lost as exudation from plants, and excretion from animals, whereas the particulate matter is derived from the death of organisms. Figure 34a illustrates the flow of organic matter through the estuarine ecosystem.

Newell (1979) suggests that the bulk of organic debris in estuaries comprises faecal material composed of indigestible chitin, cellulose and lignin. The faecal material undergoes a cycle in which bacteria colonize its surface and are later eaten by deposit-feeders. Bacteria then recolonize the excreted faecal material thus making it available again as a food.

The carbon content of sediment was investigated both in relation to transect profile and distance from the sea (along the estuary).^{Figure 34b} The expected result was that as one moved upshore from tidal levels with large median particle

Figure 33. Major pathways for the cycling of organic matter in an estuary (After Head, 1976).

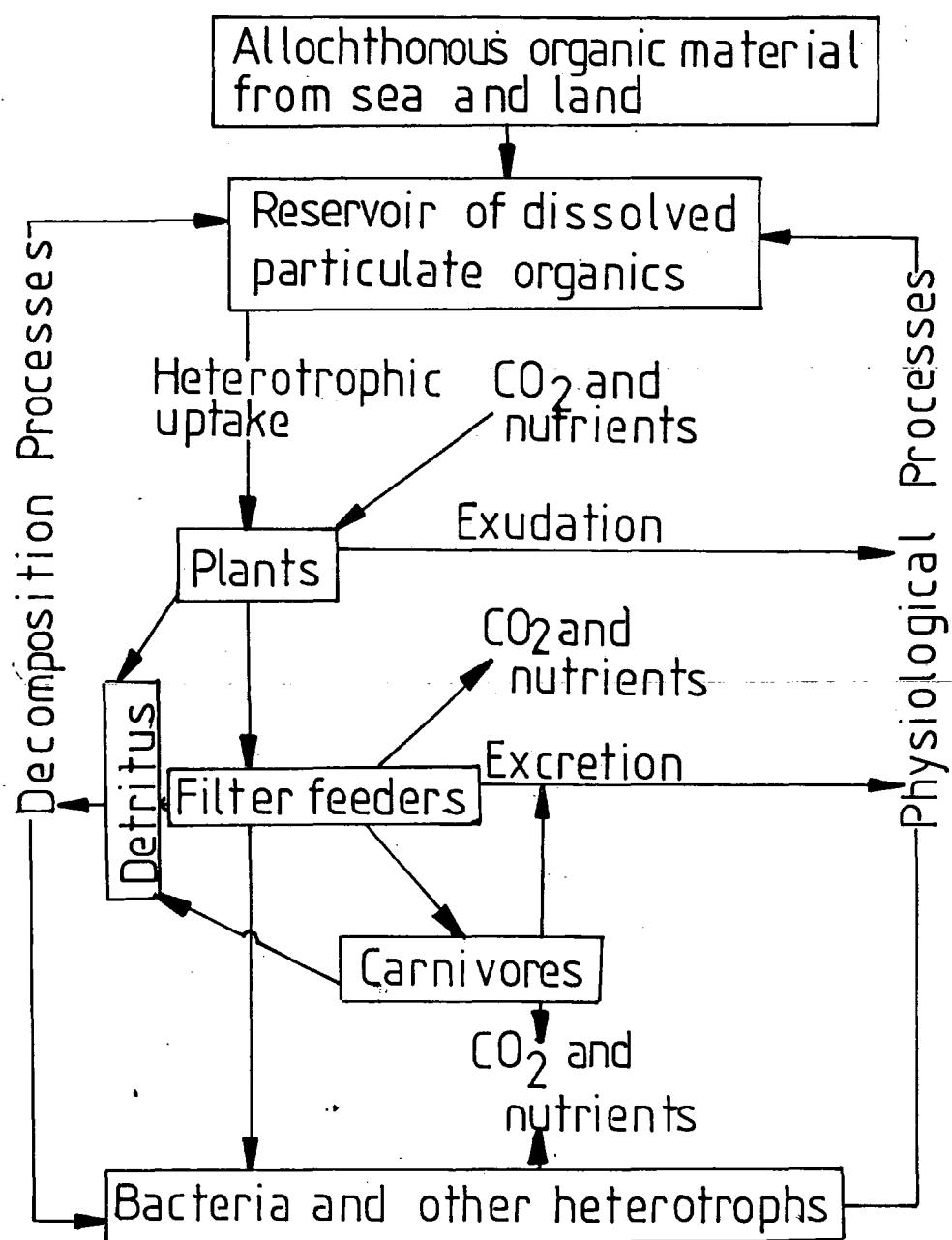
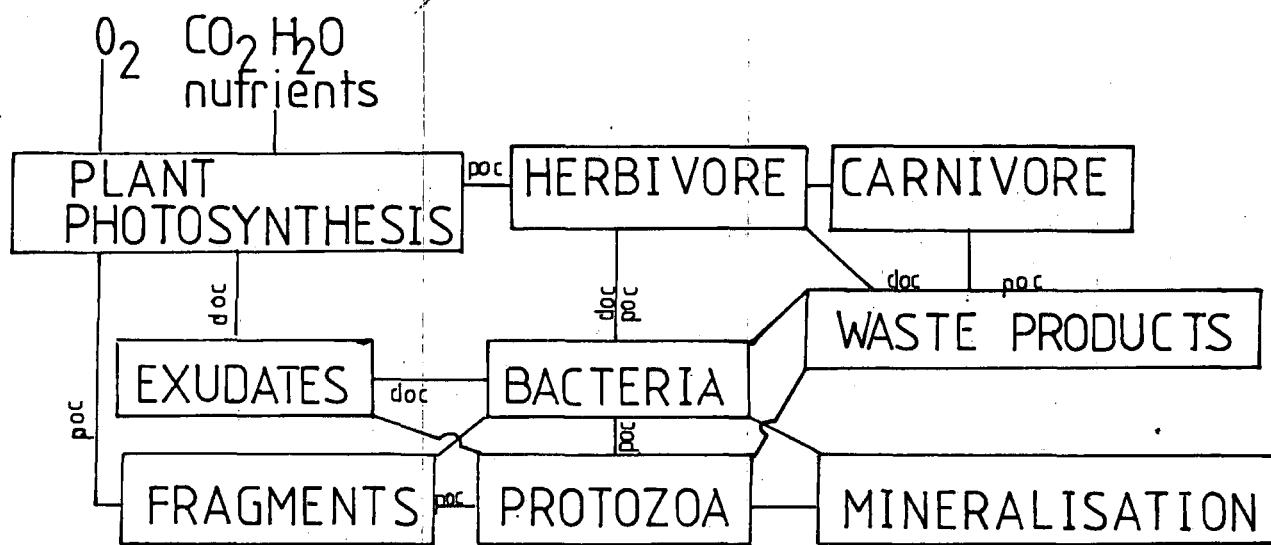
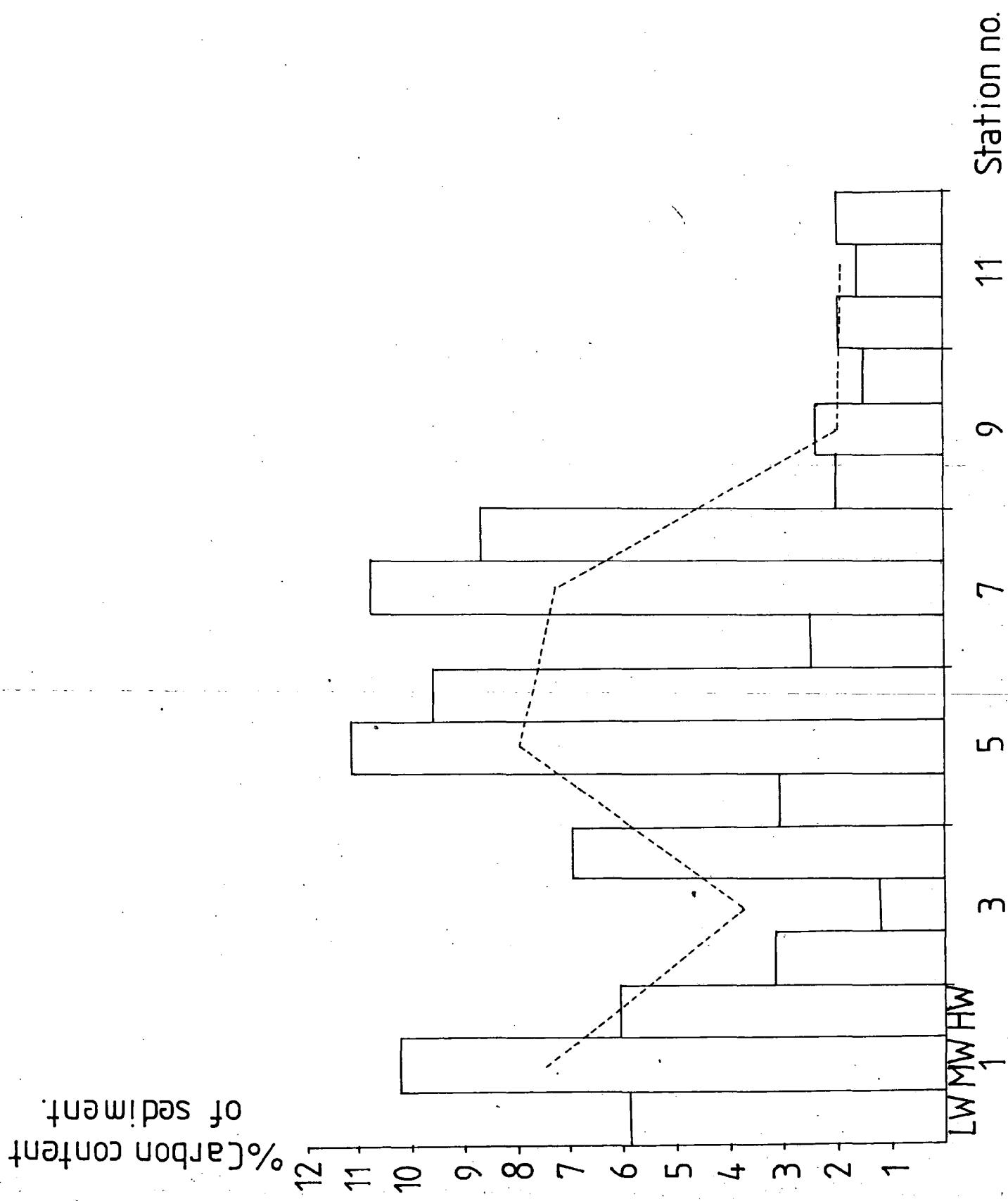


Figure 34a The flow of organic matter through an estuarine food web. (After Head, 1976).



doc = dissolve organic carbon, poc = particulate organic carbon

Figure 34b Carbon content of sediment samples from
Stations 1,3,5,7,9,11.
(mean value of LW,MW,HW.)



sizes to those with smaller, carbon content of the sediment would increase. However, this was not found to be the case because the Aln estuary is partially exposed to wave action and maximum and minimum carbon content were found to occur at LW and MW respectively. Particle size decreases from LW-HW mark only if the estuary is sheltered from wave action. No marked gradient in organic carbon along the estuary was found. The likely explanation for this is that there is equally no distinct gradient in median particle size with distance along the estuary. According to Tenore (1972), levels of organic matter are generally higher up-river, probably associated with flocculation of suspended materials at the point where fresh water meets saline.

The negligible variation in the carbon content of sediment along the shore is not likely to account for any variations in species number since the correlation between species and sediment carbon content only produced a rho value of 0.39 (Table 5).

Newell (1979) reports a significant and positive relationship between the abundance of deposit feeders and the amount of organic matter in the sediment. However, this relationship was not found at Alnmouth since a Spearman's Rank correlation only produced an r_s value of 0.257 (Appendix 7). A possible interpretation of this is that the abundance of deposit-feeding animals is limited more by sediment particle size, as indicated by an r_s value of -0.71 ($p = 0.01$) (Appendix 8).

The explanation as to why abundance of deposit-feeders is inversely correlated with median particle size lies in the fact that fine-grained deposits present a greater surface

area for the attachment of organic matter than a coarser sediment. Organic matter in turn provides the colonization potential for micro-organisms and hence potential food. The organic carbon therefore reflects mainly the debris upon which the microheterotrophic community depends. Particles with a median diameter of 0.1 mm support numbers of micro-organisms of about one order of magnitude higher than particles with a median diameter of 1 mm, the reason being that micro-organisms mainly occur on the outer surface of the particles (Newell 1979).

(iii) Depth of the water table

The depth of the water table in a soil is dependent upon particle size and degree of sorting which in turn influences the porosity, permeability, soil compactness and capillarity. The capillarity of a soil is related to porosity and permeability. It is a surface tension feature; hence, water will rise higher in a column of fine soil than in coarser soil. Thus the water table is shallower in fine-grained sediment than in coarser. Soil compactness also depends on the porosity of the sediment, and can be an important factor influencing the penetrability of a sediment.

The horizontal variation in water table depth along the Aln estuary and the vertical variation up the beach profile is presented in Table 4. The depth of the water table was distinctly greater in the sandy soils of the lower reach characterized by relatively large particle size and high permeability. Water table depth covaried significantly with the R.P.D. ($r = 0.7$, $p = 0.01$) (Table 5) since the depth of the oxygen penetration is limited by the interstitial water. The horizontal and vertical variation in

water table depth was not related to the transect gradient.

The variation in water table depth at the three shore levels showed the general situation expected - a distinct gradation from deep to shallow water table as one proceeds from H.W. to L.W. Variations in sediment type can cause deviations from this generalised norm. In the Aln estuary H.W. was associated with a small median particle size of 3.7 mm (i.e. average result calculated from sediment samples from Stations 1,3,5,7,9 and 11), and a relatively poorly sorted sediment (mean $QD\phi$ value for the six stations = 1.32) (Table 22). This result was anomalous because fine-grained sediments are generally associated with a shallow water table, but poorly-sorted sediment is related to a deep water table (Day 1981).

(iv) Depth of the Redox Potential Discontinuity

The depth of the R.P.D. is a measure of the extent of soil aeration. This black deoxygenated layer is produced by ferrous sulphide, which is oxidizable to ferric oxide. The top of the R.P.D. is a level at which there is a balance between sulphide production at depth in the soil and oxidation in the more superficial layers. The transition from the upper oxidized layer into the lower sulphide zone is connected with drastic changes in the physico-chemical environment and these have been reported to be significant in limiting the occurrence of interstitial fauna since the discontinuity presents an impenetrable ecological barrier to further downward movement of air-breathing species (Fenchel and Riedl 1970, Newell 1979).

The depth of the R.P.D. was directly related to water table depth in the Aln estuary ($r = 0.7$, $p = 0.01$) (Table 5),

and the two factors covaried both along and up the shore. Hence, R.P.D. depth was greatest at the H.T. level of the lower reaches of the estuary (Figures 35 and 36).

It was expected that R.P.D. depth would be positively correlated with particle size, but the coefficient indicated no correlation ($\rho = 0.08$) (Table 5). The relationship between small median particle size and shallow R.P.D. depth is widely accepted (Wolff 1973, Millard 1976, Fenchel and Riedl 1970), and in general sandy sediments are deeply oxygenated (5-40 cm), whereas muddy sediments are oxygenated only very superficially (Wolff 1973).

Millard (1976) claims that since the level of the discontinuity is associated with a fine-grained sediment and hence high silt-clay content, that the R.P.D. depth also reflects a high organic content of the sediment. The absence of correlation at the Aln estuary ($\rho = 0.1$) does not support their proposal (Table 5).

Correlation between the number of species and depth of the reducing layer (both vertically up the beach profile and horizontally along the estuary) was not significant, consequently the degree of aeration is not thought to have been important in controlling the species richness. However, in Chapter 5, Section C, a discussion of the role of interstitial oxygen penetration will be highlighted with respect to certain species.

(v) Gradient of the shore

The slope of the shore at each station is illustrated in the profile diagrams (Figures 5b-16b). The shore angle was found to be linearly correlation with $QD\theta$ ($r = 0.58$, $p = 0.05$) Skq ($r = 0.61$, $p = 0.01$), interstitial salinity



Figure 35 Variation of water table depth, R.P.D. depth and angle of profile along the shore.

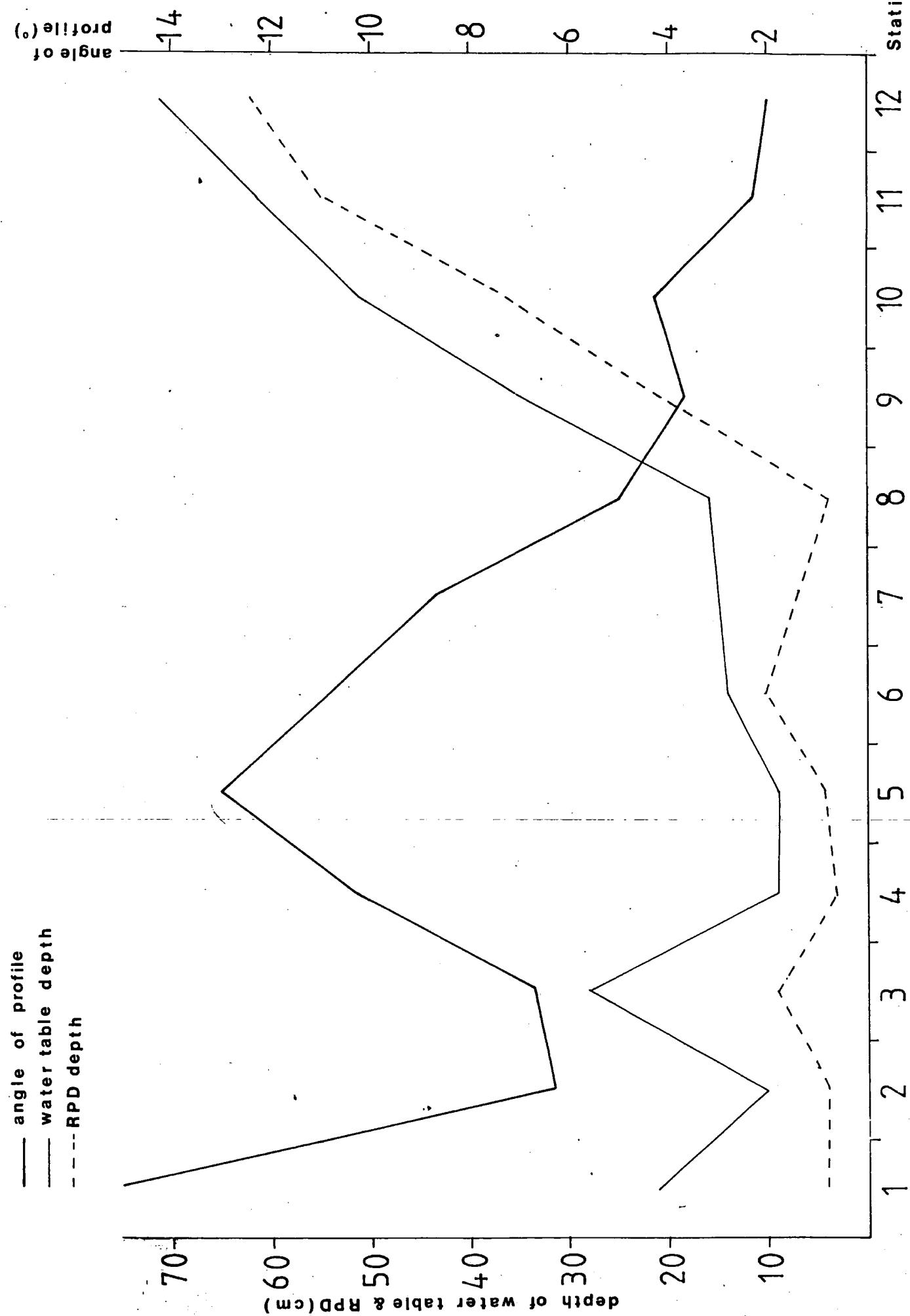
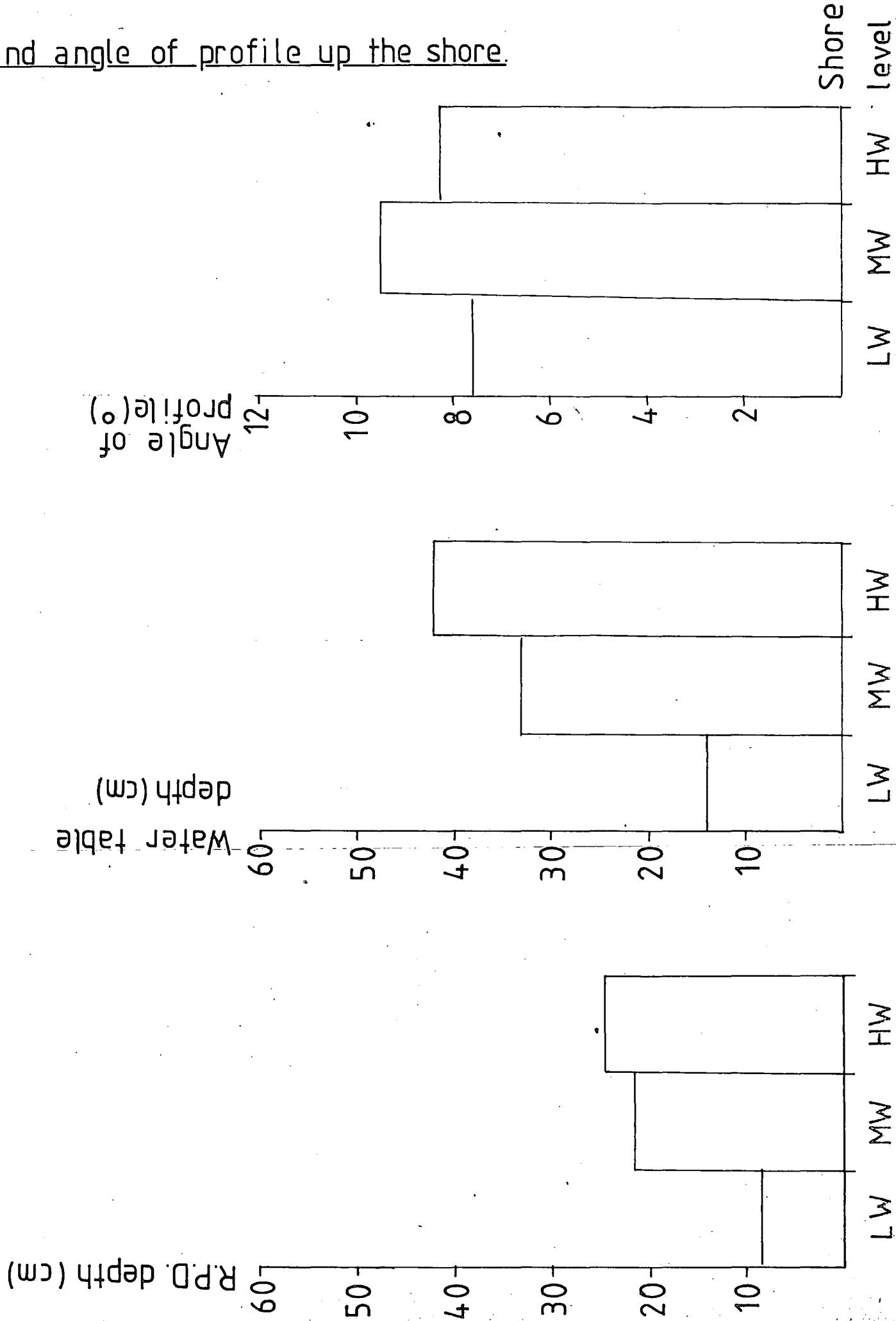


Figure 36 Variation of water table depth, R.P.D. depth and angle of profile up the shore.



($r = -0.5$, $p = 0.05$) and % carbon content of the sediment ($r = 0.64$, $p = 0.01$) (Table 5). However, none of these relationships are thought to be causal in relation to the distribution of the fauna.

C. Species

(i) Horizontal distribution of species along the estuary

The spatial and temporal distribution of species within the estuary is a product of polyfactorial gradient changes within the estuary and the constraints imposed by these gradients on the genotypic physiological tolerance and behaviour of the total available number of species (Day 1951; Carriker 1967; Potts 1954). The distribution of all species cannot be based on the same single factor, if indeed a single factor alone is ever implicated.

Conversely, an animal's tolerance of a few factors may be extended to where most factors are optimum (Day 1951).

Estuaries are generally characterized by reduced diversity but increased abundance relative to the marine situation. Increased abundance within a species is related to the high productivity of the estuarine ecosystem. Estuaries act as nutrient traps and can consequently maintain high rates of primary production and also benefit from the energy subsidies of tidal flow. However, the environmental unpredictability imposes stresses which strongly control the diversity of fauna.

Results from the quantitative sampling of species penetration up river are summarized by kite diagrams (Figures 18a-e) which indicate both the species penetration and density of species occurrence (m^{-2}), and by the graph of ζS against Station number (Figure 37). Highest and lowest ζS

values occurred at Stations 10, 11, and at 7, 8, 9 respectively.

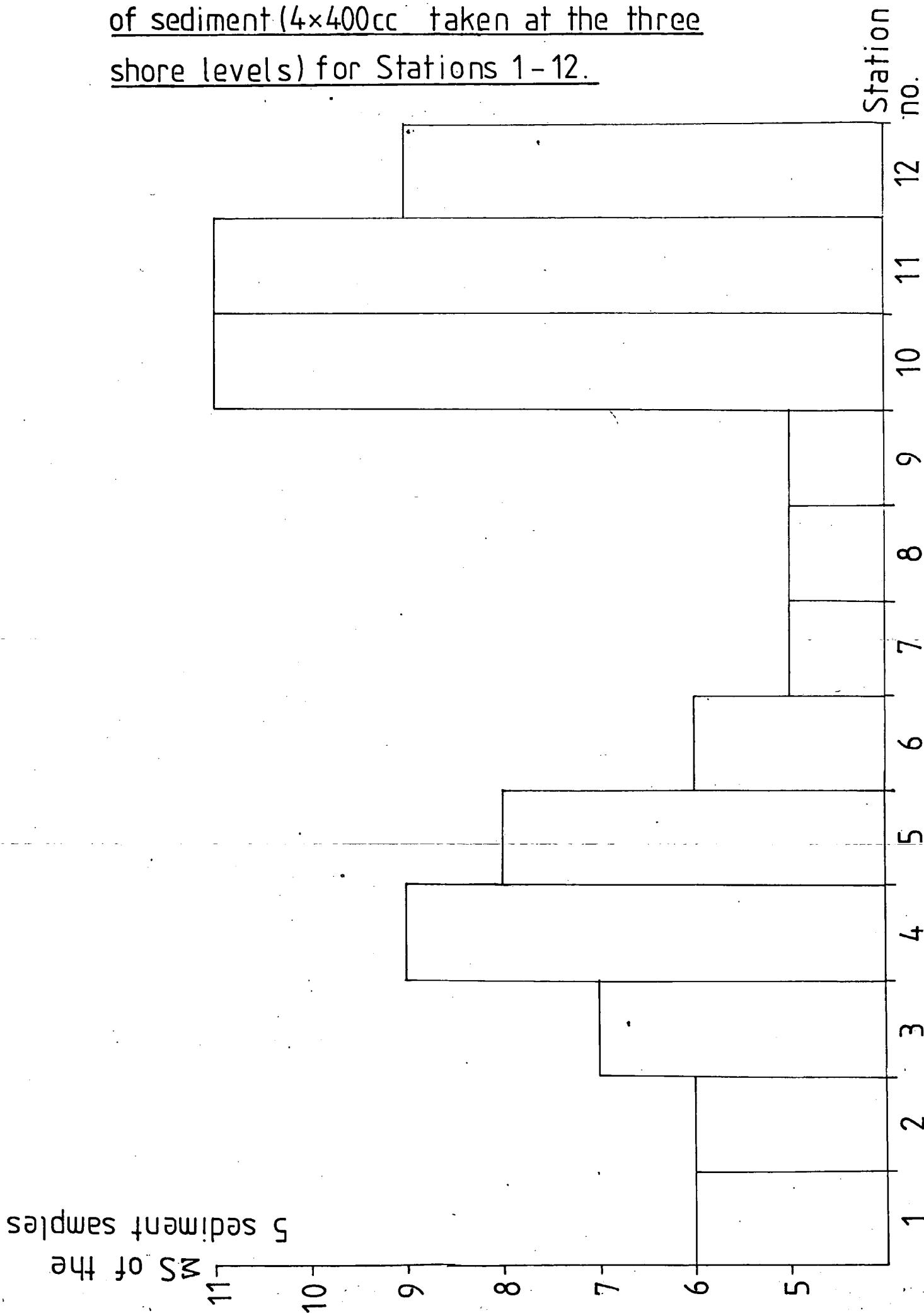
It can be seen from Figures 18a-e that most species are fairly continuously distributed within the main regions in which they occur. A few species such as Mya a. and Lineus spp. were less continuously distributed. The true burrowers were of relatively regular occurrence over the length of the estuary investigated e.g. Corophium v. and Nereis d. Within the zone it occupied perhaps the most uniformly distributed species was the surface-living Hydrobia j., and accordingly Spooner and Moore (1940) report that this species is very independent of the nature of the substratum. One apparent feature in relation to the relative density of species is the dominance of Corophium v. with the highest density of $3,175 \text{ m}^{-2}$ at Station 8.

The order of species penetration up-river (Figure 19) points to a large group of species tolerant of the more marine parts of the estuary (Stations 9-12). The middle reach (Stations 5-8) supported fewer species, and the upper reach (Stations 1-4) an intermediate number (Figure 37).

The fact that the middle reach was only inhabited by a few species poses an ecological problem, i.e., the extent to which the biological factors override the physico-chemical factors in determining species distribution. For example, are there few species in the middle reach because these species competitively exclude other species?, or because the middle reach species are excluded from other sites?, or because only they can tolerate the physico-chemical stresses and variability of the middle reaches of the estuary? This project could only attempt to investigate the latter

Figure 37 Graph to show ΣS of the 5 samples of sediment ($4 \times 400\text{cc}$ taken at the three shore levels) for Stations 1-12.

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alternative, however, one must be aware of potential control of biological factors over species distribution.

The lowest number of species is generally not quite halfway between fresh water and marine salinity, but is displaced towards fresh water at about 5-7% S. This asymmetric position in the species minimum is believed to reflect the different problems faced by colonists from fresh water and marine sites. While the number of fresh water species drops rapidly, the decrease in the reduction of marine species takes longer (Remane and Schlieper 1971). The typical situation is illustrated in Figure 38. This asymmetry in species abundance was also apparent at Alnmouth with the lowest mean number of species per Station coinciding with fairly low surface water salinities of 7.6 and 9.6% S at Stations 7 and 9 respectively.

The stability-time hypothesis of Sanders (1968) is offered as a possible explanation for the paucity of species in the middle reach of the Aln estuary. The middle reach experiences the greatest fluctuations in physico-chemical conditions since it lies mid-way between the fresh-water and marine environments. This harsh environment is associated with high unpredictability, which, according to Sanders, renders successful invasion improbable and potential speciation slow. His principle is illustrated in Figure 39.

The role of competition, predation and other biological phenomena in determining the middle reach-species-minimum, and indeed in determining the distribution of species along the rest of the estuary, could not be studied within the scope of this project. Biological factors undoubtedly influence species distribution along Aln estuary and interact

Figure 38 Penetration of marine, fresh-water and brackish-water animals into an estuary in relation to salinity. (After McLusky, 1971.)

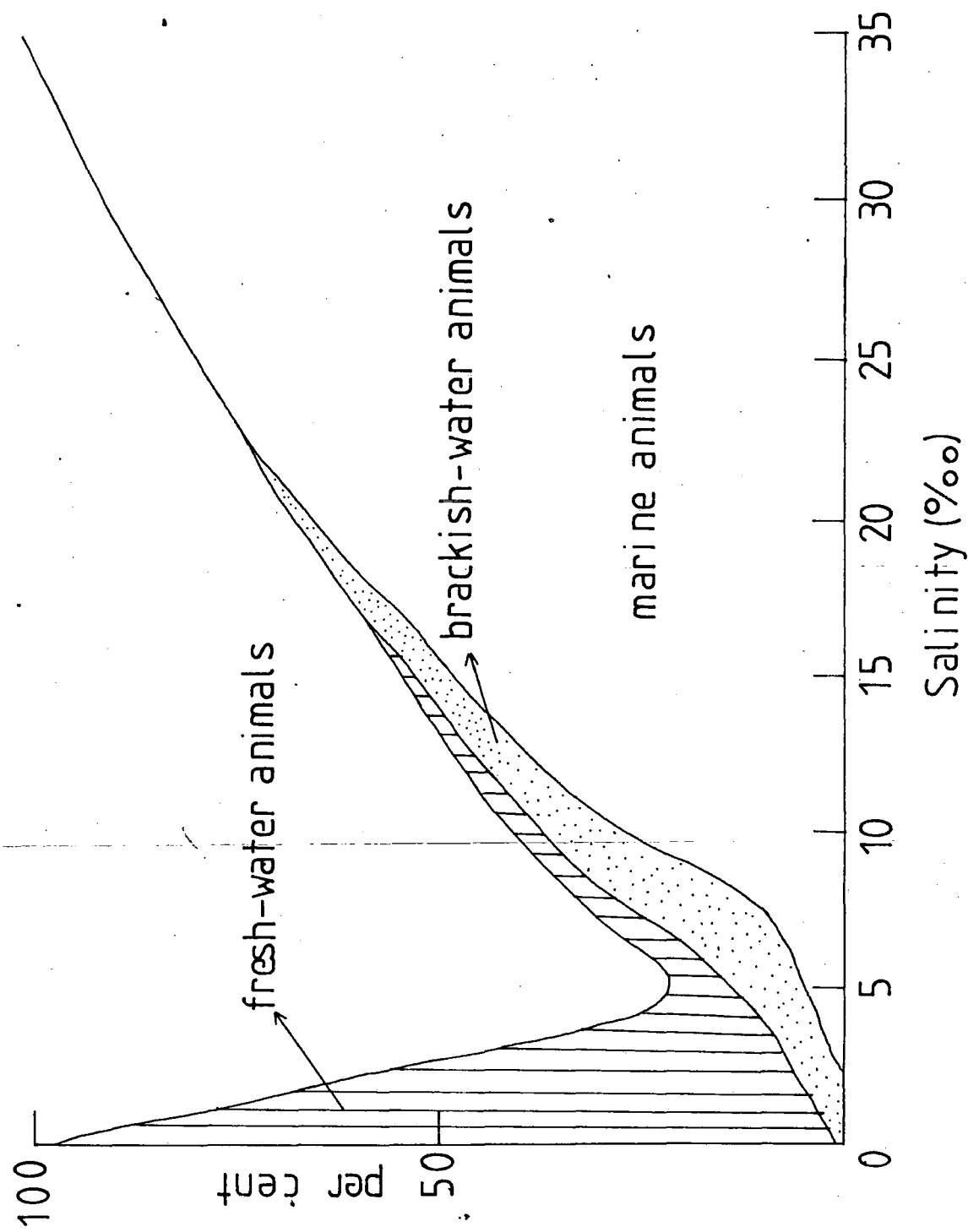
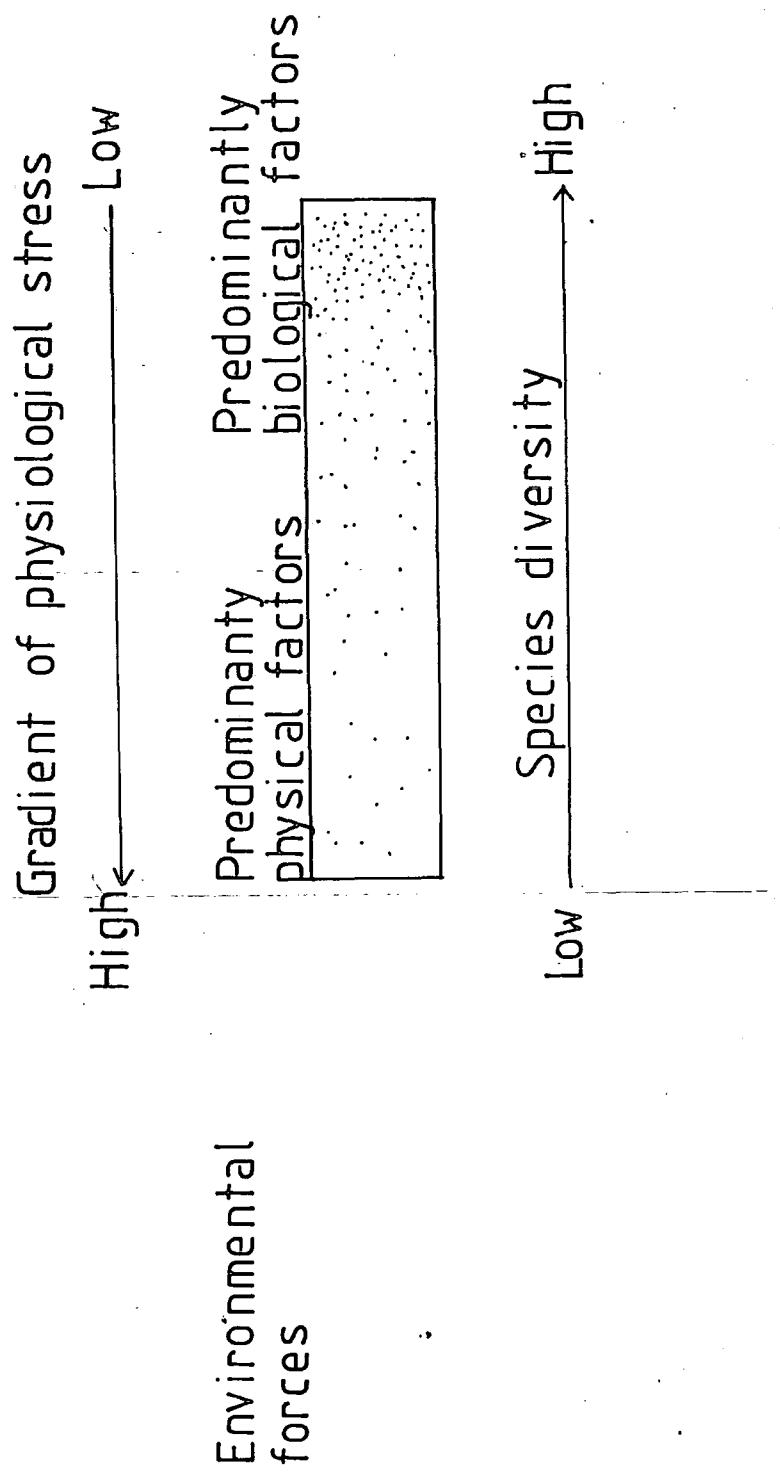


Figure 39 Stability-time hypothesis of Sanders (1968). The number of species (stippling) will decrease continuously along a stress gradient.



with the physico-chemical conditions. Investigation of the biological factors and their importance relative to the physico-chemical factors in influencing species distribution along Aln estuary would prove a viable extension of this research.

(ii) Distribution of species in relation to shore level

The vertical distribution of species up the shore is presented in Figure 40.

Species abundance was highest at M.W. and lowest at H.W. It is probable that the reduction in species at H.W. was a consequence of the stresses imposed by exposure and desiccation.

(iii) Distribution of *Corophium volutator*

Corophium volutator is a euryhaline amphipod and is the dominant component of the Aln estuarine ecosystem in terms of abundance (maximum average density = 3175 m^{-2} at Station 9). It occurs within the upper 7 cm of mud and lives within a 'U'-shaped burrow. Within the burrow it creates a slow water current which acts as a respiration stream, from which food particles are filtered off (Figure 41). At low tide the animal acts as a selective deposit feeder and may emerge to collect detritus from around the burrow (Figure 42).

In studying Corophium distribution it is first necessary to deal with what sets the limits to its distribution, then to look at what effects density within its distribution, and finally to investigate what controls its micro-distribution.

The laboratory experiments to determine substrate-choice and salinity tolerance provide evidence that Corophium distribution was limited to a salinity regime between the

Figure 40 Histogram of mean no. of species at the three shore levels,

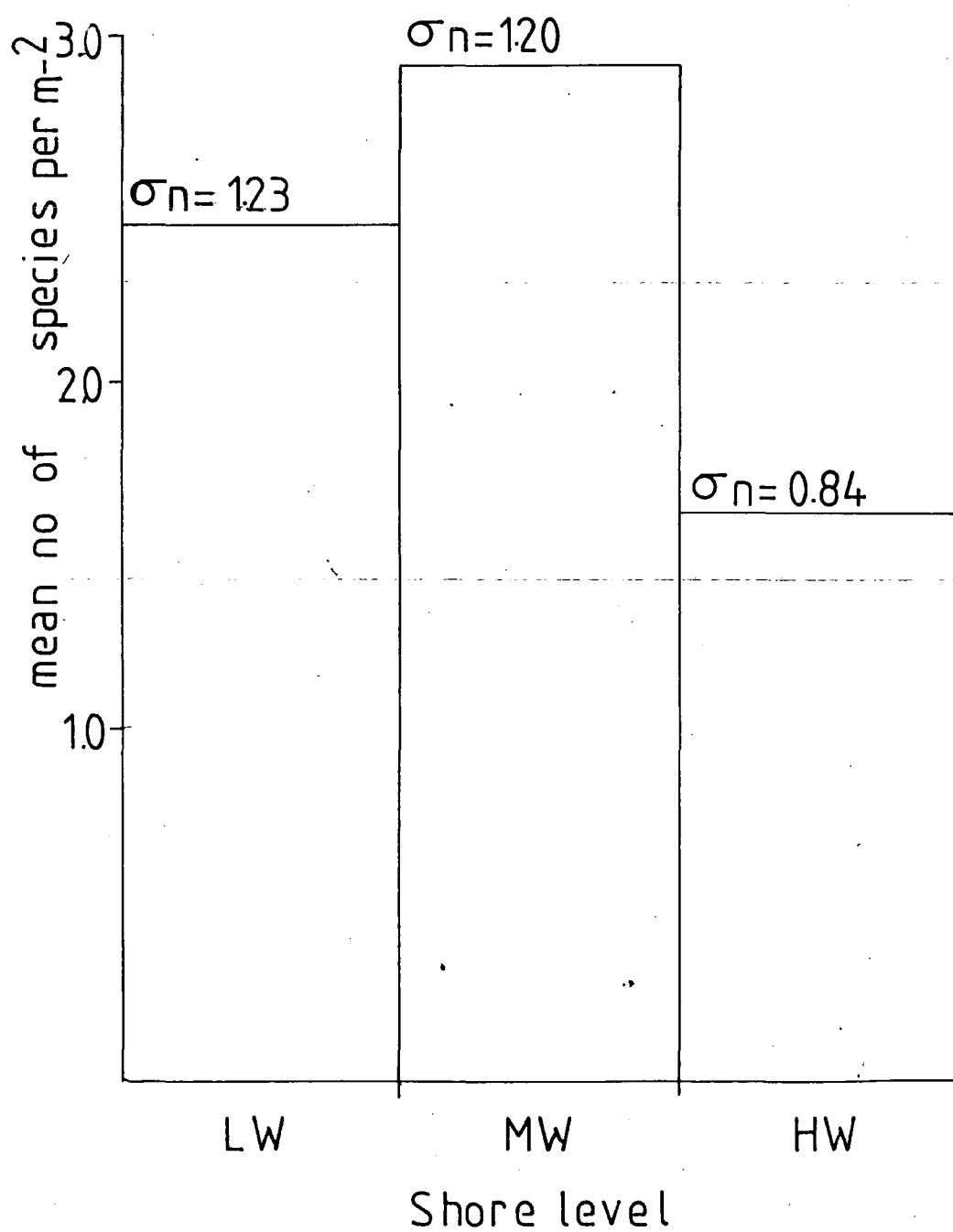
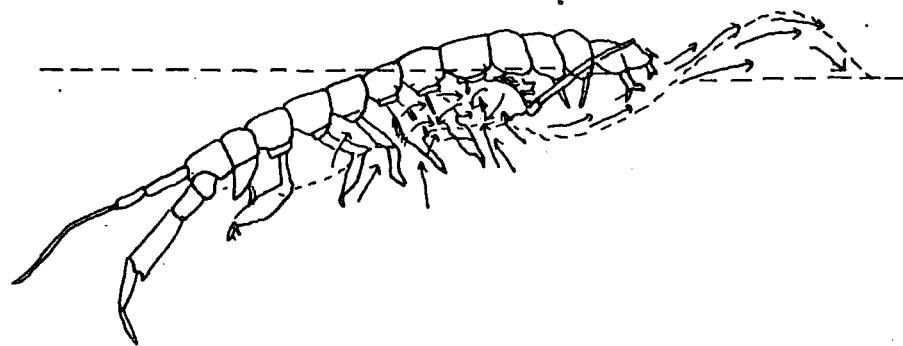
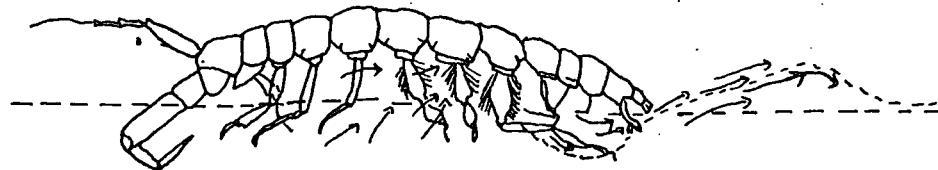
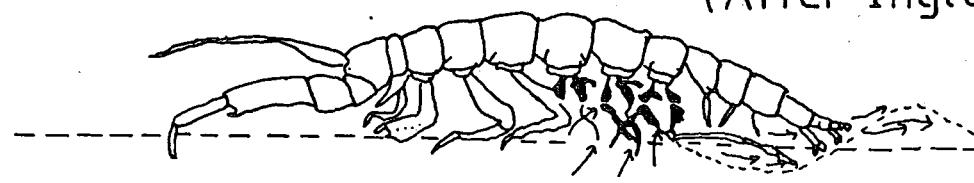


Figure 41 Burrowing sequence of Corophium.

(After Ingle 1966)



---level of substratum
→water current direction

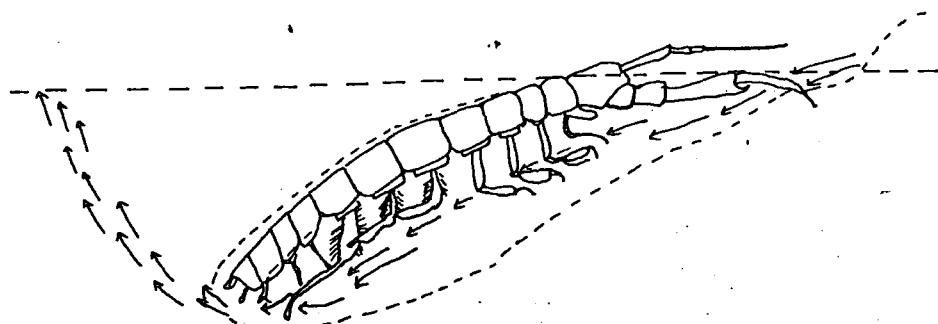
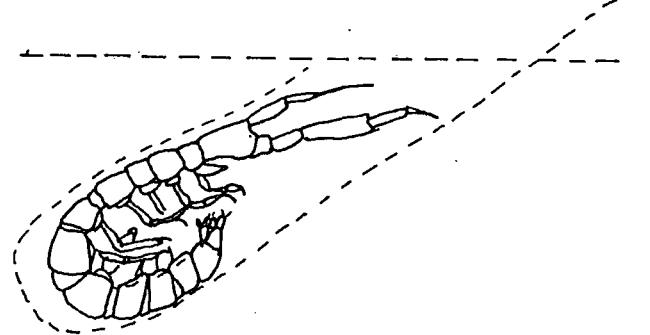
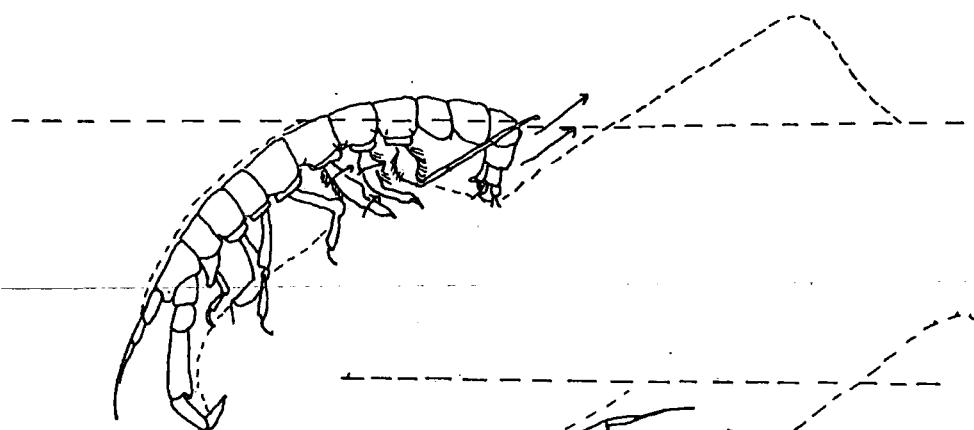
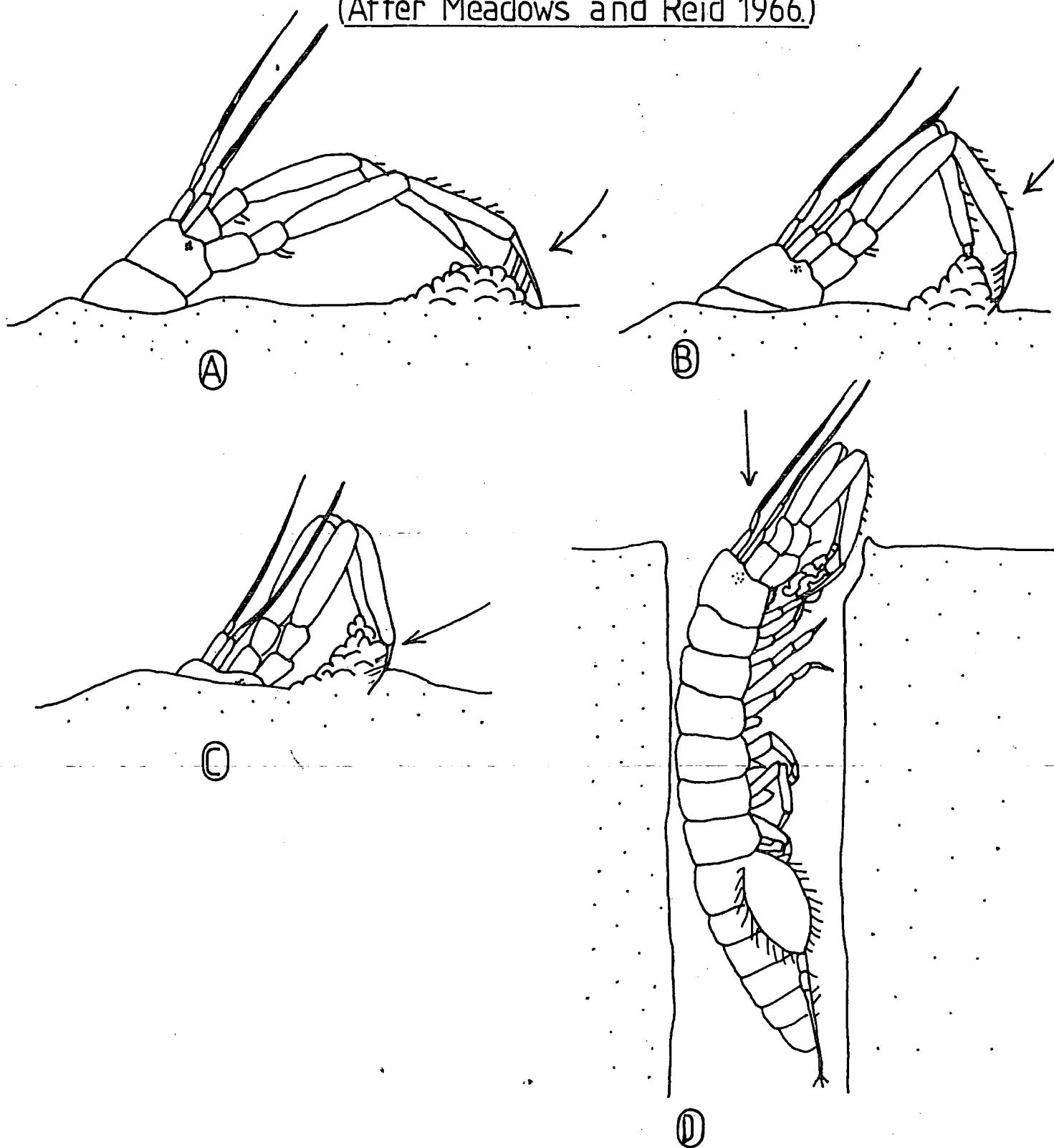


Figure 42 Diagram illustrating how *Corophium volutator* removes organic debris from the surface of the substratum (A,B,C) and retreats into its burrow (D).

(After Meadows and Reid 1966.)



limits of 6.96-36.4 and 6.96-37.9% S for Station 1 MW and Station 9 MW animals respectively. The substrate-choice experiment showed that Corophium distribution was mainly limited to muddy sediment ($Mdmm = 0.29$ mm, $\chi^2 = 92.48$, $p = 0.001$). Only an insignificant proportion of Corophium were found in the sand ($\chi^2 = 10.58$), sand + 1cm mud ($\chi^2 = 8.0$) and silt ($\chi^2 = 12.5$). In the field, the species occurred over an interstitial salinity range of 17.49-35.00 % S which lies within the tolerance range determined in the laboratory. In the estuary Corophium occurred within substrates ranging from 0.39-0.59 $Mdmm$, which is consistent with the limits determined in the laboratory. It therefore appears that salinity and substrate particle size can limit Corophium distribution, because where conditions outside these laboratory-determined limits prevailed in the field, Corophium were absent.

Perkins (1974) proposes that the discrimination of particle size may be due to one of three factors: (1) an appreciation of particle size; (2) an appreciation of increased content of organic matter and micro-organisms on fine sand grains and (3) the difficulty of constructing permanent burrows in sand of coarser grade. Perkins concludes that sediment selection is based on a combination of any two or three of these factors. The Aln study has demonstrated the importance of the first factor in limiting Corophium distribution. However the fact that Corophium density was not significantly related to the carbon content of the sediment ($\rho = -2.0$) (Table 12), suggests that the second factor is not as influential as the first in determining Corophium distribution. Perkins' third factor was found to

be effective because in the laboratory, the majority of animals had not burrowed into the sandy sediment but were lying on the surface.

In order to study what affects the density of Corophium within its distribution, correlations were calculated between Corophium density and the various physico-chemical factors (Table 12). No significant associations were found. However, Millard (1976) reported an increase in Corophium density with decreasing silt-clay content. On this basis one would predict the highest Corophium density at Station 9 with an average silt-clay content of zero (see Table 3b). However, other important features of Station 9 which could be potentially limiting to Corophium include the very low water table of 35.0 cm which possibly does not render the sediment sufficiently thixotropic, and the comparatively low carbon content of 1.93% which could limit food availability.

By combining the results from the Aln estuary with the literature reports, it seems feasible that Corophium is distributed according to sediment particle size and silt-clay content, but is only found in a particular sediment if the salinity is suitable. The distribution of Corophium thus reinforces the feature of the polyfactorial control of the distribution and abundance of estuarine animals.

The distribution of Corophium is known to change seasonally. Quatrefage (cited by Millard, 1976) reported upshore migration at the end of April and a sudden return at the end of October. Since Corophium at Alnmouth were sampled from the latter part of April to July, it is possible that the population were migrating upshore during

this period, and hence the spring-summer distribution sampled might well differ from the autumn-winter distribution.

In addition to overall population migrations, small scale movements of individual Corophium have been observed by Meadows and Reid (1966). They found that larger animals occasionally move to new burrows. In the Aln estuary, Corophium were seen to migrate to the surface and swim when the tide came in. Morgan's (1965) explanation for this movement is that the swimming reaction is induced by reduced hydrostatic pressure. Corophium were observed to be carried upshore over distances greater than a metre, and so it is quite probable that Corophium do not return to their original burrows on the ebbing tide. The Corophium distribution sampled probably reflects the average spring-summer distribution, but minor variations are likely to occur with each tide.

Results from the microdistribution survey suggest that the vertical distribution within the sediment is due to the topographical separation of size classes. The size frequency of the population also determines the horizontal spacing in terms of minimum individual distance, since older and thus larger animals require a greater diameter of burrow than do younger animals.

It is also conceivable that within the Aln estuary the distribution of Corophium both along and up the shore may be influenced by predators. Corophium is common prey to Redshank, Blackheaded gull and flat-fish (Green 1968). However, Millard (1976) found that at Budle Bay, Northumberland, predation alone could not account for the Corophium distribution.

To summarize, Corophium distribution was limited by salinity and sediment particle size. Although results were not significant, the density of Corophium within its distribution was expected to be high in relation to high silt-clay content and percentage carbon content. The microdistribution was found to be related to the size frequency of the population.

(iv) Distribution of Haustorius arenarius

Haustorius was restricted to the lower reach of the estuary, being most abundant at Station 10 L.W. At Stations 10, 11 and 12 Haustorius became scarcer towards H.W.

Haustorius swims on its back by beating its powerful pleopods, the metachronal rhythm of which increases their efficiency. Burrowing is a modification of the swimming movements and is dependent upon the explosive action of the swimming current. Burrowing is rendered ineffective in sand which is not completely saturated with water, hence the species was generally found in thixotropic sediment at LW level.

Feeding is accomplished by two methods - one filtratory and the other being the more usual amphipod type on large food masses. In general however, Haustorius feeds on small food particles in the interstitial water by means of the filter-mechanism formed by a series of mouth appendages, the maxillae producing and filtering an anteriorly-directed water current.

Williams, Perkins and Hindle (cited by Perkins 1974) report that Haustorius falls prey to flat fish. However, the degree to which this predation acts to control Haustorius distribution is not known.

Results from the laboratory experiments and correlations between Haustorius densities and field physico-chemical factors suggest that Haustorius could have survived a salinity regime in parts of the estuary where it was absent, notably, Stations 5, 7 and 9. Therefore, the species must have been restricted in distribution by other factors such as preference for a set sandy thixotropic sediment with a relatively high carbon content.

A similar distribution was recounted by Dennell (1933) at Robin Hood's Bay, Yorkshire. Here, Haustorius distribution was further influenced by scar formation. The species was most abundant on the scar nearest L.W. and numbers progressively decreased on succeeding scars towards H.W. (D^2). This was thought to be due to the tendency to congregate in the wettest sands. Figure 43 illustrates the primary diminution (D^1), up the beach as a whole, which was found at Alnmouth, and the secondary diminution (D^2), in the reverse direction in individual scars, as was found at Robin Hood's Bay. Both distributions are accounted for by the water content of the sand.

(v) Distribution of other individual species

The following section is a discussion of the distribution of species which were recorded at more than one station.

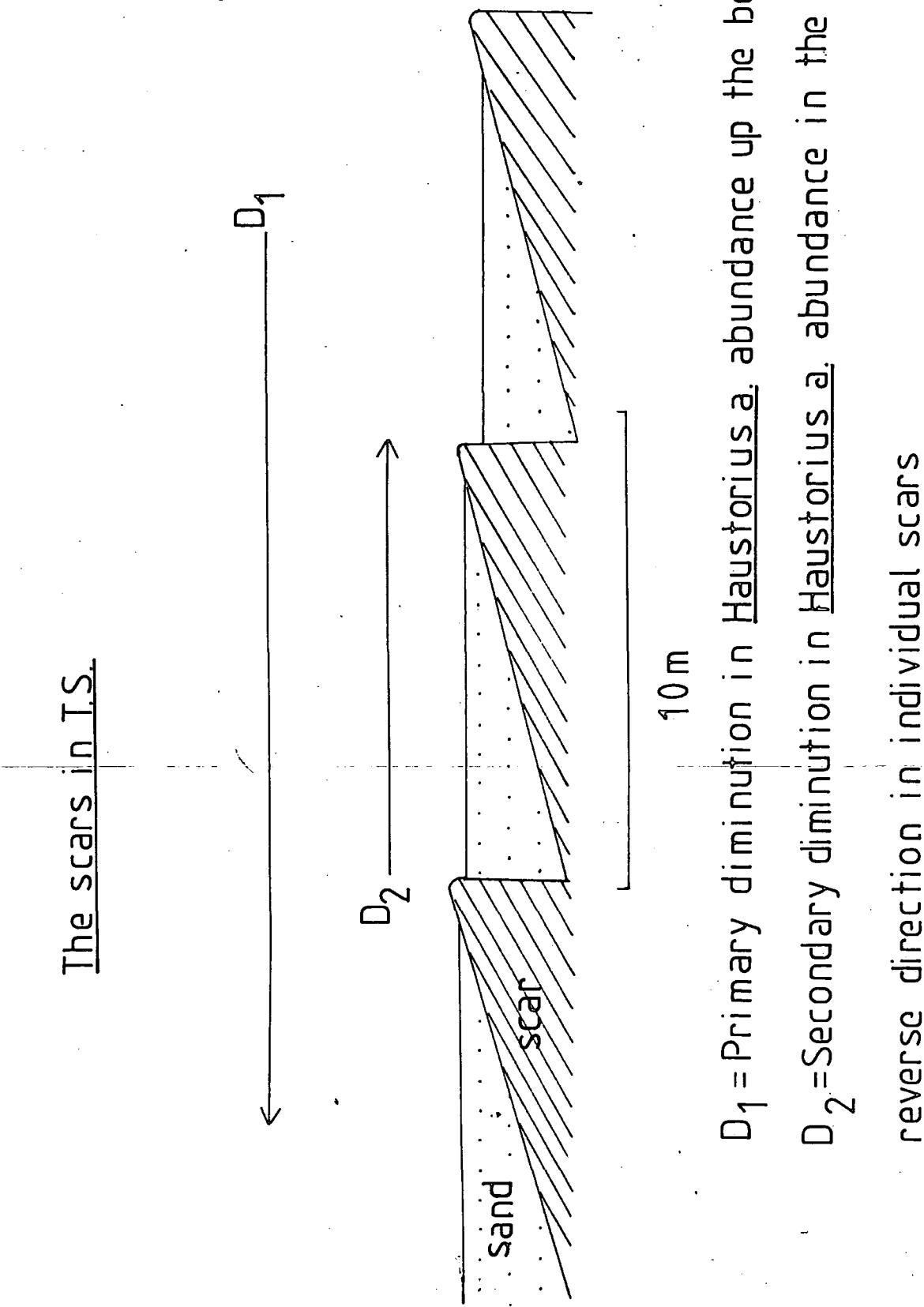
Nemertini

Lineus spp. (Figure 44)

This animal is most likely to be Lineus ruber since this species is the most widespread of estuarine nemertines (Coe 1943, cited by Green 1968).

Lineus spp. seems to prefer L.W. and M.W. habitats

Figure 43 The distribution of *Haustorius arenarius* in relation to scar formation. (After Dennel, 1933)



within the lower reach of the estuary, occurring in greatest density at Station 12 (47 m^{-2}). A few specimens were also recorded at Stations 4 and 5 (Figure 18a).

Remane (Green 1968) claims that the minimum salinity tolerance of Lineus is 8‰ S. This minimum was not encountered at Alnmouth, and Lineus occurred over the salinity range of 23.33-35.00‰ S. Salinity, therefore, does not limit Lineus distribution at Alnmouth. Sediment particle size is also unlikely to influence its distribution since Barrett and Yonge (1980) report its occurrence over a range of sand to fine mud.

It is conceivable that any one or combination of other factors, including biological factors, could control Lineus distribution. The marked absence of the species from the middle reach suggests that Lineus is unable to tolerate the rapidly fluctuating physico-chemical factors experienced within this section.

Nemertopsis flava (Figure 45)

This species occurs at Stations 4 and 5, at very low densities of 13 and 20 m^{-2} respectively (Figure 18a). At these stations it showed preference for a L.W. habitat.

Annelida

Arenicola marina (Figure 46)

Arenicola lives in an L-shaped burrow at a depth of some 20-30 cm (Newell 1979) (Figure 47). Since only the top 8 cm of sediment was sampled the densities recorded are unlikely to be representative of the total population, and probably reflect the densities of only the shallower-burrowing juveniles.

The species occurred in the middle reach at Stations

FIGURE 44

NEMERTINI- LINEUS SPP. Magnification xII

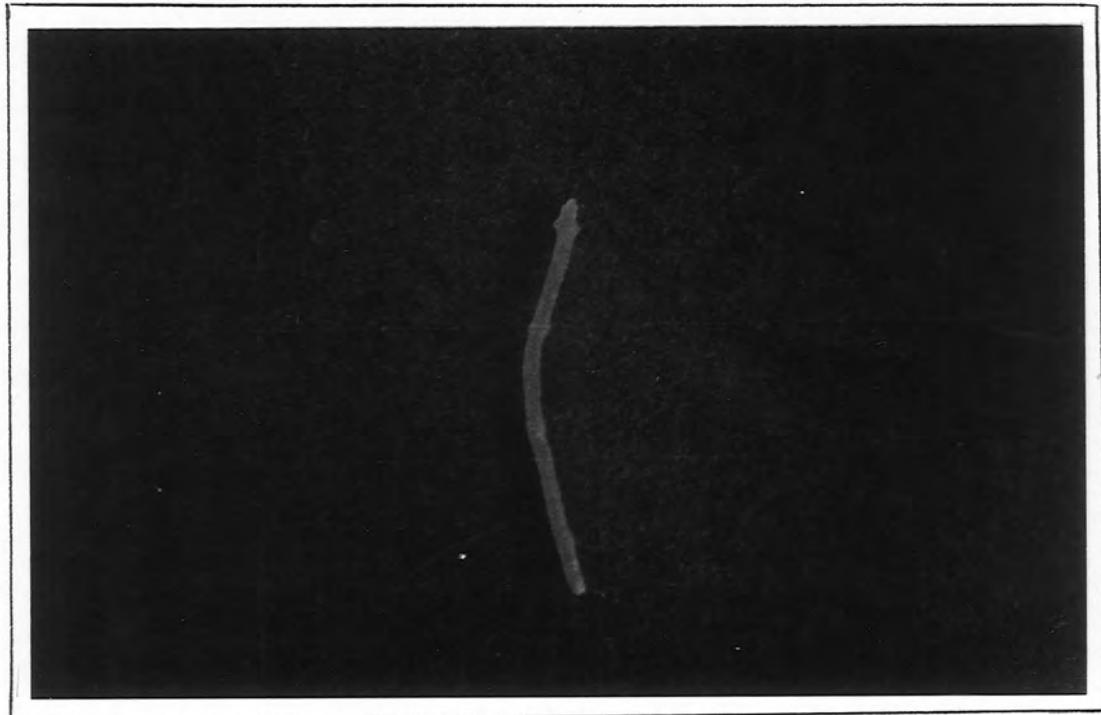


FIGURE 45.

NEMERTOPSIS FLAVIDA. Magnification x 7

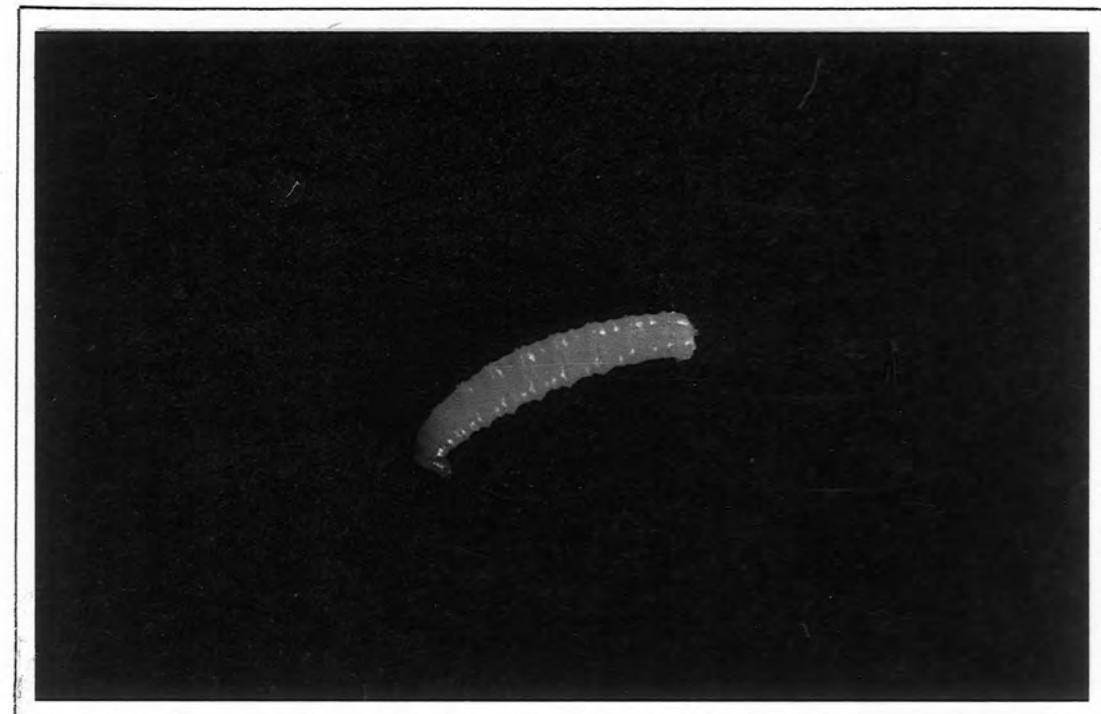


FIGURE 46

ANNELIDA- ARENICOLA MARINA. Magnification x 5

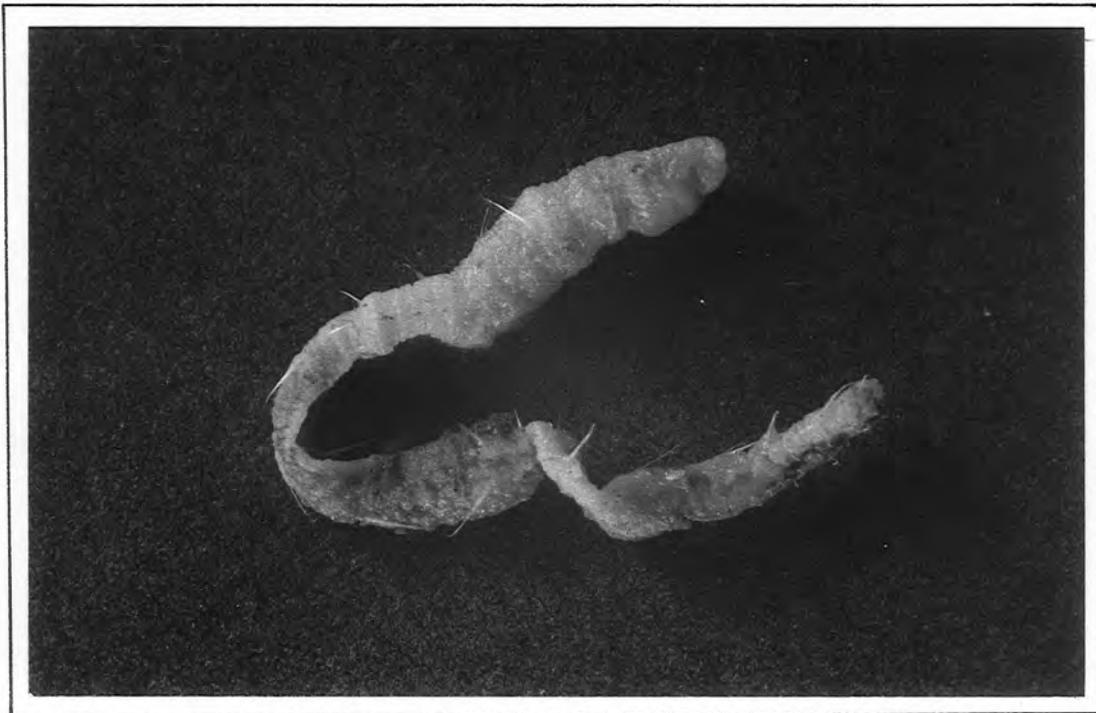


FIGURE 48

LANICE CONCHILEGA. Magnification x 5

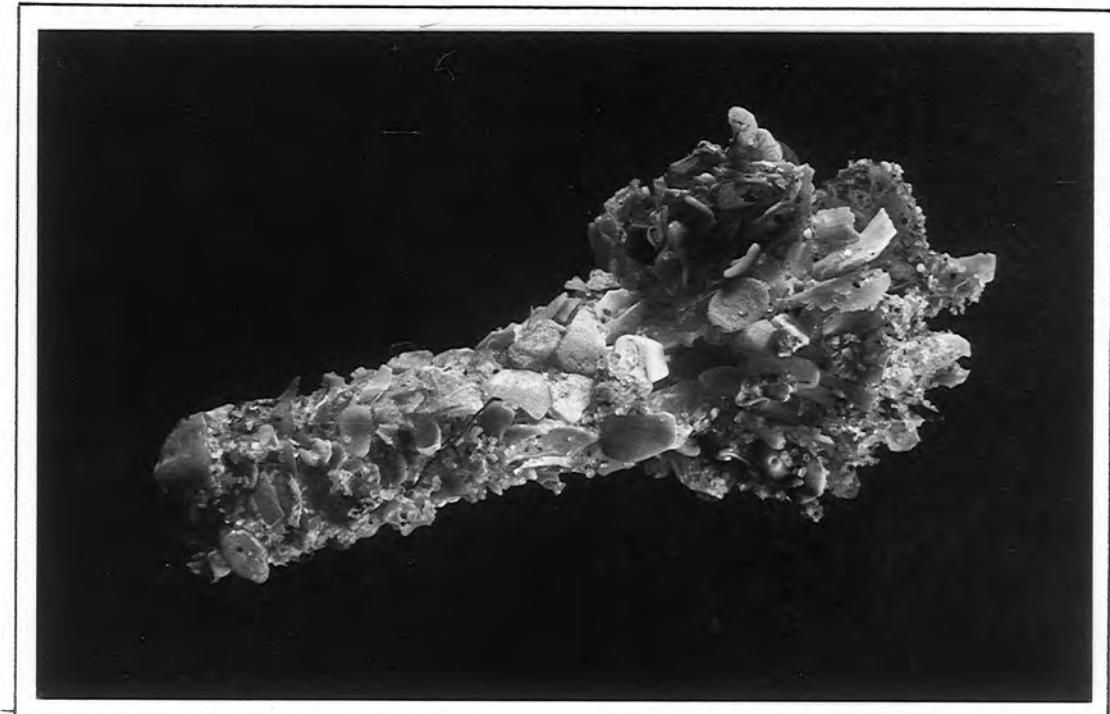
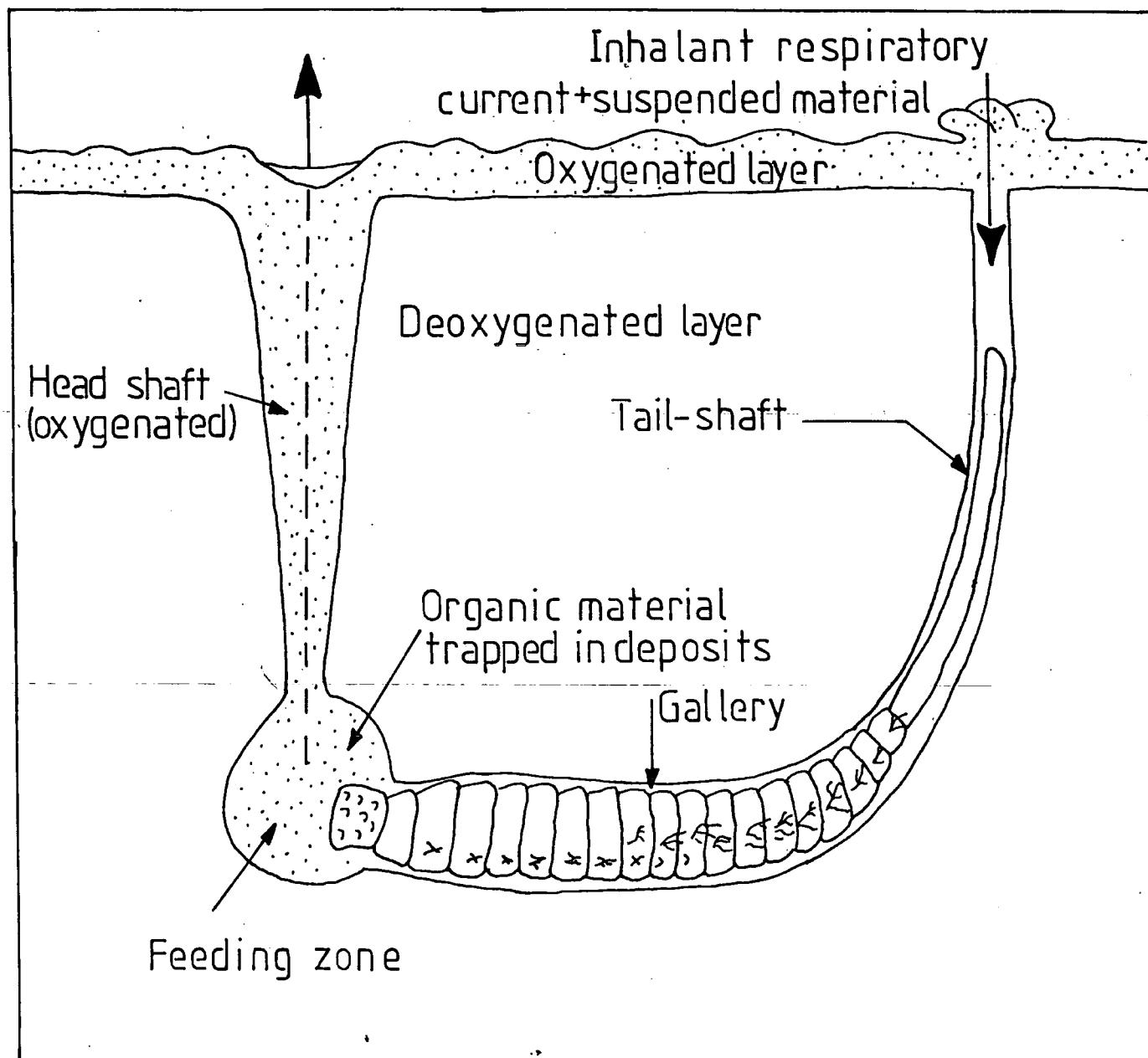


Figure 47 Diagram showing the L-shaped burrow of *Arenicola m.* (From Perkins, 1974).



6, 7 and 8 ranging from L.W.-H.W., but showing preference for M.W. habitats. Due to the H.W. penetration by Arenicola it is assumed that the animal makes use of oxygen diffusing into the burrow or performs aerial respiration (Wells 1949). In addition, Arenicola has a remarkable resistance to anaerobic conditions and can survive without oxygen for several days (Hecht 1932, cited by Green 1968). When subjected to anaerobiosis Arenicola carries out glycolysis without the usual accumulation of lactic acid (Dales 1958). These adaptations may explain the distribution of Arenicola in the relatively harsh and rapidly fluctuating conditions of the middle reach.

Arenicola is euryhaline and is reported to tolerate between 8-35‰ S (McLusky 1981, Barnes and Green 1971). It has no powers of osmoregulation, the body fluids being isosmotic with the external medium. Experimental work by Beadle (1971) demonstrated the wide salinity tolerance of the body tissues. Holme (1949) suggests that because Arenicola is an 'open' burrow species, it will be exposed to the salinity of the overlying water rather than to the interstitial salinity. At Alnmouth, Arenicola occurred at stations with overlying water salinity values of 5.83, 7.58 and 9.33‰ S. In view of the salinity tolerance reported by McLusky, Barnes and Green, it is not easy to interpret Arenicola occurrence at these low salinities. However, Wolff (1973) partly refutes Holme's claim and proposes that the surface water salinity conditions are buffered to some extent by Arenicola within the sediment.

From the above results and literature reports, one can hypothesize that Arenicola is excluded from the upper

reach of the estuary because of the low salinity there. However, its distribution seawards of Station 8 must be controlled by another factor(s).

The preference by Arenicola for finer sediments is well known. In the Dutch Delta area Wolff (1973) recorded the species occurrence over a range of grain size of Mdmm 0.07-1.2, the majority occurring in sediments of Mdmm 0.11-0.13. At Alnmouth, most Arenicola occurred in sediments of Mdmm 0.29 and 0.26 at 7 M.W. and 7 H.W. respectively. Seaward of 8 M.W., the sediment is distinctly coarser. It is therefore possible that sediment grade is an operative factor in controlling the seawards expansion of Arenicola.

The lug-worm is considered to be a non-selective deposit-feeder (Wolff 1973) and Longbottom (1970) has shown significant association between Arenicola abundance and carbon content of the sediment. At Alnmouth, Arenicola occurred in sediments of relatively high carbon content of 10.75 and 8.70% at 7 M.W. and 7 H.W. respectively. Seaward of Station 8, the amount of organic matter in the sediment dropped dramatically from 1.93% at Station 9 to 0.51% at Station 12. Low carbon contents of the sediments may thus be responsible for the absence of Arenicola from the lower reach.

Lanice conchilega (Figure 48)

The sand-mason occurs in the sandier part of the estuary on the lower shore at Stations 9, 10 and 12.

Lanice burrows up to 30 cm deep with a small tube of approximately 2 cm protruding above the sand surface. Due to Lanice burrow depth, the abundance recorded will not reflect the true density because of the shallow sampling

technique employed.

Lanice is a selective deposit-feeder and is also capable of some suspension-feeding (Wolff 1973). Because of its deposit-feeding mode one would expect Lanice distribution to be restricted to sediment of high carbon content. This was not the case at Alnmouth because the species occupied sediment of relatively low carbon content ranging from 0.26 at 12 H.W. to 1.88%C at 9 L.W.

The occurrence of Lanice in medium grade sands (Mdmm 0.40-0.66) is also reported by Wolff (1973). He also maintains that Lanice prefers less well-sorted sediments. This was not the case at Alnmouth since the more poorly sorted sediments were in the upper reach.

Salinity is not a limiting factor to Lanice distribution since its minimum tolerance is at 7.7-7.9‰S (Wolff 1973). At Alnmouth the species occurred in sediments of interstitial salinity well above this level.

Nereis diversicolor (Figure 49)

Nereis may burrow to a depth of up to 20 cm (Green 1968) and so the density data from the Aln is not representative of the adult population.

This polychaete was exceptionally tolerant of the range of estuarine conditions and occurred in the middle to lower shore at Stations 1-8, with maximum density of juveniles at Station 4 (see Figure 18a). Bogucki and Smith (cited by Wolff 1973) suggest that the upstream limit of distribution of Nereis is set by the distance the larvae are transported upstream by the flood tide, because Nereis is unable to reproduce below about 1.7‰S. Had the Alnmouth survey extended further up river, this possible controlling

factor could have been investigated. However, the salinity of the overlying water at Station 1 is 2.28‰ S, so it is likely that Nereis was close to its up-river limit.

Nereis is generally considered a species inhabiting muddy substrates. This was confirmed by its distribution over a Mdmm range of 0.29 mm (at Station 7 M.W.) to 1.10 mm (at Station 5 L.W.). The sorting coefficient is not thought to be of importance to Nereis distribution (Wolff 1973).

Wolff (1973) concludes that the seaward limit of Nereis distribution is set either by predation from waders and flat fish, or by competition. The same situation could exist at Alnmouth, and had biological factors been studied, Wolff's claim could have been tested.

Evidently this euryhaline polychaete exhibited a large potential distributional range. It had a relatively large vertical distribution, inhabited a variety of sediments and employed catholic feeding habits. Thus it was able to tolerate the low salinity of the upper reach in addition to the rapidly fluctuating environment of the middle reach.

Polydora spp. (Figure 50)

The photograph shows the minute tube of this worm which protrudes about 1 cm out of the surface.

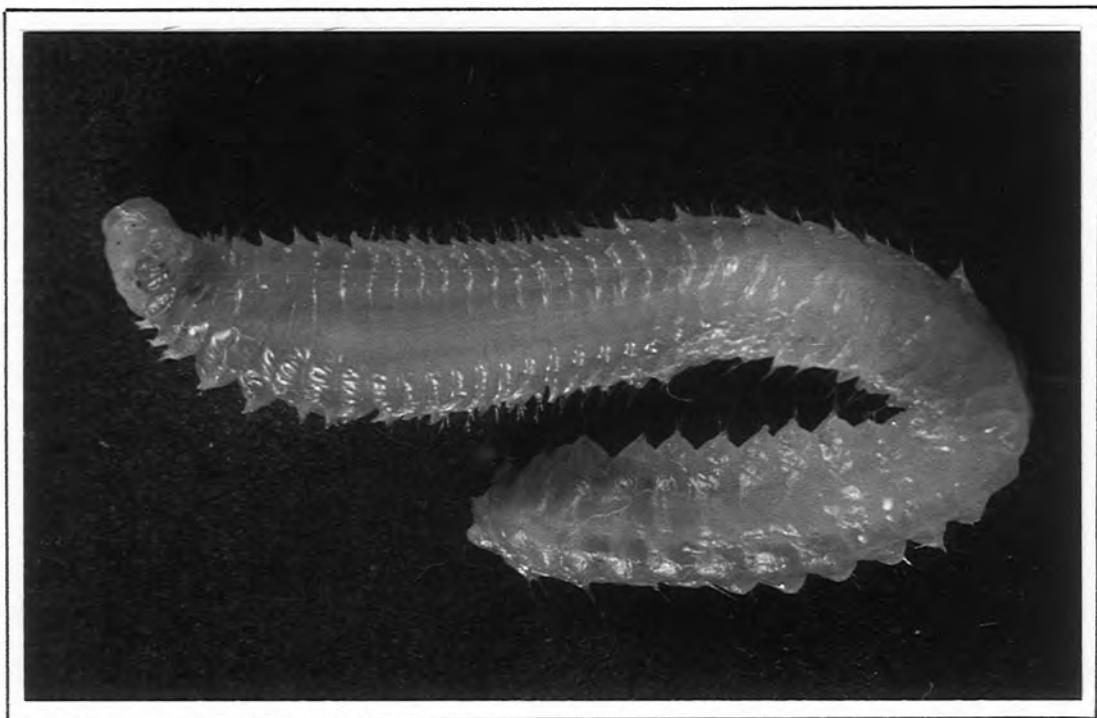
Sabellidae (Figure 51)

The photograph illustrates part of the tube of this fan worm which protrudes above ground at low tide. The worm itself is 10-25 cm long with a pale grey-green body with orange and violet tints towards the tail (Barrat and Younge 1980).

Sabellidae appeared to be restricted to the lower shore

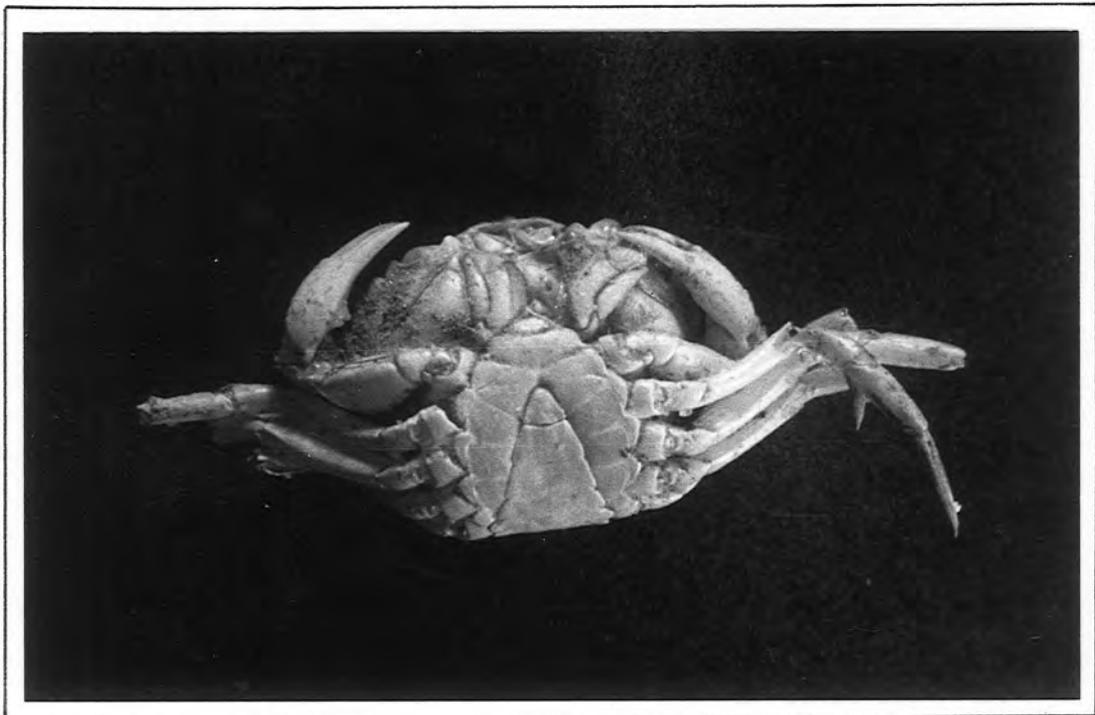
FIGURE 49

NEREIS DIVERSICOLOR. Magnification x 5

FIGURE 50

POLYDORA SPP. Magnification x 8



FIGURE 51SABELLA PAVONIA. Magnification x 10FIGURE 52ARTHROPODA- CRUSTACEA- CARCINUS MAENAS. Magnification x 6

of the lower reach of the estuary (Figure 18a). At Station 9 L.W. it occupied a muddy sediment ($Mdmm = 0.41$), whereas at Station 11 L.W. it inhabited a distinctly sandy sediment ($Mdmm = 0.50$). Thus, sediment grain size did not restrict this species' distribution.

It is possible that predation by flat fish could control its seaward extension (Green 1968).

Crustacea

Carcinus maenas (Figure 52)

This is the only species of crab which is known to enter estuaries. It is a member of the epifauna and is therefore less influenced by the substratum than are the infauna. Carcinus is considered to have colonized from rocky shores (Eltringham 1971) and exhibits a characteristic feature of estuarine organisms, the reduction in size relative to its marine counterpart.

Carcinus occurred where shelter was available under stones at Stations 1-4, and was most abundant at Station 4 (40 m^{-2}) (Figure 18b). Carcinus favoured the muddy sediment of the upper reach which permits easy burrowing.

Carcinus is hyperosmotic, being poikilosmotic at high salinities and homoiosmotic at low salinities. It tolerates salinities down to 2‰ S (Floodgate 1964). Because Carcinus is epifaunal, it is the salinity of the overlying water which is important. The salinity ranged from 2.28-4.49‰ at Stations 1-4, therefore, Carcinus was near its minimum at Station 1.

Restriction of Carcinus to the upper reach could have been due to several factors including reduced shelter, a sandy substrate, a decrease in available food and increased

predation. Salinity did not limit the seaward extension of this species.

Carcinus is a generalised predator. Its variety of feeding habits is linked with its ability to osmoregulate at salinities below blood concentration during the summer, so that the crab is well adapted to the estuarine environment. During the winter Carcinus migrates seawards.

Eurydice pulchra (Figure 53)

This isopod occurred in the outer area of the estuary (Stations 10, 11 and 12) where it spends the majority of its time buried in sand (Figure 18c).

Eurydice was most abundant at L.W. where the water table was highest and the sediment most likely to be thixotropic. This supports Jones' demonstration of Eurydice abundance in disturbed sediments (Newell 1979). Disturbance induces the isopod to emerge, swim and begin its active feeding phase. Fish has shown that the intertidal distribution changes in relation to the semi-lunar tidal rhythm. The vertical distribution of Eurydice is modified by a semi-lunar migration up and down the shore coincident with tidal amplitude, together with a circatidal rhythm which encourages emergence at high tide (Newell 1979).

Salinity was not operative in restricting the up-river extension of this species in the Aln since 5.6‰ S is its minimum salinity tolerance (Newell 1979).

Wolff (1973) reports Eurydice's preference for medium-fine sands of Mdmm 0.21-0.26 mm. At Alnmouth, Eurydice occurred in coarser sediments ranging up to Mdmm 1.34. Wolff also found that Eurydice abundance was not correlated with the sorting coefficient. Eurydice occurrence at Alnmouth

FIGURE 53

EURYDICE PULCHRA. Magnification x 8

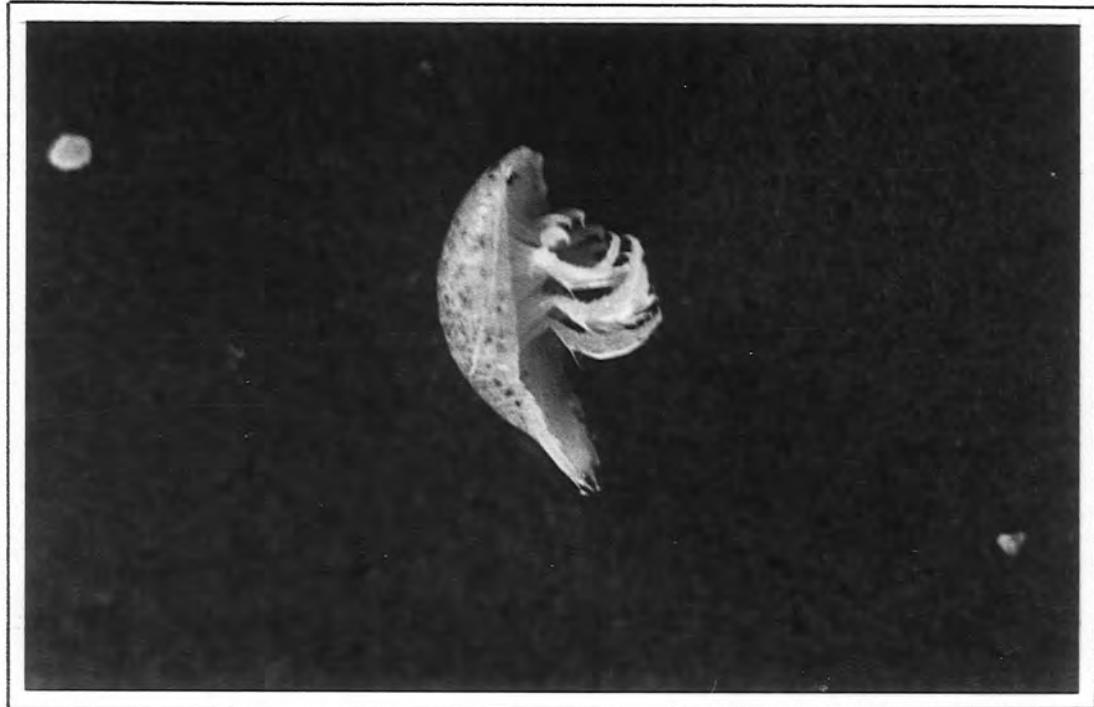


FIGURE 54

GAMMARUS SPP. Magnification x 7



in sediments ranging from QDØ 1.54-0.47 supports Wolff's conclusion.

This species is a predator and scavenger and therefore not dependent upon high sediment carbon content. It occurred in sediments with only 0.52-1.99%C.

A combination of factors are probably responsible for the distribution of Eurydice. Primarily, it is restricted to medium-fine sands, within this sediment range it was further confined to a low shore position characterized by a disturbed thixotropic substrate.

Gammarus spp. (Figure 54)

Gammarus showed a decline in abundance (MW-LW) from Station 9-12 (Figure 18c).

Since Gammarus is epibenthic the interstitial salinity will not be relevant. Salinity did not restrict the distribution of Gammarus at Alnmouth because Gammarus is euryhaline and hyper/isosmotic (McLusky 1971).

Talitrus saltator (Figure 55)

This species occurred in low densities in the lower reach (Figure 18c). Within the lower reach it was restricted to H.W. because it scavenges on organic debris thrown up by the tide. During the day it remains in its burrow and consequently evades stresses of temperature, dessication and predation. At night it is an opportunistic feeder and emerges to scavenge.

Talitrus is associated with the well-drained sandy sediments of 10 H.W., 11 H.W. and 12 H.W. This distribution supports Wolff's conclusion (1973) from the Dutch Delta area, that Talitrus is dependent on a sandy sediment and on a certain amount of organic matter washed ashore. The

lower reach of the estuary was semi-exposed and it is likely that more organic matter was washed-up than further inland. Therefore, the amount of washed-up debris, which is in turn controlled by the degree of exposure, may limit the extension of Talitrus up river.

Gastropoda

Acmaea virginea (Figure 56)

Gibbula umbilicalis (Figure 57)

Hydrobia jenkinsi (Figure 58)

Hydrobia is a member of the epifauna and burrows down to 2 cm during low tide.

It was observed at Stations 1-6 at L.W. and M.W. (Figure 18d). It is likely that Hydrobia is excluded from higher shore levels by dessication, because Stopford (quoted by Millard 1976) found that Hydrobia can only tolerate dryness for about 4 days.

Wolff (1973) concluded that H. ulvae preferred sediments with a median grain size ranging from 0.089 to 0.17 mm. This was not the case at Alnmouth where the species occupied coarser sediments ranging from Mdmm 0.33 to 0.66. However, the sediments of Stations 1-6 were relatively fine-grained compared to the other stations.

Hydrobia is a selective deposit feeder. It would therefore be expected to favour sediments of high carbon content, which are consequently also fine-grained. Since there was no significant correlation between grain size and %C, the association between high Hydrobia densities and high %C was not found.

The depth of the RPD was not significant in determining Hydrobia distribution because the animal does

FIGURE 55

TALITRUS SALTATOR. Magnification x 9

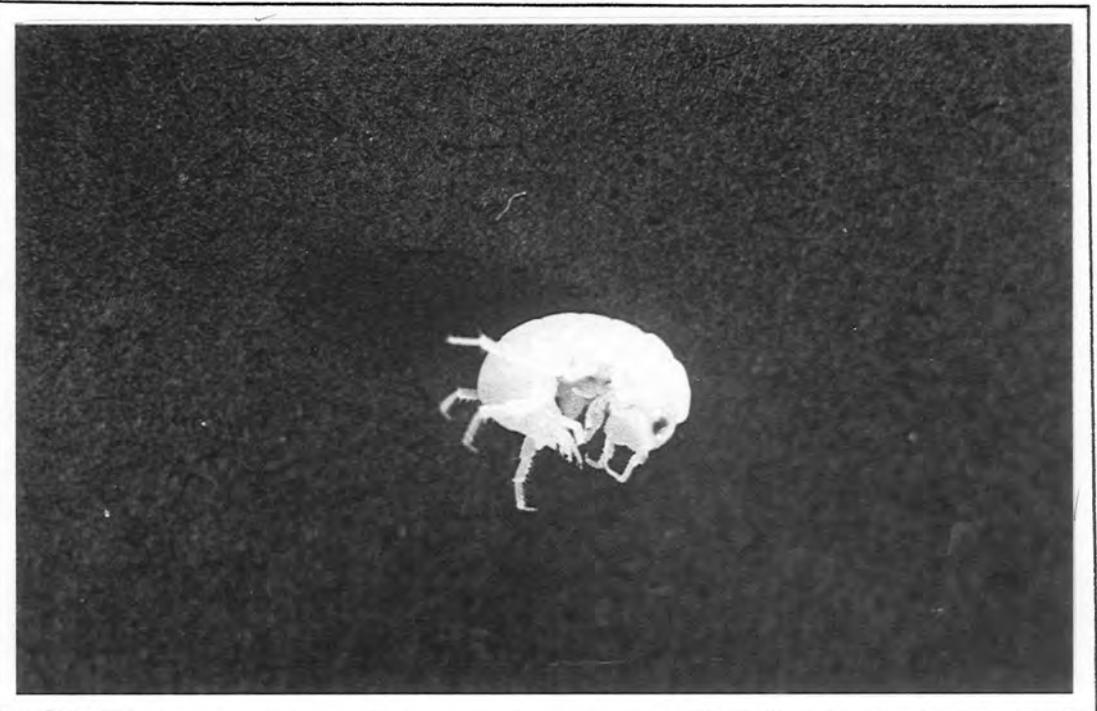


FIGURE 56

MOLLUSCA- GASTROPODA- ACMAEA VIRGINEA. Magnification x 8



GIBBULA UMBILICALIS. Magnification x 6

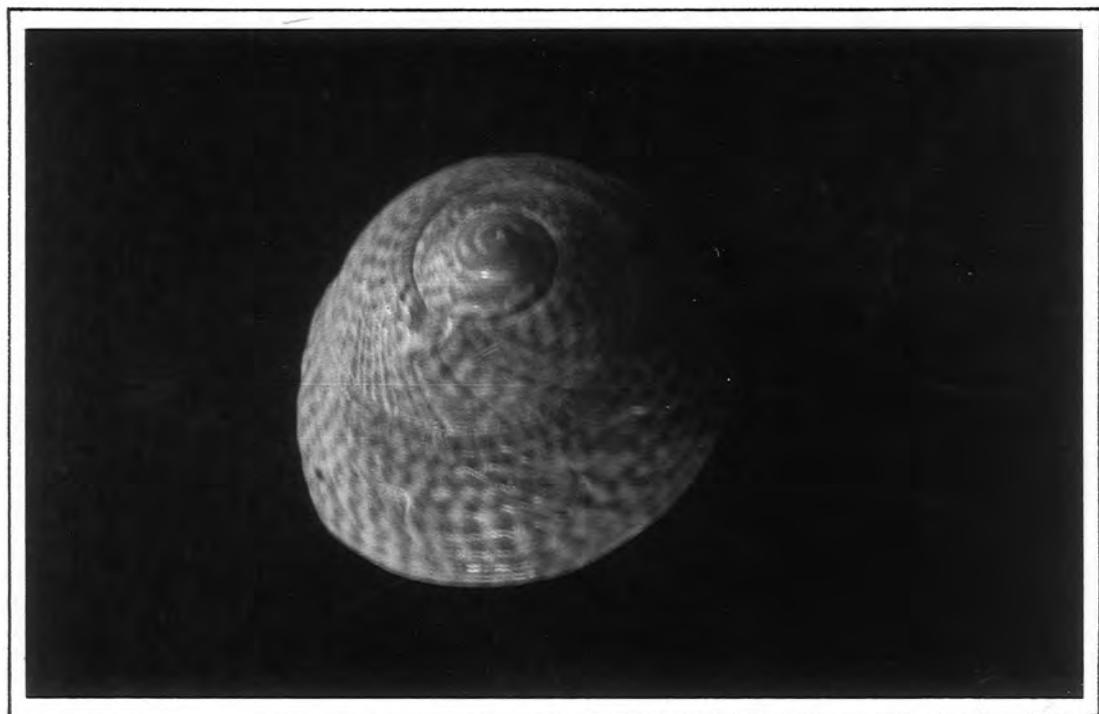
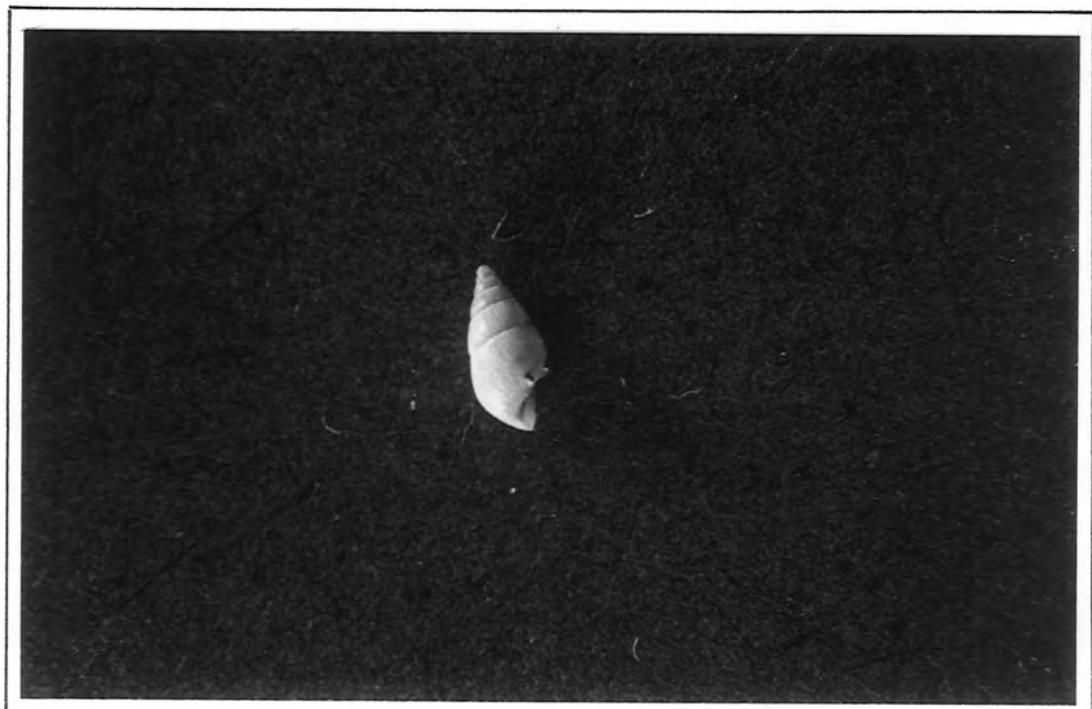


FIGURE 58

HYDROBIA JENKINSI. Magnification x 8



not burrow deeply enough.

Hydrobia is markedly euryhaline and can tolerate wide ranges of salinity. Data from Avens (Eltringham 1971) suggest that the animal does not osmoregulate but merely tolerates salinity extremes by closing its operculum. Since Hydrobia burrows, it is affected by the salinity of the surface water and interstitial salinity. The lower salinity limit is 1.97% S or 5.6% S according to Muus (1963) or McMillan (19480, respectively (cited in Milland 1976). Salinity did not limit this species at Alnmouth since 2.28% S was the lowest value for salinity of the overlying water.

The Redshank is a common predator of Hydrobia, but Milland (1976) found that the impact of bird predation is negligible and unlikely to control Hydrobia distribution.

To conclude, the distribution of Hydrobia is determined chiefly by an acceptable salinity regime, within which optimal development probably occurs within the finer-grade sediments.

Littorina littoralis (Figure 59)

Nassarius incrassatus (Figure 60)

Natica alderi (Figure 61)

Lamellibranchia

Donax vittatus (Figure 62)

This animal occurred at L.W., M.W. and H.W. at Stations 11 and 12 (Figure 18e). Donax alternates between lying buried and actively emerging, hence it experiences both interstitial salinity and that of the surface water. Its tolerance of 29.17-35.00% S is in accordance to the minimum isohaline of 9.86% S described by Wolff (1973) working in the Dutch Delta area. Absence of Donax from

FIGURE 59

LITTORINA LITTORALIS. Magnification x 6



FIGURE 60

NASSARIUS INCRASSATUS. Magnification x 7

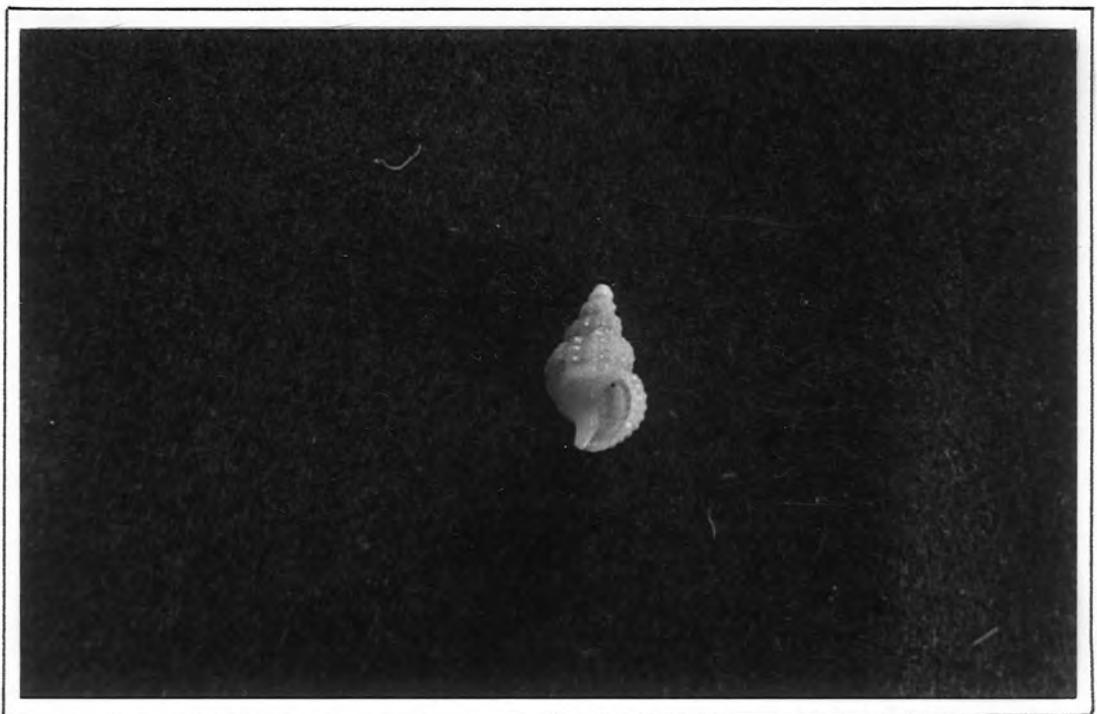


FIGURE 61

NATICA ALDERI. Magnification x 7

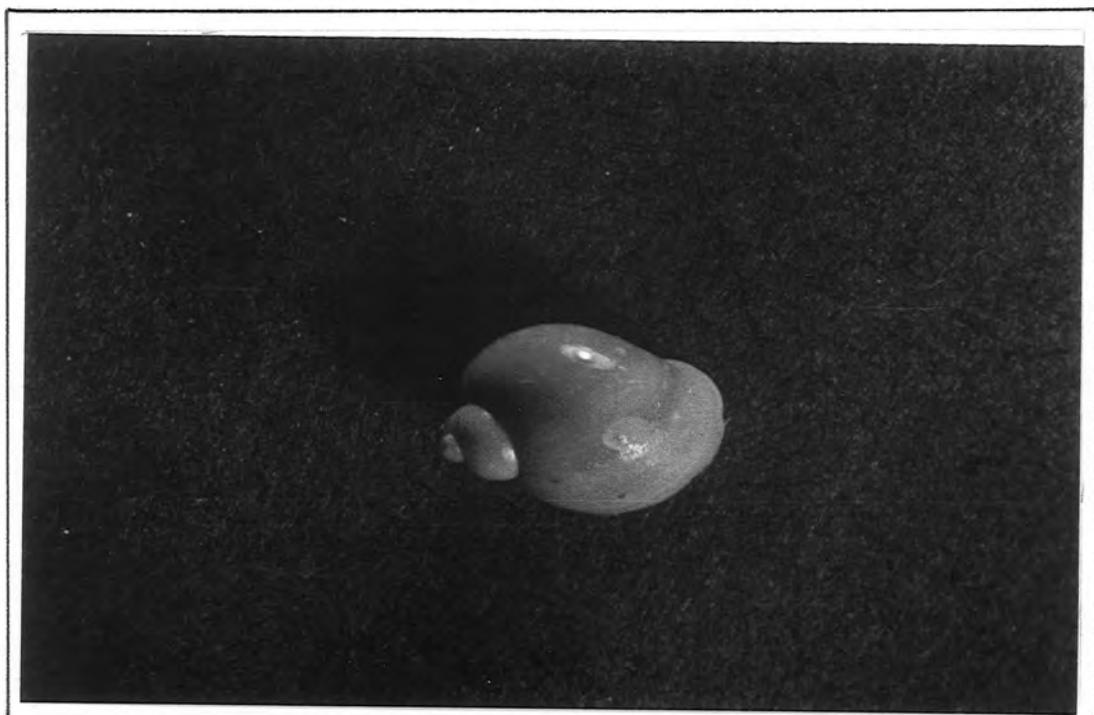
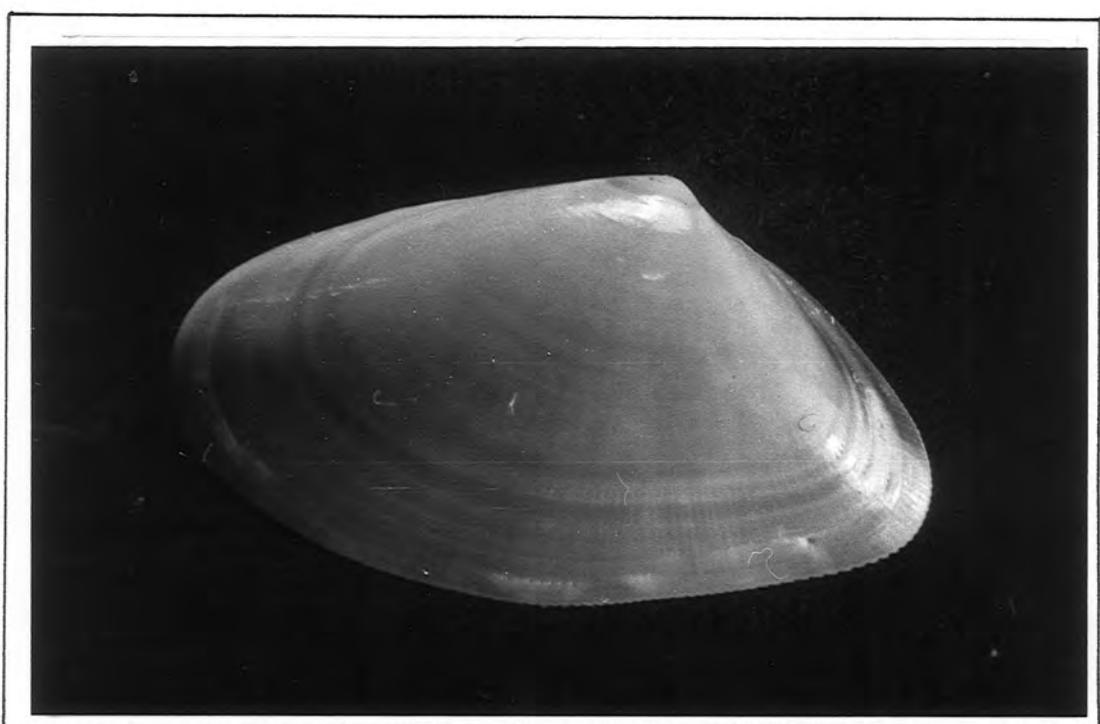


FIGURE 62

MOLLUSCA- LAMELLIBRANCHIA- DONAX VITTATUS. Magnification x 5



Station 10 (salinity of overlying water = 8.46‰ S) may therefore be ascribed to intolerance of the lower salinity.

Eisma (Wolff 1973) reports that Donax prefers well-sorted medium sand of $Mdmm$ 0.15-0.3. At Alnmouth the species inhabited relatively well-sorted coarser sand ranging from $Mdmm$ 0.40 to 0.66, and $QD\phi$ 0.35-0.61.

The occurrence of Donax at 12 H.W. is not easy to explain because Donax is generally reported to favour the surge zone where suspended food concentrations are probably enhanced by the backwash from surface deposits (Newell 1979).

To conclude, the landwards extension of Donax is controlled by salinity of the surface water, and its occurrence at Stations 11 and 12 is explained by preference for a well-sorted sandy sediment lying within the surge zone.

Macoma balthica (Figure 63)

Macoma occupied a belt at low-tide level at Stations 7 and 8 (Figure 18e). It lies 5-10 cm below the surface, maintaining surface contact by means of separate inhalent and exhalent siphons. The species is known to move extensively about the sand surface undergoing horizontal migrations, and this habit confers the advantage of bringing the animal into contact with surrounding areas whilst maintaining its station on the shore (Brafield and Newell 1961).

Macoma is tolerant of low salinities and Wolff (1973) recorded a minimum isohaline of 1.13‰ S in the Dutch Delta area. Since the species occupies its burrow but feeds from the sediment surface it is subjected to both surface water salinity and interstitial salinity. Station 7 L.W. had the lower salinity values of the two stations with a surface

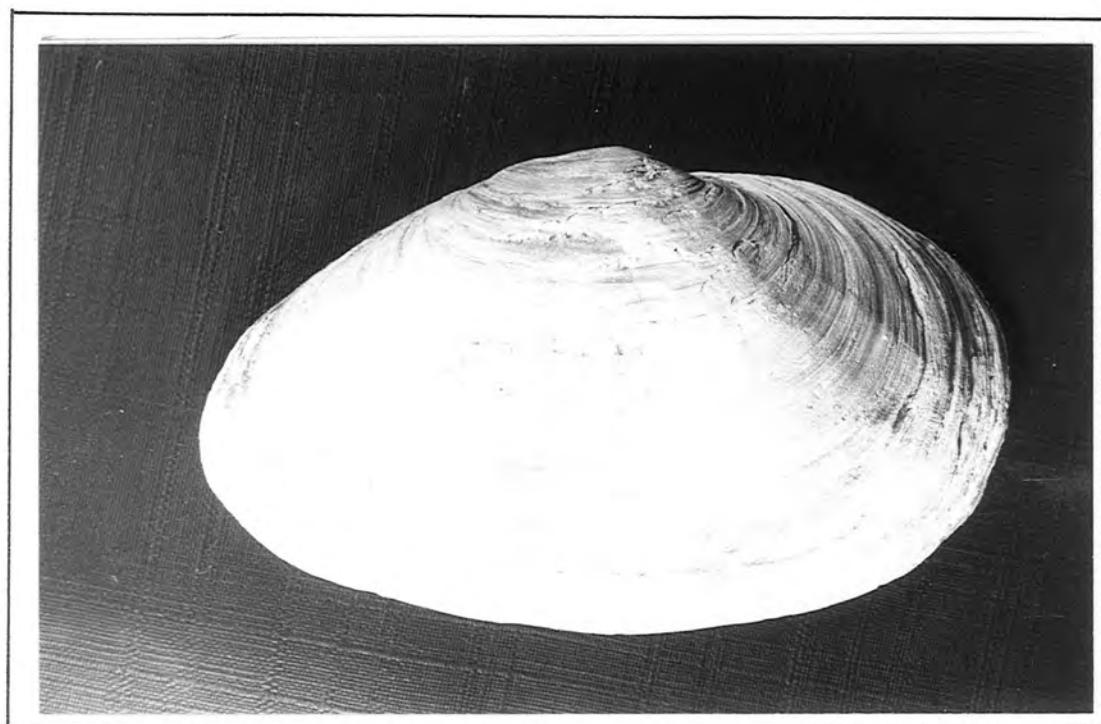
FIGURE 63

MACOMA BALTICA. Magnification x 7



FIGURE 64

MYA ARENARIA. Magnification x 1



water salinity of 7.78‰ S and an interstitial salinity of 33.83‰ S. Since these values are well above the minimum isohaline cited by Wolff, it is concluded that salinity was not effective in determining Macoma distribution at Alnmouth.

Newell (1965) found that fine deposits, with associated high silt-clay content, were directly correlated with Macoma density. He attributed the higher populations (in fine deposits) to increased abundance of micro-organisms. Macoma is principally a deposit-feeder, and the amount of its food is therefore directly related to the surface area of the deposit. Wolff (1973) found that Macoma inhabits all types of sandy sediments, but prefers finer badly sorted sediments of Md_{mm} 0.06-0.13. At Alnmouth at 7 L.W. this preference was not evident, since Macoma occurred in a coarse sediment of Md 0.76 mm. However, this sediment was badly sorted ($QD\phi$ = 1.66). As a consequence of the relatively coarse substrate at 7 L.W. and 8 L.W. the % carbon was comparatively low with values of 2.5% and 4.7% carbon respectively. Seaward of Station 8, the carbon content of L.W. sediments was distinctly lower. It is therefore possible that seaward colonization was prevented by the lack of sufficient food.

Penetration of Macoma further up the estuary may be limited by competition. It is well documented that Macoma competes with Scrobicularia plana (Newell 1979, Green 1968). The latter species occurred at mid-water level at Stations 4, 5, 6 and 7. It is possible that the L.W. Macoma zone overlapped slightly with the M.W. Scrobicularia zone and that Scrobicularia outcompeted Macoma at Station 6.

Thus, seaward extension of Macoma may be limited by

low carbon content of the sediment, and landward penetration may be prevented by competition with Scrobicularia plana.

Mya arenaria (Figure 64)

Density recordings for the soft clam probably only reflect the juvenile density, because adults are known to burrow up to 600cm below the surface (Green 1968). Not all adults were sampled by the technique I employed.

The abundance of juvenile Mya reflected the same pattern as found by Wolff (1973) in the Dutch Delta area - that of a decrease seawards. Juveniles were densest at Station 2 and numbers rapidly declined to Station 8. (Figure 18e). At these positions juveniles chiefly occurred at L.W. and M.W.

Mya is influenced by salinity of the surface water when as a pelagic larva, and when adult because it retains contact with the surface by means of its siphons. At Alnmouth it experienced a salinity range of 3.30-9.33‰ S. Howard and Walden (Perkins 1974) claim that below 4.0‰ S Mya stops feeding, and consequently the abundance of Mya at Station 2 (3.30‰ S) would seem anomalous. However, Eisna reported that Mya's salinity tolerance ranges from estuarine values of 1.13-9.3‰ S up to the salinity of the North Sea (Wolff 1973). So in the light of Eisna's data, the occurrence of Mya at Station 2 is quite credible.

Eisna believed that the seaward extension of Mya is not restricted by salinity, but by other factors. The sandy sediments of Stations 9-12 could possibly be unfavourable to Mya since Kuhl found that the species occurs chiefly in muddy sediment (Wolff 1973).

Both the carbon content of the sediment and depth of the R.P.D. are ineffective in determining the distribution of Mya, since the animal is in constant contact with the sediment surface. As long as the sediment is relatively easy to penetrate, water table depth will not be a crucial factor in limiting Mya's distribution.

Juvenile Mya were most abundant at L.W., and this suggests that predation by waders was ineffective in determining the intertidal distribution of Mya at Alnmouth. The carbon content of the sediment, predation, depth of the R.P.D. and the water table, have been discounted as being likely to control the distribution of Mya. The seaward extension of the soft clam could however be influenced by the absence of a suitable muddy substrate.

Mytilus edulis (Figure 65)

At Alnmouth the species occurred at Stations 1-5 mainly at L.W.-M.W. (Figure 18e). The lower density of Mytilus at H.W. could be due to lack of sufficient food, as was proposed by Baird. He also concluded that temperature may also be an important factor inhibiting the occurrence of mussels on the higher tidal flats (Wolff 1973).

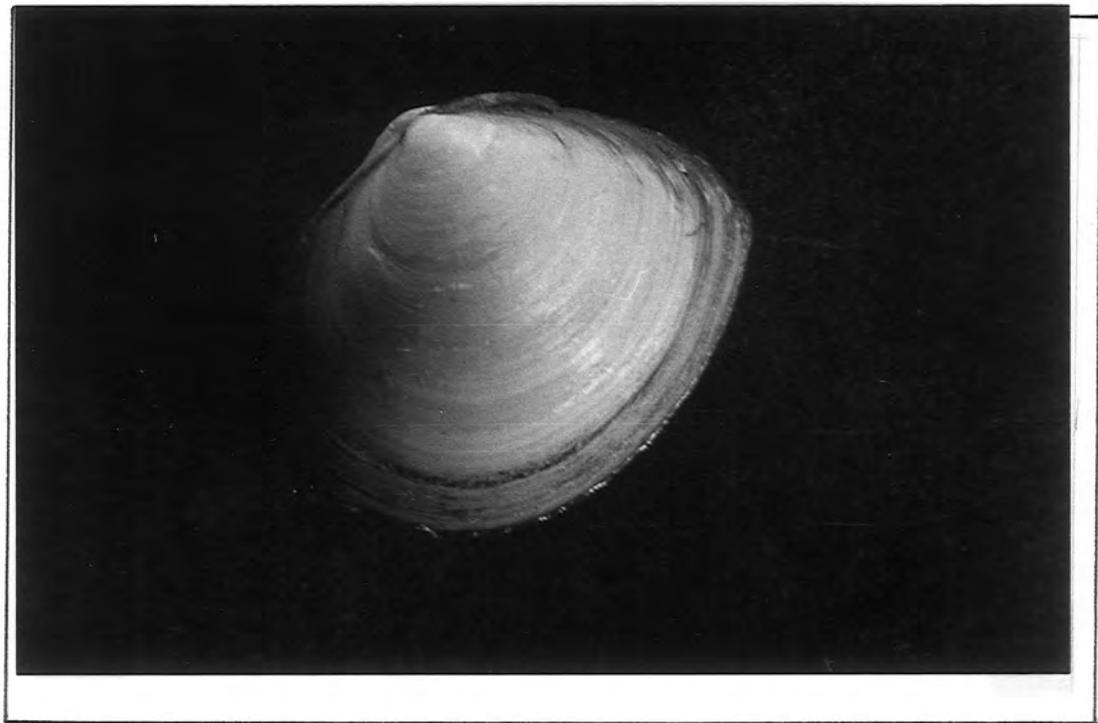
Mytilus is classified as being polyhaline-mesohaline, having a minimum isohaline at 10‰ S with 4‰ S being the lethal minimum (Nelson Smith 1965, cited by Parkins 1974). Mytilus is influenced by salinity of the surface water and its occurrence over the range 2.28-4.67‰ S is not in accordance with the salinity limit proposed by Nielson Smith. The progressive decline in size of Mytilus with reduced salinity is documented by Segerstrale in the Baltic (McLusky 1971). Accordingly, minute specimens of

MYTILUS EDULIS. Magnification x 13



FIGURE 66

SCROBICULARIA PLANA. Magnification x 6



approximately 2 mm in length were found to be characteristic of the upper reach of the Aln estuary. Salinity is unlikely to be responsible in controlling the seawards extension of Mytilus and so we turn to studying the sediment preference of the species.

Mytilus prefers badly-sorted muddy sediments and Wolff (1973) concluded that it does not occur on sandy flats with strong currents or wave action. The substrate at Stations 1-5 was distinctly muddy and poorly sorted with a mean QDØ of 1.29 for the lower reach compared with a mean QDØ of 0.72 seawards of Station 5.

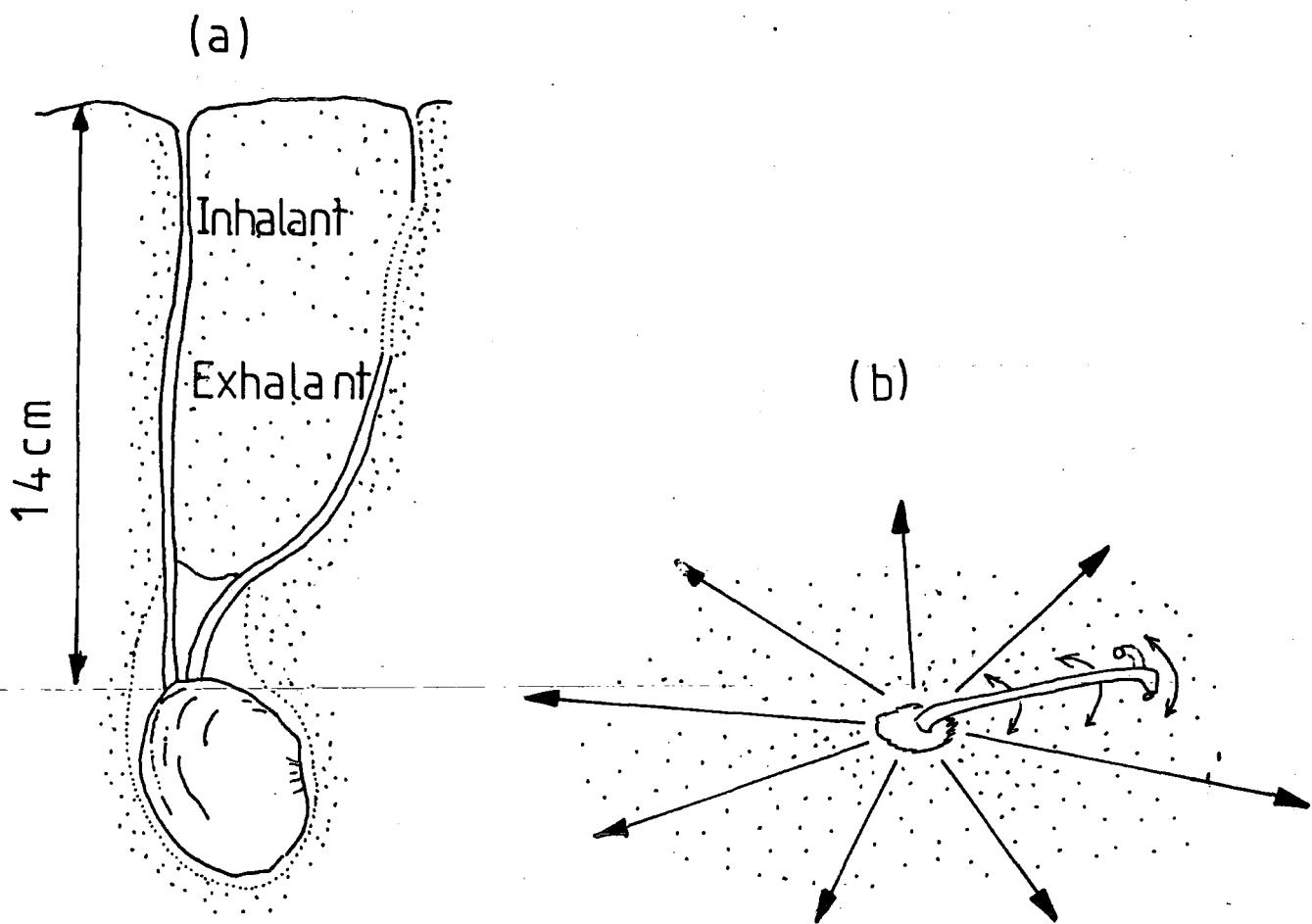
The availability of food is another potentially limiting factor. Mytilus is a suspension feeder and relies on phytoplankton and small organic particles as its food source. The reduced shelter seawards of Station 5 may prevent the settlement of sufficient food and thereby inhibit the distribution of Mytilus.

Scrobicularia plana (Figure 66)

Adult Scrobicularia are known to burrow up to a depth of 30 cm, therefore not all specimens present were sampled by the technique employed. Scrobicularia is a selective deposit-feeder which may act as a suspension-feeder during high tide (Thamdrup and Hughes in Wolff 1973). The burrowing mode and feeding activity of Scrobicularia is illustrated in Figure 67.

This species was recorded at M.W.-H.W. at Stations 4, 5, 6 and 7 (Figure 18e). Wolff considers this vertical distribution to be determined by its preference for finer muddy sediments together with its intolerance of semi-permanent immersion.

Figure 67 (a) The burrow of *Scrobicularia plana*
(b) Inhalant siphonal activity when deposit feeding
along mud surface (After Hughes, 1969).



Scrobicularia maintains contact with the surface by means of its siphons and is therefore influenced by the salinity of the surface water. At Alnmouth it was present within a salinity range of 4.49-7.58% S which is within the 2-20% S tolerance limit proposed by Freeman and Rigler (Perkins 1974). However, the species can withstand these extremes only for short periods during which it retracts its siphons and closes its shell. The salinity regime experienced by Scrobicularia at Alnmouth is dilute. Freeman and Rigler found that the animal commences osmoregulation at 10% S, so that low salinity might account for the position of the landwards boundary of Scrobicularia distribution, but not for its seawards boundary.

The occurrence of Scrobicularia in mud (Mdmm 0.26-0.33) is in accordance with the distribution found by Wolff and Tebble (Wolff 1973). However, Guerin and Schulz report its presence in a variety of sediments ranging from coarse sand to silt (Wolff 1973). Thus Scrobicularia may not require a specific substrate, but prefers the environmental conditions associated with a muddy bottom, i.e. a continuous source of fine particulate organic matter.

Tellina crassa (Figure 68)

This bivalve occurred mainly M.W.-H.W. at Stations 10-12 (Figure 18e). It remains burrowed within the sediment and is in constant contact with the surface by means of its siphons. It is therefore affected by the salinity of the surface water which ranged from 8.46-35.0% S.

Tellina occurred in relatively coarse sands (Mdmm for: M.W.-H.W. Station 10 = 0.43, for M.W.-H.W. Station 11 = 0.54 and for L.W.-M.W. Station 12 = 0.59). Its distribution at

FIGURE 68

TELLINA SPP. Magnification x 5

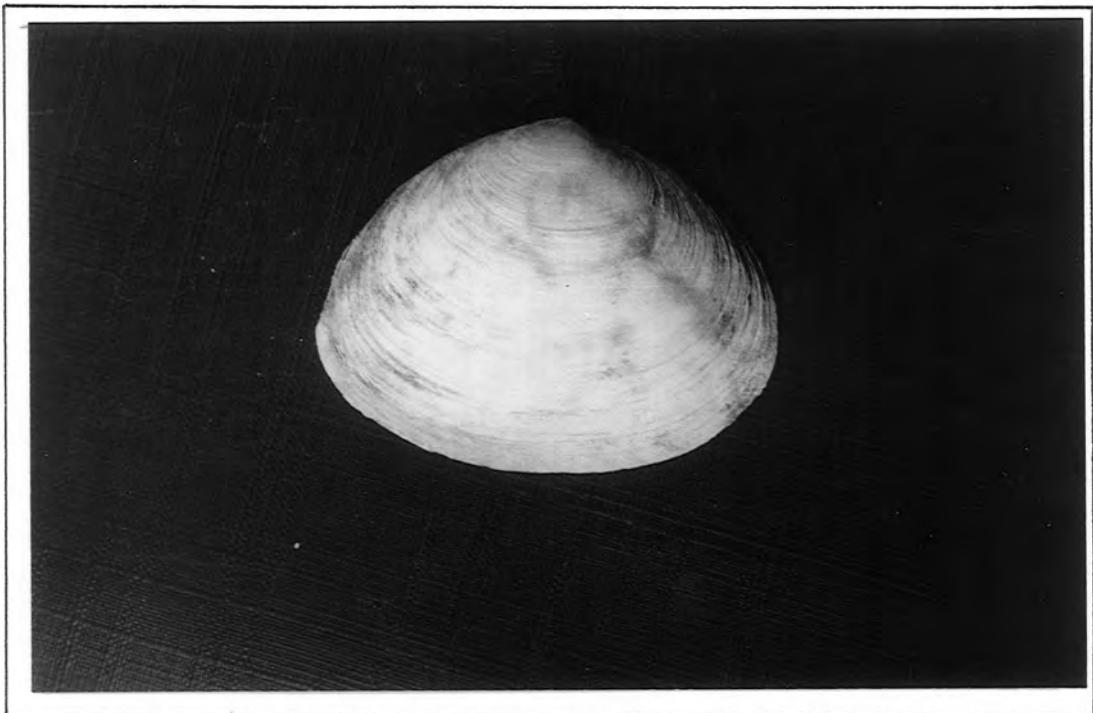
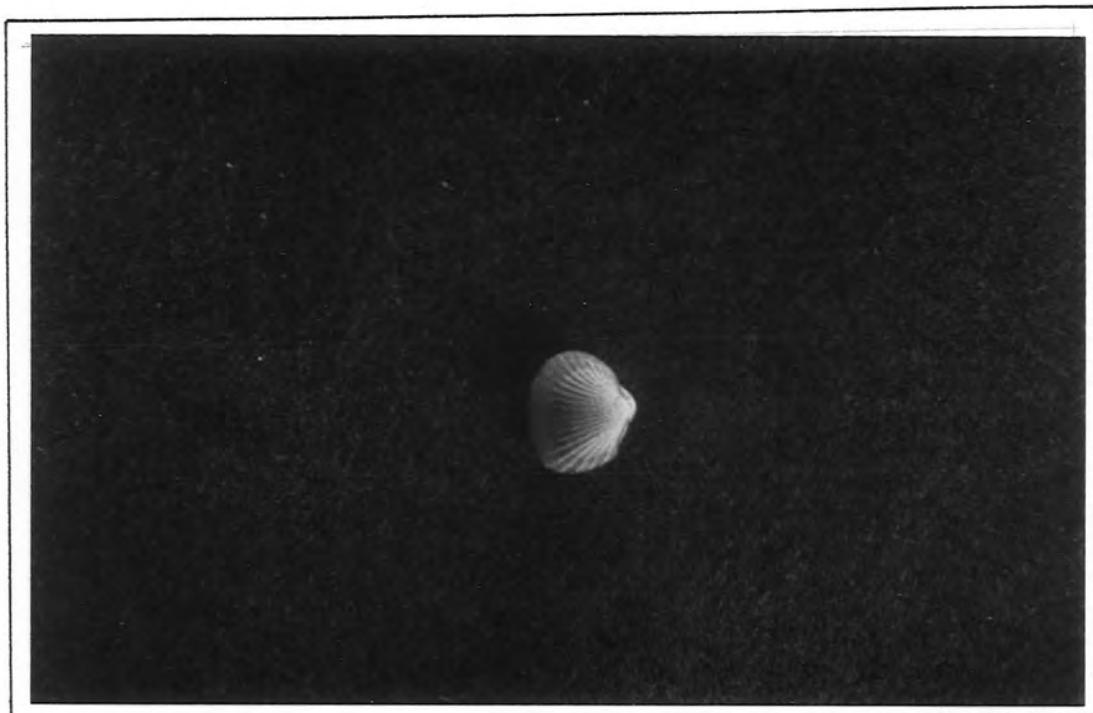


FIGURE 69

VENUS OVATA. Magnification x 8



Alnmouth is in accordance with that forecast by Barrett and Yonge (1980), and the animal's preference for coarse sands could be the factor preventing its penetration further up the estuary.

Venus ovata (Figure 69)

Venus is a shallow-burrowing bivalve which retains siphonal contact with the surface. It occurred chiefly at M.W. at Stations 10-12 (Figure 18e).

Venus experienced the salinity range of 8.46-35.0‰ S and occurred in coarse sand ranging in Mdmm from 0.43 to 0.66. The finer grade of sediment further up the estuary could possibly be responsible for the lack of Venus from the middle and upper reaches.

CHAPTER 6 : CONCLUSION

The estuarine environment is a multivariate system wherein factors combine to exert cumulative control over species distribution. Consequently the elucidation of single factor control is made impossible by the existence of confounding variables.

Salinity is a factor to which all estuarine species must respond. Salinity was found to be especially important in controlling the distribution of Corophium volutator and Arenicola marina. However, within the salinity regime tolerated by a particular species, the distribution is related to some optimal combination of physico-chemical factors. High interstitial salinity was associated with a gentle shore gradient. Surprisingly, salinity was not found to correlate with sediment particle size or with water table depth. Salinity did correlate significantly with R.P.D. depth, but not in a causal way. Salinity was not associated with species richness, characteristic breaks in species abundance were found at the oligohaline-mesohaline and mesohaline-polyhaline boundaries. Species richness was lowest where salinity fluctuation was greatest, in the middle reaches of the estuary. It was proposed that this region was habited only by a few specialist species which were adapted to tolerate large salinity fluctuations.

Sediment particle size was significantly inversely correlated with % carbon content of the sediment and the sediment sorting coefficient. Data did not exhibit the significant relationship expected between median particle diameter and water table and R.P.D. depth, and salinity.

I would therefore suggest that more extensive sampling is necessary. A significant correlation was calculated between % silt-clay content of the sediment and the number of deposit feeders. This suggested that sediment particle size gives some indication of the potential food available.

Sediment grade was found to significantly affect the distribution of Corophium volutator and Haustorius arenarius. Sediment grade was also found to be important in influencing the distribution of Euyridice pulchra, Tellina crassa and Venus ovata.

The % carbon content of the sediment was not found to be significant in controlling the distribution of species since variation was negligible and there was no correlation with species richness. However, at the level of individual species, the organic content of the sediment was proposed influential in determining the distribution of Arenicola marina and Macoma balthica.

The depth of the water table was distinctly greater in the sandy soil of the lower reach which was characterized by relatively large particle size and high permeability. Water table depth covaried significantly with R.P.D. depth. Water table depth displayed a marked gradation from deep to shallow as one proceeded from HW to LW. Water table depth was an important factor in relation to the distribution of a few individual species, for example, Euyridice pulchra and Haustorius arenarius which rely on a thixotropic sediment for burrowing.

R.P.D. depth was greatest at HT level within the lower reaches. Surprisingly, it was not significantly correlated with sediment particle size or with % carbon

content. The degree of sediment aeration was not thought to have been significant in determining species distribution at Alnmouth.

It was not possible to measure all the potentially important factors which could affect species distribution. Factors which could not be measured within the time scale were physico-chemical factors of seasonal fluctuations in salinity, water temperature, light, oxygen saturation, current velocity, turbidity and wave action, and the biological factors of availability of optimal conditions for reproduction and settlement of larvae and juveniles, competition, predation and parasitism.

Undoubtedly, biological factors combine and are interrelated with physico-chemical factors and influence the distribution of estuarine species. From the field situation at Alnmouth and from literature reports, it was likely that the seaward limit of Nereis diversicolor was set either by predation or by competition, and in the case of Macoma balthica, that penetration of the species up-river was prevented by competition from Scrobicularia plana.

Corophium volutator was the predominant species at Aln estuary, and occurred in greatest abundance at Station 8 (3175 m^{-2}).

Laboratory and field reports indicated that Corophium volutator was distributed according to sediment particle size and silt-clay content, but that Corophium v. was only found in a particular sediment if the salinity was suitable. The distribution of Corophium thus reinforces the feature of multi-variate control of the distribution and abundance of estuarine animals. Results from the micro-

distribution survey suggested that vertical distribution within the sediment was due to the topographical separation of size classes. The size frequency of the population also determined the horizontal spacing in terms of minimum individual distance, since the older and larger animals required a greater burrow diameter than younger animals.

Studies on Haustorius arenarius suggested that Haustorius could have survived in a salinity regime in parts of the estuary where it was absent. It was therefore proposed that the species must have been restricted in distribution by other factors such as preference for a wet sandy thixotropic sediment with a relatively high organic content.

The lower reach of the estuary supported most species, the upper reach supported an intermediate number, and the middle reach supported fewest species. Species paucity in the middle reach could have been due to physico-chemical stresses and fluctuations and/or to biological factors such as competitive exclusion. Lowest species richness did not occur midway between fresh water and sea water.

The asymmetric position of the species minimum was believed to reflect the problems faced by colonists from fresh water to sea water: while the number of fresh water species declines rapidly, the decrease in the reduction of marine species takes longer. On a vertical scale upshore, species richness was highest at MW and lowest at HW - the reduction in the number of species at HW was a consequence of the stresses imposed by exposure and dessication.

Despite the fact that all estuarine species must respond to salinity, salinity is not paramount in determining

the distribution of all macrobenthos at Aln estuary.

The estuary does not give up its secrets too easily, and only after a relatively long term intensive study can one begin to appreciate the fine balance of the estuarine ecosystem and the subtle polyfactorial control of the distribution of the intertidal invertebrates.

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SAMPLE 1

	STN.11			STN.12		
	LW	MW	HW	LW	MW	HW
L.spp.				1		
N.f.						
A.m.						
L.c.			1			
N.d.						
P.spp.						
<i>Sabellida</i> .p.						
C.m.						
C.v.						
E.p.		1	3			
G.spp.	5		1			
H.a.	2					
T.s.			2			
A.v.						
G.u.						
H.j.						
L.l.						
N.i.						
N.a.						
D.v.	1		1			
M.b.						
M.a.						
M.e.						
S.p.						
T.c.			1			
V.o.						

SAMPLE 2

	STN.11			STN.12		
	LW	MW	HW	LW	MW	HW
L.spp.				1	1	
N.f.						
A.m.						
L.c.				1		
N.d.						
P.spp.						
<i>Sabellidae</i> .p.						
C.m.						
C.v.						
E.p.	3	2	1	5		
G.spp.	1					
H.a.	3			1		
T.s.		1	1	3		
A.v.						
G.u.		1				
H.j.						
L.l.						
N.i.						
N.a.						
D.v.	1			1	1	
M.b.						
M.a.						
M.e.						
S.p.						
T.c.			1			
V.o.						

SAMPLE 3

	STN.6			STN.7			STN.8			STN.9			STN.10		
	LW	MW	HW	LW	MW	HW									
L.spp.										1					
N.f.															
A.m.	1				1	1									
L.c.													2		
N.d.				3	3			2							
P.spp.															
Sabellaa.p.															
C.m.															
C.v.	8	5		38	42		51	55		19	9				
E.p.													2	4	
G.spp.										3					
H.a.													7		
T.s.															2
A.v.															
G.u.															
H.j.															
L.l.															
N.i.													1		
N.a.													1		
D.v.															
M.b.			1												
M.a.															
M.e.															
S.p.															
T.c.															
V.o.													1		

	STN.11			STN.12		
	LW	MW	HW	LW	MW	HW
L.spp.				2		
N.f.						
A.m.						
L.c.				1	2	1
N.d.						
P.spp.						
Sabella.p.	1					
C.m.						
C.v.						
E.p.	2	3		2	3	
G.spp.						
H.a.	2	1				
T.s.		2	2			2
A.v.						
G.u.						
H.j.						
L.l.		1				
N.i.						
<u>N.a.</u>						
D.v.		1			1	
M.b.						
M.a.						
M.e.						
S.p.						
T.c.						
V.O.			2			

SAMPLE 4

	STN.11			STN.12		
	LW	MW	HW	LW	MW	HW
L.spp.			1			
N.f.						
A.m.						
L.c.				1	1	
N.d.						
P.spp						
Sabellida.p.						
C.m.						
C.v.						
E.p.	5	4		3		
G.spp	3	1				
H.a.	7					
T.s.						
A.v.						
G.u.						
H.j.						
L.l.						
N.i.						
N.a.						
D.v.						
M.b.						
M.a.						
M.e.						
S.p.						
T.c.	1			2		
V.o.	1			1	1	

SAMPLE 5

	STN.6			STN.7			STN.8			STN.9			STN.10		
	LW	MW	HW	LW	MW	HW									
L.spp.													2		2
N.f.															
A.m.		1			1										
L.c.													1		
N.d.	4			2			1	2							
P.spp.															
Sabellap.															
C.m.															
C.v.	9	5	7	33	41	7	41	48		27	11				
E.p.													4	4	
G.spp.										2	5	2			
H.a.													8		
T.s.													1	1	
A.v.															
G.u.															
H.j.															
L.l.															
N.i.													1		
N.a.															
D.v.															
M.b.															
M.a.															
M.e.															
S.p.		1													
T.c.													1		
V.o.													1	1	

	STN.11			STN.12		
	LW	MW	HW	LW	MW	HW
L.spp	1	1		1		
N.f.						
A.m.						
L.c.						
N.d.						
P.spp.						
Sabella.p.						
C.m.						
C.v.						
E.p.	3	2	1	3		
G.spp.	2					
H.a.	6	1		1		
T.s.			1		2	
A.v.						
G.u.						
H.j.						
L.l.						
N.i.						
N.a.						
D.v.	1			1	1	
M.b.						
M.a.						
M.e.						
S.p.						
T.c.						
V.o.	1		1	1		

APPENDIX 2 : Calculation of Analysis of Variance for the experiments to investigate the salinity tolerance of Corophium volutator and Haustorius arenarius

CV 9 MW : Corophium volutator from Station 9 MW
 CV 1 MW : " " " " 1 MW
 HA 10 LW : Haustorius arenarius " " 10 LW

Variance between samples

Sample	b-c	df	sos/df
	—	—	s
CV 1 MW	4802.90	11	436.63
CV 9 MW	3707.27	11	337.02
HA 10 LW	985.97	11	89.63

Variance within samples

Sample	a-b	u(v-1)	t
	—	—	—
CV 1 MW	4394.40	108	40.69
CV 9 MW	3107.40	108	28.77
HA 10 LW	703.20	108	6.51

Total

Sample	a-c	F=s/t	Sig. level
	—	—	—
CV 1 MW	9197.30	10.73	1%
CV 9 MW	6814.67	11.71	1%
MA 10 LW	1689.17	13.77	1%

1% level at $v_1=10$, $v_2=120$, $F=2.47$

Appendix 3Preliminary Calculations for the Investigation of Penetration
of Species up-river

Station No.	Species (S)	No. of individuals recorded from 5 (12x400cc sediment) samples, each sample consisting of LW, MW and HW sub-samples					ΣN	Nos of individuals per m^2
1	N.d.	15	1	7	10		33	220
	C.v.	50	59	51	40	60	260	734
	P.spp.	1					1	7
	C.m.	1	1	1	1		4	27
	H.j.	2	2	1	3		8	53
	M.e.	1	2	2			5	34
$\Sigma S=6$								$\bar{x}: \Sigma N=311$
2	N.d.	2	3	4	5	5	19	127
	M.a.	3	1	2	1	1	8	53
	H.j.	1	2	2	3	2	10	67
	C.v.	6	27	14	15	32	94	627
	M.e.	2	1	1	1		5	33
	C.m.	2	1	1			4	27
$\Sigma S=6$								$\bar{x}: \Sigma N=140$
3	A.v.	1	1	1			3	20
	C.v.	14	27	9	16	21	87	580
	N.d.	7	5	10	4	3	29	193
	M.a.	1	1				2	13
	H.j.	2	2	2	4		10	67
	C.m.	1	1				2	13
	M.e.	1	1				2	13
$\Sigma S=7$								$\bar{x}: \Sigma N=135$
4	N.d.	5	12	14	15	14	60	400
	C.v.	8	28	11	20	27	74	494
	L.spp.	1					1	7
	N.f.	1	1				2	13
	S.p.	1	1	1			3	20
	C.m.	3	1	2			6	40
	H.j.	3	3	2	4		12	80
	M.e.	1	1				2	13
	M.a.	1					1	7
$\Sigma S=9$								$\bar{x}: \Sigma N=161$

continued ...

Appendix 3 (continued)

Station No.	Species	No. of individuals recorded from 5 (12x400cc sediment) samples, each sample consisting of LW, MW and HW sub-samples					ΣN	Nos. of individuals per m^2
5	N.d.	5	7	7	2	7	28	187
	C.v.	8	26	8	9	10	61	407
	L.spp.	1	1	2			4	27
	N.f.	1	1	1			3	20
	H.j.	1	5	5			11	73
	M.e.	1	2	2			5	33
	S.p.	1					1	7
	M.o.	1					1	7
$\Sigma S=8$ $\bar{x}: \Sigma N=114$								
6	N.d.	2	1	3	4		9	60
	H.j.	1	1				2	13
	C.v.	5	35	13	18	14	87	580
	S.p.	1	1				2	13
	A.m.	1	2	1			4	27
	M.o.	1					1	7
$\Sigma S=6$ $\bar{x}: \Sigma N=105$								
7	C.v.	65	70	80	98	81	394	2628
	N.d.	6	6	7	2		21	140
	M.b.	1	1	1			3	20
	S.p.	1	1				2	13
	A.m.	2	1				3	20
$\Sigma S=5$ $\bar{x}: \Sigma N=423$								
8	N.d.	1	2	1	3		7	47
	M.b.	1	1	1			3	20
	C.v.	74	95	106	105	96	476	3175
	M.a.	1					1	7
	A.m.	1					1	7
$\Sigma S=5$ $\bar{x}: \Sigma N=488$								
9	L.c.	1	1				2	13
	G.spp.	23	7	3	7	7	47	314
	L.spp.	1	1	1	2		5	33
	Sabellidae	2					2	13
	C.v.	39	28	32	38		114	760
$\Sigma S=5$ $\bar{x}: \Sigma N=170$								

continued ...

Appendix 3 (continued)

Station No.	Species	No. of individuals recorded from 5 (12x400cc sediment) samples, each sample consisting of LW, MW and HW sub-samples					ΣN	Nos. of individuals per m^2
10	H.o.	2	6	7	5	8	28	187
	G.spp.	7	2	4	2		15	100
	E.p.	5	6	11	8		36	240
	V.o.	1	1	2			5	33
	L.spp.	1	2				3	20
	T.c.	1	1				2	13
	T.s.	2	2	6	2		12	80
	N.i.	1	1	1			3	20
	N.o.	1	1				2	13
	L.c.	2	1	1			4	27
	Sabellap.	1					4	7
								$\bar{x} \Sigma N = 111$
11	H.o.	2	3	3	7	7	22	147
	G.spp.	5	1	4	2		12	80
	D.v.	1	1	1			3	20
	E.p.	1	6	5	9	6	27	180
	G.u.	1					1	7
	T.s.	2	4	1			7	47
	Sabellap.	1					1	7
	L.l.	1					1	7
	T.c.	1					1	7
	V.o.	1	1				2	13
	L.spp.	2					2	13
								$\bar{x} \Sigma N = 79$
12	G.spp.	1					1	7
	C.p.	3	5	5	3	3	19	127
	L.c.	1	1	4	2		8	53
	T.c.	1	1	2			4	27
	T.s.	2	3	2	2		9	60
	L.spp.	1	2	2	1	1	7	47
	D.v.	1	2	1	2		6	13
	H.o.	1	1				2	13
	V.o.	2	2	2			6	40
								$\bar{x} \Sigma N = 62$

Appendix 4
Abundance of Species at Stations 1-12 Nos. m⁻²

Station No.	L.spp.	N.f.	A.m.	L.c.	N.d.	Sabella spp.	P.spp.	C.m.	C.v.	C.p.	G.spp.	H.a.	T.s.
1						220		7	27	1734			
2						27			27	627			
3						193			13	580			
4	7	13				400			40	494			
5	27	20				187				407			
6			27			60				580			
7			20			140				2628			
8			7			47				3175			
9	33			13		13				760	313		
10	20			27		7				240	100	187	80
11	13							7		180	80	147	47
12	47				53					127	7	13	60
Station No.	A.v.	G.u.	H.j.	L.l.	N.i.	N.a.	D.v.	M.b.	M.a.	M.e.	S.p.	T.c.	V.o.
1				53							34		
2				67						54	34		
3		20		67						13	13		
4				80						7	13	20	
5				73						7	34	7	
6				13						7		13	
7							20					13	
8							20			7			
9													
10					20	13					13	34	
11				7			20				7	13	
12											27	40	

APPENDIX 5 : Spearman's Rank Correlation between the % silt-clay content of sediment and the number of deposit feeders

Deposit feeders:

Arenicola marina, *Corophium volutator*, *Donax vittatus*, *Hydrobia jenkinsi*, *Lanice conchilega*, *Macoma balthica*, *Nereis diversicolor*, *Scrobicularia plana*.

Station No.	No. of deposit feeders	Rank	% silt-clay content	Rank	d	d^2
1	62	2	15.22	3	-1	1
3	24	4	6.75	4	0	0
5	20	5	20.46	1	-4	16
7	84	1	16.25	2	-1	1
9	29	3	0.00	5.5	-2.5	6.25
11	1	6	0.00	5.5	0.5	0.25
$\sum d^2 = 24.50$						

$$r_s = 1 - \frac{6(\sum d^2)}{n(n^2-1)}$$

$$r_s = 1 - \frac{6(24.50)}{210}$$

$$r_s = 1 - \frac{147}{210}$$

$$r_s = 1 - 0.7$$

$$r_s = 0.3$$

$$N = 6$$

The calculated value of 0.3 is not significant at the 5% level (tabulated value = 0.829, $p < 0.05$)

APPENDIX 6 : Spearman's Rank Correlation between the % carbon content of sediment and number of deposit feeders

Station No.	No. of deposit feeders	Rank	% carbon content	Rank	d	d^2
1	62	2	1.43	5	-3	9
3	24	4	1.71	3	1	1
5	20	5	1.38	6	-1	1
7	84	1	1.52	4	-3	9
9	29	3	1.79	2	1	1
11	1	6	1.87	1	5	25

$$\sum d^2 = 46$$

$$r_s = 1 - \frac{6 \sum d^2}{n(n^2 - 1)} \quad r_s = 1 - \frac{6(46)}{210} \quad r_s = 1 - \frac{276}{210}$$

$$r_s = 1 - 1.314 \quad r_s = -0.314$$

$$N = 6$$

The calculated value of -0.314 is not significant at the 5% level (tabulated value = 0.829, $p < 0.05$)

APPENDIX 7 : Spearman's Rank Correlation between median particle diameter and the number of deposit feeders

Station No.	No. of deposit feeders	Rank	Mdmm	Rank	d	d^2
1	62	2	0.403	5	3	9
3	24	4	0.503	3	1	1
5	20	5	0.596	1	4	16
7	84	1	0.440	4	3	9
9	29	3	0.390	6	3	9
11	1	6	0.520	2	4	16
						$\Sigma d^2 = 60$

$$r_s = 1 - \frac{6 \Sigma d^2}{n(n^2-1)} \quad r_s = 1 - \frac{6(60)}{210} \quad r_s = 1 - \frac{360}{210}$$

$$r_s = 1 - 1.714 \quad r_s = -0.715$$

$$N = 6$$

The calculated value of -0.714 is not significant at the 5% level (tabulated value = 0.829, $p < 0.05$)

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