W. J. WOLFF

THE ESTUARY AS A HABITAT

STELLINGEN

I

De „time-stability" hypothese van H. L. Sanders geeft een bevredigende verklaring voor de soortenarmoede van brakke wateren.

H. L. Sanders - Amer. Nat. (1968) 102 : 243-282.

II

In tegenstelling tot de gangbare opvatting is de soortensamenstelling van brakwaterfauna's niet overal ter wereld dezelfde.

M. R. Carriker - In: G. H. Lauff (ed.) - Estuaries - Publ. 83 Amer. Ass. Advanc. Sci. (1967):442-487.

G. de Lattin - Grundriss der Zoogeographie - G. Fischer, Jena, 1967, 602pp.

III

De Oosterschelde is een estuarium.

IV

Adriani en Van der Maarel (1968) maken niet voldoende aannemelijk dat een laag niveau van de „eigenlijke plantenvoedende elementen" essentiëel is voor de ontwikkeling van soortenrijke vegetaties.

M. J. Adriani & E. van der Maarel - Voorne in branding. Uitgave: Stichting Wetenschappelijk Duinonderzoek, Oostvoorne, 1968, 102 pp.

V

De uitspraak van Westhoff (1969) dat "Gause's principle" niet opgaat in gestructureerde fytocoenosen, berust op een onjuiste interpretatie van deze regel.

V. Westhoff - Verandering en duur, beschouwingen over dynamiek van vegetatie. Inaugurele rede, Nijmegen, 1969, 19 pp.

VI

Het verwaarlozen van de biomassa van de jongste stadia van een organisme bij de berekening van de produktie door sommering van de gewichtstoenames (Crisp, 1971) kan tot aanzienlijke onderschatting van de grootte van de produktie leiden.

D. J. Crisp - Energy flow measurements - In:
N. A. Holme & A. D. McIntyre - IBP-Handbook
No. 16 (1971): 197-279.

VII

Het is noodzakelijk dat een veel groter deel van de gehandicapte kinderen die in staat zijn onderwijs te ontvangen, in de normale schoolgemeenschap wordt geïntegreerd.

VIII

Davenport (1972) heeft niet voldoende aangetoond dat er een verschil in tolerantie van lage zoutgehalten bestaat tussen grote en kleine heremietkreeften (Pagurus bernhardus).

J. Davenport - Mar. Biol. (1972) 17:222-227.

IX

Trekkende vinken geven in het gebied van de Duitse Bocht een draaiing van de voorkeursrichting van zuid naar west te zien. De mogelijkheid dat dit kan worden verklaard door de invloed van in zuidelijke richting toenemende aantallen vinken met individueel een westelijke voorkeursrichting is door Perdeck (1965, 1967) ten onrechte niet in zijn verklaring betrokken.

A. C. Perdeck - Limosa (1965) 38:113-117;
Limosa (1967) 40:158-162.

X

Milieubeheersing is niet hetzelfde als milieubeheer. Daarom is het onjuist de grotere mogelijkheden tot milieubeheersing te hanteren als argument voor de afsluiting van de Oosterschelde.

XI

Artikel 19 van de Wet op de Ruimtelijke Ordening wordt op grote schaal onjuist gebruikt.

5 juli 1973,
W. J. Wolff.

THE ESTUARY AS A HABITAT

AN ANALYSIS OF DATA ON THE SOFT-BOTTOM MACROFAUNA OF THE ESTUARINE AREA OF THE RIVERS RHINE, MEUSE, AND SCHELDT

THE ESTUARY AS A HABITAT

AN ANALYSIS OF DATA ON THE SOFT-BOTTOM MACROFAUNA OF THE ESTUARINE AREA OF THE RIVERS RHINE, MEUSE, AND SCHELDT

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN
DOCTOR IN DE WISKUNDE EN NATUURWETENSCHAPPEN
AAN DE RIJKSUNIVERSITEIT TE LEIDEN,
OP GEZAG VAN DE RECTOR MAGNIFICUS
DR. A. E. COHEN,
HOOGLERAAR IN DE FACULTEIT DER LETTEREN,
VOLGENS BESLUIT VAN HET COLLEGE VAN DEKANEN
TE VERDEDIGEN OP DONDERDAG 5 JULI 1973
TE KLOKKE 16.15 UUR

DOOR

WILLEM JAN WOLFF

geboren te Eelde in 1940

LEIDEN
E. J. BRILL
1973

Promotor: Prof. Dr. D. J. Kuenen
Co-referent: Dr. M. Brongersma-Sanders

Dit proefschrift verschijnt tevens als no. 126 van de Zoölogische Verhandelingen uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden.

Aan mijn ouders
Aan Ineke

SAMENVATTING

Gedurende de jaren 1958-1970 is descriptief oecologisch onderzoek verricht aan de diergroepen die de zand- en modderbodems van de estuaria in het Deltagebied en van het aangrenzende deel van de Noordzee bewonen. Dit onderzoek is beperkt tot de grotere soorten (Coelenterata, Mollusca, Echiuroidea, Polychaeta, Archiannelida, Crustacea Malacostraca).

Met behulp van 0,1 en 0,2 m^2 Van-Veen-bodemhappers werden 1751 monsters genomen, terwijl in de getijzone enkele honderden monsters werden uitgegraven. Voorts werden aparte monsters verzameld voor de studie van interstitiëel levende polychaeten en archianneliden. Van de milieufactoren werden speciaal zoutgehalte, sedimentsamenstelling, stroomsnelheid, watertemperatuur, zuurstofverzadigingspercentage, watertroebeling, waterverontreiniging, expositie t.o.v. de golfslag en de invloed van ijs onderzocht. Het zoutgehalte vertoont een gradient van $19{,}0^0/_{00}$ Cl′ in de Noordzee tot onder $0{,}3^0/_{00}$ Cl′ in het zoetwatergetijdengebied. Het sediment bestaat meestal uit middel-, fijn of zeer fijn zand; modder- en veenbanken komen ook voor. Stroomsnelheden liggen meestal onder 1,5 m/sec. De watertemperatuur varieert in de loop van het jaar gewoonlijk tussen 1° en 22°C. Het zuurstofverzadigingspercentage ligt laag (0-70%) in de rivieren; in het brakke gedeelte van de estuaria vindt een stijging plaats tot over 100%, welke waarde bereikt wordt in de mariene gedeelten. Waterverontreiniging vertoont het omgekeerde patroon. De troebelheid van het water is het hoogst in de brakke delen van de estuaria. Het merendeel van de oevers in het Deltagebied ligt beschut tegen zware golfslag, doch de stranden langs de Noordzee liggen tamelijk geexponeerd. IJs oefent de grootste invloed uit in het zoetwatergetijdengebied. In de estuaria komt een overvloed aan voedsel voor; in de Noordzee zijn de hoeveelheden echter kleiner.

Taxonomische opmerkingen worden onder andere gemaakt over *Polinices polianus, Venus gallina striatula, Eteone foliosa, Nereis virens, Nephtys caeca, Aricidea minuta, Spio martinensis, Streblospio shrubsolii, Tharyx marioni* en *Ophelia borealis.*

Voor 2 holtedieren, 19 slakken, 44 tweekleppigen, 1 echiuride, 76 polychaeten, 4 archianneliden, 6 bloedzuigers, 15 kreeften, krabben en garnalen, 2 aasgarnalen, 8 cumaceëen, 1 tanaide, 9 isopoden, 31 amphipoden, 8 stekelhuidigen en 1 lancetvisje wordt het verspreidingspatroon in het Deltagebied in verband gebracht met de onderzochte milieufactoren of worden andere publicaties waarin dit verband is behandeld, opgesomd. Voor vele soorten is de vergelijking tussen verspreidingspatroon en milieufactoren uitgevoerd met behulp van een "maximum-likelihood" methode.

De volgende hoofdlijnen kunnen worden ontdekt in de verspreidingspatronen.

De biologische grens van het estuariene habitat kan aan de zeezijde worden geplaatst in het gebied waar de min of meer vlakke zeebodem overgaat in een topografie met getijgeulen en ondiepten. Aan de zijde van de rivier kan geen duidelijke begrenzing worden gevonden.

Het minimum in het brakke water dat wordt gevonden wanneer men het aantal soorten uitzet tegen het zoutgehalte en dat de eerste maal werd aangetoond door Remane (1934), komt ook voor in de estuaria van het Deltagebied. Het blijkt dat vrijwel alle soorten die in de brakke gedeelten van de estuaria voorkomen, ook voorkomen of kunnen voorkomen in de mariene delen van het estuarium of in zoet water. Daarom kunnen waarschijnlijk alle worden beschouwd als euryhaliene mariene of zoetwatersoorten.

De onderzochte fauna kon worden verdeeld in een relatief stenotherme component welke alleen ver van de kust voorkomt en een relatief eurytherme component die zowel voor de kust als in de estuaria te vinden is.

Van geen enkele soort kon worden aangetoond dat de verspreiding beneden de laagwaterlijn wordt beïnvloed door de hydrostatische druk. Slechts drie soorten bleken vrijwel beperkt tot de getijzone.

Vele soorten bleken beperkt te zijn tot een bepaald sedimenttype. Van de soorten die in het brakke gedeelte van de estuaria voorkomen, bleken de meeste modderige sedimenten te verkiezen. Daarom zijn soorten die als brakwatersoorten worden beschouwd in werkelijkheid waarschijnlijk vaak euryhaline bewoners van zeer fijne sedimenten.

Van geen enkele soort kon worden aangetoond dat de verspreiding rechtstreeks afhankelijk is van de mate van golfslag, doch vele soorten bleken wel indirect hiervan afhankelijk te zijn door hun binding aan een bepaald type sediment.

Waarschijnlijk worden enkele soorten in hun voorkomen negatief beinvloed door de grote troebelheid van het water. Waterverontreiniging en lage zuurstofverzadigingspercentages kunnen verantwoordelijk worden gesteld voor het ontbreken van verschillende soorten in het zoetwatergetijdengebied, doch van slechts zeer weinige in het brakke gebied.

Tekort aan voedsel is waarschijnlijk de reden dat enkele soorten die talrijk voorkomen in de estuaria, ontbreken in de Noordzee.

Het bleek onmogelijk enige biologische brakwaterindeling toe te passen op de estuaria van het Deltagebied. De eerder voorgestelde indelingen kunnen in verband worden gebracht met hydrografische onregelmatigheden van de estuaria.

De soorten die karakteristiek zijn voor het brakke gedeelte van de estuaria van het Deltagebied, blijken ook in vrijwel alle andere estuaria en brakke wateren langs de Atlantische kusten van Europa voor te komen. Enkele van deze soorten komen ook in het westelijke deel van de Middellandse Zee voor. Deze europese brakwaterfauna verschilt in haar soortensamenstelling echter vrijwel volledig van vergelijkbare brakwaterfauna's in Zuid-Afrika, Zuidoost-Azië, Nieuw-Zeeland, Noord-Siberië, de Pacifische kust van Noord-Amerika en de Atlantische kust van Noord-Amerika. Er is dus geen sprake van één kosmopolitische brakwaterfauna.

De soortendiversiteit is het laagst in de brakke delen van de estuaria en in de getijdenzone van het zoetwatergetijdengebied. Met name de zandbodems in de getijzone vertonen een gradient van een groot aantal soorten in de stranden langs de Noordzee naar vrijwel geen soorten in de zandplaten van het zoetwatergetijdengebied. Modderbodems in de getijzone en zandbodems beneden de laagwaterlijn vertonen een dergelijke gradient. Aangezien in brakwatergebieden een relatief hoog aantal uit andere werelddelen geïntroduceerde soorten voorkomt, wordt verondersteld dat de europese brakke wateren a.h.w. onderverzadigd zijn met betrekking tot het aantal soorten dat er in voorkomt.

Omnivoren zijn relatief talrijk in de brakke delen van de estuaria, zodat moet worden aangenomen dat de weinige soorten die er voorkomen relatief brede niches bezetten.

Het percentage soorten met pelagische larven neemt sterk af van de zee naar de rivier; het percentage soorten met een niet-pelagische ontwikkeling vertoont uiteraard het omgekeerde verloop.

Waterverontreiniging, troebelheid, de grootte van brakke wateren en de „kritische-zoutgehalte-hypothese" van Khlebovich kunnen niet worden gebruikt ter verklaring van het minimum aan soorten in brakke wateren. Instabiliteit van temperatuur en zoutgehalte verklaren het verschijnsel gedeeltelijk, doch een bevredigende verklaring voor de uitzonderingen wordt alleen verschaft door de „tijd-stabiliteit-hypothese" van Sanders.

Het wordt waarschijnlijk gemaakt dat de geschiedenis van de Noordwesteuropese estuaria gedurende de pleistocene ijstijden de soortenarmoede van deze estuaria voldoende kan verklaren. Voor andere brakwaterfauna's vormt de geologische geschiedenis waarschijnlijk ook een goede verklaring voor hun armoede aan soorten.

THE ESTUARY AS A HABITAT
AN ANALYSIS OF DATA ON THE SOFT-BOTTOM MACROFAUNA OF THE ESTUARINE AREA OF THE RIVERS RHINE, MEUSE, AND SCHELDT

Communication nr. 106 of the Delta Institute for Hydrobiological Research

by

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CONTENTS

1. INTRODUCTION

After the disastrous storm flood of February 1st, 1953, the Netherlands' Government decided to dam up four of the six estuaries in the southwestern part of the Netherlands, since then called the Delta area (fig. 1). By carrying out this scheme, generally known as the Delta Plan, these tidal estuaries, containing salt or brackish water, will be changed into stagnant freshwater lakes. The Delta Institute for Hydrobiological Research was founded to study the hydrobiological changes accompanying these large works (Vaas, 1961).

The present study aims to be a descriptive investigation of the soft-bottom fauna, i.e. the fauna living in and on soft sediments such as sand, clay and peat, of the Delta area before any changes occurred.

This study has been confined to the macrofauna, defined as the animals retained by a sieve with a mesh width of 1 mm. Of the Polychaeta also the meiofauna representatives have been studied. The meiofauna has been defined as those animals not retained by a sieve with a mesh diameter of 1 mm, but larger than about 100 μ.

The macrofauna was chosen because it is investigated easier than the other groups and because the species belonging to it in general offer less taxonomical difficulties.

The investigations were carried out in the Delta area and in the adjacent part of the North Sea.

The data for this study have been collected from 1958 until 1969.

The aims of this study may be defined as:

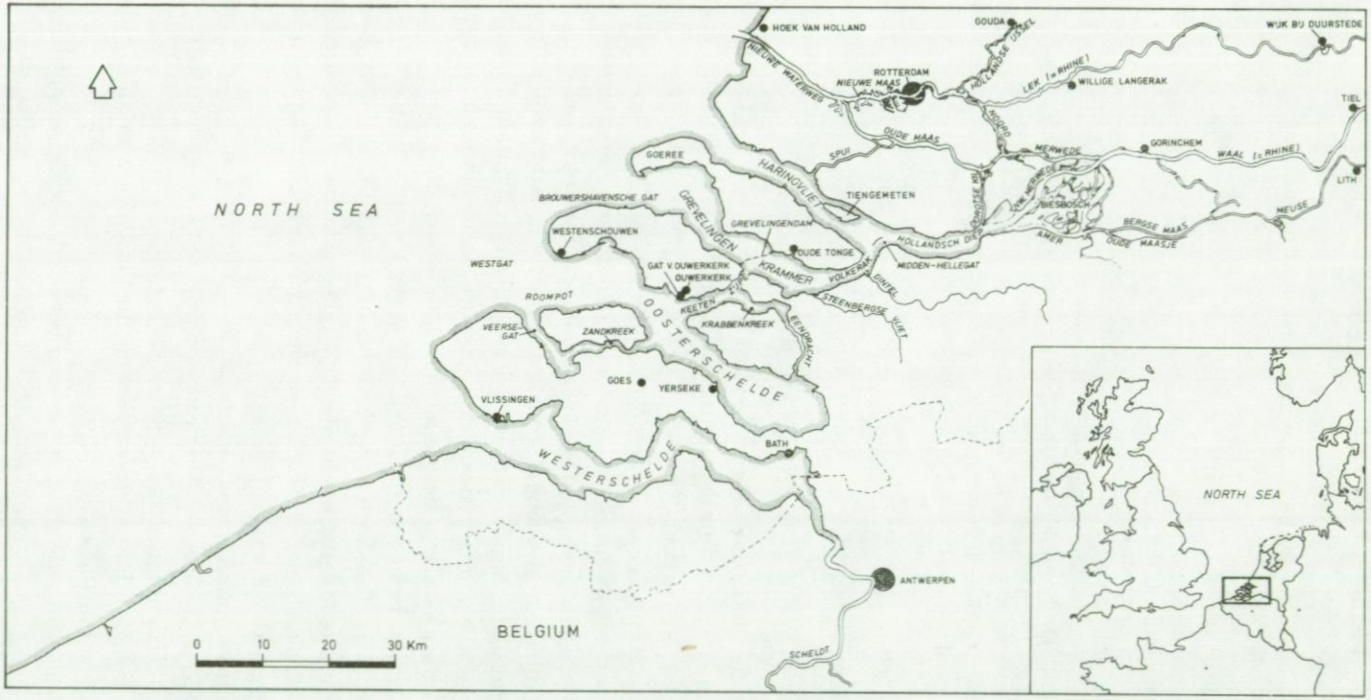

Fig. 1. Map of the Delta area. In 1960/1961 the Veerse Gat and the Zandkreek were dammed up. The resulting new lake has been called Veerse Meer (Lake Veere).

1. to list the species belonging to the soft-bottom macrofauna of the Delta area;
2. to establish the relationships with the environment of as many of these species as possible, with special reference to salinity, sediment, water movements, and climate;
3. to investigate the phenomenon that in different parts of an estuary in the same series of habitats, viz. the whole area between the high water mark and the bottom of the main tidal channel, the number of species differs widely, creating, in the brackish areas, a situation with a low number of species, in which probably either a single species occupies several niches or some niches remain unoccupied;
4. to investigate the possible causes for the paucity of species in the brackish and freshwater tidal parts of the estuaries.

Acknowledgements. — In the early part of this study the investigations were conducted by Dr. C. den Hartog and later by Mr. W. J. M. Vader, who made their data available when they left the Delta Institute. The field-work and the sorting of the samples as well as part of the identifications of the material were carried out by Messrs. L. de Wolf and A. J. J. Sandee with additional support by Messrs. P. de Koeijer, J. Nieuwenhuize and W. J. L. Robër. Messrs. J. Nieuwenhuize, A. J. J. Sandee and J. van Liere analyzed the sediment samples. Mr. C. de Rooij, captain of the institute's research vessel, directed the grab-sampling. Dr. D. Eisma offered hospitality aboard the vessels employed by the Netherland's Institute for Sea Research for offshore sampling. Mrs. C. H. Borghouts and Dr. K. F. Vaas made available additional data on the fauna of the Delta area.

Messrs. C. Bakker, Dr. W. G. Beeftink, P. H. Nienhuis, R. Peelen, and F. Vegter and Dr. M. Bilio (Marine Biological Institute, Venice) provided environmental data and gave advice on their fields of knowledge. Mr. E. Meelis (Institute for Theoretical Biology, Leiden) helped with the mathematical treatment of the data and wrote the computer programs.

Mrs. C. H. Borghouts (Yerseke), Dr. K. Fauchald (Los Angeles), Dr. M. Glémarec (Brest), Dr. G. Hartmann-Schröder (Hamburg), Mr. G. R. Heerebout (Leiden), Prof. Dr. L. B. Holthuis (Leiden), Dr. J. van der Land (Leiden), Dr. A. D. McIntyre (Aberdeen), Dr. M. H. Pettibone (Washington), Dr. C. O. van Regteren Altena (Leiden), Prof. Dr. J. H. Stock (Amsterdam), Dr. N. Tebble (London), Mr. R. M. van Urk (Leiden), Mr. W. J. M. Vader (Bergen), Dr. W. Vervoort (Leiden), and Dr. W. Westheide (Göttingen) helped with the identification of the material.

Miss E. C. Kanaar and Mrs. E. S. Nieuwenhuize typed the various drafts

of the manuscript, whereas Messrs. J. van de Ende and A. A. Bolsius prepared the drawings. Mrs. C. H. Borghouts, Mrs. Dr. M. Brongersma, Prof. Dr. D. J. Kuenen and Dr. K. F. Vaas read the manuscript critically and gave many valuable suggestions. Dr. K. F. Vaas improved the English translation.

The author would like to present his sincere thanks to all mentioned, but he feels that special thanks are due to Messrs. A. J. J. Sandee and L. de Wolf, who did the larger part of the field and laboratory work, and to Dr. K. F. Vaas, who encouraged this study as much as possible.

2. METHODS

2.1. Sampling methods

As pointed out by Holme (1964) the choice of a grab has to be based on: 1) the size, density, and habits of the animals to be collected; 2) the nature of the sediment; 3) the size of the ship and facilities for working heavy gear. Therefore, the Van Veen grab was chosen for these investigations.

It has, however, several disadvantages, viz.:

1) Rapidly moving animals may escape the grab and may normally not be be caught (Thorson, 1957). Although fast-moving animals, for instance *Ammodytes, Crangon,* and mysids, regularly were caught, it is difficult to ascertain how large a proportion of such animals escaped.
2) The grab used sampled 0.1 m^2, digging only to a depth of about 15 cm maximally. Normally, however, it will not dig deeper than about 10 cm, which means that deeper burrowing animals, for instance large *Arenicola marina* and *Mya arenaria* will not be caught.
3) On very hard sandy bottoms and on bottoms of stiff clay the grab will only dig a few centimeters. However, the clay bottoms, consisting of subfossil clay layers eroded by the tidal currents, never contain burrowing animals. Consequently this disadvantage of the grab is not important here. In cases when judging from the volume of sand in the grab, it had dug only a few centimeters into a sand bottom, the sample was discarded. Fortunately, the larger part of the animals seems to live in the topmost few centimeters of the sediment, so the majority of the species is most probably sampled adequately. Beukema (1971) observed for a 0.2 m^2 Van Veen grab that the species living in the surface layers were sampled with an efficiency of nearly 100%, whereas the deeper living species were caught with an efficiency of about 80%.
4) Sometimes samples contained too small a volume of sediment, because the grab did not hit the bottom in the right way, owing to drifting of the ship by the tidal currents. Such samples always were discarded.

5) According to Wigley (1967) the Van Veen grab produces a shock wave when it is lowered, resulting in tiny animals being pushed away in front of the sampler. This effect may be important on muddy bottoms with slight water movements. In the tidal Delta area, however, nearly all animals live inside tubes or buried in the sediment, where they will not be washed away by the tidal currents, nor by the shock wave of a bottom grab. Some observations on this effect were made by SCUBA-divers, who also did not notice that animals were pushed away. This is in accordance with the observations by Lie & Pamatmat (1965).

It may be concluded that the Van Veen grab is a reasonable instrument to sample the bottom fauna of the estuaries of the Delta area, but it has to be borne in mind that fast-moving and deep-burrowing animals may not be sampled quantitatively.

Finally it should be emphasized that the jaws of the Van Veen grab approach each other horizontally when closing rather than digging a semicircular cut (Lie & Pamatmat, 1965; Gallardo, 1965). This means that animals from all depths in the sediment are equally well represented in the samples, and also that it is better to use a unit of area for comparison than a unit of volume.

The grab samples were sieved aboard through two sieves with mesh widths of 2 and 1 mm diameter, respectively, while water was sprayed over the sample. Often a rocking apparatus was used to carry out the sieving rapidly.

On the upper 2 mm sieve large animals, remains of plants and pieces of peat were retained; the animals were picked out aboard. On the second 1 mm sieve a residue of animals, plant remains, and other small objects was retained; this residue was collected as a whole to be sorted in the laboratory. However, Reish (1959) found that through an 1 mm sieve many species of polychaetes disappeared. This problem seems to be less serious for molluscs and malacostracan crustaceans.

The sediment of the estuaries of the Delta area nearly always passes without difficulties through the 1 mm sieve.

To take an intertidal sample a fixed area was dug out and sieved through a 1 mm sieve in a nearby pool. The residue was freed from empty shells and taken to the laboratory to be sorted. The sampling depth usually was about 25 cm, except when large specimens of *Mya arenaria* or large polychaetes were present: these were dug out. The area of surface sampled varied in relation to the nature of the locality investigated. In muddy sands and in muds of brackish and marine areas usually a sample of 0.05 m^2 was taken. In sandy sediments in the marine and brackish areas the area of the samples sometimes was fixed at 0.25 m^2, because the number of individuals is smaller in such areas. In the freshwater tidal area sometimes an area of 1 m^2 was sampled, but in these cases the depth of the samples was less, being about 5 cm.

To sample the interstitial meiofauna the method described by Boaden (1963) was used.

For observations in the sublitoral environment SCUBA-divers sometimes assisted.

2.2. Sorting and preservation of the samples

Directly after sampling a small quantity of neutralized formalin 40% was added to the samples, covered beforehand with some water from the locality sampled.

The samples preserved in this way were sorted by hand in the laboratory. After sorting most of the animals were preserved in alcohol 70 %, except for the amphipods which were preserved in neutralized formalin 4%.

2.3. Measuring methods for the environmental factors

2.3.1. Introduction

The following environmental factors were measured: the grain-size distribution of the sediment, the amount of organic matter in the sediment, the salinity of the interstitial water, and the depth of the sample in relation to low or high water level.

Data on hydrography of the Delta area, including information on river discharges, tidal differences, current velocities, salinity and turbidity, were mostly derived from the extensive literature available in connection with the large engineering works of the Delta Plan. Data on salinity, turbidity, and oxygen saturation of the Delta waters also were derived from studies of colleagues of the author, particularly Messrs. C. Bakker, R. Peelen and F. Vegter. Methods to measure the exposure to waves will be discussed in paragraph 2.3.5.

2.3.2. The grain-size data

From samples procured by bottom grabs a small subsample was always taken for sediment analysis (about 200 gr.). In intertidal sampling this subsample was mostly taken just outside the area sampled. From the samples used for the study of the interstitial fauna the sediment subsample was mostly taken from the top of the sediment after the animal sampling had been finished. The subsamples from the bottom grabs mostly consisted of three or four still smaller samples taken at random from the main sample.

The sediment sample from intertidal localities also consisted of several smaller samples taken at various depths, unless the layering of the sediment proved to be inhomogeneous.

For the determination of grain-size distributions a series of graded sieves was used. Folk (1966) concluded that sieving is more accurate than other methods. The mesh width of the sieves adopted by various workers, however, varies greatly. Although at first this seems to present a difficulty for comparing the results of their investigations, as was believed by Morgans (1956), this may be overcome by expressing the grain-size distribution as a median grain-size, combined, if necessary, with a sorting coefficient.

Before sieving the samples were dried in a stove at 105°C, but as was advocated by Morgans (1956), not treated otherwise. Of these dried samples a quantity of known weight was sieved through a series of graded sieves with mesh diameters of 1000, 600, 420, 300, 210, 150, 105, and 75 μ, respectively, during 10 minutes. Although Krumbein (cited from Morgans, 1956) believes that dry sieving is the best method, the more muddy samples had to be sieved wet. A large, well-mixed sample was tested for differences originating from different "treatments". The results are summarized in fig. 2.

It may be concluded that the grain-size distribution of the sample investigated is already determined after about 2 minutes of dry sieving. Using the wet sieving method the grain-size distribution of the sample was also known

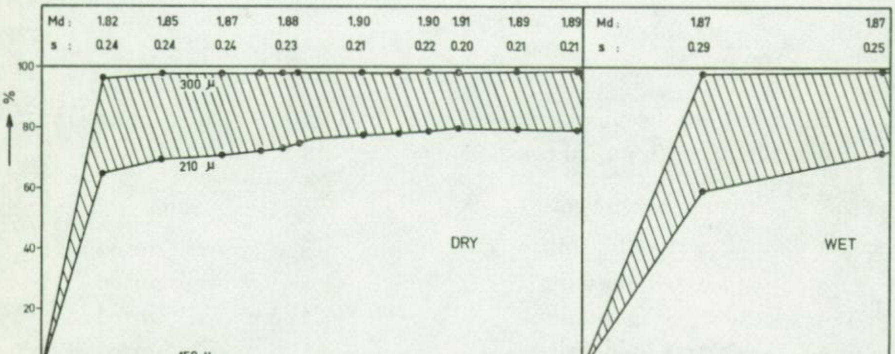

Fig. 2. Influence of prolonged sieving on the grain-size distribution. The vertical axis shows cumulative weight percentages; the horizontal one the time of sieving applied. The left part shows the results of dry sieving; the right part wet sieving. The values obtained for median grain-size (Md) and sorting coefficient(s) after different periods of sieving are shown in phi-units on the top rows.

after 1-2 minutes. Therefore, wet or dry sieving during 10 minutes certainly gives valuable information for sandy sediments.

The results of an analysis by means of graded sieves have been expressed in the phi notation where $\varphi = -\log_2$ of the ratio between the diameter of the grains in millimeters and a standard grain diameter of 1 millimeter (Inman, 1952; McManus, 1963). A comparison between microns and phi-units is given below. The percentage frequencies of the various grain-size classes are plotted cumulatively against the limits of the classes which are expressed in phi-units, to obtain the median diameter of the grain-size distribution. The distance between the places where the cumulative graph crosses the values of 16% and of 84% is nearly equal to two times the standard deviation. Therefore half this value has been taken as a good approximation of the standard deviation of such nearly normal distributions. This standard deviation constitutes a measure for the sorting of a sediment.

The quantity of particles $<75\,\mu$ has been used as a measure for the amount of silt and clay present. Partly in accordance with the Wentworth-scale the following names are used for the sediments of the Delta area:

median diameter between		name
phi-units	microns	
0—1	500-1000	coarse sand
1—2	250- 500	medium sand
2—3	125- 250	fine sand
3—3.75	75- 125	muddy sand
>3.75	<75	mud

The following terminology, partly derived from Folk (1966), is used for the rate of sorting of the sediments:

Sorting coefficient	name
<0.35 phi-units	very well sorted
0.35-0.50 phi-units	well sorted
0.50-2.00 phi-units	less well sorted
>2.00 phi-units	poorly sorted

2.3.3. AMOUNT OF ORGANIC MATTER

The quantity of organic matter was determined from the same samples as used for the determination of the grain-size data. A wet oxidation method, viz. the method of Kurmies, being a modification of the method of Schollenberger, was used in this investigation (Mebius, Dekker & Ten Have, 1957).

It is especially suitable for marine soils because there is no need to correct for loss of carbonates and for loss of constitutional waters of soil colloids. The errors introduced by the presence of ferrous minerals, and by the loss of sodiumchloride proved to be unimportant after extensive experiments (Mebius et al., op. cit.). The analysis runs as follows:

A known quantity of well ground sediment, with less than 150 mg organic matter, is brought into a boiling tube of 250 ml, and 40 ml concentrated sulphuric acid is added. During 10 minutes the tube is shaken a few times; after this 25 ml of a 2 N potassium dichromate solution is slowly added, while the tube is cooled. Then the tube is heated for 1½ hour in a bath of boiling water and gently shaken each quarter of an hour. After cooling, water is added to 250 ml and the contents are mixed. When the mineral parts of the sediment have settled, 25 ml of the solution is pipetted into a beaker glass containing 25 ml of 0.22 N solution of ferrous ammonium sulphate. The surplus is titrated with a 0.1 N solution of potassium permanganate, until the first colour change from green to blue-green. Addition of 5 ml of a 2 N solution of $BaCl_2$ can make this titration easier. A blank determination without soil is carried out in the same manner. The percentage of organic matter than is calculated as follows:

$$\frac{(a\text{-}b) \times 0.3 \times 1.724 \times f}{g} = \%\ \text{organic matter}$$

with a = ml 0.1 N potassium permanganate used for the sample, b = ml 0.1 N potassium permanganate used for the blank, f = Kurmies factor and g = gr. soil.

The Kurmies factor was established to be 1.03; it represents the ratio between the percentage of organic matter obtained by the method of loss-on-ignition and that obtained by the Kurmies method. It was found empirically by Mebius et al. This is also true for the factor 1.724 which represents the ratio between the total percentage of organic matter and the percentage of carbon. Presumably this factor is too low, particularly for sandy sediments. Nevertheless it has been maintained because it gives at least the minimal values of organic matter present. The factor 0.3 results from the reagents used in this method.

The most important drawback of this method is that it presents a more or less exact figure, but that it is unknown what relation exists between this figure and the quantity of matter which actually can serve as food for animals.

2.3.4. THE INTERSTITIAL WATER

The most simple method for sampling interstitial water is burrowing a hole in the sediment and collecting the inflowing water. This was often done to gain an insight into the general salinity conditions of a sediment rapidly. Salinity then may be determined by titration.

For more detailed studies another method, described below, was adopted. The samples required for this method were obtained from various depths in the sediments by a corer. For each depth in the sediment about 10 subsamples were combined into one main sample. The latter was brought to the laboratory in a closed plastic bag for analysis. The routine starts with very thoroughly mixing of the soil sample. From the resulting "cake" two subsamples are taken and brought into 150 ml bottles. After weighing, the bottles with their contents are dried at 105°C until constant weight. After cooling the sample is weighed again. From the loss of water a figure may be calculated for the amount of water per 100 gr of stove-dry soil.

After this a small spoonful of gypsum (free of chlorides) and 75.0 ml of water are added to the sample. Then the bottles are closed and shaken during 4-8 hours. When this is finished the bottles have to stand for at least 12 hours to let the sediment settle down. From the clear upper layer of fluid 10.0 ml are pipetted into a beaker glass. K_2CrO_4 is added as an indicator and the sample is titrated with 0.1000 N $AgNO_3$ until faint red. From this titration and the weighings a figure may be obtained, which represents the amount of sodiumchloride per l of soil water.

2.3.5. EXPOSURE TO WAVES

To obtain comparative data on the exposure to wave-action of the shores of the Delta area the method described by Baardseth (1966) has been employed. This method is based on the assumption that exposure is related to the amount of open sea around a certain place, because there exists a relation between the height of the waves and the length of the fetch of the wind.

In this study Baardseth's method was modified as follows. For each locality along the shore it was determined on a coastal map how many degrees of a circle were lying entirely over open sea for at least 100 km (the distance to the English coast is only slightly more). Localities of 20 or more degrees have been considered as semi-exposed, contrary to the others which were classified as sheltered.

This procedure has been carried out for the low-tide situation and for the high-tide situation separately, because many offshore shallows uncover during falling tide, thus interrupting the waves from the North Sea.

2.4. MATHEMATICAL METHODS

Various statistical methods have been employed when making a choice between alternative hypotheses (De Jonge, 1964). To describe the abundance of a number of common species in relation to certain environmental factors a mathematical model has been developed by Mr. E. Meelis (Institute for Theoretical Biology, Leiden University), who also wrote the computer program. The details of this model will be given below. The unknown parameters occurring in the model are estimated by the maximum likelihood estimates. The computations were carried out by means of the I.B.M. 360-50 computer of the Leiden University.

The habitat of the subtidal environment of the Delta area, — where the grab-samples were taken —, has been divided into a number of environmental classes. This division has been based on watertype (comprising salinity, rate of change of salinity, percentage of dissolved oxygen, turbidity and pollution), median grain-size of the sediment and sorting of the sediment. This resulted in twelve classes based on water type, four on median grain-size and two on sediment sorting, combined into $12 \times 4 \times 2 = 96$ environmental classes (section 5.1.). Some of these classes have not been sampled or even do not exist in the Delta area.

For each species considered, it has been assumed that at a certain moment the eggs, larvae, or whatever other stage of dispersal may occur, will be extremely abundant and occur in groups of unknown size, the members of one group reacting in the same way to the environment. No assumptions have been made about the size or the frequency distribution of such groups.

The 12 water classes will be represented by the index i; $i = 1, 2 \ldots\ldots 12$; the four classes of the median grain-sizes by j; $j = 1, 2, 3, 4$; the two classes of the sediment sorting by k; $k = 1, 2$.

The environmental classes will be denoted as (i, j, k) for the sake of simplicity.

Let $N_{i,j,k}$ be the number of groups of dispersion stages in the population of dispersion stages in the Delta area that are potential adults in a future grab-sample in the environmental classes (i, j, k).

Let $p_{i,j,k}$ be the chance that a random chosen group of this population will be represented as at least one adult in a future grab-sample, then $1\text{-}p_{i,j,k}$ is the chance that no adult of the group considered will be found in this grab-sample.

It has been assumed that the groups of dispersion stages are stochastically independent, in a sense that the success in development of one group will not influence the success of another group of the population. When the surface area of the sample is relatively large as compared to the size and number of developing dispersion stages, this assumption will be approximately justified.

Thus, the chance that no adult of the species considered will be found in a grab-sample, equals

$$(1 - p_{i,j,k})^{N_{i,j,k}}$$

It has further been assumed that 1) for each group the chance to produce at least one adult (= the chance to be represented in a grab-sample) differs for the various environmental areas in accordance with unknown constants; 2) the three environmental factors considered (watertype, median grain-size, sorting) are mutually independent in their influence upon the development towards adulthood; 3) the chances of a successful development are approximately inversely proportional with the number of groups in the population mentioned above; or: the expected number of adults does not depend on the number of dispersion groups, but solely on the environmental factors.

Therefore, the chance $p_{i,j,k}$ may be written as:

$$p_{i,j,k} = \frac{\alpha_i \beta_j \gamma_k}{N_{i,j,k}}$$

wherein $\alpha_1, \alpha_2, \ldots\ldots \alpha_{12}, \beta_1, \beta_2, \beta_3, \beta_4, \gamma_1$ and γ_2 represent the ratios of the chances to find at least one adult of a randomly chosen group of the population above in a grab-sample in the various environmental classes.

The chance to find no adult of the species considered in a grab-sample then is:

$$(1 - p_{i,j,k})^{N_{i,j,k}} = \left[1 - \frac{\alpha_i \beta_j \gamma_k}{N_{i,j,k}} \right]^{N_{i,j,k}} \approx e^{-\alpha_i \beta_j \gamma_k},$$

where e = 2.71828.....
Therefore, the chance to find at least one adult of the species considered is

$$1 - e^{-\alpha_i \beta_j \gamma_k}$$

The unknown parameters $(\alpha_1, \alpha_2 \ldots\ldots \gamma_2)$ are estimated by likelihood estimates.

For *Macoma balthica* the actual observations of the number of times this species was represented in the samples have been compared with the values which could be computed as an estimate of this frequency of occurrence based on the estimates of $\alpha_1 \ldots\ldots \gamma_2$. These frequencies did correspond to a very large degree.

By means of a likelihood ratio test (Wilks, 1966) it could be concluded then, that within the frame-work of a more general model, this model with only a small number of parameters provides in fact a very good description of the occurrence of the species. In the more general model it is supposed that each environmental combination has its own parameter, e.g. $q_{i,j,k}$ denoting the chance of at least one adult in a grab-sample in class (i, j, k). The hypothesis tested is

$$q_{i,j,k} = 1 - e^{-\alpha_i \beta_j \gamma_k} \text{ for } i = 1, .., 12; j = 1, .., 4; k=1, 2.$$

One of the main conclusions to be drawn from this circumstance is that the environmental factors listed up to a certain degree are mutually independent in their influence on the development of *Macoma balthica.* Also for several other species the correspondance between observed values and the values predicted on the base of the model described above, is very impressive. Hence, this model apparently may be applied to a large number of species. Nevertheless, for some species the predicted values deviate considerably from the observed ones. This may be caused by either invalidity of the model or by interference by some environmental factor not represented in the model.

For some species the computer program devised to calculate the constants $\alpha_1 \ldots\ldots \gamma_2$ did not work, owing to the large number of zero observations. In these cases some of the watertypes and sediment classes with no or very few observations were left out of consideration.

Within the frame-work of the model described above the following hypotheses have been tested by means of a likelihood ratio test (Wilks, 1966; especially p. 402 and further).

The first hypothesis tested is that for one species the values for γ_1 and γ_2 are identical ($\gamma_1 = \gamma_2$).

The second hypothesis tested is that of two different species the corresponding parameters are identical ($\alpha_1 = \alpha'_1$; $\alpha_2 = \alpha'_2 \ldots\ldots \gamma_2 = \gamma'_2$).

The results of these tests will be discussed in chapter 5 .

3. THE ENVIRONMENT

3.1. WEATHER AND CLIMATE

The Delta area has a climate strongly influenced by the vicinity of the sea. This results in absence of extreme temperatures and precipitation values (Table 1).

Frost is rather a rare phenomenon in the Delta area. At Vlissingen (Flushing) temperature falls on the average only on 31 days a year below zero. Here also the monthly average of the daily minimum temperatures is above 0°C for all months of the year. On the other hand, only 10 days a

TABLE 1

Average monthly temperatures in centigrades at Goes, calculated for the period 1901/30 (Den Hartog, 1959a) and average monthly water temperatures in the Oosterschelde, calculated for the period 1921/30 (Korringa, 1941).

	air	water		air	water
January	2.9	3.0	July	16.7	19.1
February	3.2	2.9	August	16.4	18.8
March	5.2	4.9	September	14.1	16.6
April	7.9	8.5	October	10.4	12.1
May	12.4	13.3	November	5.7	7.1
June	14.5	16.9	December	3.6	3.6

year the maximum temperature exceeds 25°C at Vlissingen (Van der Sluijs, Steur & Ovaa, 1965).

There are no important differences in temperature between the various parts of the Delta area.

During the period of sampling two more or less aberrant years occurred. Firstly, the summer of 1959 was very warm and dry. The average temperatures for the months of June, July, August, and September were 15.7°C, 18.5°C, 18.5°C and 16.8°C, and the precipitation was low during this period (compare Table 1). This warm and dry summer was favourable for the breeding of many southern species.

In the second place the winter of 1962/1963 was extremely cold. The average temperatures for the months of December, January, February, and March were +1.5°C, —4.1°C, —2.5°C, and +4.0°C (compare Table 1). During 44 days temperature did not rise above zero. This winter had a disastrous effect on many species. Several even disappeared for many years from the Delta area, for instance the polychaete *Nephtys cirrosa* and the snail *Brachystomia scalaris*.

The average yearly precipitation is 689 mm, the larger part falling in the second half of the year (Van der Sluijs, Steur & Ovaa, 1965). This amount has no significant, direct influence on the salinity of the estuaries, although an indirect influence may be felt through the increased discharges (Korringa, 1941).

Winds from the West, the South-West, and the South occur during about 50% of the year. Therefore, the estuaries of the Delta area, with their main axis approximately in the direction NW-SE, are protected to a high degree against the influences of the wind. The beaches along the North Sea proper are most exposed to the wave-action caused by the wind.

Winds with an average velocity surpassing 50 km/h are observed along the coast of the Delta area on 50 days a year (Van der Sluijs, Steur & Ovaa, 1965). More landinward the number of such days decreases strongly.

3.2. THE MORPHOLOGY OF THE DELTA AREA

The Delta area may be thought to be built up by five main estuaries (fig. 1), all with their main axis about ESE-WNW. Their morphology has been described by Peelen (1967, 1969). His data, together with some data on the offshore area, will be summarized below.

1. The Nieuwe or Rotterdamse Waterweg has been dug in the period 1864-1868 in order to provide an acces to the sea for the port of Rotterdam. Nowadays the average depth varies between 15 and 20 m; shallows emerging during low tide hardly occur and only very small salt-marshes and reed-beds may be found along the edges. The width varies and is, on the average, slightly more than 500 m. This estuary is fed with fresh water from the Rhine through the branches Lek—Nieuwe Maas, Waal—Merwede—Noord—Nieuwe Maas, and Waal—Merwede—Oude Maas.

2. The Haringvliet—Hollands Diep is the main estuary of the Rhine and the Meuse. The length of the area with brackish water is about 40 km; the freshwater tidal area with alternating tidal currents occupies another 35 km. The width varies between 2 and 4 km. The maximal depth is about 45 m, but at low tide only 15% of the remaining area of water is deeper than 10 m. The outlet to the North Sea is very shallow with an uninterrupted sandbar at a depth less than 4 m lying across the outlet. During low tide large areas of shallows emerge.

This estuary has two unimportant side-branches, the Spui and the Dordtse Kil, and one extremely important branch, the Volkerak, to be discussed in the next paragraph. The Haringvliet—Hollands Diep estuary is fed with fresh water from the Rhine via the Waal—Nieuwe Merwede, and from the Meuse via the Bergse Maas—Amer. At the head of the estuary and at the confluence of the branches Nieuwe Merwede and Amer the large freshwater tidal area of the Biesbosch is found. The width of the Nieuwe Merwede is about 900 m, of the Amer nearly 800 m, their maximal depths are 12 m and 20 m, respectively. At low tide less than 1% of the remaining area of water has a depth over 10 m. Along the edges of Haringvliet—Hollands Diep estuary large salt-marshes, reed-beds and willow-coppices occur.

3. The Grevelingen—Krammer—Volkerak system may be considered as a branch of the Haringvliet—Hollands Diep system. Its length is about 55 km, its width varies between 7.5 and slightly more than 1 km. Its maximal depth is 45 m, but at low tide only 17.5% of the remaining area of water is

deeper than 10 m and only 6% deeper than 20 m. At low tide about 43% of the area covered with water at high tide emerges as sandy and muddy shoals. Some salt-marshes are found along the edges.

4. The Oosterschelde estuary is about 50 km long and has a width varying between 9.2 and 3 km. The maximal depth is 49 m, but at low tide only 33% of the remaining area of water has a depth over 10 m and only 6.5% over 20 m.

The channels Keeten, Zijpe, Krabbekreek, Eendracht, and before 1961 also Veerse Gat and Zandkreek may be considered as branches of the Oosterschelde. In general their width is smaller, but their depth is considerable, because about 10% of the area with remaining water at low tide is deeper than 20 m.

During low tide about 43% of the Oosterschelde area covered with water during high tide emerges as shallows. Along the edges of the estuaries relatively small areas of salt-marshes occur.

5. The Westerschelde estuary has a length of about 80 km up to Antwerpen, where the boundary of the brackish water area usually is found. Its width varies between 7.8 km and about 1 km. The maximal depth, also the maximal depth of the Delta area, is 57 m. At low tide about 45% of the remaining area of water has a depth over 10 m and only about 6% over 20 m.

During falling tide about 40% of the area covered with water during high tide emerges as shoals. Extensive salt-marshes occur at a few places along the edges of the estuary.

6. The offshore area. Offshore of the Delta area the bottom of the North Sea gently slopes down in a westerly direction. Near the shore a pattern of shallows and tidal channels is still found, but this situation abruptly ends at about 5-15 km offshore. The depth contour of 10 m below low water spring level approximately limits the region with an estuarine topography. West of this border several sand-banks still occur, but they are part of the subtidal marine environment.

3.3. Substrate and sediments

3.3.1. Types of sediments and substrate

Only loose sediments occur in the Delta area. Rocks are absent, and only a few isolated boulders occur offshore in the North Sea (Jarke, 1955).

The types of soft sediments occurring in the Delta area are enumerated in paragraph 2.3.2. Additional categories are the substrates formed by peat and by live or dead organisms.

Peat is found in small banks in places where the tidal currents erode older layers, often at depths of about 2-5 m. In the same localities subfossil clay layers also often occur.

Shells and shell fragments also may be important as a substrate. Empty shells and shell fragments behave to some degree like sediment grains, and may be concentrated at places with strong currents (Postma, 1957). This, however, is a rare phenomenon in the Delta area; shell gravels are only found in the Roompot and in parts of the Westerschelde. More important

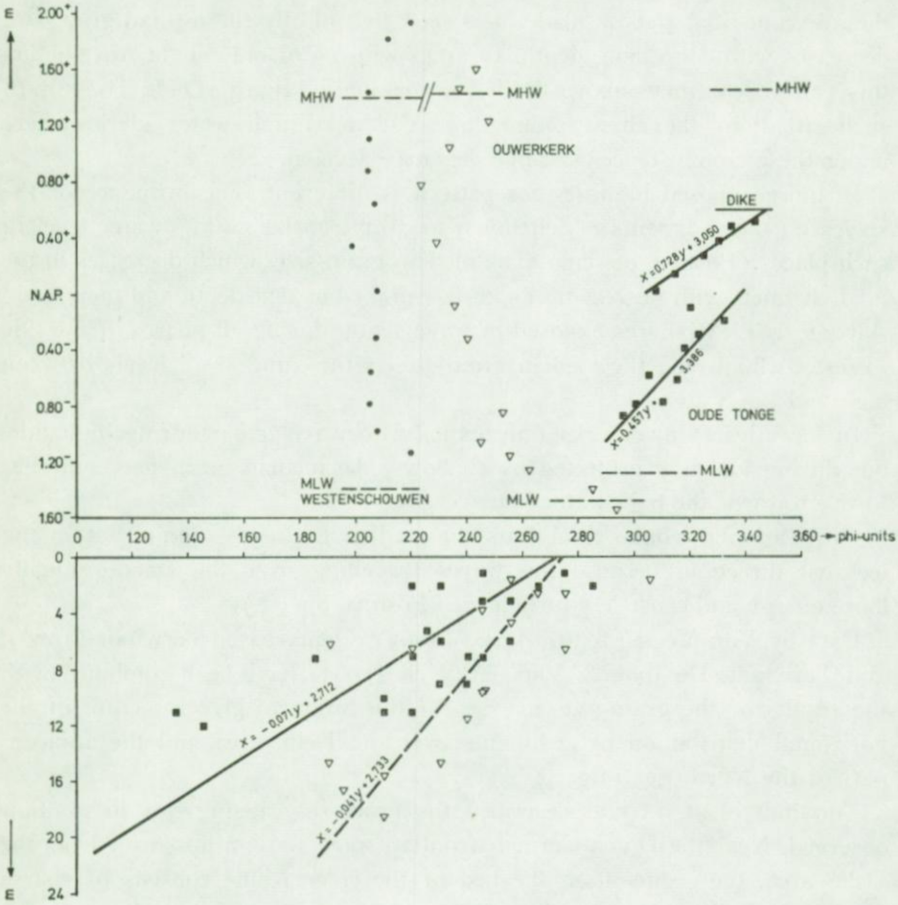

Fig. 3. Vertical distribution of the median grain-size on tidal flats and in tidal channels: near Oude Tonge (■, solid line), near Ouwerkerk (▽, dashed line) and near Westenschouwen (●). The median grain-size, expressed in phi-units, is represented horizontally. The level with regard to Dutch Ordnance Datum (NAP) is shown vertically in the upper part of the figure, whereas the depth below mean low water level is shown in the lower part. The vertical scale of both parts is not equal.

as a substrate are the oyster- and musselbeds; Korringa (1951) gave a detailed description of their importance as a substrate.

3.3.2. Distribution of sediments

Postma (1957) has shown that the sediment distribution in an estuarine area is governed by wave action as well as by the currents. The coarsest sediments are found in the deepest parts of the tidal channels, where the highest current velocities prevail. When a cross-section of such a channel and the adjacent tidal flats is made, it is seen that ideally the median grain-size decreases with decreasing depth. In areas with no or only slight wave-action this pattern continues above the low water mark (fig. 3; Oude Tonge). In such situations the finest sediments occur near high water mark, where under these circumstances salt-marshes may develop.

In more exposed localities the pattern is different. The influence of the waves on the sediments is felt down to 1 or 2 m below low water level in such places (Postma, op. cit.). The median grain-size, which decreases in the tidal channels with decreasing depth, is minimal at that depth and then again starts to rise. At shores exposed to wave-action during all phases of the tide (Westenschouwen), the median grain-size is the same at all levels between high and low water.

In localities (Ouwerkerk) only exposed to wave-action during high tide, but during low tide protected by shallows, the median grain-size continues to rise towards the high water line.

On nearly horizontal tidal flats the median grain-size diminishes in the leeward direction, because the waves travelling over the flats gradually loose energy and cause less turbulence (Postma, op. cit.).

Data by Van Veen (1936), Jarke (1955), Oomkens & Terwindt (1960), and Terwindt, De Jong & Van der Wilk (1963) have been combined with the results of the grain-size analyses of this study to give a picture of the horizontal distribution of sediments over the Delta area and the adjacent part of the North Sea (fig. 4).

Terwindt et al. (1963) described the processes causing the distribution observed. Near the Dutch-German frontier, some 100 km upstream from the Delta area, the sediment in the bed of the river Rhine consists of coarse sand and small pebbles (median diameter — 1.00-0.00 φ), which are transported downstream. Near the fluvial tidal zone the transporting power of the river diminishes, owing to the regular slowing down of the current velocity under the influence of the tides. Only the finer fractions of the sediments still are transported and, consequently, the bed of the river consists of finer sediments (median grain-size 0.00-1.00 φ). This trend of a declining median grain-size is continued in the zone forming the transition to the estuarine zone of the river. In this transitional zone reversing currents already occur, but the upstream currents are still too weak to cause a transport of sand in this direction. It is only in the estuarine zone of the river that the flood current is able to transport sandy sediments, a process favoured by the occurrence of a wedge of salt flood water near the bottom of the gully in the middle reaches of the estuary. The importance of this inshore transport and the grain-size of the material transported increase towards the sea, and this determines to a large degree the distribution of sediments in an estuarine area. Thus, larger φ-values are found when going downstream along the river, but also when going upstream along the estuary. Hence, a maximum in the φ-values is to be expected and this is found in the area of the Hollands Diep and the eastern part of the Haringvliet, where very fine sands occur (Terwindt et al., 1963).

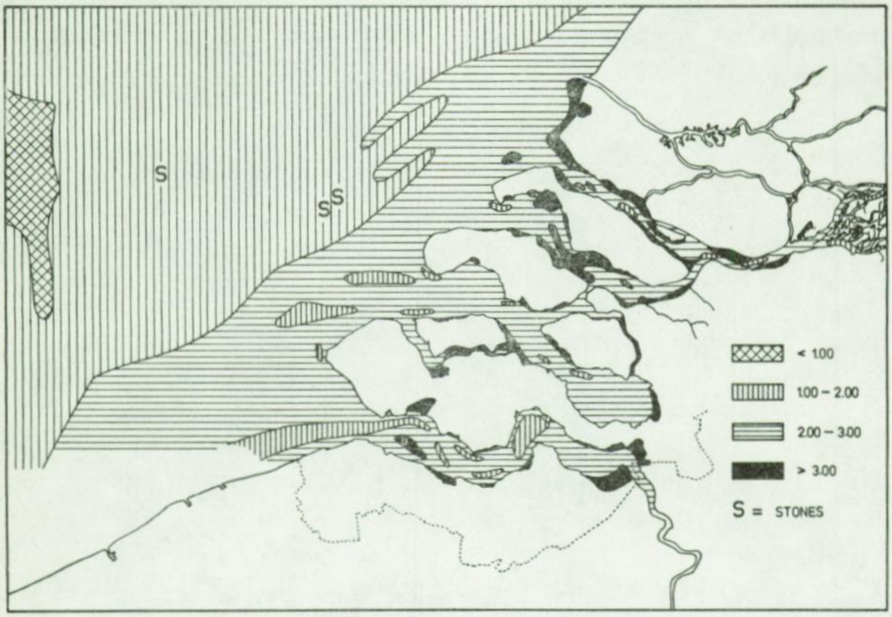

Fig. 4. Simplified horizontal distribution of sediments in the Delta area. The limits of the grain-size classes are expressed in phi-units.

In the other estuaries of the Delta area this pattern of sediment distribution is not so clear, but a trend of rising φ-values when going inshore, may be observed. The lowest φ-values occur at the entrances of the estuaries near the North Sea. Just outside these entrances, the values are higher again, but further to the West the φ-values are declining continually.

To summarize, coarse and medium sands occur offshore in the North Sea, fine sands in the area just outside the beaches and fine sands intermingled with medium sands in the entrances of the estuaries. Further inward fine sands occur which eventually change into muddy sands, and even into true muds still further upstream. Medium sands are found upstream in some very deep gullies. Intertidally, the median grain-size of the sediment is also influenced by the exposure to wave-action. According to Krumbein, whose findings were summarized by Newell (1970), there exists a linear relationship between the mean particle size of a sediment and the amount of wave-action. The occurrence of sandy beaches indeed is restricted to the semi-exposed shores (fig. 18).

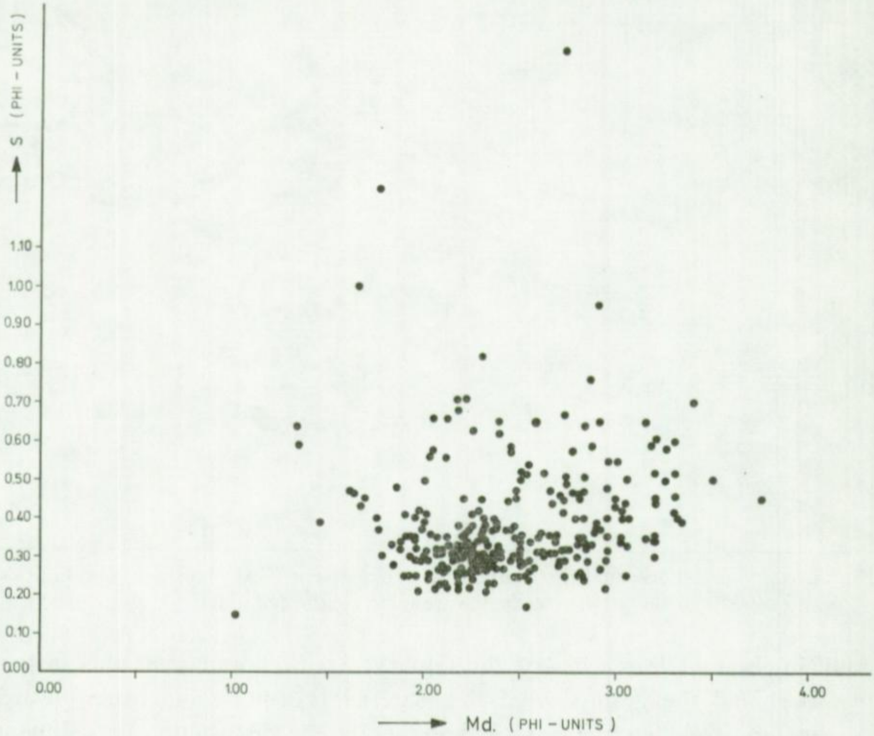

Fig. 5. Relation between median grain-size (Md) and sorting coefficients (s) for sediments from the Oosterschelde.

It has to be stressed that fig. 4 only presents an overall picture. In more or less homogeneous areas large deviations from the "normal" values regularly occur, but, of course, could not be shown in the map. For all correlations between the fauna and the sediment, use has been made of the data calculated for each sample separately.

3.3.3. SORTING OF SEDIMENTS

Although the sorting of sediments is determined by many factors, it is nevertheless possible to distinguish some general trends. The best sorting occurs at the inlets of the estuaries and along the beaches, where sorting coefficients under 0.30 phi-units are normal. However, in the North Sea proper the sorting coefficient usually is over 0.40 phi-units. Within the estuaries the sorting coefficient occupies a large range. Very well sorted sands with coefficients under 0.25 phi-units occur, but also poorly sorted sediments. In the brackish area of the Haringvliet and in the freshwater tidal area of the Hollands Diep and the Biesbosch the less well and poorly sorted sediments even preponderate, although very well sorted sands still occur. Insufficient data are available on the sorting of the sediments occurring in the rivers. The sands sorted best appear to be those with a median grain-size of about 2.50 φ (fig. 5), probably because this size of grains is most easily moved by the currents (Sanders, 1958).

3.3.4. IMPORTANT CHARACTERISTICS OF SEDIMENTS

3.3.4.1. WATER CIRCULATION

Water movements in sediments are caused by hydraulic gradients, which may be set up by the tides, by waves and by currents; their magnitude and velocity are governed by 1) the size of the grains, 2) the arrangement of the grains, 3) the sorting of the grains, and 4) the shape of the grains. For the study of watermovements in sediments these characteristics may be expressed by the porosity and the permeability. Porosity may be defined as the ratio between the volume of the voids and the total volume of the sediment; permeability as the rate of water flow through the sediment per unit of time (Callame, 1963). Although these parameters probably should be determined directly, as was done by Webb (1969), it was in this study only possible to infer them from the grain-size distributions as follows.

1) Theoretically, for spherical grains of uniform size, the porosity of a sediment is independent of the diameter of the grains, since the ratio between the volume of the voids and the volume of the spherical grains is independent of the diameter of the grains. This was confirmed experimentally by Webb (1958). Permeability, however, is not primarily dependent on porosity, but on pore size. A decreasing grain-size is connected with a decreasing pore size and thus means a decreasing permeability. In fact, permeability is proportional to the square of the diameter of the grains, which means for natural sediments that increasing φ-values for the median diameter (Md) are correlated with a strongly decreasing permeability, but do not influence

porosity. It has to be noted, however, that in clayey sediments porosity may become higher due to bridging effects, but, owing to the very small pore size, permeability remains negligible.

2) However, for uniform spherical grains porosity is influenced by the arrangement of the grains. Such grains in a cubic arrangement show a porosity of 47.64%, but similar grains in a rhombohedral arrangement have a porosity of only 25.95%. Hence, the most stable arrangement may contain the smallest volume of water. Experimentally, the water contents of saturated "sediments" always proved to be higher than that of a sediment with a rhombohedral arrangement. It may be concluded that sediments with a simple and uniform arrangement do not occur in nature (Graton & Fraser, 1935). The arrangement of a sediment is very difficult to determine, since it may already be disturbed by normal sampling procedures. Some indications, however, may be derived from studies on porosity. Ruttner-Kolisko (1962) mentions a porosity of 40% ± 3% as normal for natural sands in the range 200-2000 μ. Webb (1958) found values between 32 and 38%; Salvat (1967) between 34 and 45%. Webb (1969) published an important study on the relation between the arrangement of the grains, the porosity and the permeability. In a series of experiments he found a very clear linear relationship between the decreases of porosity and permeability when the arrangement of the grains was tightened by ultrasonic vibration. When more angular grains were present in the sediment, or when very different sizes of grains were mixed, one or two abrupt changes in the slope of these linear relationships occurred, probably corresponding with a new orientation of the grains. Webb (op. cit.) used the slope of the line representing the ratio between permeability and porosity at about maximum porosity as a new parameter called specific permeability, and found it to be correlated very significantly with the distribution of *Branchiostoma* and an interstitial copepod. Although Webb also was not able to determine the arrangement of natural sediments, he, nevertheless, has been able to estimate its effects. From his data it appears that the arrangement has a marked effect on porosity and permeability and it is regretted that his paper did not appear before the sampling for this study was finished. Therefore, it is assumed that the arrangements of the natural sediments studied were lying somewhere in between the possible extremes, and, hence, were comparable, thus causing no important differences in porosity and permeability.

3) The influence of the sorting of a sediment is difficult to quantify. Fraser (1935) and Callame (1963) arrived at the conclusion that porosity of a sediment is maximal at a maximal uniformity of the grains; it decreases as a function of the amount of deviating grains. This was confirmed experi-

mentally by Webb (1958, 1969), who found that mixing of very different types of sand resulted in very low porosities. The influence of sorting on permeability is more difficult to find out, but this may be attempted by imagining a sediment composed of uniform spherical grains in a rhombohedral arrangement. Such a sediment has a sorting coefficient of 0.00 phi-units. Now a normally distributed sediment with the same median diameter, but with a larger sorting coefficient (for instance 0.10 phi-units) may be imagined. In such a sediment the original rhombohedral arrangement will be drastically upset, because the grains do not fit each other. The small grains are generally not small enough (less than 0.414 times the diameter of the large grains: critical ratio of occupation (Graton & Fraser, 1935)) to fit in between a number of large grains without disturbing the arrangement. This will result in an arrangement with larger pores and, hence, a larger permeability. When, at the same median grain-size, the sorting coefficient is increased still more (up to, for instance, 1.00 phi-units) another effect becomes important. The number of small and very small grains (smaller than 0.164 times the diameter of the larger grains — critical ratio of entrance —, thus able to block the pores) then becomes very significant, and, moreover, much larger than the number of large and very large grains. The very small grains, with mainly a diameter below the critical ratio of entrance of the large grains, then become so overwhelming in number (— the normal distribution from which the sorting coefficient is derived, is based on weight percentages —) that they may block the pores to a very large degree. The pore size thus becomes less and, hence, permeability too. The conclusion may probably be drawn that also in natural sands of a certain median diameter with an increasing sorting coefficient permeability first increases, but later decreases. Indications for this phenomenon may be found in Webb (1969), who added different amounts of large and small grains to a uniform grade of sand. Although this also changes the median grain-size, nevertheless small quantities of slightly deviating grains already cause an increase of capillary space and hence of permeability as well. Unfortunately, it was not possible to determine exactly the value where the increase in permeability changes into a decrease.

4) The last factor influencing porosity and permeability is the shape of the grains. Webb (1958) experimentally found indications that sediments with rounded grains had a higher porosity than those with angular grains. With more angular grains however, the average pore size increases, causing also an increase in permeability. Fraser (op. cit.) and Callame (op. cit.) stated that the most angular sediments are not more than two or three times as permeable as a perfectly rounded sediment. However, for reasons of time

this factor has been left out of consideration in this study, although it is known that in the Delta area the river sands are more angular than the marine sands.

Before drawing a final conclusion it is useful to look at Webb's (1969) conclusions. He found that small differences in the grain-size distribution falling within the limits of accuracy of normal sieving procedures, may cause a doubling of his important parameter of specific permeability. This means that sands with similar median grain-sizes and sorting coefficients may vary considerably with respect to their actual permeability. On the other hand, permeability decreases with the square root of the diameter of the grains, and this dominates the other effect, as was proved experimentally by Webb (op. cit.). The influence of the other features of the grain-size distribution, however, will probably partly be obscured by the characteristics observed by Webb, and therefore the influence of the sorting coefficient only may become apparent when very large numbers of data are considered. Webb (1969) showed also that the organic epipsammic films on the sand grains influence the properties of the sediments. In most cases these organic constituents cause a decrease of the permeability and an increase of porosity.

The conclusion, therefore, has to be drawn that permeability increases with increasing median grain-size (decreasing φ-values) but that it may not easily be predicted from the grain-size distribution at similar median grain-sizes.

Various authors, for instance Webb (1958) and Clark & Haderlie (1960), related permeability to the percentage of silt or small grains. Webb, for instance, noted that the addition of 0-40% of "fine" sand to a medium-grade sand caused a parabolic decrease of the permeability. It has to be pointed out, however, that such an addition causes important changes in the parameters applied in the present study, viz. an increase of the sorting coefficient as well as a decrease of the median grain-size. Both these parameters may influence independently the permeability and therefore it seems better not to combine them into one parameter. On the other hand, it may be argued that the use of the former parameters is based on the assumption of a normal distribution, and that, therefore, these ought not to be applied to bimodal distributions, often occurring when a sand is mixed with a certain amount of mud. Therefore, to characterize such distributions use has been made of the percentage of particles $<75\,\mu$ as a measurement of its permeability and other characteristics. It is, however, clear that a large amount of mud or fine sand also will be reflected in the values calculated for the median grain-size and the sorting coefficient.

Permeability governs water circulation and this factor strongly influences temperature within the sediment, availability of oxygen in the interstitial water, salinity of the interstitial water, and availability of food in the interstitial environment.

However, water circulation does not occur without hydraulic gradients.

In the intertidal zone the tidal movements may set up such gradients causing waterflow through the sediment, because the water table within the sediment is displaced. Waves may do the same (Riedl & Machan, 1972). During this process the permeability of the sediment exercises a great influence upon the velocity and the magnitude of the water circulation.

In permanently submerged sediments, however, mostly no hydraulic gradients occur. Webb & Theodor (1968, 1972), however, revealed an important process acting upon the watercirculation within subtidal sediments. They found that turbulence and differences in hydrostatic pressure at the sea bed resulting from the passage of surface waves (height 50 cm trough to crest in a waterdepth of 3 m) caused a flow of water through the sand affecting the unconsolidated upper layer of a coarse sand. Riedl, Huang & Machan (1972) quantified the importance of this proces. Another observation was made by Fenchel (1969) who found that a laminar waterflow of 8 cm/sec was felt down to a depth of 0.5 cm in a medium sand (Md = 1.55 φ). In the deeper parts of the estuaries out of reach of the influence of the waves, the oxygen supply of the sediment is completely dependent on this process and on diffusion from the overflowing water. Of course also all other exchanges are dependent on this process. The porosity of the sediment then governs the rates of diffusion.

3.3.4.2. INTERSTITIAL TEMPERATURE

In general it can be stated that the annual as well as the diurnal temperature variation is most extreme in the upper layers of the sediment and rapidly diminishes towards the deeper layers. The higher situated parts of the tidal flats also have a more extreme variation than the lower parts, which on their turn are more extreme than the subtidal sediments. In the Delta area depth below low water level hardly influences the temperature regime owing to the mixing of the water by the tides.

The nature of the sediment also is very important for the amount of temperature variation within a sediment. Linke (1939) showed that changes in temperature proceed at least two times quicker in sandy than in muddy sediments, probably because in the former the heat is conducted by waterflow which is much slower in muddy sediments (compare sub-paragraph 3.3.4.1.).

3.3.4.3. INTERSTITIAL SALINITY

According to Smith (1956) the salinity of the interstitial water of intertidal sediments is the result of the salinities of the overflowing water and of the period of emersion. It is certainly not the average of the salinities of the overflowing water. This point was also stressed by Reid (1930, 1932) and Sanders, Mangelsdorf & Hampson (1965) who found that fresh water could be driven out the sediment by salt water, but that the reverse is more difficult. The result is that the interstitial water has a higher salinity than the average salinity of the overflowing water. It is possible that part of this higher salinity may be explained by ion adsorbtion on the grains.

Sanders et al. (1965) investigated the relation between the depth in the sediment and the amplitude of the variation in salinity of the interstitial water. They found that in very soft muds this amplitude decreased very strongly with increasing depths, from about 95% of the amplitude of the overflowing water in the surface layers to nearly zero at 5 cm depth. They assumed that such diurnal salinity changes would penetrate deeper in coarse, porous sands, but less deep in hard-packed stiff muds. Therefore, it may be assumed that in the Dutch estuaries the extreme diurnal variations occur exclusively in the topmost few centimeters of the sediment. The annual fluctuations, however, probably may be felt also at larger depths.

To study these diurnal and annual fluctuations an investigation into the interstitial salinity of three types of sediment was carried out on a flat in the Krammer area.

To study the annual fluctuations samples were taken once a month during 15 months at three sampling plots with different types of sediment (fig. 6). Unfortunately it was not possible to choose all sampling plots at the same tidal level. Plot A with a median grain-size of 2.50-2.57 φ had a period of emersion of about 8-9 hours; plot B with a median grain-size of 2.90-3.07 φ a period of about 4-5 hours and plot C had a period of about 3 hours and a median grain-size of 3.27-3.30 φ. Hence, the median grain-size in microns decreases together with the period of exposure.

The salinity of the water flowing along these sampling plots was measured daily at high tide at about 2 km downstream, making a maximal difference of about $1.5\,^{0}/_{00}$ Cl′. The upper part of figure 6 depicts the average salinity of the overflowing water, during the week before the sampling. The lower part of figure 6 shows the salinity of the interstitial water at each of the three sampling plots mentioned above. For each plot the salinity in three different layers is shown: 0-5 cm, 5-20 cm, and 20-40 cm.

At the sandy plot A the interstitial salinity fluctuates widely at all three levels. In the less sandy plot B the amplitude of the salinity fluctuations is less, but still considerable. In the muddy plot C the situation is much more stable. At 20-40 cm depth the salinity fluctuates only between $14.50\,^{0}/_{00}$ Cl′

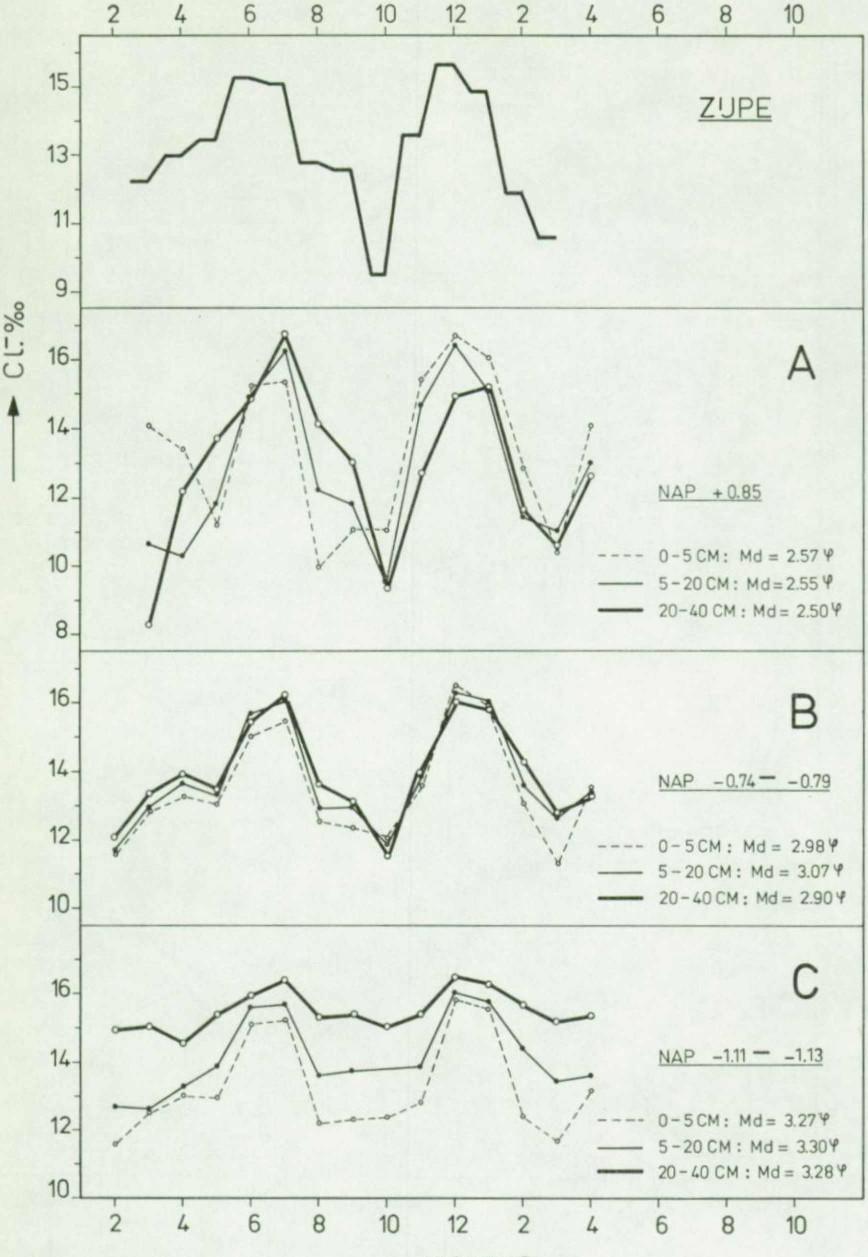

Fig. 6. Annual fluctuation in interstitial salinity of three sampling plots near Oude Tonge. The upper part of the figure shows the salinity of the overflowing water measured at Zijpe (about 2 km downstream) at high tide and averaged over the week before the observations at the three sampling plots were made. The lower parts show the interstitial salinity at three sampling plots in three different depth layers.

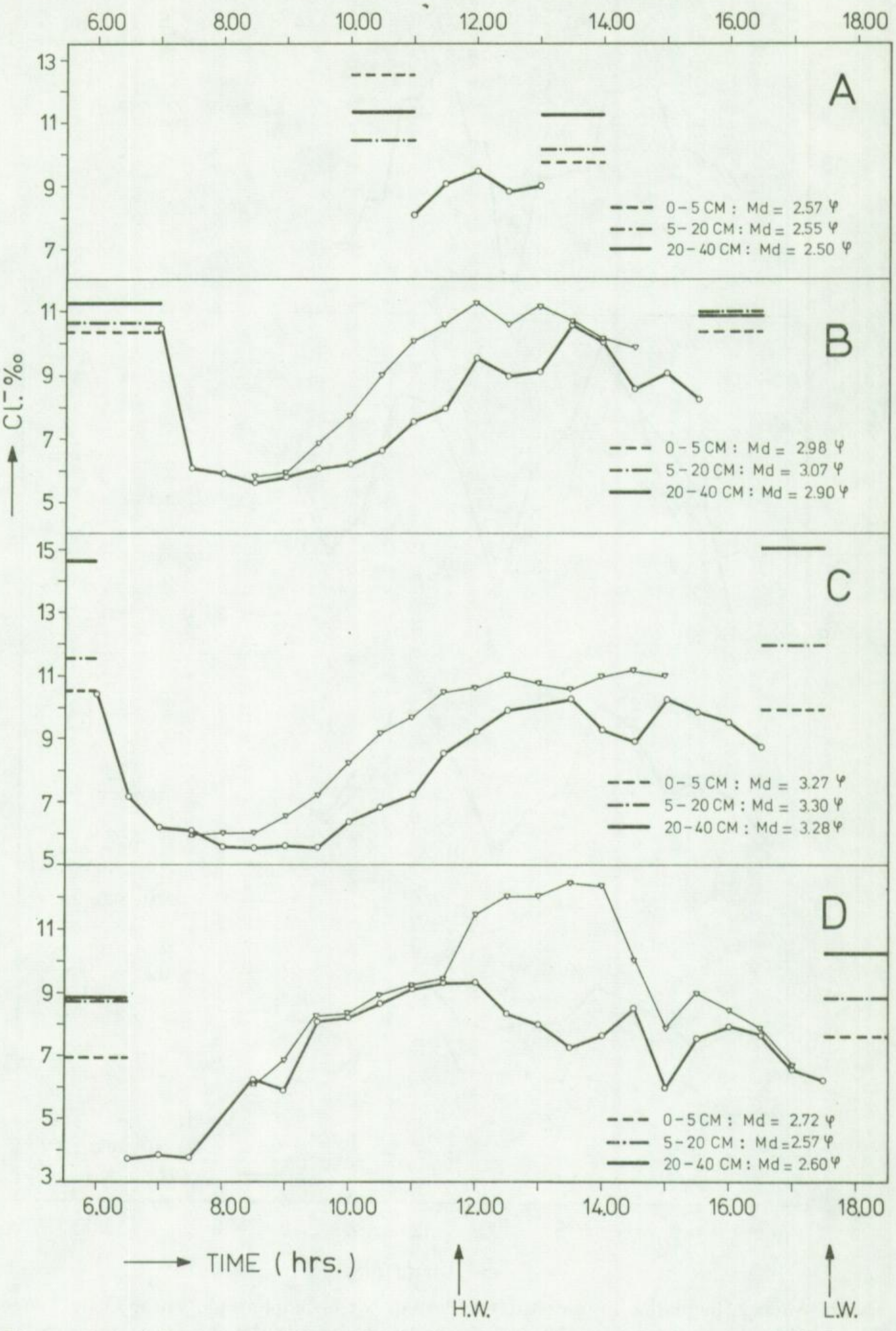

Fig. 7. Diurnal fluctuation of interstitial salinity of four sampling plots near Oude Tonge. Shown is the interstitial salinity at three different depths within the sediment before and after submersion, and the salinity of the overflowing water, measured near the bottom (thin line) and near the surface (thick line).

and 16.48$^0/_{00}$ Cl′. In the higher sediment layers the fluctuation is larger, but still does not reach the extreme values of plot A. It may be concluded that in sandy sediments the annual fluctuations of the salinity of the overflowing water exercise their influence much more thoroughly and deeper than in muddy sediments.

An impression of the diurnal fluctuations was gained at the same sampling plots plus plot D with a median grain-size of 2.57-2.72 φ and a period of emersion of 3-4 hours. The interstitial salinity was measured at each plot in three different layers before submersion (fig. 7). During the period of submersion the salinity of the overflowing water was measured each half hour at the surface and near the bottom. After emersion the interstitial salinity was measured again in the same way.

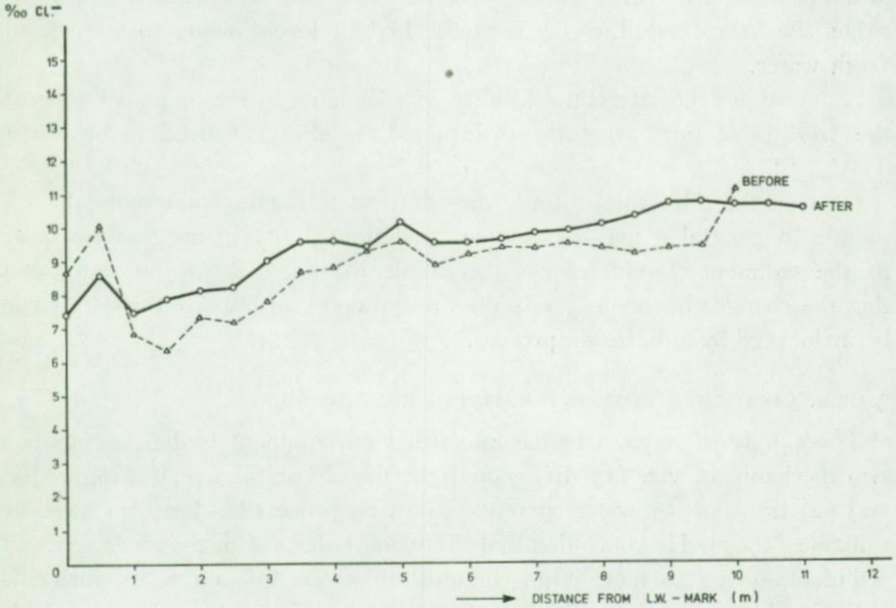

Fig. 8. Relation between tidal level and interstitial salinity in the tidal flats near Oude Tonge. Determination of salinity was carried out just before and just after the period of high water shown in fig. 7D. The vertical distance between high and low water mark was about 3 m, the horizontal distance, which is shown, about 12 m.

The main conclusions from these measurements are that (1) the interstitial salinity of the topmost layers of the sandy sediments may vary considerably but that no important changes occur in the other layers, and (2) the interstitial salinity of all layers lies higher than the salinity of the water flowing over the sampling plot during the last part of the period of submersion. This is in agreement with the conclusions reached by Reid (1930, 1932) who found that it is difficult to replace salt water in the soil by overflowing water with a lower salinity.

As in an estuary the saltest water occurs during high tide, it may be expected that in sandy sediments the highest interstitial salinities may be found near the high water mark, because the salinity of the overflowing water just before uncovering becomes less with decreasing tidal level. Indeed this could be found in a traverse from plot A to plot D (fig. 8), where the highest interstitial salinities occurred at the highest level. In localities along the North Sea, however, especially on beaches before a dune-ridge, the lowest salinities occur at the highest levels owing to seepage of fresh water.

A few times the interstitial salinity of sediments in the intertidal zone of the freshwater tidal area was determined. It always proved to be under $0.2^0/_{00}$ Cl′.

Data on the interstitial salinity are difficult to obtain from subtidal sediments. In general it may be assumed that the salinity in the topmost layer of the sediment closely follows the salinity of the overflowing water, but that the changes in the deeper layers are unimportant because these only can be influenced by a diffusion process.

3.3.4.4. OXYGEN IN THE INTERSTITIAL ENVIRONMENT

The supply of oxygen to the interstitial environment is dependent upon two mechanisms, viz. (1) diffusion from the air or the overflowing water, and (2) transport by water currents. The first process has been reviewed by Callame (1967). He concluded that diffusion is largest in the finer types of sediment, owing to their large contents of water. Of course, diffusion is only possible via the interstitial water, which diminishes the surface available for the diffusion process with a large percentage. As diffusion, moreover, is a slow process, counteracted in the sediment by the consumption of oxygen by bacteria and other organisms, it is understandable that in estuarine sediments with their relatively large amounts of organic matter, diffusion only may allow for oxygenation of the topmost few millimeters of a sediment. This conclusion was also reached by Teal & Kanwisher (1961) for the muds of a Georgia salt-marsh. It has to be stressed that diffusion is dependent on porosity, not on permeability.

In the estuarine sediments of the Delta area the transport of oxygen by interstitial water currents seems much more important. These currents are dependent on permeability, not on porosity (see sub-paragraph 3.3.4.1.). Brafield (1964, 1965) and Jansson (1967) arrived also at the conclusion that the oxygen supply of similar sediments depended chiefly on waterflow. Brafield (op. cit.) was able to correlate the oxygen availability at 5 cm depth in sandy beaches positively with a factor influencing permeability, viz. the amount of small grains in a sediment. He found significant correlations between oxygen content and the weight percentage of grains smaller than 250 μ and 125 μ, respectively, but failed to discover a significant correlation between oxygen content and the median grain-size, although indications for a correlation with the rate of sorting were found. Probably, this failure has to be ascribed to the comparatively small number of sediments investigated by this author and the extremely wide range of median grain-sizes and sorting coefficients of these sediments. Jansson (op. cit.) was able to demonstrate the positive effects of water flow, and hence of permeability, on oxygen supply in the field. Without doubt the conclusions reached above may be applied to the sediments of the Delta area. A check on this may be provided by the depth of the black layer, resulting from the activity of sulphur bacteria, causing the fixation of sulphides as ferrous sulphides. The upper boundary of this black layer is not completely identical with the lower limit of the oxygenated zone (Fenchel, 1971), but their depths are very well correlated. It was always found that the depth of the black layer correlated well with the median grain-size of the sediment, and, therefore, the latter parameter may be considered as a rough indication for the oxygen contents of a sediment. In general, sandy sediments are deeply oxygenated (5-40 cm), whereas muddy sediments are oxygenated only very superficially. Contrary to Brafield (1964), no important influence of the rate of sorting was found, but the differences in the rate of sorting in the Delta area are far less than in the sediments investigated by Brafield.

3.3.5. ORGANIC MATTER

Organic matter in sediments may consist either of live organisms or of detritus. In most methods of determination, the method applied in this study inclusive, both components will be measured.

Deposition of organic detritus may be expected in areas with slight water movements, and, hence, in areas where the finer grades of sediment tend to be found. Thus, a positive correlation between the median grain-size of a sediment (in φ-units: negative for microns) and the percentage of organic matter in the sediment may be expected.

Moreover, it has been argued that dissolved organic matter in seawater tends to be concentrated by adsorbtion to surfaces (ZoBell, 1943), thus providing quantities of organic matter large enough to be used by bacteria.

This also may be true for sediment surfaces. Wood (1965) indeed has shown that micro-organisms tend to adhere to fine sediment particles and a positive correlation between the contents of organic matter and the median grain-size of sediments in φ-units has been demonstrated often (Southward, 1953; Rullier, 1959; Newell, 1965, 1970; Longbottom, 1970). Meadows & Anderson (1968) indeed demonstrated the existence of a rich microflora on sediment grains. Later (Anderson & Meadows, 1969) they concluded, however, that no relationship could be found between bacterial numbers and particle size. As they remarked, this could be due to disturbing factors acting in the intertidal zone where they collected their samples. This becomes more probable, because Hickel & Gunkel (1968) found a good correlation between the number of bacteria and the median grain-size of sediments with higher numbers in finer sediments. Also Newell (1965) found evidence for a similar relationship. From this the tentative conclusion may be drawn that in subtidal sediments the number of bacteria is correlated positively with the internal surface area of the sediment. Fenchel (1969) computed this internal surface area for a number of sediments and found a linear relationship between the logarithm of this internal surface area and the median grain-size in φ-units (which is also a logarithmic parameter). Because Hickel (1969) demonstrated a high and significant positive correlation between bacterial number and the percentage of organic matter in the sediment, such a correlation also may be expected to occur between median grain-size as a parameter of internal surface area and the percentage of organic matter.

This hypothesis was tested for a large number of sediment samples taken in the second part of November 1968 from all over the Delta area. A statistically significant correlation between median grain-size and the logarithm of the weight percentage of organic matter was found for sediments originating from five different areas, viz. the Grevelingen ($r = 0.70$; $n = 14$), the Keeten-Krammer-Volkerak area ($r = 0.59$; $n = 13$), the Oosterschelde ($r = 0.65$; $n = 26$), the western part of the Westerschelde ($r = 0.66$; $n = 14$), and the eastern part of the Westerschelde ($r = 0.57$; $n = 10$). Fig. 9 presents the regression lines of these five relationships. Longbottom (1970) found a similar correlation.

A covariance analysis showed that the slopes of these lines did not differ significantly but that their general level did. This means that, although a relationship between median grain-size and contents of organic matter can be demonstrated for certain restricted areas, the median grain-size cannot be used as an overall measurement of the percentage of organic matter in the sediment. This becomes even more evident when the relationship between median grain-size and organic contents in the Haringvliet area is considered. In three hydrographically differing stretches of this estuary the correlation coefficient was 0.02 (n = 25), 0.34 (n = 12), and — 0.11 (n = 10), respectively, none of which is statistically significant. Apparently,

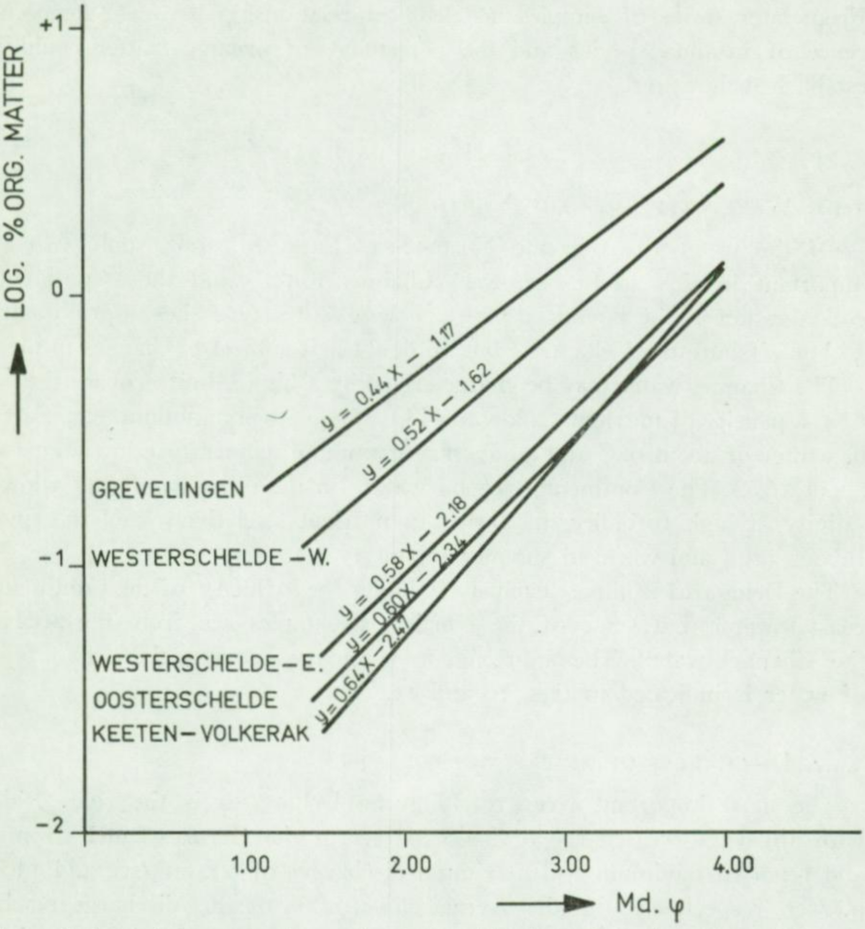

Fig. 9. Relation between median grain-size in phi-units and the logarithm of the percentage of organic matter in sediments. Shown are the regression lines for five areas where a statistically significant correlation could be detected.

the amount of organic matter in the sediments of this estuary, where the influence of river discharge is felt most directly, is determined by other processes than in the more marine parts of the Delta area. The fact that bacterial numbers in sediments may differ 10 — to 100 — fold in the course of a year (Hickel, 1969) is another warning against the use of median grain-size as a parameter of organic contents. Indeed, Longbottom (1970) found seasonal variations in the amount of organic matter. The percentage of organic matter in a sediment apparently has to be determined directly and has not to be inferred from the grain-size data. Unfortunately, the earlier samples for this study have not been subjected to direct determination. From later series of samples no clear-cut relationship between the occurrence of infauna species and the percentage of organic matter could be established, however.

3.4. Hydrography

3.4.1. Water types of the North Sea

Of the water types in the North Sea (Laevastu, 1963) only two are important in this study, viz. the "Channel water" and the "Continental coastal water". The boundary between these water types lies approximately 30 km offshore the Delta area, but no doubt it is subject to changes in place.

The Channel water may be characterized by a high salinity (over 18.5 $^0/_{00}$ Cl'), a paucity of nutrients, a low turbidity, an average minimum temperature in winter of about 6°C and an average maximum temperature in summer of about 16°C. The Continental coastal water, on the other hand, has a lower salinity, a high turbidity, it is rich in nutrients, relatively cool in winter (about 3°C) and warm in summer (about 17°C).

The Delta area is almost exclusively under the influence of the Continental coastal water, but some of the North Sea samples are from the area of the Channel water. The approximate boundary between these two types of water is indicated in figs. 10 and 11.

3.4.2. Discharges of rivers and polders

The most important river reaching the Delta area is the river Rhine with an average discharge of 2200 m^3/sec at the German-Dutch frontier and reported minimum and maximum discharges of 600 m^3/sec and 13000 m^3/sec, respectively. On the average about 90% of this discharge reaches the Delta area along the branches Lek (about 400 m^3/sec) and Waal (about 1600 m^3/sec). The water from the Lek reaches the North Sea through the Nieuwe Waterweg. The Waal, however, branches again and until 1969 (compare paragraph 3.4.13) about 880 m^3/sec reached the Hollands Diep, whereas the remaining volume of water mainly flowed to the North Sea along the Nieuwe Waterweg.

The average discharge of the river Meuse is 330 m^3/sec with observed maximum and minimum discharges of 3000 m^3/sec and less than 10 m^3/sec, respectively. This average discharge of the Meuse unites with the average 880 m³/sec from the Waal, thus constituting an average discharge of over 1200 m³/sec through the Hollands Diep (Peelen, 1967). Until 1969 an average freshwater discharge of about 50 m³/sec branched off from the Hollands Diep through the Volkerak (Peelen, 1969), but the larger part reached the North Sea through the Haringvliet.

To the freshwater discharge of the Volkerak an insignificant quantity (about 15-20 m³/sec on the average) of water from the small rivers Dintel and Steenbergse Vliet was added. The resulting 65-70 m³/sec reached the North Sea until 1964 through the Grevelingen-Brouwershavense Gat (compare paragraph 3.4.13), but, after the closure of the secondary dam in the Grevelingen, through the Oosterschelde.

The average discharge of the Westerschelde is about 90 m³/sec with maximum and minimum discharges of 500-600 m³/sec and less than 10 m³/sec, respectively.

To the enormous river discharge the freshwater discharge from the polders has to be added. The polder discharge, especially from low-lying areas, however, is more or less brackish due to seepage. The average fresh water discharge of the polder areas, however, may be calculated from the difference between evaporation and precipitation. It has been found that the freshwater discharge from the polder areas, averaged over the whole year, is maximally a few m³/sec even for the largest islands of the Delta area. Compared to the enormous discharges of the rivers this quantity is insignificant and may be left out of consideration. The same is true for precipitation in the open water, also because the yearly evaporation from a free surface is nearly equal to the yearly precipitation (Van der Sluijs, Steur & Ovaa, 1965).

Locally and during short periods, however, precipitation and polder discharge may have some influence on the salinity and other characteristics of the water of the estuaries.

3.4.3. TIDES

The tides of the Delta area belong to the semi-diurnal type with high and low water twice a day. The vertical difference between neap and spring tides is at Vlissingen about 35% of the range at spring tide.

The tidal amplitude differs throughout the Delta area. Along the shore of the North Sea the mean amplitude decreases from 3.90 m at Vlissingen to 1.74 m at Hoek van Holland, with intermediate values in between.

In the estuaries the mean tidal amplitude becomes slightly larger in a landinward direction, reaching for instance 4.53 m at Bath and about 1.90 m near the Biesbosch area.

During average river discharge the vertical component of the tidal movements could be observed until 1969 upstream as far as Wijk bij Duurstede along the Lek, Tiel along the Waal, Lith along the Meuse (further propagation of the tidal wave is inhibited by a barrage) and Gent along the Scheldt. Den Hartog (1963) called this the tidal limit. Alternating tidal currents could be observed until 1969 as far as Willige Langerak in the Lek and Gorinchem in the Waal. This limit was designated by Den Hartog as the "stuw" limit. Between this limit and the tidal limit the riverflow twice a day slows down, but does not reverse. Terwindt, De Jong & Van der Wilk (1963) called this area the fluvial tidal zone.

3.4.4. Currents

In general, maximum current velocities in the Delta area vary between 0 and 2.0 m/sec (Anonymous, 1951), but in the main gullies the maximum current velocity usually lies between 0.7 and 1.5 m/sec.

The highest maximum current velocities usually are found at the entrances of the tidal inlets with a rapid decline towards the North Sea and a slow decline in a landinward direction. The maximum current velocities during a tidal cycle near the Biesbosch area, for instance, still are 0.8-0.9 m/sec.

This means that along the main axis of the estuaries differences in current velocity are relatively unimportant.

Maximum current velocities in the North Sea offshore vary between 0.5 and 1.0 m/sec. In this area no still water period occurs, because the tidal currents do not alternate, but show a rotating pattern.

3.4.5. Salinity

Detailed information about the pattern of salinity distribution was obtained from Den Hartog (1963), Peelen (1967, 1970), Van der Burgh (1968), Anonymous (1966, 1968) and from personal information of colleagues.

Salinity has been expressed as chlorinity or the weight in grams of the chloride ions in one liter of water.

The salinity of the water of the Rhine in the years 1965-1968 amounted to 128 mg Cl′/l or 0.128$^{0}/_{00}$ Cl′ on the average. Owing to variations in river discharge, this figure temporarily raised to about 0.3$^{0}/_{00}$ Cl′ during short periods. The salinity of the Meuse in the years 1965-1968 amounted to 45 mg Cl′/l or 0.045$^{0}/_{00}$ Cl′ on the average. On the salinity of the water of the Scheldt, no detailed information is available, but it may be assumed that it is similar to that of the Meuse.

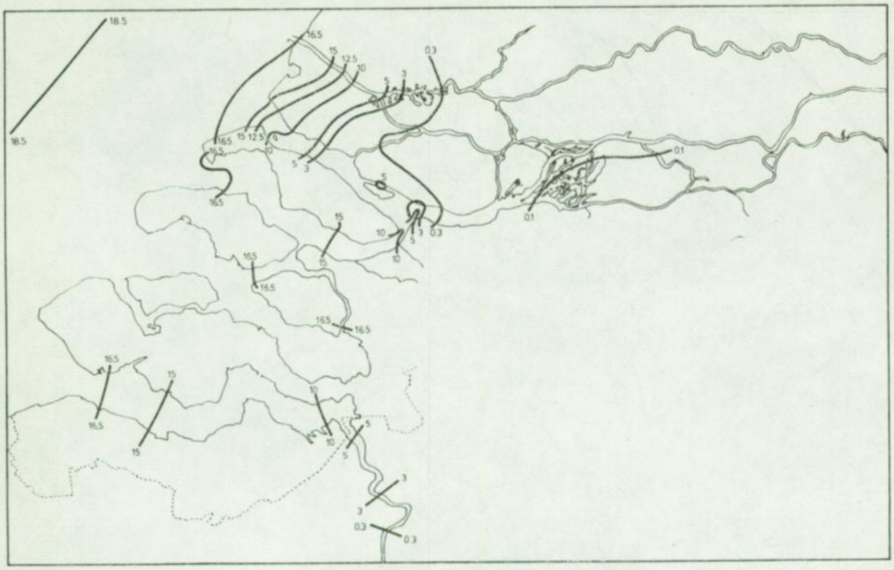

Fig. 10. Salinity of the bottom waters of the Delta area at high tide during an average river discharge. The isohaline of $18.5\,^0/_{00}$ Cl′ represents the boundary between the "Channel water" and "Continental coastal water".

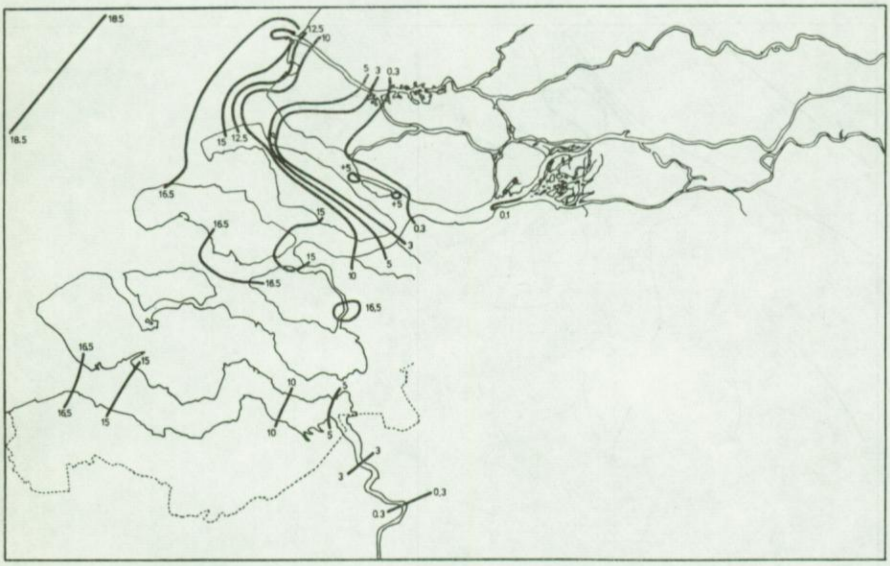

Fig. 11. Salinity of the bottom waters of the Delta area at low tide during an average river discharge. The isohaline of $18.5\,^0/_{00}$ Cl′ represents the boundary between the "Channel water" and the "Continental coastal water".

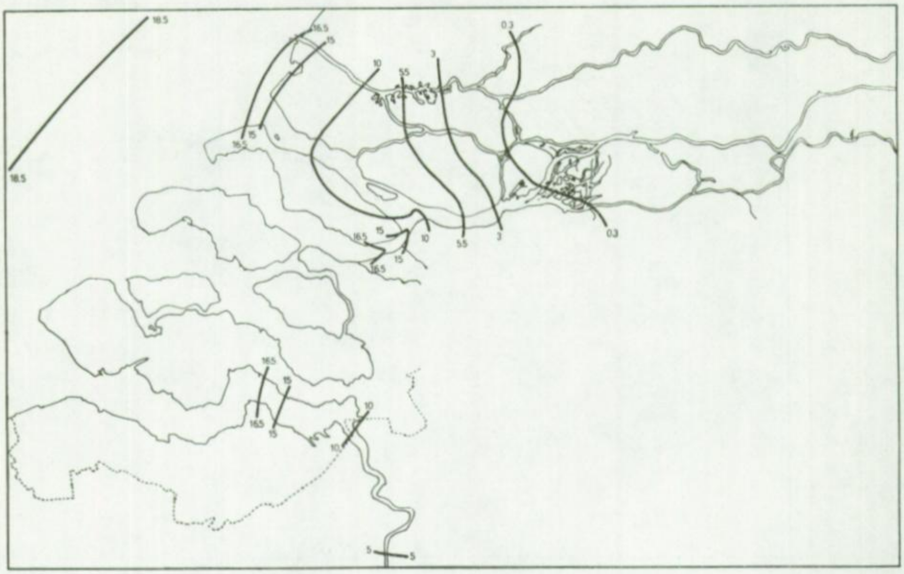

Fig. 12. Salinity of the bottom waters of the Delta area at high tide during a low river discharge.

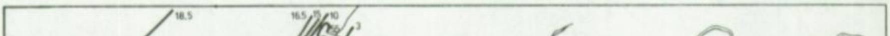

Fig. 13. Salinity of the bottom waters of the Delta area at low tide during a high river discharge.

The salinity of the "Channel water" in the North Sea (compare paragraph 3.4.1.) is over 18.5‰ Cl′.

In the estuaries the water masses are usually vertically well-mixed, but in areas with a steep horizontal salinity gradient a vertical salinity gradient often is also present. This is the case at the mouths of the Nieuwe Waterweg and the Haringvliet and in the Volkerak—Hollands Diep area. In these areas bottom salinity usually is much higher than surface salinity.

The following data seem important for the distribution of animals: the salinity at high and low tide during average river discharge, the maximum salinity at high tide during the lowest river discharge of the year, the minimum salinity at low tide during the highest river discharge of the year, and possibly the maximal difference in salinity during one tidal cycle and during one year (figures 10, 11, 12, 13, 14 and 15). In all figures the salinity of the bottom waters is shown, contrary to the publications of Den Hartog (1963) and Peelen (1967), which showed surface salinities.

Estuarine animals experience different salinities through the impact on their system for physiological adjustment. From the reviews by Schlieper (1958) and Kinne (1964) some ideas may be gained about the relationships between the distribution of animals, their physiological capacities and the distribution of salinity.

Marine species lacking any form of protection to low salinities, may be limited in their distribution by the salinity at low tide during high river discharge (fig. 13), or, when they are short-living, by the salinity at low tide during average river discharge (fig. 11). When such species are able to retreat into burrows, or to close their shells during periods of unsuitably low salinity, their distribution is governed by the length of the period with water of sufficiently high salinity, allowing them to feed. The length of this period could not be shown on a map, but it is reflected in the salinities at high and low tide during average river discharge as well as during high or low river discharge (figs. 10, 11, 12, 13).

In osmoregulating species from marine and brackish waters a lower salinity limit may occur, below which their osmoregulating apparatus falls short. Such species may be limited by the salinity at low tide during average or high river discharge (figs. 11, 13). The freshwater species, which all have to osmoregulate, mostly have an upper salinity limit above which their osmoregulating capacity breaks down. These species may be limited in their distribution by the salinity at high tide during average or low river discharge (figs. 10, 12).

The volume regulating species are likely to be influenced by the velocity of the change in salinity during one tidal cycle, which is related to the

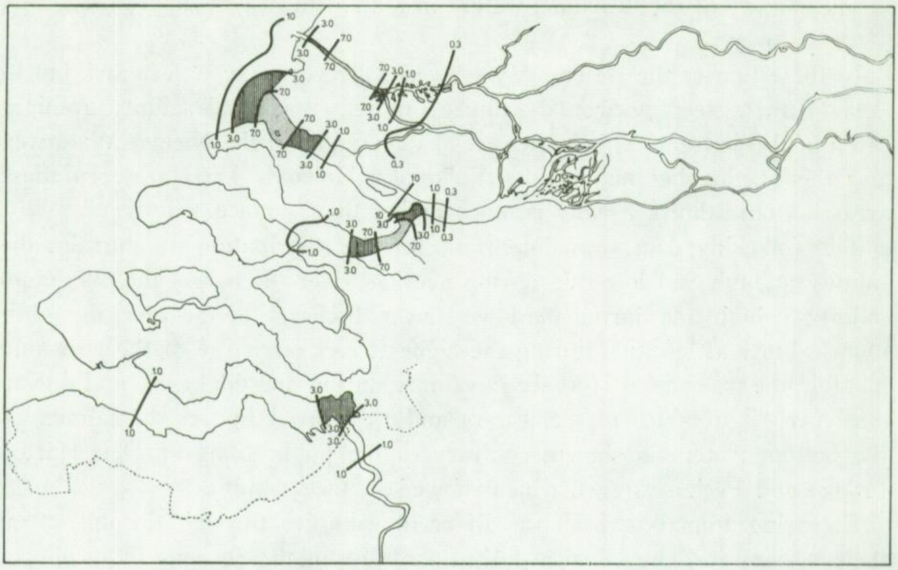

Fig. 14. Maximal difference in salinity of the bottom waters of the Delta area during one tidal cycle at an average river discharge. The differences have been derived from the data shown in figs. 10 and 11.

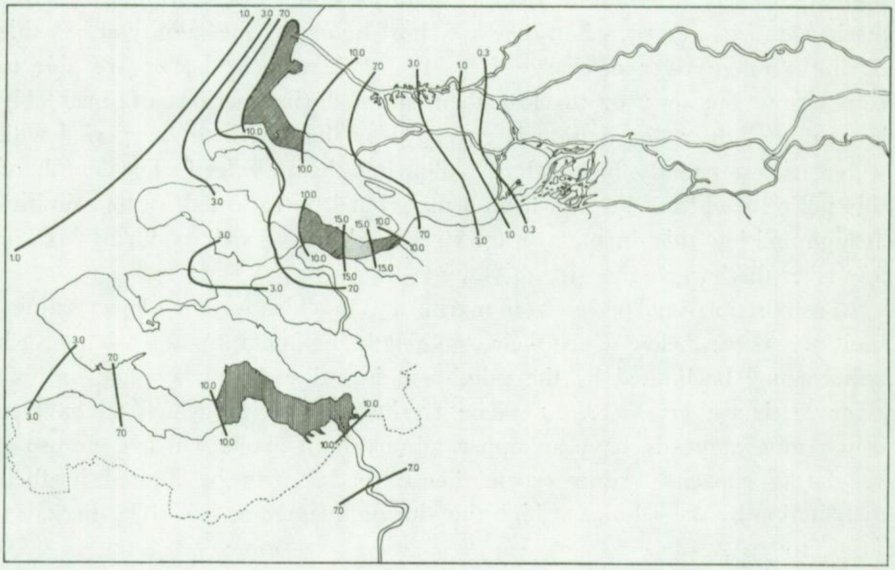

Fig. 15. Maximal difference in salinity of the bottom waters of the Delta area during one year. The differences have been derived from the data shown in figs. 12 and 13.

amplitude of salinity during one tidal cycle (fig. 14). It seems possible that such species are not able to correct very rapid changes of the external medium.

3.4.6. WATER TEMPERATURE

The yearly temperature amplitude of the Oosterschelde (Table 1), is over 16°C. Due to the good vertical mixing of the estuary this is true for the surface waters as well as for the bottom waters. Offshore in the Channel water the yearly temperature amplitude is less than 10°C. The waters in between have intermediate temperature amplitudes.

The minimum water temperature in winter is on the average about 6°C in the Channel water, but below 3°C in the water of the estuaries. Values below zero, however, are very rare and were only reached in the extremely cold winter of 1962/1963.

The maximum water temperature offshore mostly does not rise over 16°C, but in the estuaries it may be over 20°C for many days and even weeks.

TABLE 2

Data on the pollution of the rivers Rhine, Meuse and Scheldt. The quantities mentioned are given either in percentages, or in quantities per liter. The data have been derived from the reports of the International Rhine Commission and from personal information by the State Institute for the Purification of Sewage.

	Rhine			Meuse			Scheldt near Antwerp		
	average summer values 1965–68	average winter values 1965–68	average 1965–68	average summer values 1965–68	average winter values 1965–68	average 1965–68	average summer values 1962–67	average winter values 1962–67	average 1962–67
percentage oxygen saturation	48 %	71%	58 %	73 %	88 %	81 %	20 %	20 %	20 %
biological oxygen demand (BOD_5^{20})	5.6 mg	4.2 mg	6.2 mg	7.2 mg	3.8 mg	6.2 mg	10.5 mg	5.5 mg	8.0 mg
NH_4^+	1.1 mg	2.0 mg	1.7 mg	1.2 mg	1.4 mg	1.5 mg			
NO_3^-	10.0 mg	11.9 mg	11.1 mg	14.0 mg	11.2 mg	13.0 mg			
total PO_4^{3-}	0.8 mg	0.8 mg	0.8 mg	0.8 mg	0.7 mg	0.8 mg			
Cl^-	122.0 mg	122.0 mg	128 mg	55 mg	30 mg	44.5 mg	slightly brackish		
SO_4^{2-}	70.5 mg	69.0 mg	70.5 mg	66 mg	51 mg	58.5 mg			
phenoles	10 µg	18.5 µg	14.2 µg	9 µg	8 µg	8.7 µg			
suspended matter	31 mg	42 mg	36.5 mg	32 mg	49 mg	48 mg			
synthetic detergents	0.15mg	0.31mg	0.22mg	0.31mg	0.25mg	0.30mg			
			average 1963–65						
Mg^{2+}			20 mg						
Na^+			78 mg						
K^+			7.4mg						
Ca^{2+}			163 mg						

In shallow waters and in pools in the intertidal zone during low tide temperature conditions usually are more extreme. In winter these shallow waters may freeze, but in summer they may reach temperatures well over 30°C. These extremes, however, are smoothed again by the next incoming flood.

3.4.7. OXYGEN

The water of the rivers reaching the Delta area is polluted (compare paragraph 3.4.9.). Owing to this the oxygen saturation of these rivers is nearly always below 100% (Table 2).

In the freshwater tidal area the water is sometimes super-saturated (Parma, 1968).

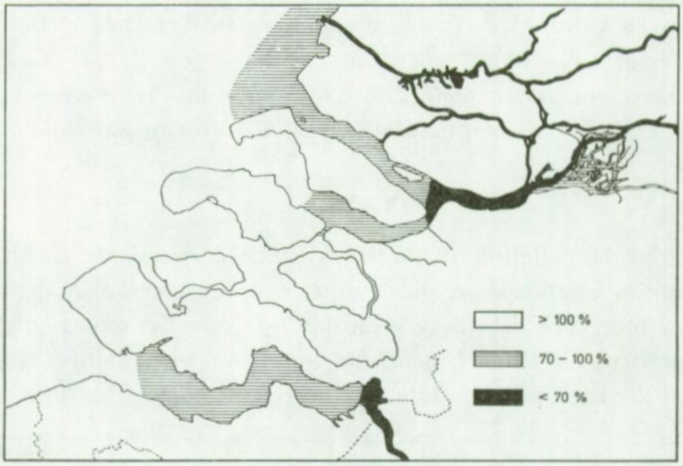

Fig. 16. Percentage of oxygen saturation in the Delta waters. Shown is an overall picture of the percentage of saturation at daytime and half tide during average river discharge and normal meteorological conditions for the situation round about 1964.

The water of the marine parts of the estuaries and of the North Sea usually is super-saturated with maximum values up to about 150% (Bakker, 1964, 1967).

In the zone between the marine parts of the estuaries and the freshwater of the rivers the percentage of saturation gradually decreases with the decreasing salinity (Fig. 16). Locally and temporarily large deviations from this picture may occur, and fig. 16 only is intended to give an impression of the average conditions.

3.4.8. TURBIDITY

A process of mud circulation and accumulation is the cause of the higher mud content of estuarine water compared with both river and sea water

(Postma & Kalle, 1955; Postma, 1967; Meade, 1968). This feature especially occurs where the salt wedge reaches the entirely fresh river water, e.g. where a steep vertical salinity gradient is present. In the seaward direction the concentration of suspended matter decreases owing to the dilution of river water by sea water. This phenomenon may also be observed in the Delta area.

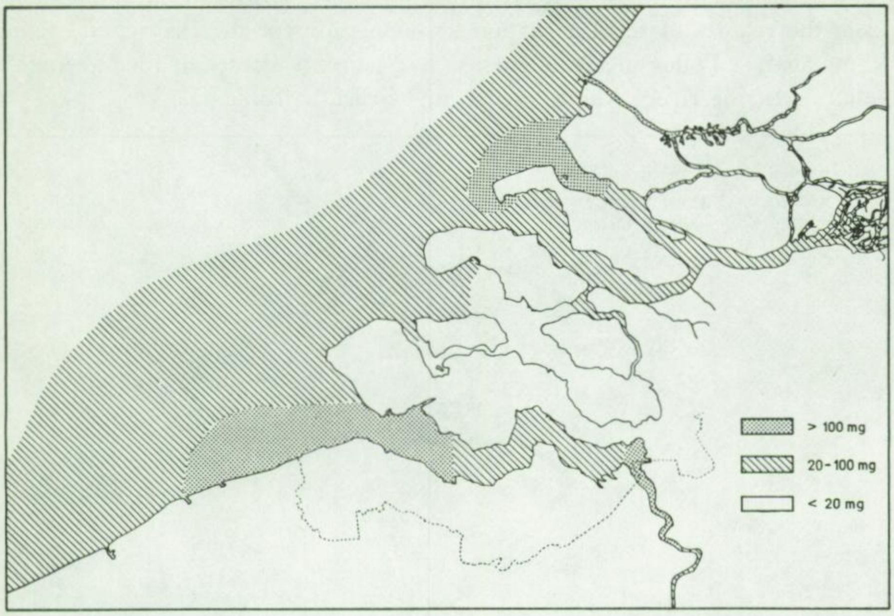

Fig. 17. Turbidity of the Delta waters. Shown is an overall picture of the amount of mud in suspension (dry weight) at half tide during average river discharge and normal meteorological conditions for the situation round about 1964.

Data on the turbidity of the waters of the Delta area were derived from Terwindt (1967), Lee & Folkard (1969) and from personal information from colleagues. In the offshore parts of the North Sea the amount of suspended mud is in the magnitude of 10 mg/l. Such values also may be found in the middle and eastern parts of the Oosterschelde (fig. 17). Areas where the quantity of mud in suspension is over 100 mg/l mostly correlate with steep salinity gradients, but in the western part of the Westerschelde the high content of mud is caused by erosion of old clay layers. Owing to a circular course of the tidal currents in this area, the suspended material is trapped in this area and the amount of mud in suspension is kept on a high level (Terwindt, 1967).

The variations in the quantity of mud in suspension are large, for instance from 50 to 1000 mg/l, but it is possible to indicate a certain level of turbidity in each locality. Nevertheless, due to these large fluctuations and also to the insufficient number of data, it is not possible to delimit the areas of high and low turbidity exactly.

3.4.9. WATER POLLUTION

Data derived from the State Institute for the Purification of Sewage and from the reports of the International Commission for the Protection of the Rhine against Pollution (Anonymous, 1967) give a picture of the "average" pollution of the rivers Rhine, Meuse, and Scheldt (Table 2).

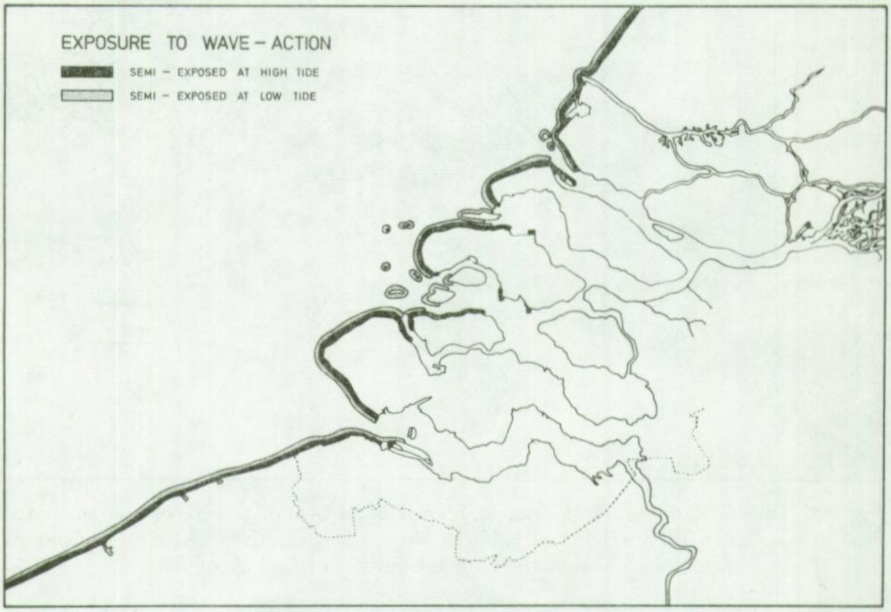

Fig. 18. Exposure to wave-action of the shores of the Delta area. The situations at high tide (black) and at low tide (hatched) are shown separately.

In the marine and brackish parts of the estuaries no major sources of pollution occurred in the period of this study.

It may be assumed that the pollution in the zone between the marine and the freshwater parts of the estuaries decreases with the rate of dilution of riverwater by seawater. Thus it may be measured by parameters such as the salinity (fig. 10-13) or the percentage of oxygen saturation (fig. 16).

3.4.10. EXPOSURE TO WAVES

Ballantine (1961) proposed a biologically defined exposure scale of eight classes for the comparative description of rocky shores. According to this scale the artificial rocky shores of the Delta area may be classified as ranging from semi-exposed to extremely sheltered, i.e. within the last five classes. Lewis (1964) proposed a similar scale of five classes; in his scale the artificial rocky shores of the Delta area belong to the last three classes, viz. ranging from semi-exposed to very sheltered. According to these methods of classification the beaches and mudflats in between the artificial rocky shores of the Delta area also could be classified as semi-exposed to very sheltered.

With the method described in paragraph 2.3.5. the shores of the Delta area were divided in semi-exposed and sheltered shores. This was done separately for the high and the low tide situation, because shallows emerging during the falling tide considerably change the situation (fig. 18).

Only the shores near the entrances of the estuaries are really exposed to wave-action. The more inland shores of course show minor differences in their exposure to wave-action, but, nevertheless, they all may be considered as sheltered.

This method of measuring the exposure of the shore produces a result which proves to be in good accordance with a classification by means of the scales of Ballantine or Lewis.

The effect of exposure to wave-action of soft sediments varies with the median grain-size of the sediment, the coarser sediments being influenced to a greater depth. For sediments with a median grain-size in the range of that of the beaches of the Delta area each foot of wave height gives a disturbance of 1 cm depth in the sediment (King, 1951).

3.4.11. INFLUENCE OF ICE

Ice may be formed in the Delta area proper or it may be transported by the rivers to this area.

In the freshwater tidal area and in the slightly brackish areas the ice formation may proceed very rapidly, but in the more seaward reaches of the estuaries it is a slow starting process, occurring especially in the shallows.

According to observations on January 26th, 1966, the following phenomena are connected with the formation of ice in the freshwater tidal area. During falling tide an ice cover is formed on all firm substrates. During low tide the upper layers of muddy sediments rich in water may freeze, together with an overlying thin layer of water. During the next tides a new layer of ice is added to this layer, until the whole packet of ice, together with the upper layer of the sediment is lifted by the flood and may be carried away. Specimens of *Pisidium* frozen in such ice floes, were observed.

Ice floes carried by the currents may strand on sandbanks. Owing to the forces exerted by the currents, they may plough up the sediment very thorougly. Similar ice floes stranded on the sandbanks may force the water currents through small openings and this may be another cause that deep gullies erode in these sandbanks and that the sediment is disturbed thoroughly.

3.4.12. DEFINITION, CLASSIFICATION AND DELIMITATION OF ESTUARIES

According to Twenhofel (1950): "An estuary is that part of the course of a river which is affected by the tides", whereas Pritchard (1967) states: "An estuary is 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".

This means that the waters of the Delta area, perhaps with the exception of the Oosterschelde, may be defined as estuaries. According to the older classifications of estuaries, summarized by Emery & Stevenson (1957) and Bowden (1967), these waters have to be classified as "positive or normal estuaries" with a net landward flow of salt bottom water. The Oosterschelde also may be fitted into this category, but it approaches to the group of "neutral estuaries" without any net transport of bottom water.

Bowden (1967) and Pritchard (1967a), who consider positive estuaries to be the only real estuaries, present a scheme of classification based on the estuarine circulation pattern of salt and fresh water. They distinguished 1) and 2) the highly stratified estuaries where river flow dominates the tidal water movements; 3) the partially mixed or moderately stratified estuaries; 4) the vertically homogeneous estuaries.

The entrance of the Haringvliet, the Keeten—Krammer—Volkerak—Hollands Diep-system, and the eastern part of the Westerschelde clearly belong to the third type, whereas the Oosterschelde, the Veerse Gat—Zandkreek-system, and the western part of the Westerschelde may be classified in the fourth type. Until the closure of the Grevelingendam in 1964 the Brouwershavense Gat—Grevelingen area was intermediate between the types 3 and 4; afterwards it approached the fourth type. Of course, changes in the amount of river discharge may influence this classification.

Sanders, Mangelsdorf & Hampson (1965) classified estuaries according to the horizontal displacement of the watermasses and distinguished between a) stable, b) gradient, and c) fluctuating estuaries. The second type, to which the estuaries of the Delta area belong, shows isohalines moving over a restricted distance in the course of a tidal cycle.

The estuaries of the Delta area have been classified by Peelen (1970) according to their geomorphological characteristics. He distinguished:

1) bar-built estuaries with a continuous subsurface-bar, viz. the Haringvliet;
2) estuaries with a subsurface-bar, transected by one or more tidal channels,

viz. the Grevelingen, and the Oosterschelde. Also the Westerschelde belongs to this type;

3) estuaries without a subsurface-bar, thus consisting only of a tidal channel, viz. the Keeten. Also the Nieuwe Waterweg belongs to this type, which may be considered as a special case of 2.

It seems logically to set the abiotic limits of the estuarine environment exactly there where the influence of the sea and of the river, respectively, ends.

In a river mouth the sea can exercise an influence by its salinity as well as its tidal movements. The effect of the tides is normally felt much further inland than that of salinity and therefore the riverward limit of the estuaries may be set by the definition by Twenhofel (1950) at the tidal limit.

The seaward limit of the estuary is more difficult to define. The influence of the river in an estuary appears from the dilution of the sea water with fresh water. To use the presence of diluted sea water as an indication of estuarine conditions, as has been done by some authors, would lead to strange results, because it would imply that large parts of the North Sea and the whole of the Baltic were estuarine. Nor is it very well possible to delimit the estuarine environment by means of the term "a semi-enclosed body of water" (Pritchard, 1967), since, according to Bird (1969) "The ideal estuary is funnel-shaped, opening seawards, subject to tidal fluctuations, and influenced by the salinity of the sea". Therefore, it seems useful to introduce some other more or less general characteristic of estuaries, for instance the aberrant temperature conditions or the estuarine topography of flats and channels.

Temperature conditions in rivers as well as in the sea are remarkably constant and change very slowly only in the course of the year. In the estuary, however, owing to the large areas of tidal flats, temperature may vary considerably in the course of a tidal period and, hence, relatively large and rapid changes of water temperature are one of the features of an estuary. The tidal currents filling and emptying the estuarine basin shape a coastal morphology quite different from that of the sea. Its main features are deep channels and large areas of shallows. When including temperature and the estuarine topography into the definition, it becomes possible to delimit the estuarine area in a seaward direction.

Doing so, the seaward limit of an estuary may be set at the limit where rapid and relatively large changes of the temperature of the bottom water occur and where the topography of tidal shoals and channels changes into a more or less level sea floor. In this way the estuarine environment of the Delta area is perfectly limited by abiotic factors, which also may be applied to other estuaries, for instance the Elbe, as was pointed out by Caspers (1967).

3.4.13. Hydrographical changes due to the delta works

The following hydrographical changes due to the Delta works occurred during this investigation:

In 1960 the dam in the Zandkreek (fig. 1) was built, whereas in 1961 the dam in the Veerse Gat was closed and as a result of this and the former closure the Veerse Gat and the Zandkreek became stagnant.

In 1964 the secondary dam in the Grevelingen was closed and thus the Brouwershavense Gat—Grevelingen area was separated from the Krammer—Volkerak area. This meant that the Brouwershavense Gat—Grevelingen area no longer received fresh water from the rivers. Only a minor amount of fresh water flowing around the island of Goeree and originating from the Haringvliet reached this area since this closure. The water coming down from the rivers Rhine and Meuse through the Volkerak and Krammer ran through the Zijpe and Keeten to the Oosterschelde and then to the North Sea from 1964 onwards (Peelen, 1967, 1970).

In 1969 the dam in the Volkerak was closed and in 1970 the Haringvliet sluices became operational. The connection between the waters of the main Rhine-Meuse estuary and the estuaries to the south was disrupted completely by this. The Hollands Diep-Haringvliet area freshened largely, but the area to the south acquired a much more marine character (Peelen, 1970).

3.5 Food

The best classification of feeding types seems to be (Hunt, 1926; Sanders, Goudsmit, Mills & Hampson, 1962): 1. suspension-feeders; 2. deposit-feeders, divided into a. selective deposit-feeders and b. non-selective deposit-feeders; 3. scavengers; 4. carnivores; 5. herbivores; 6. omnivores. Pearson (1971) gives essentially the same classification but uses different names.

Most suspension-feeders, which feed on edible matter suspended in the water, select organisms of a certain size-range; moreover it has been shown that not all species of algae have nutritional value. On the other hand the importance of bacteria as a source of food has only been realized during the last years (Jørgensen, 1966).

Unfortunately, there exist no published accounts of the densities of planktonic organisms in the Delta waters. However, Messrs. C. Bakker and R. Peelen, studying distribution and ecology of plankton in the Delta waters, have confirmed that the total plankton populations, dead and dying specimens inclusive, are of about the same order of magnitude in the various parts of the estuaries of the Delta area, and that the general level is high. In the offshore part of the North Sea, however, the total densities seem to be less, due to the lower nutritional value of the Channel water (Laevastu, 1963; Johnston & Jones, 1965).

Even less information is available on the abundance of bacteria. It may be assumed that the numbers of bacteria are high in polluted rivers emptying into the estuaries of the Delta area. Towards the marine parts of the estuaries and the North Sea a gradual decline probably will be found. The main conclusion is that for suspension-feeders food is abundant in the estuaries, but less in the offshore parts of the North Sea.

Deposit-feeders live on the organic matter present on or in the sediment. Doing so, they are ultimately dependent on the organic detritus. Species directly dependent on the detritus probably are rare (Newell, 1965; Fenchel, 1969). Adams & Angelovic (1970), however, showed that three species inhabiting seagrass beds ingested and assimilated considerable amounts of detritus and that the associated bacterial flora formed a source of food of less importance. For quite a number of other species it could, nevertheless, be shown that they are dependent either on bacteria, or on algae or fungi. The microflora is preyed upon by many representatives of the micro- and meiofauna and also some macrofauna species. Other macrofauna species, however, feed indiscriminately on the microflora as well as on the micro- and meiofauna by ingesting the sediment as a whole, and thus act as non-selective deposit-feeders. The selective deposit-feeders select the particles of food from the sediment and reject other things.

A rough estimate of the quantities of organic detritus available may be obtained in two ways. The first is based on the amounts of organic matter present in the water, which may be deposited. The abundance of this material is identical to that of the food of suspension feeders, viz. high in the estuaries and low in the offshore parts of the North Sea.

The second estimate is based on the amounts of organic matter actually present in the sediments (paragraph 3.3.5.; fig. 9).

Scavengers feed on dead animal remains. This type of feeding is rather rare in its pure form.

Carnivores feed on living animals. Typical carnivores are less frequent than was formerly assumed (Sanders et al., 1962).

Herbivores have not been met with among the soft-bottom macrofauna of the Delta area. Species feeding on microscopic algae have been considered as suspension- or deposit-feeders.

Omnivores employ two or more of the feeding techniques mentioned above. According to Sanders et al. (1962) many "carnivores" are really omnivores. The most frequent combinations are predator and scavenger, predator and deposit-feeder, and deposit-feeder and suspension-feeder.

Since many years dissolved organic matter has also been mentioned as a source of animal food. The value of this type of food seems questionable mainly because the organisms quoted apparently also need other methods of feeding. Southward & Southward (1972) record that some polychaetes are able to take up dissolved organic matter, but they add that it seems improbable that this uptake covers more than a small percentage of the requirements of the worms. It might be more important for juvenile stages.

3.6. VEGETATION

The phanerogamous vegetation of the estuaries of the Delta area has been described by Zonneveld (1960) for the freshwater tidal area and by Beeftink (1965) for the marine and brackish areas. Their results may be summarized as follows.

Seagrasses (*Zostera marina* fo. *stenophylla* and *Z. noltii*) occur on the tidal flats in areas with an average salinity over about 10-12$^0/_{00}$ Cl′. Below low water level no seagrasses occur. Similar plants do not occur in the brackish area, but in the freshwater tidal area pond weeds (*Potamogeton* spp.) occur in some creeks below low water level.

Typical salt-marsh vegetation occurs only near mean high water level in the marine area. The most important species are *Salicornia stricta, Spartina townsendii, Puccinellia maritima,* and *Halimione portulacoides*. In the brackish area species like *Scirpus maritimus, Cochlearia officinalis* and *Phragmites communis* are added to these species and gradually replace them. These species also descend to a lower level in the intertidal zone, reaching nearly mean sea level. In the freshwater tidal area the most important species are *Typha* spp., *Scirpus* spp., *Phragmites communis* and several species of *Salix*. Vegetation in the freshwater tidal area descends to about mean "sea" level.

In the area with a salinity over 10-12$^0/_{00}$ Cl′ the tidal flats are inhabited by several species of macroscopic algae (Nienhuis, 1970).

Diatoms and flagellates inhabiting the upper layer of the sediment are found in the marine areas as well as in the brackish and the freshwater tidal areas. They occur on all types of sediments, but are most common on the very muddy ones.

Also species of *Vaucheria* are found at all salinities, but mostly only between the erect vegetation of phanerogams on clay bottoms.

4. MATERIAL

4.1. SURVEY OF THE SAMPLES

The data for this study have been collected from 1958 until 1970. The samples taken may be classified into four groups, viz. 1) subtidal samples taken with the Van Veen grab; 2) intertidal samples obtained by sieving; 3) meiofauna samples, and 4) various other types of samples (section 2.1.).

A survey of the grab-samples may be found in table 3; their distribution is shown in fig. 19.

Intertidal samples usually were taken in transects from high to low water mark. Such transects have been sampled along the Westerschelde, the Oosterschelde, the Grevelingen, the Krabbekreek, the Krammer, the Midden-Helle-

TABLE 3

Distribution and numbers of grab-samples.

Year	Month	Area	Number of samples	sample-size
1959	August	Oosterschelde, Veerse Gat, Zandkreek	50	0.2 m^2
1960	Sept.-Dec.	Zandkreek	44	0.1 "
1961	April	Zandkreek	37	0.1 "
	June	Haringvliet, Hollands Diep	41	0.1 "
1962	September	Oosterschelde, Eendracht, Krabbekreek	168	0.1 "
	October	Brouwershavense Gat, Grevelingen	76	0.1 "
	November	North Sea, Westgat, Oosterschelde	36	0.1 "
1963	September	Haringvliet, Hollands Diep, Biesbosch, Krammer,	190	0.1 "
		Keeten	43	0.1 "
	Sept.-Oct.	Brouwershavense Gat, Grevelingen	89	0.1 "
	October	Krammer, Volkerak	83	0.1 "
1964	June-July	Oosterschelde	152	0.1 "
	July	Krabbekreek, Eendracht, Keeten	50	0.1 "
	August	Westgat	28	0.1 "
1965	April	Westerschelde	55	0.2 "
			31	0.1 "
	June-July	Biesbosch, Amer, Oude Maasje	99	0.1 "
1966	June-July	North Sea	108	0.2 "
	September	Hollands Diep	71	0.1 "
		branches of the Rhine	37	0.1 "
		branches of the Meuse	6	0.1 "
1967	February	Oosterschelde - eastern part	10	0.1 "
1968	November	Haringvliet	33	0.1 "
		Krammer-Volkerak	10	0.1 "
		Westerschelde	15	0.1 "
1969	April	Haringvliet, Hollands Diep, Volkerak	189	0.1 "
			1751	

gat, in the Biesbosch, and on the beaches along the North Sea. Several of these transects have been sampled many times in the course of the years 1963-1970.

The meiofauna samples have been taken in the winterperiods of 1968-1969 and of 1969-1970. The localities were scattered more or less evenly all over the Delta area. Usually 4-6 samples were taken at one locality, intertidally as well as subtidally.

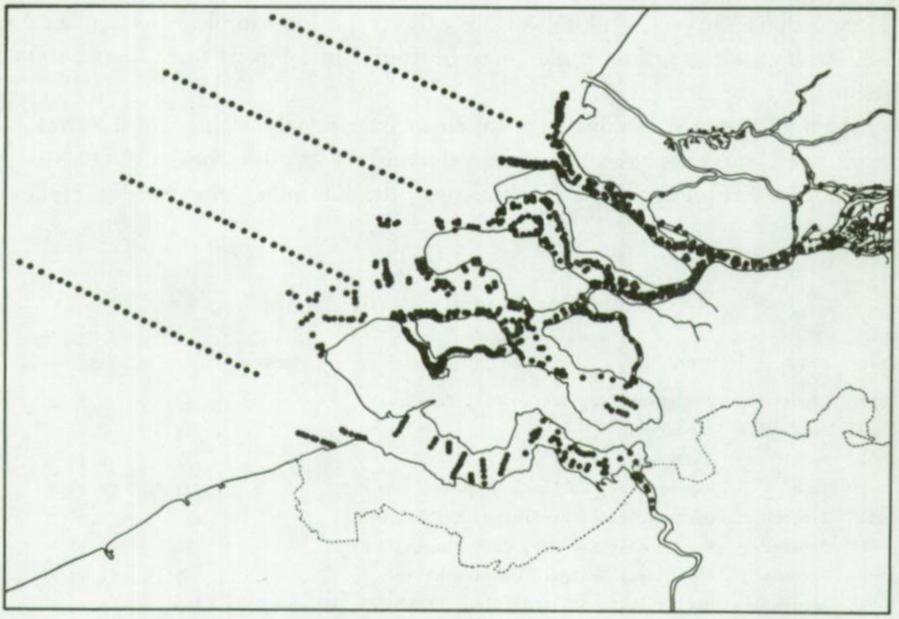

Fig. 19. Localities where one or more grab-samples have been taken.

Other samples were obtained in several different ways. For instance, SCUBA-divers sampled by hand on subtidal bottoms. The distribution of a species like *Arenicola* was established by visual inspection of the mudflats. Data on epifaunal species were derived from about 1500 hauls with a shrimp-trawl with a beam of 3 m. Records of some rare species were obtained from local fishermen and amateur biologists.

4.2. DEFINITION OF A SOFT-BOTTOM SPECIES

Every species able to maintain itself during all of its life or at least during some important part of its life within or upon bottoms consisting of loose particles smaller than 1000 μ diameter, has been considered as belonging to the soft-bottom fauna. This means that species attached to shells and stones, for instance many species of sea-anemones, bryozoans, and hydrozoans, have been excluded. In fact, these might be considered as inhabitants of extremely small areas of hard bottom.

There exist some groups which present some difficulties when this definition is applied, viz. mysids, some isopods and amphipods, prawns, shrimps, and some fishes. These species divide their time between alternating free-swimming and bottom-living periods. When the latter period normally is spent within or upon soft sediments, these species are considered as soft-bottom fauna, except for the fishes.

4.3. GROUPS NOT STUDIED

Because this study has been confined to the macrofauna, Protozoa, Plathelminthes (Turbellaria, Gnathostomulida), Nemathelminthes (Gastrotricha, Rotatoria, Nematodes, Kinorhyncha), Tardigrada, Halacaridae, Ostracoda, and Copepoda were not investigated. An exception is formed by the interstitial polychaetes and archiannelids. The following groups with benthic species have no soft-bottom representatives in the Delta area: Porifera, Kamptozoa, Loricata, Pantopoda, Cirripedia, and Tunicata and thus have not been included. Owing to taxonomical difficulties species belonging to the Nemertini, Oligochaeta, and Insecta (Chironomidae) also had to be omitted. Representatives of the Priapulida, Brachiopoda, Phoronida, Holothuroidea, Crinoidea, and Hemichordata do not occur at all in the Delta area.

4.4. DEPOSITION OF THE MATERIAL

Nearly all material was preserved as described in section 2.2. and deposited for the time being in the collection of the Delta Institute.

Afterwards the whole collection of samples of each species or at least a representative part of it, was or will be deposited in either the Rijks Museum van Natuurlijke Historie (State Museum of Natural History) at Leiden, or the Zoölogisch Museum (Zoological Museum) of the University of Amsterdam.

4.5 NOMENCLATURE

The nomenclature of not too old a handbook has been adopted for most groups of species.

Author's names and years of first description have been given at the beginning of the ecological description of each species in chapter 5.

4.6. TAXONOMICAL REMARKS

Polinices polianus (Delle Chiaje, 1830) — There is no reason for distinguishing a subspecies *alderi* Forbes as often has been done in The Netherlands (Altena, Bloklander & Pouderoyen, 1956). *Lunatia nitida* of German authors is identical with this species.

Cardium edule Linné, 1758 — Høpner Petersen (1958) redescribed the closely related species *Cardium lamarcki* Reeve, 1844 from brackish water in Denmark. This author already indicated that *C. lamarcki,* presently known as *C. glaucum,* also occurred in The Netherlands. However, it proved to be confined to brackish inland waters; it is absent from all tidal waters, also the brackish ones. Therefore, all data on *Cardium* refer to *C. edule* Linné, 1758 sensu Høpner Petersen (1958).

Spisula elliptica (Brown, 1827) — Three species of *Spisula* occur in Dutch coastal waters (Van Urk, 1957). Besides the wellknown *S. solida* and *S. subtruncata,* the species *S. elliptica* also appeared to be common. The difference between *S. elliptica* and *S. subtruncata* proved to be clear-cut and these are certainly two valid species.

Venus gallina striatula Da Costa, 1778 — Many authors consider *V. gallina* L. and *V. striatula* Da C. as separate species. Owing to their close resemblance and to the fact that these species do not seem to occur together in the same geographical area, Dr. C. O. van Regteren Altena (pers. comm.) has been followed in considering the two forms as of subspecific rank.

Eteone foliosa Quatrefages, 1865 — The only important difference between *Eteone foliosa* and *Eteone lactea* Claparède, 1868 lies in the armature of the proboscis, bearing three rows of soft papillae in *E. foliosa,* and being smooth in *E. lactea* (Fauvel, 1923). As such a character is subject to deformation by preservation, and because Eliason (1962) also is of the opinion that *E. foliosa* and *E. lactea* represent the same, variable, species, the specimens collected have been called *E. foliosa,* this being the oldest available name.

Nereis virens (M. Sars, 1835) — In 1955 Abdel Moez & Humphries described a new species *Nereis southerni.* All specimens of *Nereis virens* obtained closely resembled this description. Nevertheless, the name *N. virens* has been maintained, because it seems that *N. southerni* constitutes merely a form of *N. virens.* It may have subspecific status, but this seems questionable. Also Muus (1967) and Hartmann-Schröder (1971) are of the opinion that *N. southerni* should be regarded as a synonym of *N. virens.*

Nepthys caeca (Fabricius, 1780) — The specimens of *N. caeca* from the Delta area differ slightly from specimens from other parts of Europe in having no bilobed acicular lobes. These lobes are simply flattened on their tops. Nevertheless, these specimens have been identified as *N. caeca.* Dr. K. Fauchald (Washington) confirmed this identification (pers. comm.).

Glycera capitata Oersted, 1843 — Several of the specimens of *Glycera* showed characteristics of *G. lapidum* Quatrefages, 1865, especially with regard to the shape of the jaws. Following Friedrich (1940), no specific value is attached to these characteristics.

Aricidea minuta Southward, 1956 — The specimens of *Aricidea* from the Delta area have modified neurosetae in the posterior part of the body.

Also with regard to the other morphological details *A. minuta* shows the closest resemblance with the Delta specimens. However, they have a three-lobed median antenna and 12-15 pairs of branchiae. Southward (1956) does not give a clear picture of the antenna and mentions only 10 pairs of branchiae. Eliason (1962) as well as Hartmann-Schröder (1971) picture a bilobed antenna and record 10-12 pairs of branchiae. Gibbs (1965) also pictures a bilobed antenna and records 7-12 pairs of branchiae. The other characters closely resemble those in the Dutch material. In a second paper Gibbs (1969) describes the juvenile stages of *A. minuta*. The number of branchiae increases with length and the antenna makes its appearance at the same moment as the 6th pair of branchiae. Hence, it may be concluded that such characters as the shape of the antennae and the number of branchiae are subject to variation due to the growth of the animal. Therefore, the Delta specimens of *Aricidea* are considered to belong to the species *A. minuta* Southward, 1956. The length of the antenna and the number of branchiae apparently do not constitute reliable specific characters in the genus *Aricidea* and probably in the whole family Paraonidae. Better characters seem to be the shape of the various setae, of the branchiae and of the notopodial cirri.

Drs. A. D. McIntyre (Millport) and M. Glémarec (Brest) shared the opinion that these specimens belonged to *A. minuta* (pers. comm.).

Spio martinensis Mesnil, 1896 — Hannerz (1956) writes that *S. martinensis* Mesnil, 1896 and *S. filicornis* (Müller, 1776) differ with regard to the occurrence of the ventral hooded crochets (from segment 10 onwards in *S. filicornis* and from segment 13-15 in *S. martinensis*), and also in their larval development. Although the value of these characters is uncertain, it appears that the Delta specimens show the arrangement of the hooded crochets typical for *S. martinensis*.

Streblospio shrubsolii (Buchanan, 1890) — Horst (1909) described the species *Streblospio dekhuyzeni* from The Netherlands. Fauvel (1927) and Friedrich (1940) already expressed their doubt about the validity of this species. Because all transitions between *S. shrubsolii* and *S. dekhuyzeni* were found in the Haringvliet area, it seems certain that they represent one and the same species.

Magelona papillicornis F. Müller, 1858 — At least six species of *Magelona* occur in European seas (Glémarec, 1966). Nevertheless, only *M. papillicornis*, easily identifiable by its characteristic setae on the 9th segment, was found.

Tharyx marioni (St. Joseph, 1894) — Using the keys provided by Fauvel (1927), a common cirratulid from the Delta area was identified as *T. marioni.* Korringa (1951), however, named apparently the same species from the Oosterschelde *Tharyx multibranchiis* (Grube, 1863). Moreover, it seems that *Cirratulus filiformis* Keferstein, 1862 also represents the same species, because the descriptions of the two species by Fauvel (1927) and Hartmann-Schröder (1971) are nearly identical. Apparently, the family Cirratulidae seriously needs a thorough revision.

Ophelia borealis Quatrefages, 1865 — Tebble (1952) established that *O. borealis* is distinct from *O. limacina* (Rathke, 1843). Pettibone (1954), however, found that these species are connected by intermediates in Alaskan waters. However, in European waters the difference seems to be constant and the areas of distribution mutually exclusive, so one is tempted to consider the two forms at least as subspecies. Therefore, the distinction between the two species has been maintained.

5. ECOLOGY OF THE INDIVIDUAL SPECIES

5.1. INTRODUCTION

In this chapter a short description will be given of the distribution and ecology of all soft-bottom species belonging to the macrofauna of the Delta area. For each species this description begins with an enumeration of the most important previous publications on the occurrence of the species in this area. Then are described:

- reproduction, larval stages and metamorphosis, mostly based on an investigation of the literature;
- food, also mostly derived from the literature;
- relations with hydrographical characteristics, viz. salinity, turbidity, current velocity, wave exposure, water pollution;
- relations with the sediment;
- vertical distribution, especially in the intertidal zone.

The Gastropoda have been treated rather shortly, because in future more extensive data will be published by Mrs. C. H. Borghouts.

All species have been considered to be monotypic (Mayr, 1963) since nearly nothing is known about the genetic variation.

The description of the ecological distribution of a large number of species was greatly facilitated by the method described in section 2.4. To this end the estuaries of the Delta area were split up into twelve different types of water (fig. 20, Table 4), based on differences in salinity, fluctuation of salinity, turbidity, oxygen saturation, pollution, and temperature (section

3.4). The sediments in these estuaries were divided in eight different types, based on differences in the median grain-size and the sorting coefficient

TABLE 4

Water types in the Delta area.

Name	range of temperature	level of salinity	range of salinity	turbidity	pollution	oxygen saturation
1. Channel water	small	high	small	low	low	high
2. coastal water	large	high	small	medium	low	high
3. mouth of the Haringvliet	large	medium	large	high	low	medium
4. transitional areas of the Haringvliet	large	low	large	high	medium	medium
5. central area of the Haringvliet	large	low	medium	medium	medium	medium
6. Hollands Diep and Rhine	large	fresh	small	medium	high	low
7. Brabantse Biesbosch and Meuse	large	fresh	small	medium	low	medium
8. Krammer	large	medium	medium	medium	low	medium
9. Grevelingen, Keeten, Krabbekreek, and Eendracht	large	high	medium	medium	low	high
10. Oosterschelde, Zandkreek	large	high	small	low	low	high
11. Westerschelde - western part	large	high	small	high	low	high
12. Westerschelde - eastern part	large	medium	large	high	high	medium

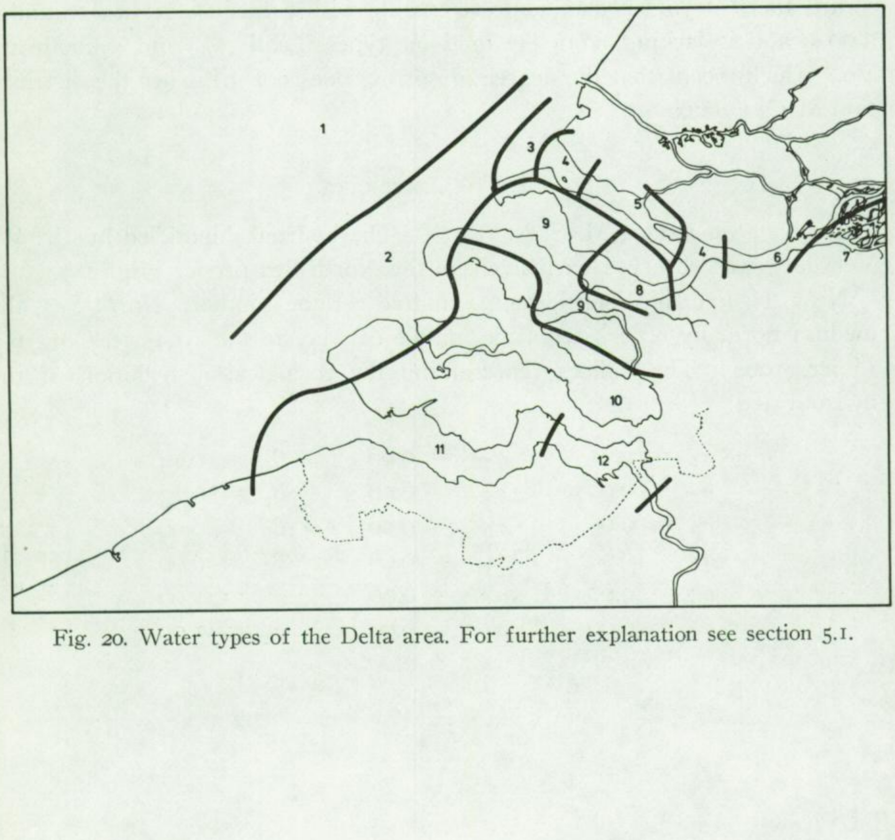

Fig. 20. Water types of the Delta area. For further explanation see section 5.1.

(section 3.3.). According to the median grain-size of the sediment the following classes were distinguished:

1. median grain-size $\leqslant 2.00\ \varphi$ (β_1)
2. median grain-size 2.01—$3.00\ \varphi$ (β_2)
3. median grain-size 3.01—$4.00\ \varphi$ (β_3)
4. median grain-size $> 4.00\ \varphi$ (β_4)

According to the sorting coefficient of the sediment a division was made in:

1. sorting coefficient $\leqslant 0.45$ phi-units (γ_1)
2. sorting coefficient $\geqslant 0.46$ phi-units (γ_2)

In this classification of the environment $12 \times 4 \times 2 = 96$ classes thus may be distinguished. The indices α, β, and γ provide information about the relative abundance of the species investigated in the twelve different water types, the four classes of median grain-size, and the two classes of sorting coefficient, respectively.

This may be explained with *Corymorpha nutans* (p. 62) as an example. α_2 up to α_{12} are zero, which means that *C. nutans* is absent from these water types. The species occurs only in the Channel water which is reflected by α_1 being 2.21. $\beta_1 = 0.14$ and $\beta_2 = 0.13$, while β_3 and β_4 are zero. This means that *Corymorpha* inhabits sediments with a median grain-size under $3.00\ \varphi$, and is lacking from the muddier types. Lastly, γ_1 and γ_2 both are 1.00, which means that the degree of sorting does not influence the distribution of *C. nutans*.

5.2. COELENTERATA

Corymorpha nutans M. Sars, 1835 — The hydroid, identified by Dr. W. Vervoort, was observed exclusively in the North Sea proper (fig. 21).

Near the lightship Texel, representative for the southern North Sea, the medusa normally occurs from the middle of May to the first week of July (Boer, 1968). The indices representing the ecological distribution of the hydroid are:

$\alpha_1 = 2.21$
$\alpha_2 = 0.00$
$\alpha_3 = 0.00$
$\alpha_4 = 0.00$
$\alpha_5 = 0.00$
$\alpha_6 = 0.00$

$\alpha_7 = 0.00$
$\alpha_8 = 0.00$
$\alpha_9 = 0.00$
$\alpha_{10} = 0.00$
$\alpha_{11} = 0.00$
$\alpha_{12} = 0.00$

$\beta_1 = 0.14$
$\beta_2 = 0.13$
$\beta_3 = 0.00$
$\beta_4 = 0.00$
$\gamma_1 = 1.00$
$\gamma_2 = 1.00$

The exclusive occurrence of the hydroids in the North Sea points to a preference for high salinities or stable temperature conditions, or both.

Indeed, the species was not found at salinities under 17.0⁰/₀₀ Cl′. Kramp (1935) records *C. nutans* from the Sound and the Belts, but the salinity of the bottom waters in the area where *C. nutans* was found, normally does not fall much below 16.5⁰/₀₀ Cl′ (Brattström, 1941).

C. nutans does not seem to require a special type of sediment. Ford (1923) records the species from silty sand, clean sand and clean shell gravel. Boer (1968) mentions sediments with median grain-sizes ranging from 135 to 305 μ (= 1.70-2.90 φ). In this study the species was found on sediments ranging from 1.40 to 2.25 φ. Sands coarser than 1.40 φ were repeatedly sampled, but did not contain *Corymorpha.* Sands with median grain-sizes over 2.90 φ were also sampled, but only in the near vicinity of the coast with possibly adverse salinity or temperature conditions. This also seems to be case in the Oosterschelde, where sands in the range 1.40-2.90 φ are abundant, but where *C. nutans* was never found. From the γ-indices it appears that the degree of sorting of the sediment does not influence significantly the distribution of *Corymorpha.* Thus it may be assumed that the distribution of

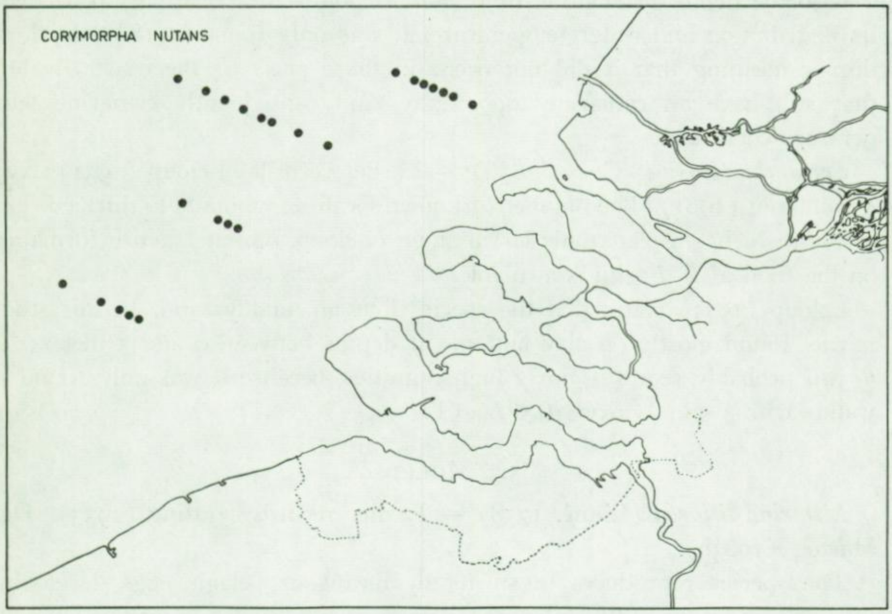

Fig. 21. Distribution of *Corymorpha nutans.* Black dots denote subtidal finds.

C. nutans in the Delta is not governed by the nature of the sediment, but by some characteristic of the water.

Because the Oosterschelde is very well comparable to the part of the North Sea where *C. nutans* lives, as far as salinity, turbidity, and oxygen saturation are concerned, it seems probable that temperature restricts the distribution of this species. As the species was not effected seriously by the cold winter 1962/1963 (Boer, op. cit.), it probably is susceptible to the high summer temperatures in the Delta waters.

Also the depth distribution of *C. nutans* points to a relationship between its distribution and water temperature. It was only found at 18 m depth or deeper meaning that it did not occur in those parts of the coastal waters that still have an estuarine topography, and consequently estuarine temperature conditions.

Cerianthus lloydii (Gosse, 1859) — Earlier records: Leloup (1931); Van Vlimmeren (1961). The number of known localities amounts to thirteen.

C. lloydii has a planktonic larval stage (Leloup, op. cit.). No information on the food of *C. lloydii* is available.

Leloup (1931) states that the species lives in muddy sand. In this study it was found mostly on clay bottoms at depths between 0 and 5 meters. *C. lloydii* probably requires fairly high salinities, because it was only found in waters with a salinity over $16.5^0/_{00}$ Cl′.

5.3. Mollusca

Littorina littorea (Linné, 1758) — Earlier records: Jutting (1933); Den Hartog (1963b).

The species reproduces in spring by means of pelagic eggs developing into pelagic larvae with a planktonic stage of two weeks or more (Thorson, 1946). The diet of *L. littorina* consists mainly of algae, but also small animals (Schäfer, 1950).

L. littorina is restricted to areas with a salinity of at least $10^0/_{00}$ Cl′ (Den Hartog, 1963b). Todd (1964) showed experimentally that the tolerance to lowered salinities is influenced by temperature. From her publication a lower limit of tolerance of about $9^0/_{00}$ Cl′ may be assumed to occur in the climate of The Netherlands. Nevertheless, Jaeckel (1952) records $5^0/_{00}$ Cl′ as the lower limit in the Baltic. The species does not seem to be bound to a special type of substrate (Moore, 1937); in the Delta area it has been found on stones, *Zostera*-leaves, and muddy bottoms. On the tidal flats its distribution seems to be governed by the availability of shelter; it is absent from the bare areas, but it is numerous on musselbeds, seagrass-meadows and salt-marshes.

In the Delta area like elsewhere (Moore, op. cit.), *L. littorea* is mainly a littoral species. The few specimens obtained from sublittoral samples may have been brought there with mussels, relaid for better growth.

Littorina saxatilis (Olivi, 1792). Earlier records: Jutting (1933); Beeftink (1957); Den Hartog (1963b).

L. saxatilis is a viviparous species, reproducing in summer (Thorson, 1946). The food consists of small algae, growing on some kind of hard substrate, and occasionally pieces of *Ulva* and *Enteromorpha*. Diatoms are not digested (Berry, 1961).

L. saxatilis has a distribution similar to that of *L. littorea* (Den Hartog, 1963b). This means that it lives in salinities above at least $10^{0}/_{00}$ Cl′. From the experiments of Todd (1964) and Avens & Sleigh (1965) it may be concluded that the lower limit of tolerance lies near about $9^{0}/_{00}$ Cl′. Nevertheless, Jaeckel (1952) records $3.5\text{-}4^{0}/_{00}$ Cl′ as the lower limit in the Baltic.

In the Delta area the species inhabits the stones covering dikes and breakwaters, but it also occurs in salt-marshes (Beeftink, 1957) and dense vegetations of *Zostera noltii*. It does not inhabit the lower parts of tidal flats, nor the musselbeds, as does *L. littorea*. Below low water level the species was never found. This is in accordance with Berry (1961) who saw that the species did not feed, move, or copulate when submerged.

Valvata piscinalis (Müller, 1774). Earlier records: Jutting (1933).

It reproduces by means of eggs laid in a gelatinous cocoon on waterplants. The young snails hatch from these eggs without any larval stage. It is a suspension-feeder on detritus, diatoms, and filamentous algae (Fretter & Graham, 1962; Jørgensen, 1966).

Valvata piscinalis was found only in fresh water in the Meuse as well as in the Rhine, withstanding considerable pollution. It lives also in the freshwater tidal area, even along the Spui and the Hollands Diep, where normally fresh water is found, but where inflows of brackish water occur at irregular times.

Apparently *V. piscinalis* is very tolerant to its substrate, because it may be found on a large range of types, but it seems to prefer rather soft muds (Fretter & Graham, op. cit.). It is absent from places with strong water movements.

In the freshwater tidal area it was not found in the intertidal zone, except for some finds in pools retaining water during low tide.

Assiminea grayana Fleming, 1828. Earlier records: Jutting (1933); Leloup & Konietzko (1956); Beeftink (1957); Den Hartog (1963b).

The species deposites its egg-cocoons on the mud on which it lives. When these cocoons are reached by the flood — often only once in a fortnight —

the veliger-larva hatches (Sander & Siebrecht, 1967). The larva is able to live for 2-3 days in fresh water (Sander, 1950), but about the normal duration of the planktonic stage no data are available. Probably it is only short. The food consists of micro-organisms, animals as well as plants (Jutting, 1933).

According to the authors mentioned above *A. grayana* inhabits a large range of watertypes from fully marine to completely fresh. Its optimum, however, lies undoubtedly in the brackish parts of the estuaries, where thousands of individuals may inhabit a square meter.

The species is able to live and to deposit its eggs in salinities ranging from that of tapwater to $30^0/_{00}$ Cl′ (Seeleman, 1968a).

In the predominantly marine parts of the estuaries *A. grayana* is confined to the high water mark. Schäfer (1941) even considers it as an indicator species for this region. In the brackish water area, however, *A. grayana* still has its optimum near high water mark, but descends to much lower levels when appropriate shelter is available (Den Hartog, 1963b). Apparently, the species is vulnerable to water movements. *A. grayana* was never found below low water level.

Lithoglyphus naticoides (Férussac, 1827). Earlier records: Jutting (1933); Adam (1938).

Due to water pollution (Krause, 1949) the species has disappeared from nearly all its former localities and Den Hartog (1963b) only knew one locality, where it was lost in the extremely cold winter 1962/63.

The species reproduces by means of eggs deposited on a firm substrate and giving rise to young snails without a pelagic stage. The food consists of organic debris, mainly originating from plants (Krause, op. cit.).

This freshwater species lives mainly on muddy bottoms with low current velocities (Jutting, op. cit.; Krause, op. cit.). As far as it was possible to ascertain *L. naticoides* did not occur in the intertidal zone of the freshwater tidal area.

Hydrobia ulvae (Pennant, 1777). Earlier records: Jutting (1933); Beeftink (1957); Den Hartog (1963b).

The species reproduces by means of eggs often deposited on the shells of the own species. The larvae hatch after 8-10 days and they may go through a short (a few hours) pelagic phase. This phase may also be suppressed completely (Pilkington, 1971). The floating behaviour of the snails, however, forms an efficient means of dispersal (Anderson, 1971). The food of *H. ulvae* probably consists of diatoms (Perkins, 1958), small algae and bacteria (Newell, 1965).

H. ulvae is a marine species penetrating into the brackish part of the estuaries until a salinity of about $10^0/_{00}$ Cl′ at high tide during average river discharge or about $3^{0}/_{00}$ Cl′ during high river discharge. Its sparse occurrence in areas still further upstream probably is not of a permanent nature (Beeftink, 1957; Den Hartog, 1963b). Newell (1964) finds experimentally a salinity of about $3.5^{0}/_{00}$ Cl′ as the limit of the physiological tolerance of *H. ulvae*. The floating behaviour stopped in salinities below about $2^{0}/_{00}$ Cl′. The partly still lower data quoted by him from literature, should not be taken in consideration, as they may relate to the recently described species *Hydrobia neglecta* Muus, 1963. Avens (1965) found experimentally a salinity of about $6^{0}/_{00}$ Cl′ as the lower limit of tolerance of *H. ulvae*.

Towards the North Sea, however, *H. ulvae* most probably is limited by the increased water movements at the exposed shores. In summer considerable numbers may be found on the exposed sandy beaches, but in winter these populations probably are exterminated by severe wave-action.

H. ulvae seems to be rather indifferent about the nature of the substratum (Spooner & Moore, 1940; Fretter & Graham, 1962; Newell, 1962), but rather susceptible to the amount of watermovements accompanying some types of substrate. This may clarify the occurrence of the species in such varied habitats as muddy sediments, seagrass meadows and salt-marshes. The tidal cycle of burrowing, pelagic feeding, sinking, crawling, and burrowing again (Newell, 1962; Anderson, op. cit.), probably also plays an important role in the pattern of distribution. On the tidal flats the species was mainly found on sediments with a median grain-size ranging from 2.50 to 3.50 φ. Judging from the enormous numbers of individuals, this seem to form an optimal habitat. Newell (1965) is of the opinion that the preference of *H ulvae* for such fine-grained sediments is due to the larger surface area of the grains, supporting a larger flora of bacteria, and therefore offering a larger source of food.

When the vertical distribution of *H. ulvae* is considered, maximal numbers are found in the salt-marshes, on the upper half of the tidal flats, and in dense vegetations of *Zostera*. These places in general coincide with the area with the finest sediments (paragraph 3.3.2.), so the conclusion of Newell (1965) seems to be confirmed. However, the animals are accumulated in this zone by the same transportation process which acts upon the small sediment particles, especially when they behave as was demonstrated by Newell in 1962. In his 1964 paper Newell confirms that the specimens from the lower tidal flats are accumulated on the highest available shallow slope. Of course, this does not mean that fine-grained sediments cannot be optimal for *H. ulvae*.

H. ulvae often was quite numerous in grab-samples originating from depths down to 25 m. Most of these samples originated from muddy bottoms, indicating only slight water movements. The same phenomenon is recorded by Kristensen (1959) and Caspers (1952). Thorson (1946) records *H. ulvae* from depths varying between 6 and 20 m where the species lives permanently submerged. The conclusion has to be drawn that the distribution of *H. ulvae* is determined chiefly by salinity and water movements, but that optimal development probably occurs at places with muddy sediments.

Potamopyrgus jenkinsi (Smith, 1889). Earlier records: Jutting (1933); Adam (1942); Heyligers (1961); Den Hartog (1963b).

P. jenkinsi is a parthenogenetically reproducing viviparous species. The adults probably breed all the year round, but one or two distinct breeding peaks may occur (Thorson, 1946; Michaut, 1968). The food consists of a large variety of plants and plant-remains, except for living phanerogams (Michaut, op. cit.). *P. jenkinsi* behaves in the estuaries of the Delta area as a freshwater species, tolerating slightly brackish water (Den Hartog, 1963b). It lives in the rivers, in the freshwater tidal area, and in the brackish area in salinities up to about $2^0/_{00}$ Cl′. Nevertheless, *P. jenkinsi* is able to tolerate much higher salinities, as was shown experimentally by Todd (1964a) and Duncan & Klekowski (1967).

It lives mainly on soft sediments. It is found repeatedly between vegetations of rushes, reeds and other plants and also just below mean high water level in the willow-coppices of the freshwater tidal area (Heyligers, 1961). *P. jenkinsi* was not observed to live below low water level, where the strong water movements probably inhibit its occurrence.

Pseudamnicola confusa (Frauenfeld, 1863). Earlier records: Altena (1958); Butot (1960); Den Hartog (1960).

No information on reproduction and food is available.

Den Hartog (1960) showed that *P. confusa* is restricted to the freshwater tidal area and the oligohaline part of the estuaries. It does not occur in the non-tidal rivers.

P. confusa lives just below high water level on sheltered places, often between vegetation. Sometimes it may descend to lower levels when sufficient shelter is available. Below low water level the species was never found.

As in *Hydrobia ulvae* the nature of the substrate does not seem to be very important, contrary to the amount of watermovements which largely determines the distribution of *P. confusa.*

Polinices polianus (Delle Chiaje, 1830). Earlier records: Jutting (1933); Den Hartog (1963b).

The records by Jutting (op. cit.) of the species living in the estuaries of the Delta area seem to be erroneous.

This species has a long lasting pelagic larval stage (Thorson, 1946). Its food consists mainly of lamellibranchs with smooth shells (Ziegelmeier, 1954: sub nom. *Lunatia nitida*); especially *Spisula* seems to be important (Davis, 1923).

P. polianus was found only in the North Sea proper. Its absence from the Oosterschelde with its water of high salinity points to temperature as the factor governing the distribution of this species. In this respect it is interesting that Ziegelmeier (op. cit.) found that the species became inactive and did not take food above 20°C, but that it was able to tolerate temperatures down to 1°C.

The species was found in sediments with a median grain-size ranging from 1.13 to 2.90 φ. As this is only slightly less than the range of the sediments sampled in the North Sea it seems that the nature of the sediment is relatively unimportant. Muddy sediments were not sampled in this area.

The depth distribution of *P. polianus* ranges from 9 to 32 m, no deeper places having been sampled. The shallowest localities are in the outer reaches of the area with an estuarine topography.

Clathrus clathrus (Linné, 1758). Live specimens of *C. clathrus* have been recorded from the Delta area by Walrecht (1951), viz. from the eastern part of the Oosterschelde, probably imported with oysters, and off the island of Walcheren. Possibly the latter record means a temporary colonization by this species which has pelagic larvae (Thorson, 1946).

Buccinum undatum Linné, 1758. Earlier records: Jutting (1933).

The species reproduces in winter by means of eggs, deposited on a firm substrate. From these eggs the young develop without a larval stage. The whelk is a scavenger (Newell, 1970).

B. undatum is a common species on all substrates in the Delta area as well as in the North Sea proper (Jutting, 1933; Kristensen, 1959). Normally, it does only occur in water with a salinity over about 15 $^0/_{00}$ Cl′ during normal river discharge. It was never found on soft bottoms in the intertidal zone.

Ovatella myosotis (Draparnaud, 1801). Earlier records: Jutting (1933); Beeftink (1957); Den Hartog (1963b).

It reproduces in summer by means of eggs developing without a pelagic larval stage into young snails in 3-7 weeks. It may reach an age of 3-4 years. *O. myosotis* takes green algae (*Enteromorpha*), diatoms, detritus, mud, and sand grains (Meyer, 1955; Seeleman, 1968).

O. myosotis occurs along the seaward reaches of the estuaries upstream to the isohaline of about 10 $^0/_{00}$ during high tide and normal river discharge (Den Hartog, 1963b; Beeftink, 1957). It lives on the muddy soil of the salt-marshes between the vegetation of phanerogams. In general it occurs just above MHW-level, where it is subject to fairly frequent flooding (Meyer, op. cit.; Seeleman, op. cit.).

O. myosotis tolerates much more extreme salinities than appears from its ecological distribution. The eggs still develop in salinities down to about $3^0/_{00}$ Cl′, and the adults even may live in completely fresh water (Seeleman, op. cit.).

Limnaea peregra (Müller, 1774). Earlier records: Jutting (1933); Den Hartog (1963b, 1968).

It reproduces by means of eggs deposited on a firm substratum, from which the young hatch without a pelagic larval stage. The food consists of fresh and decaying parts of waterplants and dead animals (Frömming, 1956).

L. peregra is a freshwater species, tolerating temporary influxes of brackish water. Its occurrence in the oligo- and mesohaline parts of the estuaries is of a temporary nature, caused by individuals swept downstream by the current (Den Hartog, 1968).

The species lives on all kinds of sediments, except for coarse sands and very soft muds. It is not a characteristic soft-bottom species, but it is often found on such bottoms. In the freshwater tidal area *L. peregra* is very common throughout the intertidal zone.

Limnaea palustris (Müller, 1774). In the upper part of the intertidal zone of the freshwater tidal area a species of *Limnaea* occurs, called *L. truncatula* (Heyligers, 1961), as well as *L. palustris* (Den Hartog, 1968).

The species lays eggs, from which the young snails hatch without any pelagic stage. *L. palustris* is primarily herbivorous, but also shows some scavenging habits (Frömming, 1956).

It is a freshwater species, possibly able to bear a slightly elevated salinity. It lives on muddy sediments, often between vegetation, in the upper part of the intertidal zone, even above mean high water level. In the lower part of this zone, and below low water level, this species was not met with.

Agriolimax reticulatus (Müller, 1774). Earlier records: Heyligers, (1961). The species deposites eggs in the bottom; the young snails directly hatch from these eggs. It feeds on several species of higher plants (Pallant, 1969).

A. reticulatus is a terrestrial species. In the freshwater tidal area it is able to descend below high water mark when the vegetation provides sufficient shelter.

Perforatella rubiginosa (A. M. Schmidt, 1853). Earlier records: Jutting (1933).

This terrestrial species lays eggs, giving rise of the young snails without any pelagic stage. No data about the food are available.

It is confined to the freshwater tidal area, where it occurs exclusively in a narrow zone just around mean high water level. Garms (1961) mentions it from the same habitat along the Elbe estuary. Generally, it is found between the vegetation creeping or burrowing in the muddy soil. Normally the animals are frequently reached by the flood and hence covered with a thin layer of mud. According to Steusloff (1949) it inhabits a very similar habitat — very wet meadows and river banks — along the lower Rhine in Germany.

Retusa obtusa (Montagu, 1803). Earlier records: Jutting & Engel (1936).

The species has a non-pelagic development (Thorson, 1946; Smith, 1967). In the Netherlands it reproduces in early summer (Swennen, 1963). As food species may be listed: *Hydrobia ulvae,* juveniles of *Retusa obtusa,* Foraminifera, and copepods (Swennen, op. cit.; Linke, 1939; Smith, op. cit.). *Hydrobia ulvae* is the principal food.

R. obtusa was only met with in the marine reaches of the estuaries; it was not found below salinities of about $12^0/_{00}$ Cl′ during normal river discharge.

In general it occurred in fine and muddy sands; its sediment range varied between 1.61 and 3.02 φ, but the bulk of the observations originated from the range 2.60-3.00 φ.

The species lives in the intertidal zone as well as in the tidal channels down to a depth of 12 m, but is lacking from the zone just below mean high water level where *Hydrobia ulvae* is abundant. Probably it is not able to tolerate the long period of emersion of that zone.

Limapontia depressa (Alder & Hancock, 1862). Earlier records: Den Hartog (1959).

Egg-masses of this species were found from April to November (Den Hartog, 1959). The larval development includes a fairly long pelagic stage (Seeleman, 1967). The species feeds upon the algae *Vaucheria* and *Rhizoclonium* (Den Hartog, op. cit.).

The var. *pellucida* Kevan of this species has a distribution similar to that of *Assiminea grayana.* The var. *depressa,* however, is only found in the marine reaches of the estuaries (Den Hartog, 1963b). The lower limit of its salinity tolerance lies near $1.5^0/_{00}$ Cl′, but reproduction does not occur below $3^0/_{00}$ Cl′ (Seeleman, 1968a).

The species is only found upon the algal mats in the lower parts of the salt-marshes, often between the vegetation of phanerogams.

Alderia modesta (Lovén, 1844). Earlier records: Den Hartog (1959).

The eggs are deposited from April to December (Den Hartog, 1959); they give rise to pelagic larvae, staying for about four weeks in the plankton (Seeleman, 1967). The food of the species consists of *Vaucheria* sp. div. (Evans, 1963; Den Hartog, op. cit.).

A. modesta has in the Delta area a distribution similar to that of *Assiminea grayana* (Den Hartog, 1959, 1963b). The species is euryhaline, but the individuals rather stenohaline (Seeleman, op. cit.). It is able to live and to reproduce in salinities ranging from about 3 to about $35\,^0/_{00}$ Cl′ (Seeleman, 1968).

Like *Limapontia depressa A. modesta* is only found upon the algal mats in the salt-marshes, i.e. just below high water mark.

Mytilus edulis Linné, 1758. Earlier records: Jutting (1943).

Mussels reproduce in spring and summer; large numbers of larvae, with a pelagic phase of 3-4 weeks, then occur in the plankton (Jørgensen, 1946). Settlement especially occurs on threadlike structures, like hydroids and algae (De Blok & Geelen, 1959). After a period of growth the young mussels detach themselves from this substratum and are transported by the tidal currents to places where a secondary settlement takes place (Geesteranus, 1942; Verwey, 1952; Bayne, 1964). This secondary settlement gives rise to new musselbeds or reinforces the existing ones. The formation of new beds seems to be promoted by the occurrence of shells of *Cardium edule* and, especially, of the tubes of the polychaete *Lanice conchilega* (Verwey, 1952). *M. edulis* is a typical suspension-feeder (Jørgensen, 1966).

The ecological distribution of *M. edulis* in the subtidal part of the Delta area may be represented as:

$$\begin{array}{lll}
\alpha_1 = 0.00 & \alpha_7 = 0.00 & \beta_1 = 0.04 \\
\alpha_2 = 2.54 & \alpha_8 = 2.55 & \beta_2 = 0.05 \\
\alpha_3 = 0.00 & \alpha_9 = 2.74 & \beta_3 = 0.13 \\
\alpha_4 = 0.19 & \alpha_{10} = 2.71 & \beta_4 = 0.24 \\
\alpha_5 = 0.44 & \alpha_{11} = 0.00 & \gamma_1 = 0.32 \\
\alpha_6 = 0.00 & \alpha_{12} = 1.00 & \gamma_2 = 1.00
\end{array}$$

Although the natural subtidal distribution of mussels in the Delta area is difficult to ascertain due to the extensive cultures, it may be concluded that *M. edulis* is lacking from the offshore waters and from the areas with predominantly freshwater. It is about equally abundant in the coastal waters and in those parts of the estuaries with a salinity over about $10\,^0/_{00}$ Cl′ during average river discharge and at high tide. Juvenile specimens occasionally may be found in the brackish parts of the estuaries. However, these do not survive the high freshwater discharges during winter and early spring.

Dodgson (1928) observed that a salinity of about $11\,^0/_{00}$ Cl′ did not have any detrimental effect upon the animals. At lower values byssus formation and pumping rate are affected and below about $8\,^0/_{00}$ Cl′ the animals will not open at all. Lassig (1965), however, reports a salinity of $3\text{-}4\,^0/_{00}$ Cl′ as the lower limit of occurrence in the Baltic. The distribution of mussels in the Delta area in general is in accordance with these values. As stated above, their normal occurrence is limited by the isohaline of about 10‰ Cl′ at high tide during normal river discharge or about those of 4 or 6‰ during high river discharge.

The absence of the species from the waters of the North Sea possibly may be explained by its relatively low pumping rate (Winter, 1969), making it impossible to obtain enough food from this poor environment (section 3.5).

From the β-indices it may be concluded that *M. edulis* is able to inhabit many different types of sediment, but that it prefers the muddier ones. However, its pseudofaeces production may be the cause of this picture. This also may explain its predominant occurrence on badly sorted sediments, because it may be imagined that the pseudofaeces add a large mud fraction to a sandy sediment, thus causing a high sorting coefficient.

Kuenen (1942) studied the distribution of musselbeds on the tidal flats near Den Helder, where *M. edulis* occurred in relatively narrow, bandlike beds. He concluded that the sandy lower flats were too unstable to permit the permanent occurrence of mussels, and that the muddy higher flats were unfavourable, because the mussels were unable to retain enough food, probably due to the slight watermovements. Baird (1966) also concluded that a high level on the shore formed a drawback for retaining sufficient food, owing to the long periods of emergence. According to his observations mussels are not able to live on tidal flats above about mid-tide level. Temperature also may be an important factor inhibiting the occurrence of mussels on the higher tidal flats. Read & Cumming (1967) record 27°C and Van Winckle (1970) 26°C as the upper limit of tolerance and this value is easily reached on the higher parts of the tidal flats in summer.

The distribution of mussels on the tidal flats of the Delta area is very similar to the situation described by Kuenen (op. cit.). They do not occur on the sandy flats with strong currents or heavy wave-action, but they may be abundant on fairly sheltered flats with, at least originally, a bottom of muddy sand. Due to the presence of the mussels, however, the sediment changes to a muddier nature. On very sheltered places no mussels occur, nor at high tidal levels.

Unio crassus batavus Maton & Rackett, 1807; *U. pictorum*, Linné, 1758, *U. tumidus* Retzius, 1788, *Anodonta anatina* (Linné, 1758), *Pseudanodonta complanata* (Rossmaessler, 1835), *Pisidium amnicum* (Müller, 1774), *P. moitessierianum* Paladilhe, 1866, *P. supinum* A. Schmidt, 1850, *P. henslowanum* (Sheppard, 1825), *P. casertanum* Poli, 1791, *P. personatum* Malm, 1855, *P. nitidum* Jenyns, 1832, *P. milium* Held, 1836, *P. subtruncatum* Malm, 1855, *Sphaerium rivicola* (Leach, 1818), *S. solidum* (Normand, 1844), *S. corneum* (Linné, 1758). The ecology and distribution in the Delta area of these freshwater mussels have been discussed in a series of earlier papers (Kuiper & Wolff, 1970; Wolff, 1968, 1970).

Montacuta ferruginosa (Montagu, 1808). Earlier records: Jutting (1943).

In summer the planktotrophic larvae are released as veligers after incubation within the adults, and they may spend several months in the plankton before settlement and metamorphosis (Gage, 1966a). *M. ferruginosa* is a suspension-feeder (Newell, 1970). It occurs regularly together with several species of echinoids (Boss, 1965; Gage, 1966), but the only species available in the Delta area is the heart-urchin *Echinocardium cordatum* (Wolff, 1968a). Apparently *Montacuta* is also able to live in the absence of this echinoid — as was also pointed out by Gage (1966) — because it was also found in places where *E. cordatum* probably does not occur.

M. ferruginosa was found exclusively in areas of high salinity, viz. in the Oosterschelde, and in the North Sea proper. It was never observed in salinities below $16.5\,^0/_{00}$ Cl′.

M. ferruginosa was only found on sandy sediments with median diameters ranging from 1.72 to 3.00 φ, meaning medium and fine sands. The sorting coefficient varied from 0.21 to 0.54 phi-units. According to Tebble (1966) the species inhabits mainly fine muddy sands. Eisma (1966) records a preference for sands with a median grain-size of 1.75-2.30 φ and only 0.5-1% silt-clay. This is, however, not in accordance with the results of the authors reviewed by him, who in several cases recorded fine or silty sand.

Mysella bidentata (Montagu, 1803). Earlier records: Jutting (1943).

The earliest development takes place in the mantle cavity of the adult, whence the veligers are ejected 0.15 mm long. These occur in the plankton from June-July to September-November, often in large quantities. The larval stage apparently takes a long time (Jørgensen, 1946). *M. bidentata* is a suspension-feeder.

Also *M. bidentata* is recorded as a commensal from a number of hosts (Boss, 1965). From these only *Barnea candida* and *Nereis* sp. div. occur in the Delta area. However, it seems that *M. bidentata* is able to live very well without any host.

M. bidentata seems to have suffered from the extremely cold winter 1962/'63, because the records were markedly more scarce in the first years after this winter.

The distribution of *M. bidentata* may be represented as:

$\alpha_1 = 0.70$ $\alpha_7 = 0.00$ $\beta_1 = 0.08$
$\alpha_2 = 2.36$ $\alpha_8 = 0.00$ $\beta_2 = 0.31$

$\alpha_3 = 0.00$ $\alpha_9 = 0.23$ $\beta_3 = 0.67$
$\alpha_4 = 0.00$ $\alpha_{10} = 0.73$ $\beta_4 = 0.00$
$\alpha_5 = 0.00$ $\alpha_{11} = 0.51$ $\gamma_1 = 0.40$
$\alpha_6 = 0.00$ $\alpha_{12} = 0.01$ $\gamma_2 = 1.00$

It is absent from waters with a low salinity. The isohaline of $15^0/_{00}$ Cl' at high tide during average river discharge marks the limit of its distribution. It is also absent from the parts of the North Sea farthest offshore. Also Eisma (1966) found the species in the North Sea only in the near vicinity of the shore.

Apparently, *M. bidentata* has a preference for the finer grades of sand. The bulk of our observations originates from sands with a median grain-size of 2.20-3.30 φ. Eisma (op. cit.) records a preference for sediments with a median grain-size of 2.75-3.30 φ and over 10% silt-clay. Similary, most of the authors reviewed by him also record *M. bidentata* from muddy sand. In the Baltic the species was found in fine sand and sandy mud (Schulz, 1969). Also the preponderance of the species in poorly sorted sediments, as appears from the γ-values, may be explained by a preference for sands mixed with a certain amount of mud. A few specimens were found on sands with median grain-sizes down to 1.02 φ, but these sands mostly proved to be mixed with mud. Tebble (1966) even records the species from muddy gravel and also from muddy sand.

In the estuaries of the Delta area *M. bidentata* has been found from mid-tide level down to the largest depth sampled: 48 m.

Cardium edule Linné, 1758. Earlier records: Jutting (1943); Eisma (1965).

Cardium edule spawns in late spring and summer. The planktonic larvae may be found during a large part of the summer (Jørgensen, 1946). In the Waddensea, some 300 km from the Delta area, spatfall took place from the first half of May till, at least, the second half of July, with the maximum during the end of May. After their metamorphosis, however, the young cockles are liable to transport by the currents during about 4 weeks until they have reached a size of about 1800-2000 μ. This transports tends to accumulate the young cockles in quiet places with fine-grained sediments (Baggerman, 1953). *C. edule* is a suspension-feeder (Jørgensen, 1966).

The very severe winter 1962/1963 nearly exterminated the whole population of the Delta area. Only a few specimens apparently were able to survive in the deeper parts of the tidal channels. Nevertheless, an abundant spatfall occurred in the next summer.

The ecological distribution of the cockle in the subtidal parts of the Delta area may be represented as:

$$\begin{array}{lll}
\alpha_1 = 0.00 & \alpha_7 = 0.00 & \beta_1 = 0.04 \\
\alpha_2 = 0.63 & \alpha_8 = 0.22 & \beta_2 = 0.19 \\
\alpha_3 = 0.00 & \alpha_9 = 0.30 & \beta_3 = 0.30 \\
\alpha_4 = 0.00 & \alpha_{10} = 0.48 & \beta_4 = 0.00 \\
\alpha_5 = 0.00 & \alpha_{11} = 0.36 & \gamma_1 = 1.54 \\
\alpha_6 = 0.00 & \alpha_{12} = 0.10 & \gamma_2 = 1.00
\end{array}$$

The species is absent from the offshore parts of the North Sea and from those parts of the estuaries with an average salinity below about $12^0/_{00}$ Cl′ at high tide or $10^0/_{00}$ Cl′ at low tide during normal river discharge (fig. 22).

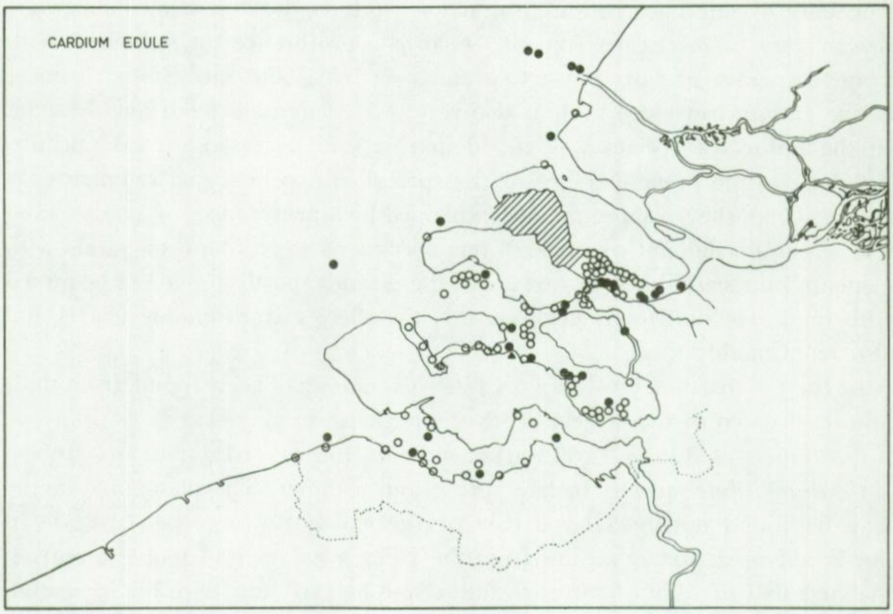

Fig. 22. Distribution of *Cardium edule*. Black dots denote subtidal finds, open circles intertidal ones. In the hatched area the intertidal sampling grid was very dense and *C. edule* was found in nearly all samples. Some data have been derived from Eisma (1966).

Tebble (1966) and Muus (1967) also record $10\text{-}12^0/_{00}$ Cl′ as the lower limit of occurrence. During high river discharges some populations become subjected to salinities down to $1\text{-}2^0/_{00}$ Cl′ and consequently mass mortalities then occur. Lower limits of tolerance mentioned in the literature probably concern the species *C. glaucum* (Eisma, 1965).

The absence of *C. edule* from the offshore parts of the North Sea (Eisma, 1966) probably may be explained by the observation of Winter (1969), who found that the relatively slow pumping rate of this species does not permit it to obtain sufficient food in such an environment (compare also *Mytilus edulis* and section 3.5.).

As appears from the indices calculated and from the work of Kreger (1940) and Kristensen (1957), the cockle tolerates a fairly large range of sediments, but its main habitat seems to consist of muddy sands. Eisma (1966) found a preference for sediments with a median grain-size of 2.75-3.30 φ and over 5% silt-clay. The large range of sediments inhabited by *C. edule* reflects that it is not influenced so much by the nature of the sediment, but mainly by the hydrodynamical conditions accompanying the sediment. The currents must not be so fast that the cockles are washed out, but fast enough to provide enough food and to prevent the deposition of a layer of detritus.

Cardium edule is abundant on most intertidal flats. Also in rather shallow water below MLW-level it may be fairly common, but it is nearly absent from the deeper part of the tidal channels. The deepest record is from about 20 m depth in the Westerschelde. Kristensen (op. cit.) supposes that the preference of the cockle for shallow water is not due to a preference for light. He assumes that cockles living completely in the dark easily fall victim to predators. This does not seem very probable because exploitable cockle banks occur at a maximum depth of 1-2 m in the very clean Oosterschelde and of 3-4 m in the turbid Westerschelde (pers. comm. Mr. C. de Rooy). More probably, the scarcity of the cockle in the deeper part of the tidal channels is caused either by the strong tidal currents washing the cockles out, or — in the channels not used any longer by the tidal currents — by the deposition of detritus, having a deleterious effect upon the cockles (Kristensen, op. cit.).

Cockles are infrequent in the higher parts of the intertidal zone. As in the Waddensea (Kristensen, op. cit.) nearly no cockles are found at places with a submersion time less than 3-4 hours. Moreover, the cockles found at such places invariably prove to be small specimens.

Venus gallina striatula (Da Costa, 1778). This is a rare species in the Delta area and the adjacent part of the North Sea, although live specimens regularly are washed ashore near Hoek van Holland.

V. gallina reproduces in Plymouth in early spring, but in Kames Bay, Scotland, in May-June (Ansell, 1961) and in the Sound in summer and autumn (Jørgensen, 1946). In the North Sea its planktonic larvae are found in September, October, and November (Ansell, 1960). It is a suspension-feeder (Jørgensen, 1966).

It is not clear why *V. gallina* is so rare in the Delta area. It is generally considered an inhabitant of sandy bottoms in deeper water (Petersen,

1915) and this type of environment exists plentiful in the offshore part of the North Sea. Moreover, Eisma (1966) found large numbers in the more northern parts of the North Sea, where they inhabited bottoms with a median grain-size of 1.75-2.00 φ and a silt-clay fraction of more than 10%. According to the authors reviewed by him, *V. gallina striatula* inhabits a fairly large variety of sandy sediments.

The only two specimens found originated from sandy bottoms in the Oosterschelde and in the North Sea, about 4 miles off the mouth of the Haringvliet.

Venerupis pullastra (Montagu, 1803). Earlier records: Jutting (1943).

Quayle (1952, 1952a) observed at Millport, Scotland, spawning from May to August and found the planktonic larvae from June to September. The larvae of probably this species occurred in the North Sea from September to December (Ansell, 1960). Quayle (1952) estimated the duration of the planktonic stage to be about 30 days. The larvae do not seem to be very selective when settling. *V. pullastra* is a suspension-feeder (Jørgensen, 1966).

V. pullastra is fairly common on the bottom of the tidal channels of the Oosterschelde and the Grevelingen. Because it is absent from the other estuaries, it does not seem to tolerate salinities very much below $15^0/_{00}$ Cl′. Rasmussen (1958), however, mentions a salinity of about $10^0/_{00}$ Cl′ as the lower limit of occurrence. *V. pullastra* shows a preference for rough bottoms, e.g. peat banks, accumulations of shells, etc. Therefore, it is impossible to correlate its occurrence with a certain range of grain-sizes. Rasmussen (op. cit.) states that the species does not occur in muddy sediments (meadows of *Zostera*), but prefers hard sandy or stony bottoms.

Its depth distribution ranges from about low water level to 25 m. Deeper samples have hardly been taken.

Petricola pholadiformis Lamarck, 1818. Earlier records: Jutting (1943). It was introduced from North America around 1905.

P. pholadiformis spawns mainly in August (Duval, 1963). The planktonic larval stage lasts for 10-15 days. The species is a suspension-feeder (Jørgensen, 1966).

Duval (op. cit.) records a number of soft types of rocks and also peat as substratum for this species. In the Delta area it is found in peat, but also in muddy sand and in mussel-beds. Also Swennen (1959) records the occurrence of *P. pholadiformis* in muddy sand.

Its ecological distribution may be sketched as:

$$\begin{array}{lll} \alpha_1 = 0.00 & \alpha_7 = 0.00 & \beta_1 = 0.12 \\ \alpha_2 = 0.41 & \alpha_8 = 0.58 & \beta_2 = 0.08 \\ \alpha_3 = 0.00 & \alpha_9 = 0.11 & \beta_3 = 0.42 \end{array}$$

$\alpha_4 = 0.00 \quad \alpha_{10} = 0.67 \quad \beta_4 = 0.48$

$\alpha_5 = 0.07 \quad \alpha_{11} = 0.64 \quad \gamma_1 = 0.52$

$\alpha_6 = 0.00 \quad \alpha_{12} = 0.01 \quad \gamma_2 = 1.00$

It appears that *P. pholadiformis* occurs only in the seaward reaches of the estuaries and the coastal water. Adult individuals probably do not occur below about $15^0/_{00}$ Cl′, but in periods of high salinity spat may be found in parts of the estuaries much more landinward. Jutting (1943) records $8.5^0/_{00}$ Cl′ as the lowest salinity endured.

The species has been met with in the intertidal zone as well as down to a depth of 48 m, deeper places not having been sampled.

Mactra corallina cinerea Montagu, 1803. Earlier records: Jutting (1943).

Nothing is known about its reproduction. It is a suspension-feeder (Newell, 1970). Because there are only four records of *Mactra* in the Delta area, it is apparently a rare species. Eisma (1966) also failed to discover this species in his extensive grab survey off the Dutch coast, although the species regularly washes ashore in large numbers. Possibly the species shows large fluctuations in numbers.

The specimens obtained originated from sandy bottoms (Md = $2.60\,\varphi$) in waters with a salinity over $15^0/_{00}$ Cl′.

Spisula subtruncata (Da Costa, 1778). Earlier records: Jutting (1943); Van Urk (1957). This species probably spawns in winter and early spring (Jørgensen, 1946), but confusion with *S. elliptica* is possible. The pelagic larval stage seems to last fairly long. *S. subtruncata* is a suspension-feeder (Newell, 1970).

S. subtruncata proved to be rather rare in the Delta area. Only four specimens could be identified with certainty; another ten specimens probably also represent this species, but are too young for a correct identification. All records originate from waters with a salinity over $15^0/_{00}$ Cl′, but in several cases far landinward. Jaeckel (1952) and Haas (1928) record $7\text{-}8^0/_{00}$ Cl′ as the lower limit of occurrence of *S. subtruncata*.

The sediment has a median grain-size varying from 1.96 to $3.18\,\varphi$. The species was found at depths varying between 6 and 22 m, but Jutting (1943) records a *Spisula*, probably this species, living on the beach of the island of Walcheren.

Spisula elliptica (Brown, 1827). Earlier records: Van Urk (1957).

Because it has been confused so long with *S. subtruncata* nothing is known about its reproduction. Probably it has a planktonic larval stage. *S. elliptica* is a suspension-feeder (Newell, 1970).

S. elliptica exclusively occurs in the offshore parts of the North Sea, where it replaces *S. subtruncata* completely. There seems to be no overlap in the distribution of the two species, which never were found in the same sample.

S. elliptica always was found in water of high salinity (over 16.0$^0/_{00}$ Cl′). It occurred in the clear Channel water as well as in the more turbid Continental coastal water.

The species has been found on medium and fine sands with median grain-sizes of 1.13-2.59 φ, but the majority originated from sands with a median diameter between 1.70 and 2.30 φ. Tebble (1966) records muddy sand, muddy gravel, fine gravel and shell gravel.

Because the salinity in the Oosterschelde seems to be high enough for *S. elliptica,* it is believed that it is especially the temperature regime which inhibits the occurrence of *S. elliptica* in the estuaries. This is, however, contradicted by its distribution. *S. elliptica* has been found at depths ranging from 35 to 6 m, the latter depth occurring in the shallow area off the mouth of the Westerschelde, where temperature probably still shows an estuarine pattern.

Donax vittatus (Da Costa, 1778). Earlier records: Jutting (1943).

Data on its reproduction have not been found; probably it has pelagic larvae. *D. vittatus* is a suspension-feeder (Pohlo, 1969).

During this study adult specimens only have been found in the offshore parts of the North Sea. A few juveniles (length 1.0-2.5 mm), however, have been found in the Zandkreek. All observations from the North Sea were made in waters with a salinity over 17.5$^0/_{00}$ Cl′. The specimens from the Zandkreek probably settled in a period with a similar salinity.

The specimens from the North Sea were found in well-sorted medium sand (Md 1.86-1.92 φ). Those from the Zandkreek, however, came from fine sand with a median grain-size of 2.60-2.78 φ. Eisma (1966) records — in general in accordance with the authors reviewed by him — a preference for sands with a median grain-size of 1.75-2.75 φ, and a fraction $<50\,\mu$ of 1-5%.

Scrobicularia plana (Da Costa, 1778). Earlier records: Jutting (1943).

Green (1957) and Raymont (1955) both found very juvenile specimens in July. Hughes (1971) records spawning from June to August in North Wales. *S. plana* possesses pelagic larvae. It is a selective deposit-feeder, which, however, may act as a suspension-feeder during high tide (Thamdrup, 1935; Hughes, 1969).

In the Delta area *S. plana* inhabits a large range of salinities. It has been found at salinities permanently over 16.5$^0/_{00}$ Cl′, as well as at about 11$^0/_{00}$ Cl′ at high tide along the Westerschelde and at about 8-10$^0/_{00}$ Cl′ along the Krammer. Also Guérin (1961) noted the euryhalinity of this species. Jaeckel (1952) records about 6$^0/_{00}$ as its limit in the Baltic.

The nature of the sediment seems to be much more important for this species. All finds of *S. plana* were made in muddy sand or soft muds. In the cases that a grain-size analysis was made, the median grain-size always was over $3.00\ \varphi$. Also Tebble (1966) records the species from soft muds. However, Guérin (1961) and Schulz (1969) record the species from all sediments ranging from coarse sand to silt. Most probably *S. plana* does not require a special type of bottom, but a certain type of environmental conditions normally accompanying muddy bottoms, viz. a constant supply with fine particulate organic matter. Because muddy sediments with such conditions especially occur in the more brackish parts of the estuaries, *S. plana* is most common in those parts of the estuaries, with a salinity between about 10 and $15^0/_{00}$ Cl′. Therefore it is not a brackish water species, as has been stated many times, but rather an euryhaline, marine species.

Its vertical distribution also seems to be determined by its preference for muddy sediments. Because the muddiest sediments often occur near the high water mark (paragraph 3.3.2.), this explains why *S. plana* may be found so often in large numbers in the upper part of the tidal zone and in creeks in the salt-marshes. *S. plana* also has been found below LW-level, maximally at a depth of 5.5 m.

Abra alba (S. Wood, 1802). Earlier records: Jutting (1943).

A. alba has pelagic larvae (Jørgensen, 1946). In Kames Bay, Scotland, spawning takes place in June-July (Stephen, 1932). The species is a selective deposit-feeder (Pohlo, 1969).

Its ecological distribution in the Delta area may be represented by:

$\alpha_1 = 0.20$ $\alpha_7 = 0.00$ $\beta_1 = 0.03$
$\alpha_2 = 1.18$ $\alpha_8 = 0.00$ $\beta_2 = 0.50$
$\alpha_3 = 0.00$ $\alpha_9 = 0.12$ $\beta_3 = 1.32$
$\alpha_4 = 0.00$ $\alpha_{10} = 0.19$ $\beta_4 = 0.00$
$\alpha_5 = 0.00$ $\alpha_{11} = 0.23$ $\gamma_1 = 0.41$
$\alpha_6 = 0.00$ $\alpha_{12} = 0.01$ $\gamma_2 = 1.00$

It appears that *Albra alba* occurs in the North Sea and in those parts of the estuaries, where salinity normally does not fall below $15^0/_{00}$ Cl′. Jaeckel (1952) however, records $7^0/_{00}$ Cl′ as the lower limit of this species in the Baltic.

A. alba is absent from the parts of the North Sea further offshore, most probably because of the nature of the sediment. From the β-values it is evident that the species prefers sediments with a median grain-size of 2.00-$4.00\ \varphi$. Glémarec (1964) records muddy sands with median grain-sizes of 2.00-3.30 φ. Tebble (1966) and Schulz (1969) mention *A. alba* as an inhabitant of bottoms of mud, silty sand and soft muddy gravel. Eisma (1966) found a preference for sediments with a median grain-size of 2.75-3.30 φ and a percentage of silt-clay over 10%. Various authors quoted by him recorded the species also from mud, sandy mud, muddy sand, and fine sand. All these types of sediment do not occur in the offshore parts of the North Sea.

With the likelihood ratio test for $\gamma_1 = \gamma_2$, mentioned in section 2.4., it was tested whether the observed difference between γ_1 and γ_2 was significant. This proved to be so ($P < 0.001$).

The vertical distribution of *Abra alba* ranges from the lower part of the intertidal zone down to 48 m, being the deepest place sampled.

Abra prismatica (Montagu, 1803). The species has not been recorded earlier from the Delta area. Nothing is known about its reproduction, but probably it has pelagic larvae. It is a selective deposit-feeder (Pohlo, 1969).

Only three finds of this species are available, all from the North Sea adjacent to the Delta area. All specimens originate from water with a high salinity (16-19$^0/_{00}$ Cl′). Nevertheless, Spooner & Moore (1940) state that the species is able to tolerate a lowered salinity during short periods.

The sediment consisted at all places of well-sorted medium to fine sand with a median grain-size of 1.92-2.29 φ. Glémarec (1964) records the species from offshore deposits with well-sorted sands with a median grain-size of 1.25-2.50 φ and Toulemont (1972) from the range 1.50-2.75 φ. Spooner & Moore (op. cit.) and Raymont (1955), however, record the species from an unstable mud bottom and a muddy sand bottom, respectively, whereas Tebble (1966) mentions clean sand, fine sand, and muddy sand. Finally, Eisma (1966) found a preference for sediments with a median grain-size of 2.00-2.75 φ and 0-10% silt-clay. The various authors reviewed by him mention mud, muddy sand, fine sand, as well as sand.

The depth distribution of *A. prismatica* ranged in the North Sea from 13 to 28 m.

Abra tenuis (Montagu, 1803). Earlier records: Jutting (1943).

Data on its reproduction are not available, but probably it has pelagic larvae. Most probably it is a selective deposit-feeder.

The number of observations from the Delta area is rather low, partly due to insufficient sampling in its typical habitat.

In tidal waters it has never been found at salinities below 15$^0/_{00}$ Cl′, but in some nontidal inland waters it was found at a median salinity (Heerebout, 1970) of 11$^0/_{00}$ Cl′, with observed minimal salinities of about 6$^0/_{00}$ Cl′. *A. tenuis* apparently is an euryhaline marine species. Glémarec (1964), however, considers this a typical brackish water species, without giving salinity data.

All observations originate from the intertidal zone. Glémarec (op. cit.) describes the same situation.

Macoma balthica (Linné, 1758). Earlier records: Jutting (1943).

M. balthica spawns in April and May (Lammens, 1967) and has pelagic larvae (Jørgensen, 1946). It is a selective deposit-feeder, but it also may act as a suspension-feeder during high tide (Brafield & Newell, 1961). Newell (1965) showed that the food of deposit-feeding *Macoma balthica* consists mainly of micro-organisms.

The distribution of *Macoma balthica* may be represented as:

$\alpha_1 = 0.00$ $\alpha_7 = 0.00$ $\beta_1 = 0.07$
$\alpha_2 = 2.35$ $\alpha_8 = 1.96$ $\beta_2 = 0.23$
$\alpha_3 = 0.73$ $\alpha_9 = 4.37$ $\beta_3 = 0.39$
$\alpha_4 = 0.54$ $\alpha_{10} = 2.61$ $\beta_4 = 0.00$
$\alpha_5 = 0.24$ $\alpha_{11} = 2.20$ $\gamma_1 = 0.76$
$\alpha_6 = 0.00$ $\alpha_{12} = 1.00$ $\gamma_2 = 1.00$

Thus, subtidally *M. balthica* is most common in the seaward reaches of the estuaries, although the species is very well able to live in brackish water, because animals living at values as low as $1.7\text{-}2.1\,{}^0/_{00}$ Cl′ are recorded by Jutting (1943) from the former Zuiderzee and as low as $1.5\text{-}2\,{}^0/_{00}$ Cl′ by Lassig (1965) from the Baltic. In the estuaries of the Delta area it reaches the isohaline of $2\,{}^0/_{00}$ Cl′ at high tide during normal river discharge (fig. 23). Nevertheless, subtidally it is less common in the brackish part of estuaries than in the marine parts. As the α-indices calculated are independent from the nature of the sediment, two reasons for this phenomenon may be given. Firstly, it seems possible that low average salinities influence the settlement and maintenance of *M. balthica*. More probable, however, seems the explanation that the populations in the brackish parts of the estuaries are decimated during periods that large quantities of fresh water are carried in by the rivers. Of course, both explanations may also hold at the same time. McErlean (1964) similarly found that the average size of *Macoma* increased with increasing salinity along the Patuxent estuary, but, remarkably enough, the average size dropped again at the highest salinities. This result, at first sight indicating a detrimental influence of high salinity, probably has to be ascribed to the nature of the sediments in this estuary or other factors, but not to salinity. Also the absence of the species from the offshore parts of the North Sea probably is not due to salinity, but to the nature of the sediment or to some other factor. Segerstråle (1965) ascribes this to predation by echinoderms and other animals. However this may be, it is concluded, contrary to Spooner & Moore (1940), that *M. balthica* has a preference for those parts of the estuaries, where salinity is highest.

Various authors stated that *M. balthica* occurs indiscriminately on all types of bottom (Beanland, 1940; Smidt, 1951). This study demonstrates that *M. balthica* indeed inhabits all types of sandy sediments, but also shows a preference for the finer sediments with a median grain-size between 3.00 and 4.00 φ. Eisma (1966) found a preference for sediments with a median grain-size of 2.25-2.75 φ and 0.5-10.0% of mud. Mulicki (1957) and Schulz (1969), working in the Baltic, also found that *M. balthica* prefers fine and muddy sands and avoids gravels and soft muds. Newell (1965), however, showed that large populations of *Macoma* may occur in very fine sediments with a median grain-size of about 5.00 φ. Moreover, he demonstrated a very clear relationship between the number of specimens per m² and the median grain-size of the sediment, the numbers of *Macoma* strongly increasing towards the finer grades of sediment.

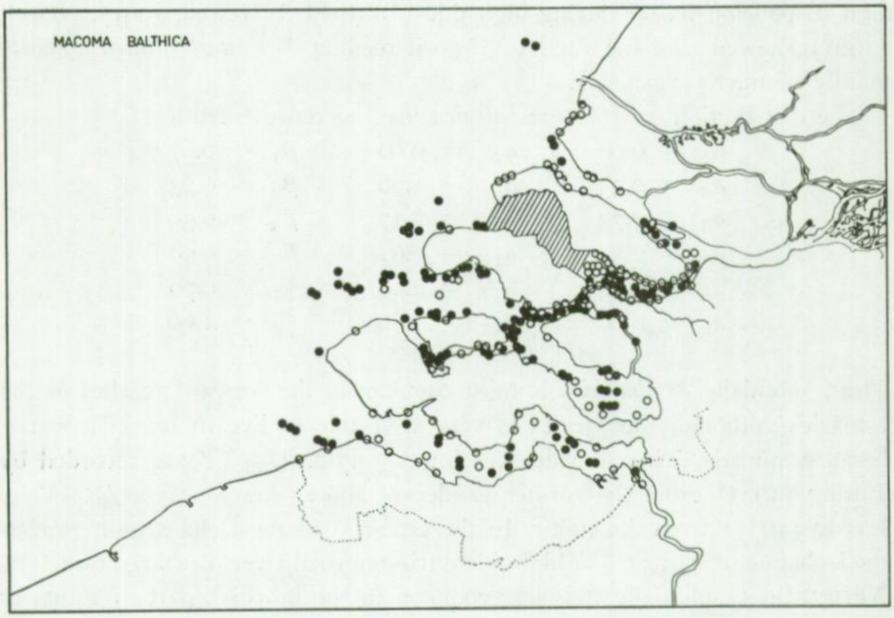

Fig. 23. Distribution of *Macoma balthica*. Symbols as in fig. 22. Some data have been derived from Eisma (1966).

In the intertidal zone fine sediments especially occur in the brackish parts of the estuaries. Consequently, *M. balthica* is numerous in many intertidal habitats of this part of the estuaries. It is concluded that this abundance is solely attributable to the nature of the sediment and not to the lowered salinity.

From the γ-indices it appears that on the average *M. balthica* has a preference for the badly sorted sediments. Perhaps this may be explained by the fact that these often contain a fair amount of much finer grained material.

The depth range of *M. balthica* is very large. It occurs from about HW-mark to the bottom of the large tidal channels. The maximum depth is 27 m. Remarkably, this species, considered by many authors as a brackish water species, does not show a "Brackwassersubmergenz" in the estuaries of the Delta area. In the marine parts with a salinity over $16.5\,^0/_{00}$ Cl′, it has the same vertical distribution as in the brackish parts with a salinity under $5\,^0/_{00}$ Cl′.

Angulus tenuis (Da Costa, 1778). Earlier records: Jutting (1943).

Spawning occurs in June-August (Ansell & Trevallion, 1967). Most probably it has a pelagic larval stage. It is a suspension-feeder with tendencies to selective deposit-feeding. It may take vegetable detritus, but diatoms also may occur in the gut (Stephen, 1928; Trevallion, 1971). Its ecological distribution in the Delta area may be represented as:

$\alpha_1 = 0.89$ $\alpha_7 = 0.00$ $\beta_1 = 0.00$
$\alpha_2 = 0.92$ $\alpha_8 = 0.00$ $\beta_2 = 0.85$
$\alpha_3 = 0.00$ $\alpha_9 = 0.15$ $\beta_3 = 0.00$
$\alpha_4 = 0.00$ $\alpha_{10} = 0.78$ $\beta_4 = 0.00$
$\alpha_5 = 0.00$ $\alpha_{11} = 0.00$ $\gamma_1 = 0.12$
$\alpha_6 = 0.00$ $\alpha_{12} = 0.01$ $\gamma_2 = 0.10$

A. tenuis has never been found in salinities below about $15\,^0/_{00}$ Cl′. Also it does not occur in the farthest offshore parts of the North Sea, but it seems to be restricted to a narrow belt along the shore, as was also observed by Eisma (1966). Probably this may be correlated with better food conditions in this area.

A. tenuis has only been found on fine and muddy sand with median grain-sizes varying between 2.10 and 3.25 φ, but the majority of the observations, as appears from the β-values, originates from between 2.10 and 2.80 φ. Also Stephen (op.cit.), Tebble (1966), Faure (1969) and Ansell & Trevallion (op. cit.) record that this species inhabits fine sands. Eisma (1966), however, found this species in a fairly large range of sediments without a preference for a special type. The authors reviewed by him mentioned widely varying types of sediment for this species as well.

A. tenuis has been found from the lower part of the intertidal zone down to 24 m. The majority of the specimens, however, originated from smaller depths.

Angulus fabula (Meuschen, 1781). Earlier records: Jutting (1943).

Pelagic larvae of probably this species may be met with in spring and summer in the Sound (Jørgensen, 1946). *A. fabula* is a selective deposit-feeder (Pohlo, 1969), although after the study of Trevallion (1971) it does not seem unreasonable to suppose that it is also capable of suspension-feeding. Its ecological distribution in the Delta area may be represented as:

$$\begin{array}{lll}
\alpha_1 = 1.14 & \alpha_7 = 0.00 & \beta_1 = 0.01 \\
\alpha_2 = 0.75 & \alpha_8 = 0.00 & \beta_2 = 0.15 \\
\alpha_3 = 0.00 & \alpha_9 = 0.00 & \beta_3 = 0.16 \\
\alpha_4 = 0.00 & \alpha_{10} = 0.33 & \beta_4 = 0.00 \\
\alpha_5 = 0.00 & \alpha_{11} = 0.00 & \gamma_1 = 1.25 \\
\alpha_6 = 0.00 & \alpha_{12} = 0.01 & \gamma_2 = 1.00
\end{array}$$

A. fabula only inhabits the most marine parts of the estuaries. It has been found in the Zandkreek, the western part of the Oosterschelde, and in the North Sea. Also Eisma (1966) found it plentiful in the North Sea. It was not found in salinities below $16.5^0/_{00}$ Cl′, hence, it seems to be less tolerant to low salinities than *A. tenuis*.

The sediment data show that *A. fabula* inhabits a larger sediment range than *A. tenuis*. The median grain-size ranges from 1.82 to 3.45 φ. Tebble (1966) mentions clean silty sand and muddy sand. Eisma (op. cit.) found a preference for sediments with a median grain-size of 2.30-2.75 φ and 1-10% silt-clay. The authors reviewed by him recorded this species, however, from a fairly large variety of sandy sediments.

In the Delta area the depth distribution of this species ranges from the intertidal zone to 32 m below low water level.

Tellina pygmaea (Lovén, 1846). Earlier records: Jutting (1943).

Data on the reproduction of this species are not available, but most probably it possesses pelagic larvae. It is a selective deposit-feeder (Pohlo, 1969).

T. pygmaea was exclusively found in the offshore parts of the North Sea at salinities over $19.0^0/_{00}$ Cl′.

All observations originate from medium sands with median grain-sizes ranging from 1.13 to 1.80 φ; the sorting ranges from 0.25 to 0.72 phi-units. Tebble (1966) reports the species to inhabit coarse sand and shell-gravel.

The depths varied from 27 to 32 m.

Cultellus pellucidus (Pennant, 1777). One specimen was found on medium sand about 40 km offshore in the North Sea. No other specimens are known from the Delta area or the adjacent part of the North Sea.

Ensis minor (Chenu, 1843). Earlier records: Van Urk (1964, 1964a), who states that this species appeared at the coast of The Netherlands around 1920.

Data on the reproduction of this species are not available, but most probably it has pelagic larvae, as is the case in at least three other species of the genus (Holme, 1954). It is a suspension-feeder.

Because the species of *Ensis* mostly are deep-burrowing, they seldom occur in a 0.2 m^2 Van Veen grab. Live specimens, however, have been found by trawling shrimp-cutters and also washed ashore on the beach. Moreover, the empty shells of this species are by far the commonest among the shells of *Ensis* washed ashore on the North Sea beaches. It is also the only species of which the empty shells may be found washed ashore on the tidal flats of the estuaries. Offshore records, on the other hand, do not exist of this species. Apparently *E. minor* is a nearshore species. However, it does not seem to tolerate salinities considerably below $16.5^0/_{00}$ Cl′.

E. minor presumably prefers sandy sediments. Data on the depth distribution are lacking.

Ensis arcuatus (Jeffreys, 1865). This species has not been recorded before from the Delta area.

It has pelagic larvae (Holme, 1954) and is a suspension-feeder.

Live specimens only have been trawled in the North Sea about 40 km offshore, most probably from a sandy bottom. Holme (op. cit.) records the species from sediments with a median grain-size ranging from about —0.50 to 2.75 φ. The salinity at the locality where the specimens were found is high; about $18\text{-}19^0/_{00}$ Cl′.

Ensis phaxoides Van Urk, 1964. This species has not been recorded from the Delta area before.

No data are available on the reproduction of this species, but probably it has pelagic larvae. It is a suspension-feeder.

About 30 km offshore a few specimens of this species (identified by Mr. Van Urk) were caught with a bottom-grab. The salinity at these localities varies between 18 and $19^0/_{00}$ Cl′. The bottom consisted four times of medium sand and once of fine sand. The depth was 28-30 m.

Mya arenaria Linné, 1758. Earlier records: Jutting (1943). It colonized the European waters in the 16th or 17th century (Hessland, 1945).

M. arenaria reproduces in summer and the larvae may be found in the plankton from June to September (Jutting, 1943). Jørgensen (1946) mentions June to October and estimates the duration of the planktonic stage to be about two weeks. The species is a slow suspension-feeder (Thamdrup, 1935; Mann, 1952), depending chiefly on flagellates (Matthiesen, 1960).

M. arenaria is able to tolerate very low salinities. Matthiesen (op. cit.) found that very small specimens (<2 mm) were able to tolerate a salinity below $0.6^{0}/_{00}$ Cl′ for at least 24 hours and larger specimens were even more tolerant. However, the pumping rate diminished at salinities below $8\text{-}9^{0}/_{00}$ Cl′ and the process stops altogether at salinities below $2.5^{0}/_{00}$ Cl′. In the Baltic the species occurs down to salinities of $2.5\text{-}3.0^{0}/_{00}$ Cl′ (Lassig, 1965). Jutting (op. cit.) even recorded the species from the former Zuiderzee living in salinities as low as $1^{0}/_{00}$ Cl′.

In the Delta area small specimens reach nearly the isohaline of $2^{0}/_{00}$ Cl′ during high tide and normal river discharge in the Haringvliet, but larger individuals only occur at higher salinities. Presumably the young specimens die in winter during periods of high river discharge. In the Delta area *M. arenaria* inhabits also a series of brackish inland waters, but only those where salinity does not fall below $5^{0}/_{00}$ Cl′ for long periods. In the estuaries adult *M. arenaria* also occurs in salinities over $16.5^{0}/_{00}$ Cl′ and it lives even in the North Sea (Eisma, 1966). Therefore it is believed that its seaward extension is not restricted by salinity, but by other factors. Its slow pumping rate (Winter, 1969) may be important, because it may result in shortage of food in the offshore areas.

M. arenaria chiefly occurs in muddy sediments, but the species seems to be able to live in all types of sediment (Kühl, 1952). This author states that the juveniles apparently need muddy sediments, but that the adults are resistant to changes in the type of sediment. Nevertheless, the bad digging capacities of the species probably restrict it to areas nearly without erosion. This probably causes the abundant occurrence of the species in the more brackish parts of the estuaries, where sedimentation of mud is the rule.

The vertical distribution ranges from the upper part of the intertidal zone, — even in creeks in the salt-marshes —, down to 16 m depth.

Mya truncata Linné, 1758. Earlier records: Jutting (1943).

The larvae occurred from October to April in the plankton of the Sound (Jørgensen, 1946). *M. truncata* is a suspension-feeder (Newell, 1970).

Because the species is missed easily by grab-sampling methods, only few records are available. It has been found in the Oosterschelde and in the coastal parts of the North Sea, thus in high salinities. In the Baltic it still occurs at a salinity of $5.6^{0}/_{00}$ Cl′ (Jaeckel, 1952).

The species has often been found in holes in peat-banks. Tebble (1966) and Schulz (1969) record it from sand, sandy mud and clay.

M. truncata has been found only subtidally at a maximal depth of 25 m.

Barnea candida (Linné, 1758). Earlier records: Jutting (1943).

Jørgensen (1946) recorded the planktonic larvae from the Sound in the months July-November. Spawning occurred at Whitstable from early to mid-September (Duval, 1963a). The species is a suspension-feeder (Jørgensen, 1966).

In the Delta area *B. candida* is restricted to peat banks and stiff subfossil clay-layers. The species may be found all over the marine parts of the estuaries. Most specimens originate from salinities over $15^{0}/_{00}$ Cl′, but one find was made at a salinity of $10\text{-}12^{0}/_{00}$ Cl′. Jaeckel (1952) records $9^{0}/_{00}$ Cl′ as the lower limit of this species in the Baltic.

B. candida has been found from the intertidal zone down to a depth ot 14 m.

Zirfaea crispata Linné, 1758. Earlier records: Jutting (1943).

Jørgensen (1946) found the pelagic larvae in the Sound throughout the year. Along the Northumberland coast Allen (1969) observed that gametogenesis occurred from March to October, but that mature animals were predominant in March-May and August-October. *Z. crispata* is a suspension-feeder.

Z. crispata lives in the same habitat as *Barnea candida*: peat banks and layers of stiff clay. It is only found in the marine parts of the estuaries of the Delta area, always living at salinities over $15^{0}/_{00}$ Cl′. It also lives in peat banks in the offshore parts of the North Sea (Jutting, 1943).

In the Delta area the vertical distribution ranges from the intertidal zone down to 11-12 m.

5.4. Vermes

Echiurus echiurus (Pallas, 1766). This species has not been recorded before from the Delta area. Most probably *E. echiurus* has pelagic larvae, as have the other species of the genus. It may be considered as a selective deposit-feeder (Kaestner, 1965).

It was found twice in the nearshore parts of the North Sea and twice in the Oosterschelde at salinities over $16.5^{0}/_{00}$ Cl′. It lived in stable bottoms of muddy sand, as was also observed by Reineck et al. (1968).

Aphrodite aculeata Linné, 1761. Earlier records: Baster (1765).

The time of spawning is unknown; possibly the species has a very short pelagic larval stage, or, more probably, a non-pelagic development (Thorson, 1946). It is a predator on other soft-bottom species (Hartmann-Schröder, 1971).

A. aculeata was repeatedly found in one particular musselbed in the western part of the Oosterschelde; moreover, it has been washed ashore a few times on the beaches along the North Sea. All observations originate from water with a salinity over $16.5^0/_{00}$ Cl′. Hartmann-Schröder (1971) records a lower limit of $10^0/_{00}$ Cl′ for the Limfjord.

A. aculeata is generally known as an inhabitant of stable mud and muddy sand bottoms (Kirkegaard, 1969). Subtidally, such bottoms are rare in the seaward parts of the estuaries of the Delta area, which explains its scarce occurrence.

Antinoella sarsi (Kinberg, 1865). This species has not been recorded before from the Delta area. The specimens were identified by Dr. M. H. Pettibone (Washington).

The species has pelagic larvae which in Finland occur in the plankton from early February to early May, and perhaps even longer (Sarvala, 1971). *A. sarsi* is a predator taking a large range of food organisms (Sarvala, op. cit.).

A. sarsi has been found at full oceanic salinity, but in the Baltic it tolerates very low salinities. Sarvala (op. cit.) records a minimal value of about $3.5^0/_{00}$ Cl′, but the various populations seem to show different tolerances. In the Delta area it was not found below salinities of about $10\text{-}12^0/_{00}$ Cl′, but this can possibly be ascribed to the distribution of its host, because *A. sarsi* was found exclusively in the burrows of *Arenicola marina*. The distribution of *A. sarsi* in the Delta area seems to be identical with that of *Arenicola* which does hardly occur below $10^0/_{00}$ Cl′. Because *Arenicola* was only rarely found below LW-level, it is not astonishing that *A. sarsi* was not found there. In the Baltic, however, Mulicki (1959) did not find the species shallower than 6 m, whereas Sarvala (1971) found the lowest numbers at a depth range of 0-10 m.

Gattyana cirrosa (Pallas, 1766). This is the first record from the Delta area.

Data on its reproduction are scarce; only Thorson (1946) records a pelagic larva possibly belonging to this species. *G. cirrosa* is a predator (Hartmann-Schröder, 1971).

Dales (1955) observed that *G. cirrosa*, living in the burrows of *Neoamphitrite figulus*, robbed the food collected by this terebellid. Also Davenport (1953) and König (1949) record it as a commensal from the burrows of this species, but Jepsen (1965) and Newell (1954) found it in *Arenicola* burrows.

In the Delta area it was never observed to inhabit the burrows of sedentary polychaetes, although it was mostly collected together with such species.

G. cirrosa was only found in the marine parts of estuaries. The lowest salinity where this species was encountered was 13-14$^0/_{00}$ Cl′. It occurred on all types of bottom, but apparently with a preference for the muddier types of sediment, often mixed with a considerable quantity of shells. Its vertical distribution reaches from the intertidal zone to the deepest place sampled: 48 m.

Harmothoe impar (Johnston, 1839). Earlier records: Korringa (1951).

In Denmark the species spawns in May (Rasmussen, 1956), but Korringa (1951) observed larvae in the Oosterschelde in June-July, and sometimes again in September. Little is known about the food of *H. impar;* only Rasmussen (1956) states that he found a 1.5 mm long *Corophium* in the intestine.

In the Delta area it is a very common species in water of high salinity. The lowest salinity it must have been able to survive was about 12$^0/_{00}$ Cl′, but the species becomes rare already below 15$^0/_{00}$ Cl′. *H. impar* is a very motile species living on all kinds of substrate, sandy muds as well as live and dead molluscs, for instance. It is absent from the offshore parts of the North Sea, probably because stable bottoms are lacking there.

It has been found in the intertidal zone as well as down to a depth of 45 m.

Harmothoe imbricata (Linné, 1767). Earlier records: Korringa (1951).

Rasmussen (1956), contesting the conclusions of Thorson (1946), states that *H. imbricata* shows a well-defined winter breeding in the Isefjord, Denmark. The larvae occur in the plankton from January to April. Daly (1972) records breeding in March and April from eastern England. Probably the larvae occur in about the same period in the Oosterschelde, because Korringa (1951) failed to discover them during his sampling in spring and summer. *H. imbricata* is a predator (Hartmann-Schröder, 1971).

H. imbricata tolerates fairly low salinities. Banse & Lefevre (1954) mention the species from salinities of 10-12$^0/_{00}$ Cl′. De Vos (1936) mentions 6.6$^0/_{00}$ Cl′ as the minimal value, whereas Hartmann-Schröder (1971) records 3$^0/_{00}$ Cl′ as the lower limit. In the Delta area it occurred plentifully in the Veerse Meer in 9-11$^0/_{00}$ Cl′. In the estuaries of the Delta area, however, it becomes less frequent below the isohaline of 15$^0/_{00}$ Cl′ at high tide and average river discharge and it is not found below salinities of 12-13$^0/_{00}$ Cl′. Probably this is caused by the periodic influxes of fresh and brackish water during periods of high river discharge.

H. imbricata is not a typical soft-bottom species; it inhabits mainly musselbeds, beds of *Lanice conchilega,* and muddy sand bottoms mixed with shells.

Its vertical distribution ranges from the intertidal zone down to a depth of 45 m.

Harmothoe longisetis (Grube, 1863). This scale-worm was not recorded before from Dutch waters. Data about its food or reproduction have not been found. This species has been recorded from the burrows of *Arenicola marina* and various terebellids and chaetopterids (Newell, 1954; Faune marine de Roscoff, 1967; Hartmann-Schröder, 1971). *H. longisetis* only was found in the offshore parts of the North Sea proper, with a distribution similar to that of *Corymorpha nutans*. All specimens were found at salinities over 18.5$^0/_{00}$ Cl'.

The specimens were found in sands with median grain-sizes ranging from 1.56 to 2.17 φ, with a variable degree of sorting. Kirkegaard (1969) found them on muddy and clayey sand and sandy clay, Hartmann-Schröder (op. cit.) on a large range of substrates. The depth varied between 25 and 35 m.

There are no indications whether these specimens lived in the burrows of some sedentary polychaete or other animal.

Harmothoe lunulata (Delle Chiaje, 1841). This species was not recorded before from the Delta area.

Data on the reproduction or the food of this species are not available. Many authors record it as a commensal of sedentary invertebrates, for instance *Lanice conchilega, Neoamphitrite figulus* and *Arenicola marina* (Davenport, 1953a; Hamond, 1966; Retière, 1967; Creutzberg, 1947). In the Delta area it was only found in the tubes of *Lanice conchilega*, often in considerable numbers.

H. lunulata has been found in the marine part of the estuaries of the Delta area — with no observations below 15$^0/_{00}$ Cl' — but also in the offshore parts of the North Sea. Logically, its distribution is identical with that of *Lanice conchilega*. Being a commensal, it has probably no preference for a special type of sediment. It has been found at depths ranging from 5 to 32 m.

Lepidonotus squamatus (Linné, 1767). Earlier records: Korringa (1951).

In Norfolk Hamond (1966) observed spawning in May and July. Korringa (1951) observed the larvae in June in the plankton of the Oosterschelde. Settling juveniles were observed by him in the midst of summer. Rauschenplat (1901) and Hartmann-Schröder (1971) mention polychaetes, crustaceans, gastropods, echinoderms, hydroids, but also seagrass and algae from the gut of this species.

It was recorded a few times as a commensal from the burrows of *Arenicola marina* (Jepsen, 1965; König, 1949; Newell, 1954).

L. squamatus is an epifaunal species (Rasmussen, 1956). It lives chiefly in the marine parts of the estuaries; only a single specimen was collected in the North Sea proper. In the Westerschelde it was found at a minimal salinity of 11-12$^0/_{00}$ Cl', but in the other estuaries it was not found below 14-15$^0/_{00}$ Cl'. Banse & Lefevere (1954) found the species at salinities of

10-12$^0/_{00}$ in the western Baltic, whereas Hartmann-Schröder (1971) mentions a lower salinity limit of about 7$^0/_{00}$ Cl′.

This scale-worm especially lives on the extensive subtidal musselbeds, but also upon other substrates providing some shelter, e.g. fields of *Sertularia* and concentrations of shells.

Its vertical distribution in the Delta area ranges from the intertidal zone to 45 m, nearly the maximum depth sampled.

Pholoe minuta (Fabricius, 1780). Earlier records: Korringa (1951).

In the Oosterschelde the main reproduction is in July-August. Pelagic larvae were observed in June, July and August (Korringa, 1951).

P. minuta probably is a predator (Southward, 1957; Hartmann-Schröder 1971).

P. minuta is locally very abundant in the marine part of the estuaries. It also occurs in the offshore parts of the North Sea. The lowest salinity observed for this species was 14-15$^0/_{00}$ Cl′. However, Banse & Lefevere (1954) found it at salinities of 10-12$^0/_{00}$ Cl′ in the Kieler Bucht.

P. minuta lives in the Delta area mainly on bottoms with a large quantity of shells and some deposition of mud and detritus. This is confirmed by Rasmussen (1956), Southward (1956) and Thorson (1946).

Its vertical distribution in the Delta area ranges from the lower part of the intertidal zone down to a depth of 27 m.

Sthenelais boa (Johnston, 1839). Earlier records: Horst (1898).

Hamond (1966) records specimens from Norfolk which on rupturing shed their ova in August, but nothing else is known about the reproduction. It is a predator (Hartmann-Schröder, 1971).

S. boa appears to have been common in the Delta area until the severe winter 1962/'63, when it disappeared completely. Since then the species has not been found again.

During its period of occurrence it was found all over the Oosterschelde and also in the Brouwershavense Gat—Grevelingen estuary. It occurred in salinities down to 15$^0/_{00}$ Cl′ but is has to be noted that in those years sampling was inadequate in the 10-15$^0/_{00}$ Cl′ zone. Below 10$^0/_{00}$ Cl′ it certainly did not occur.

All observations were made on fine and muddy sand bottoms with a slight admixture of mud. A few times the species was found on stiff, subfossil clay layers. The median grain-size of the sandy sediments ranged between 2.31 and 3.05 φ and the sorting coefficient from 0.29 to 0.65 phi-units.

In the Delta area the vertical distribution of the species ranged from 2½ to 48 m depth, that is to the deepest place sampled.

Anaitides groenlandica (Oersted, 1843). This species was not known from the Delta area.

Thorson (1946) collected the gelatinous egg-masses in the Sound from April to July. The pelagic larval stage lasts fairly long and the young bottom-stages are met with in July-October. It is a predator (Hartmann-Schröder, 1971). Its ecological distribution over the Delta area may be represented as follows:

$\alpha_1 = 3.27$ $\alpha_7 = 0.00$ $\beta_1 = 0.24$
$\alpha_2 = 0.31$ $\alpha_8 = 0.00$ $\beta_2 = 0.57$
$\alpha_3 = 0.09$ $\alpha_9 = 0.02$ $\beta_3 = 0.48$
$\alpha_4 = 0.00$ $\alpha_{10} = 0.00$ $\beta_4 = 0.00$
$\alpha_5 = 0.00$ $\alpha_{11} = 0.08$ $\gamma_1 = 0.39$
$\alpha_6 = 0.00$ $\alpha_{12} = 0.01$ $\gamma_2 = 1.00$

The species is abundant in the North Sea proper, but it has also been found at the entrances to the Brouwershavense Gat and the Westerschelde, and in the western part of the Oosterschelde (fig. 24). The lowest salinities where it has been found, are about 13-15 $^0/_{00}$ Cl′.

Eliason (1962) and Kirkegaard (1969) observed *A. groenlandica* on the most different types of bottom, but in the Delta area and in the adjacent

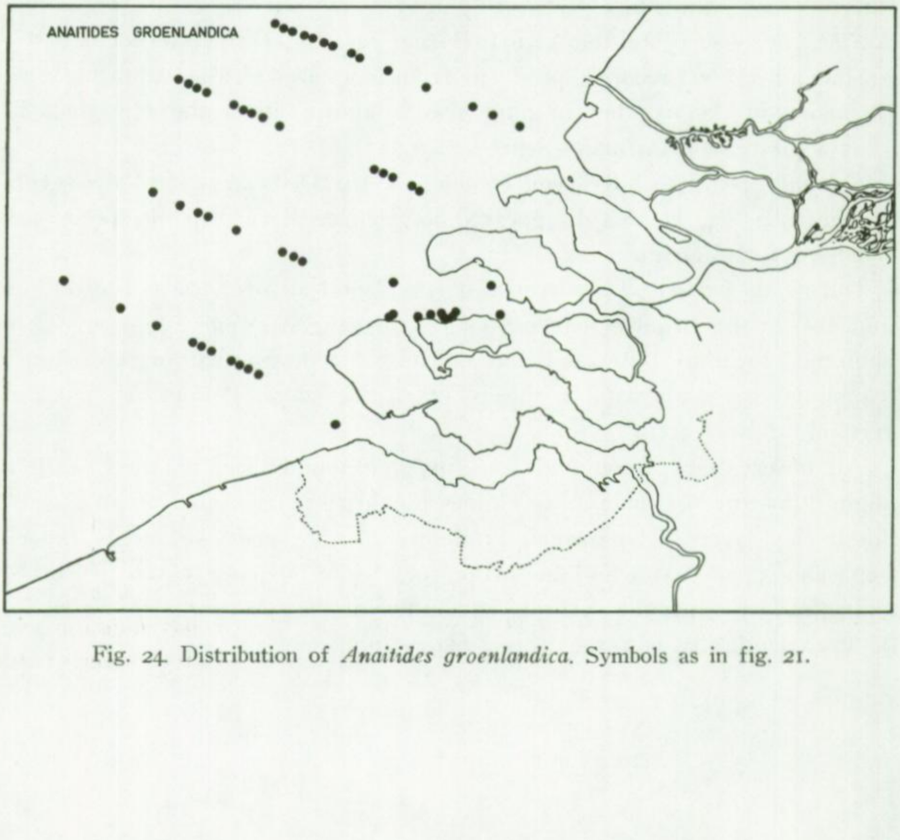

Fig. 24. Distribution of *Anaitides groenlandica*. Symbols as in fig. 21.

part of the North Sea it was only found on sandy bottoms. In the North Sea it occurred on sands with median grain-sizes ranging from 1.13 to 3.14 φ (medium to very fine sand), but in the mouth of the Oosterschelde it was often found on very fine or muddy sand. Unfortunately the median grain-sizes of these sediments were not determined.

Its vertical distribution in the Delta area ranges from 2 to 32 m depth.

Anaitides maculata (Linné, 1767). Earlier records: Korringa (1951).

A. maculata deposits its eggs in greenish gelatinous egg-cocoons at the surface of the mudflats and probably also on the sediments at the bottom of the tidal channels. In the Delta area these egg-capsules may be found from the first weeks of March until the first weeks of June. The actual period of occurrence, however, seems to depend on the temperature of the water. A second period of spawning occurs in October-November, when small quantities of egg-masses may again be found. The hatching of the egg-masses is, among other things, dependent on weather conditions, because during periods of strong winds most egg-capsules are stranded near the high-water mark, where they dry out. The larvae become free-swimming after two days to three weeks and seem to have a planktonic life of several weeks (Thorson, 1946; Smidt, 1951). Lyster (1965) found that the larvae died in salinities below 7-8$^0/_{00}$ Cl′; however, normal activity already ceased at 11-12$^0/_{00}$ Cl′.

A. maculata is a scavenger and predator (Hartmann-Schröder, 1971). The ecological distribution may be represented as:

$$\begin{array}{lll}
\alpha_1 = 3.24 & \alpha_7 = 0.00 & \beta_1 = 0.01 \\
\alpha_2 = 10.76 & \alpha_8 = 4.67 & \beta_2 = 0.06 \\
\alpha_3 = 0.00 & \alpha_9 = 9.33 & \beta_3 = 0.10 \\
\alpha_4 = 0.00 & \alpha_{10} = 7.01 & \beta_4 = 0.21 \\
\alpha_5 = 0.00 & \alpha_{11} = 1.18 & \gamma_1 = 0.36 \\
\alpha_6 = 0.00 & \alpha_{12} = 0.10 & \gamma_2 = 1.00
\end{array}$$

The distribution of *A. maculata* (fig. 25) more or less forms the complement of that of *A. groenlandica* (fig. 24). The former may be characterized as the inshore species, the latter as the offshore one. Also Spooner & Moore (1940) describe *A. maculata* as typical of the high salinity reaches of estuaries. It has been found until about the isohaline of 13$^0/_{00}$ Cl′ at high tide and average river discharge. In this respect it is interesting that Lyster (1965) found that a salinity of approximately 11-13$^0/_{00}$ Cl′ is probably near the lower limit of tolerance of *A. maculata,* both as larvae and as adults.

From the β-values calculated, it may be concluded that *A. maculata* inhabits the muddier types of sediment, contrary to *A. groenlandica* which species lives in the sandy types. Nevertheless, both species may be found on a large range of sediments. Clark & Milne (1955) found in Kames Bay, Scotland, that *A. groenlandica* replaces *A. maculata* above low-water mark. In this area the intertidal zone is a sandy beach, whereas the zone below low-water level consists of muddy sand. It is possible that one species (*A. groenlandica*?) by competition forces the other into a different type of sediment.

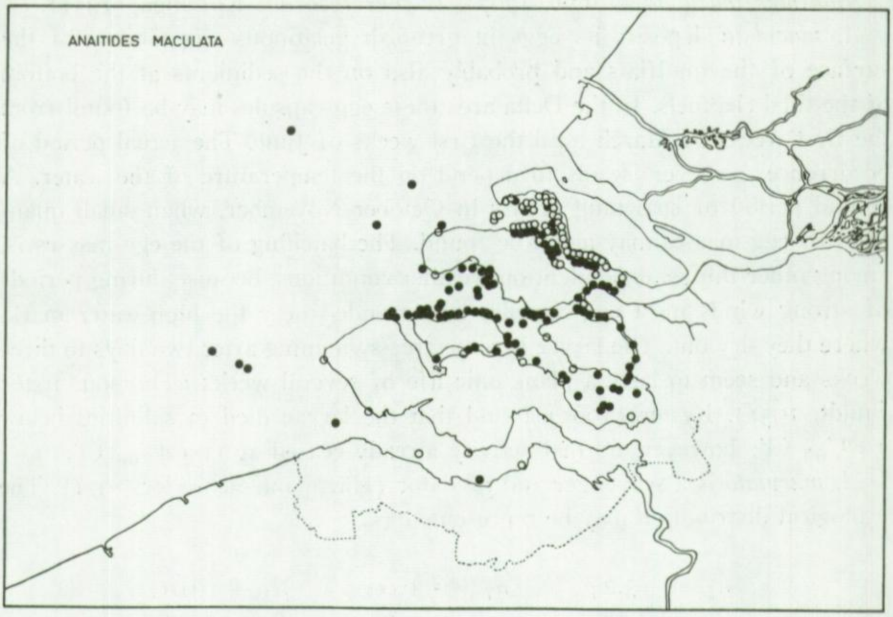

Fig. 25. Distribution of *Anaitides maculata*. Symbols as in fig. 22.

The γ-values point to a preference for less well-sorted sediments. But this fact may also be explained as a preference for sediments with an admixture of mud.

The vertical distribution of *A. maculata* ranges from fairly high in the intertidal zone down to a depth of 48 m in the tidal channels, the deepest place sampled.

Anaitides lineata (Claparède, 1868). This is the first record of this species from Dutch waters.

In Brittany Retière (1967) found sexually ripe specimens in January and April and Bhaud (1967a) found various pelagic larval stages from February to early summer in the Mediterranean.

The species was found in four grab samples originating from salinities over 18$^0/_{00}$ Cl′ in the North Sea. The bottom at these localities consisted of medium sands with median grain-sizes of 1.49-1.73 φ and a varying degree of sorting. The depth varied between 20 and 27 m.

Eteone foliosa (Quatrefages, 1865). This species was not recorded before from Dutch waters.

Data on its reproduction or food have not been found.

It has a distribution more or less similar to that of *Corymorpha nutans*, occurring exclusively in the offshore parts of the North Sea, in salinities over $18^{0}/_{00}$ Cl′. It lives in medium and fine sands with median grain-sizes varying between 1.45 and 2.90 φ and various degrees of sorting. Its depth distribution ranges from 14 to 32 m.

Eteone longa (Fabricius, 1780). Earlier records: Korringa (1951).

The eggs are deposited in a cocoon (Hamond, 1966), although the same type of cocoon has been ascribed to *Heteromastus filiformis* by Rasmussen (1956). The pelagic larvae have been found in February-June and August-October (Thorson, 1946; Smidt, 1951; Giere, 1968).

Khlebovich (1959) states that *E. longa* is a predator, feeding nearly exclusively on the polychaete *Spio filiformis*. Michaelis (1971) reports feeding on *Scolelepis squamata*. In the Delta area its food includes probably also other spionids.

The ecological distribution of *E. longa* may be represented as follows:

$$\begin{array}{lll}
\alpha_1 = 0.77 & \alpha_7 = 0.00 & \beta_1 = 0.40 \\
\alpha_2 = 0.47 & \alpha_8 = 0.63 & \beta_2 = 0.88 \\
\alpha_3 = 0.00 & \alpha_9 = 0.84 & \beta_3 = 0.82 \\
\alpha_4 = 0.13 & \alpha_{10} = 0.62 & \beta_4 = 0.00 \\
\alpha_5 = 0.00 & \alpha_{11} = 0.16 & \gamma_1 = 0.62 \\
\alpha_6 = 0.00 & \alpha_{12} = 0.10 & \gamma_2 = 1.00
\end{array}$$

E. longa penetrates until about the isohaline of $10^{0}/_{00}$ Cl′ at high tide during average river discharge, where it has to withstand periods of lower salinity during high river discharge. A single observation was made of a specimen living at salinities of 3-$5^{0}/_{00}$ Cl′. Muus (1967) records that it has its main distribution in shallow water in salinities over $10^{0}/_{00}$ Cl′. Kosler (1969), on the other hand, found three specimens at salinities as low as 4.1-$7.7^{0}/_{00}$ Cl′ in the Baltic.

The β-values show that the species prefers fine and muddy sand. It is less common in medium sand, and in the Delta area it has not been found in mud. However, the species still occurs in coarse sand (Westheide, 1966, 1967). Therefore, various authors (Smidt, 1951; Muus, 1967; Reineck et al. 1968; Schulz, 1969) state that the species occurs indiscriminately in all types of bottoms. It is concluded in this study that *E. longa* inhabits a very large range of substrates, but that it prefers the finer grades of sand.

From the γ-values it appears that the less well-sorted types of sediment are favoured. Perhaps this points to a certain preference for sand with a slight admixture of mud.

The vertical range of *E. longa* reaches from high in the intertidal zone, even from near high-water mark, down to a depth of 48 m, being the deepest place sampled.

Mysta picta (Quatrefages, 1865). Earlier records: Korringa (1951).

Korringa (op.cit.) observed the larvae in the Oosterschelde plankton in June, but Newell (1954) records the larvae already in April from the Thames estuary. Hamond (1966) records a specimen which shed its ova in August. No information on the food of this species is available.

M. picta has a scattered occurrence all over the marine parts of the estuaries of the Delta area and the adjacent part of the North Sea. It was not found beyond the isohaline of $13^0/_{00}$ Cl′ at high tide and average river discharge.

In the estuaries the species was found on fine and muddy sand and even in mud, with median grain-sizes ranging from 2.32 to about 4.00 φ. The sorting of these sediments varied widely. In the North Sea, however, the species was found in well-sorted sediments with a median grain-size ranging from 1.14 to 2.03 φ.

The vertical distribution of *M. picta* ranges from fairly high in the intertidal zone down to a depth of 25 m.

Eulalia viridis (Linné, 1767). Earlier records: Korringa (1951).

Spawning is recorded from Plymouth and Helgoland in January, February, March and April (Thorson, 1946; Hartmann-Schröder, 1971). In the Oosterschelde a specimen containing eggs was found in June. Also Hamond (1966) records such females from May and August, but possibly these do not spawn before the next winter. The eggs are deposited in a slimy egg-cocoon attached to algae, sponges, etc. The larvae hatch after 7-10 days, and probably have a long pelagic stage. *E. viridis* seems to be a scavenger (Michel, 1970).

E. viridis lives mainly on oyster- and musselbeds, in concentrations of empty shells, and between hydroids. It may be characterized as an epifaunal species, needing some shelter. In the estuaries of the Delta area the species has not been found beyond the isohaline of $13^0/_{00}$ Cl′ at high tide and average river discharge. In the Veerse Meer, however, it occurred under stable salinity conditions of about $10\text{-}12^0/_{00}$ Cl′. It is lacking from the North Sea, probably because a suitable substratum is absent.

Its vertical distribution ranges from the middle part of the intertidal zone down to a depth of 20 m.

Eumida sanguinea (Oersted, 1843). Earlier records: Korringa (1951).

In the Oosterschelde juvenile bottom-stages were observed mainly in June-July, and therefore Korringa (1951) assumes breeding in early summer. This is confirmed by Thorson (1946), although the breeding season seems to extend over the larger part of summer. The species has pelagic larvae. No data about its food have been found. The ecological distribution of *E. sanguinea* may be described as:

$\alpha_1 = 0.32$
$\alpha_2 = 1.07$
$\alpha_3 = 0.00$
$\alpha_4 = 0.00$
$\alpha_5 = 0.00$
$\alpha_6 = 0.00$
$\alpha_7 = 0.00$
$\alpha_8 = 0.06$
$\alpha_9 = 0.50$
$\alpha_{10} = 0.59$
$\alpha_{11} = 0.21$
$\alpha_{12} = 0.01$
$\beta_1 = 0.11$
$\beta_2 = 0.44$
$\beta_3 = 0.40$
$\beta_4 = 0.00$
$\gamma_1 = 0.49$
$\gamma_2 = 1.00$

The species has not been found below salinities of about $15^0/_{00}$ Cl′.

It appears from the β-values that *E. sanguinea* has a clear-cut preference for fine and muddy sand. During the identification of the material it was remarkable that a sample containing *E. sanguinea* nearly always contained also *Lanice conchilega,* thus suggesting a kind of commensalistic relationship. On the other hand *E. sanguinea* was never observed inside the tubes of *Lanice.* Obviously, the sediment preference of *E. sanguinea* resembles very much that of *Lanice.* This is also true for the sorting of the sediment. On the other hand, Korringa (1951) stated that *E. sanguinea* belongs to the normal inhabitants of the shell of the oyster.

Its vertical distribution ranges from just below LW-mark to the maximum depth sampled at 48 m.

Hesionides arenaria (Friedrich, 1937). This species has not been recorded before from Dutch waters.

Copulation and deposition of the eggs occur in June-August. Most probably, *H. arenaria* shows a direct development without a pelagic larval stage. It feeds on diatoms, Foraminifera, small algae, copepods, and detritus (Westheide, 1967). Westheide (op. cit.) found experimentally that this species was able to tolerate salinities as low as $11^0/_{00}$ Cl′ temporarily, but assumes that it is not able to do this permanently. The species was found only twice, viz. in salinities of about $15^0/_{00}$ Cl′ and over $16.5^0/_{00}$ Cl′.

Westheide (op. cit.) apparently did not find *H. arenaria* in sediments with a median grain-size above 1.00 φ. In the Delta area the species was found in well-sorted sediments with median grain-sizes of 1.66 φ and

2.10 φ, respectively. Because the great majority of the sands in the Delta area has higher φ-values, these apparently constitute an unsuitable substratum. *H. arenaria* was found only low in the intertidal zone.

Microphthalmus aberrans (Webster & Benedict, 1867). This species has not been recorded before from The Netherlands.

Ripe specimens of *M. aberrans* occur in the period November-April; the spawning takes place in February-March. It has a pelagic larval stage lasting several weeks. The food consists of diatoms (Westheide, 1967).

Only two finds of this species were made, both in the Grevelingen area in a salinity of about 15⁰/₀₀ Cl′. The animals occurred in well-sorted sands with median grain-sizes of 2.50 and 3.10 φ, respectively. One find was made in the lower part of the intertidal zone, the other at a depth of 4 m below mean low water level.

Microphthalmus fragilis Bobretzky, 1870. Earlier records: Wolff (1969).

Information on reproduction or food is not available. Only two finds of this rare species were made. The first one in the Grevelingen at a depth of 5 m on a muddy sand bottom with a median grain-size of 3.43 φ and a sorting coefficient of 0.43 phi-units. The salinity of the water in this locality was about 15-16⁰/₀₀ Cl′. A second observation is from the mouth of the Westerschelde at a depth of 16 m on a sand bottom with a large amount of mud (Md = 2.70 φ, sorting coefficient 1.10 phi-units) and at a salinity of about 16-17⁰/₀₀ Cl′.

Microphthalmus listensis Westheide, 1967. Earlier records: Wolff (1969).

M. listensis has sexually ripe specimens from December to May, and probably has a direct development. Its food consists of detritus and small algae (Westheide, 1967).

Since the records mentioned in the paper cited above, several new finds have been made in the Delta area. *M. listensis* proved to be a common species in sandy beaches along the North Sea and at the entrances to the estuaries. Subtidal finds were made in the same area and in the eastern part of the Oosterschelde. All observations were made in areas with a salinity over 15⁰/₀₀ Cl′.

It has been found in sands with median grain-sizes varying between 1.65 and 2.07 φ and widely varying sorting coefficients. Beaches with coarser sands do not occur in the Delta area. In very similar beaches with sands with a median grain-size over 2.12 φ, *M. listensis* was never found. Probably the interstices in the latter types of sand become too small to lodge this species. If this is true, it also explains its scarcity in the parts of the Oosterschelde with a high salinity, but nearly everywhere with sands with median grain-sizes over 2.20 φ.

M. listensis was found in the intertidal zone, as well as at a depth of 9 m below LW-level.

Microphthalmus similis Bobretzky, 1870. Earlier records: Wolff (1969).

Information on reproduction and food is not available. This species was found in the North Sea at a depth of 19 m. The bottom consisted of well-sorted sand with a median grain-size of 1.92 φ. The salinity at this locality was 17.8$^0/_{00}$ Cl′. A second find was made at the entrance to the Brouwershavense Gat at a depth of 6 m. The salinity at this locality was about 16.5$^0/_{00}$ Cl′.

Opisthodonta pterochaeta Southern, 1914. Until now this very rare species was only known from one specimen from Ireland (Hartmann-Schröder, 1971a). Nothing is known about its reproduction or food.

The only find was made far offshore in the North Sea on a sand bottom with a median grain-size of 1.13 φ and a sorting coefficient of 0.72 phi-units. The depth was 32 m; the salinity 19.4$^0/_{00}$ Cl′.

Exogone naidina Oersted, 1845. Earlier record: Korringa (1951, sub nom. *E. gemmifera*).

The species has a direct larval development with brood protection; breeding seems to occur in June-September (Thorson, 1946; Hamond, 1966). Data about its food have not been found.

The only finds were made in stable bottoms of fine sand with some detritus and with median grain-sizes of 2.20 and 2.50 φ and sorting coefficients of 0.34 and 0.38 phi-units. The salinity was about 13-15$^0/_{00}$ Cl′, but the species is able to withstand a salinity as low as 10-11$^0/_{00}$ Cl′ (Banse & Lefevre, 1954). The finds were made in the middle and lower part of the intertidal zone, but Hamond (1966) records it from sublittoral habitats. It is not a very characteristic soft-bottom species, but more or less a species dwelling on all types of stable bottoms.

Streptosyllis websteri Southern, 1914. This species is recorded for the first time from The Netherlands.

S. websteri has no pelagic larvae (Remane, 1952). The reproduction occurs in autumn and spring (Hartmann-Schröder, 1971); in the Oosterschelde very young specimens were found in January. The food consists of diatoms (Hartmann-Schröder, op. cit.).

S. websteri has been found in the offshore part of the North Sea, at the entrance and in the eastern part of the Oosterschelde. The salinity of the overflowing water at these localities was 15-16$^0/_{00}$ Cl′ or more. Banse & Lefevere (1954), however, record this species from 10-11$^0/_{00}$ Cl′.

The species was found in medium sand (Md = 1.46 φ) as well as in fine sand (Md = 2.07-2.36 φ), with sorting coefficients of 0.24-0.48 phi-units. The percentage of particles $<75\,\mu$ was always under 0.26%, so *S. websteri* seems to prefer clean sands. Gibbs (1969), however, records it from silty sand. The find in the North Sea was made at a depth of 23 m; the other finds were made in the intertidal zone and down to 9 m below LW-level. The scattered distribution of this species over the Delta area is remarkable and cannot be explained by one of the environmental factors investigated. Especially its absence from many seemingly suitable sands is puzzling.

Eunereis longissima (Johnston, 1840). Earlier records: Horst (1898); Korringa (1951).

Sexually ripe specimens have been observed in April and May (Horst, 1898; Newell, 1954). Most probably the larvae have a pelagic development. *E. longissima* feeds on the alga *Ulva lactuca* (Hamond, 1966), but it takes also other algae and dead animals (Goerke, 1971). Whether it may take live animals with the badly developed armature of the proboscis is a matter of conjecture. Goerke (1971) considers it as a mainly non-selective deposit-feeder.

E. longissima inhabits the marine part of the estuaries, penetrating up to the isohaline of $15\,^0/_{00}$ Cl′ at high tide and average river discharge. It is especially common at the entrances of the estuaries, but it is completely absent from the offshore parts of the North Sea.

The sediments inhabited by *E. longissima* have a median grain-size of 1.60-3.30 φ, but a large number of the observations lies between 2.25 and 3.00 φ. The sorting varies from 0.26 to 0.67 phi-units; apparently it is not very important. The amount of mud mostly varies from 2 to 9%. Kirkegaard (1969) found the species on the same types of bottom. According to Dörjes et al. (1969) this species has to be considered as a characteristic inhabitant of coarse sands, but this conclusion seems to be based on too small a number of data. *E. longissima* has never been found in the intertidal zone, but its sublittoral distribution extends from just below LW-mark down to 48 m, being the deepest place sampled.

Nereis diversicolor (Müller, 1776). Earlier records: Korringa (1951); Den Hartog (1961).

The reproduction and life history of *N. diversicolor* have been investigated by Thorson (1946), Dales (1950, 1951), Bogucki (1953, 1963), Durchon (1957), Smidt (1951), Smith (1958, 1964, 1964a), Muus (1967) and Govaere (1969).

The species is a gonochorist, with possibly very rare cases of hermaphroditism; the number of males in the population is inferior to that of the females (1-40%).

It is atokous and oviparous; the eggs are most probably shed through ruptures of the body wall, whereas the spermatozoa are almost certainly discharged through the nephridia. Most specimens spawn after 1 year, some however, after 2 years. The period of spawning is mostly placed in early spring, but Smidt (1951) and Muus (1967) and especially Govaere (1969) found that the period of spawning extends to at least August. Consequently, the larvae may be found throughout a large part of the year. The larvae are not truly pelagic, but are very easily whirled up and transported by the currents.

Smith (1964) observed that the four- and five-setiger stages are capable of swimming among the plankton. The feeding of the originally lecithotrophic larvae begins when they are some 7 weeks old. The settling of the larvae seems to happen fairly indiscriminately.

The young bottom-stages probably migrate fairly easily from one part of the intertidal zone to another (Smidt, 1951).

Goerke (1966, 1971) and Muus (1967) summarized the different feeding methods of *N. diversicolor*. The species can behave as a deposit-feeder, taking the surface layer of the sediment near the entrance of its burrow; it may take dead or live small animals, inclusive species belonging to the meiofauna, but also parts of various species of algae, and, finally, it may act as a suspension-feeder, catching edible particles in a mucus net, which is devoured afterwards. Bogucki (1953a) records cannibalism.

The ecological distribution of *N. diversicolor* below LW-mark may be represented as follows:

$\alpha_1 = 0.00$
$\alpha_2 = 0.00$
$\alpha_3 = 0.00$
$\alpha_4 = 0.24$
$\alpha_5 = 0.95$
$\alpha_6 = 0.08$

$\alpha_7 = 0.05$
$\alpha_8 = 0.03$
$\alpha_9 = 0.27$
$\alpha_{10} = 0.06$
$\alpha_{11} = 0.00$
$\alpha_{12} = 0.01$

$\beta_1 = 0.24$
$\beta_2 = 0.31$
$\beta_3 = 0.69$
$\beta_4 = 0.00$
$\gamma_1 = 1.12$
$\gamma_2 = 1.00$

It is evident that below LW-mark *N. diversicolor* is rare or lacking in the more marine parts of the estuaries and in the North Sea. The high value for α_9 (= Grevelingen, Keeten, Eendracht and Krabbekreek) has to be ascribed to finds of very juvenile specimens shortly after the ice-winter of 1962/'63 and to some samples from the shallow Eendracht area probably situated in the intertidal zone. Hence, it can be stated that *N. diversicolor* occurs subtidally only in the brackish and freshwater tidal parts of the estuaries (fig. 26). In the intertidal zone *N. diversicolor* inhabits the mudflats along the marine parts of the estuaries in fairly large numbers, especially in the upper parts. In the mudflats along the brackish parts of the estuaries it is very common, but its numbers decrease again towards the freshwater tidal area, where only occasional specimens are found in the lower part of intertidal zone (fig. 26). Moreover the species inhabits nearly all brackish inland waters. Subtidally the species is most abundant in the brackish part of the estuaries (fig. 27).

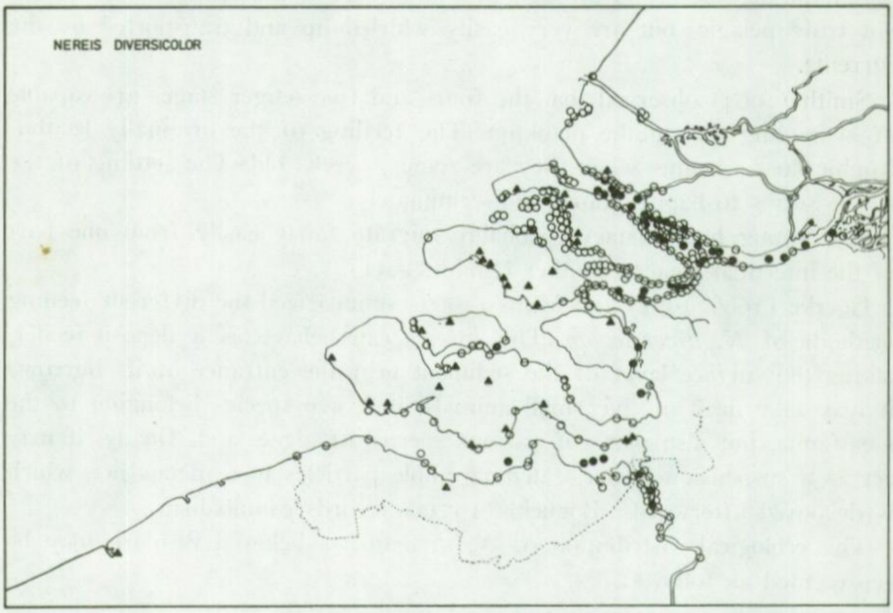

Fig. 26. Distribution of *Nereis diversicolor*. Symbols as in fig. 22. Triangles denote observations in non-tidal brackish localities.

N. diversicolor has a similar distribution in other estuaries, e.g. the Elbe (Caspers, 1949, 1952) and the Tamar (Spooner & Moore, 1940; Smith, 1956). According to the data of the late Miss A. P. C. de Vos, the species shows this type of distribution also in the Ems-Dollard estuary.

The limit of the distribution of *N. diversicolor* in an upstream direction probably is set by the distance the larvae are transported by the flood current in an upstream direction, because *N. diversicolor* is not able to reproduce below about 3⁰/₀₀ Cl′ (Bogucki, 1954, 1963; Smith, 1964a).

There exists a voluminous literature on the salinity tolerance and osmoregulation of *N. diversicolor*. Bogucki (1954) and Smith (1964a) cultured the species at various salinities and found that the developmental stages from cleavage until the three-setiger stage are most vulnerable. Below about 3⁰/₀₀ Cl′ no normal development was observed. Smith (1964a) mentions also an upper salinity limit for larval development, depending, like the lower limit, on the normal salinity experienced by the adults and, hence, by the riping gametes. Bogucki (1953), however, found that development is normal at all salinities between about 4 and 20$^0/_{00}$ Cl′. Lyster (1965) found that the larvae tolerated salinities between 3 and 35$^0/_{00}$ Cl′.

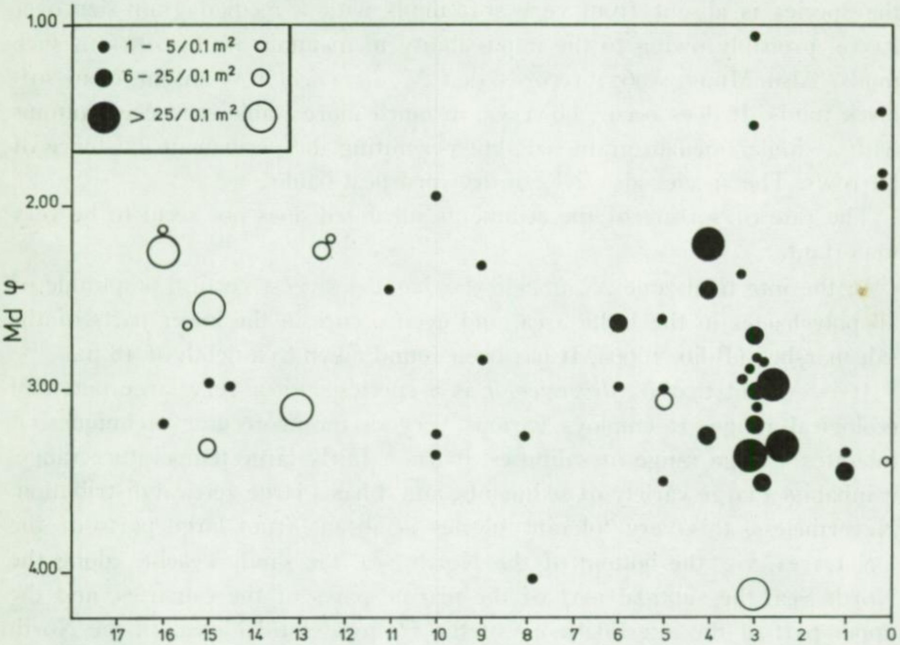

Fig. 27. Quantitative distribution of *Nereis diversicolor* in relation to median grain-size and salinity. Symbols as in fig. 22.

When the bottle-neck of the larval development has been passed, the salinity tolerance of *N. diversicolor* becomes extremely large. Bogucki (1954) held a worm during 465 days in fresh water. Jørgensen & Dales (1957) found complete volume adjustment in 0.03-0.07$^0/_{00}$ Cl′. Hohendorf (1963) records that at 10°C the adults tolerate salinities ranging from that of hard, fresh water to 30$^0/_{00}$ Cl′. Temperature, however, seems to modify this range, because the range is 0.3-27$^0/_{00}$ Cl′ at 20°C and 1-30$^0/_{00}$ Cl′ at 1°C. At 1°C osmoregulation breaks down at about 1.2$^0/_{00}$ Cl′ and at 5°C at 0.6$^0/_{00}$ Cl′. Smith (1964, 1964a), however, records that experimentally osmoregulation and survival were proved to be possible below 1$^0/_{00}$ Cl′ and below 1°C. The tolerance of sexually mature specimens was somewhat less (Bogucki, 1954). Bogucki (1963) also investigated the influence of salinity on the maturation of the gametes of *N. diversicolor*. He found that even in tap water the gametes matured normally and were suitable for fertilization.

N. diversicolor usually is considered a species inhabiting muddy sediments. This is confirmed by the calculated indices, indicating that the species has a preference for fine and muddy sands with a median grain-size between 3.00 and 4.00 φ over sands with a grain-size under 3.00 φ. Below LW-mark the species is absent from very soft muds with a median grain-size over 4.00 φ, probably owing to the impossibility to maintain its burrows in such muds. Also Muus (1967) records that *N. diversicolor* is absent from soft black muds. It does occur, however, in much more stable stiff clay bottoms with a similar median grain-size, but permitting the permanent existence of burrows. The species also lives in drowned peat banks.

The rate of sorting of the sediments inhabited does not seem to be very important.

In the intertidal zone *N. diversicolor* has the largest vertical amplitude of all polychaetes in the Delta area, and even occurs in the lower parts of the salt-marshes (Bilio, 1966). It has been found down to a depth of 18 m.

It is evident that *N. diversicolor* is a species with a very large potential ecological range. It employs various very different feeding techniques, it tolerates a large range of salinities, it has a fairly large temperature range, it inhabits a large variety of sediments, and it has a large vertical distribution. Nevertheless, this very tolerant species is absent from large parts of the Delta area, viz. the bottom of the North Sea, the sandy beaches along the North Sea, the subtidal part of the marine parts of the estuaries, and the upper part of the intertidal zone of the freshwater tidal area. In the North Sea its absence possibly may be explained by the instability of the sediment inhibiting the construction of burrows, by predation, by competition or by the scarcity of food. The sandy beaches along the North Sea evidently are too unstable to permit the permanent occurrence of *N. diversicolor.* Young stages may be found fairly often in summer, so the species is apparently able to establish and to maintain itself there for some time. During the stormy winter period, however, the species disappears completely from these beaches.

In the subtidal part of the marine reaches of the estuaries such an environmental factor inhibiting the occurrence of *N. diversicolor* cannot be found. In this area the same types of sediment and the same current conditions prevail as in the brackish part of the estuaries. The only differences are in the salinity, the percentage of oxygen and the turbidity. The latter two factors do not seem to be very important, because they are experienced to about the same extent by the animals in the intertidal zone of the marine reaches, apparently without any harmful effect. Also salinity seems unprobable as a limiting factor, because the experimental data show a very large tolerance. Also Oglesby (1965) concluded from laboratory experiments that among nereids high salinity per se has not been proved to be limiting. Zenkevitch (1963) even recorded the species from nearly $35^0/_{00}$ Cl′ in the Sea of Azov. Moreover, after the ice-winter 1962/'63 when nearly all benthic species had become extinct, young stages of *N. diversicolor* were able to establish themselves in the subtidal marine reaches of the estuaries. The next year, however, they had disappeared.

It is concluded that in the seaward reaches of the estuaries *N. diversicolor* is forced out of the subtidal environment either by predation or by competition. *N. diversicolor* is preyed upon by various species of wading birds and bottom fishes. However, it seems improbable that these would be able to exterminate a population below LW-mark, whereas they would fail to do so above LW-mark. Moreover, in the brackish area the plentifully occurring flounders (Vaas, 1969) also do not succeed in exterminating the subtidal populations there.

Therefore, it is concluded that the distribution pattern observed is determined by competition. The most probable competitors appear to be the closely related species *Nereis virens* and *N. succinea.* In the seaward reaches of the estuaries *N. virens* inhabits exactly those habitats from which *N. diversicolor* is absent (see below). Also Smith (1955) and Muus (1967) found that these two species are nearly mutually exclusive (*N. southerni* mentioned by Smith is *N. virens*; compare section 4.6.). Oglesby (1965) and Muus (1967) suggested that the same is true for *N. diversicolor* and *N. succinea.*

Clark (1959) found that between the individuals of *Nereis pelagica* fighting and competition for tubes occurs. Reish & Alosi (1968) report such behaviour between different species, e.g. *N. succinea* attacks and dominates *N. limnicola,* which is closely related to *N. diversicolor.*

Therefore, it seems probable that similar events may occur between the two species in question here. Judging from the size and the velocity of growth of *N. virens,* it seems very probable that this species will be the surviving one. It does not even seem unlikely that the relation is more of the predator-prey type.

In a simple experiment 16 *N. diversicolor* and 4 *N. virens* were brought together in a tank in November 1969. The number of *N. diversicolor* gradually declined down to 6 *N. diversicolor* on January 20, 1970. On March 17, *N. virens* still proved to be present, but all *N. diversicolor* had disappeared. However, it is possible that the reproduction of the latter species has interfered.

The upper part of the intertidal zone in the freshwater tidal area, viz. along the Hollands Diep and in the Biesbosch, also is not inhabited by *N. diversicolor*. According to Dr. C. den Hartog (personal communication) this is due to predation by the leech *Trocheta bykowski*.

Nereis fucata (Savigny, 1818). This species has not been recorded before from the Delta area.

Gilpin-Brown (1959) and Goerke (1971a) record that in Plymouth and the German Bight the species spawns from March to June. After a planktonic stage the larvae settle on the bottom and construct small tubes. It is only later that the species enters the house of the hermit crab (Gilpin-Brown, 1969; Goerke, op. cit.). Its food probably consists of material robbed from the crustacean.

Although hermit crabs are abundant in the marine reaches of the estuaries of the Delta area (Wolff & Sandee, 1971), *N. fucata* has never been found with them. The only specimens observed originated from hermit crabs caught in the North Sea, west of the border of the estuarine area.

Nereis succinea (Leuckart, 1847). Earlier records: Korringa (1951).

In the Baltic near Kiel swarming epitokous specimens were observed at night in July-September (Banse, 1954; Kinne, 1954). Also in the Delta area swarming was observed in this period. At 20-21°C the free-swimming larvae settle after about 10-14 days. Kinne (op. cit.) was not able to culture the larvae at salinities below about $8^0/_{00}$ Cl′. Also Banse (op. cit.) was not able to keep the larvae at $7^0/_{00}$ Cl′. Metamorphosis is not bound to a particular substratum. *N. succinea* is a non-selective deposit-feeder, which also may take detritus (Goerke, 1971; Hartmann-Schröder, 1971).

N. succinea has been found in salinities over $16.5^0/_{00}$ Cl′, as well as under brackish conditions (fig. 28). In the Haringvliet it has been found at a minimal salinity of about $1^0/_{00}$ Cl′ at low tide during average river discharge, and in the Westerschelde it was found at about $3^0/_{00}$ Cl′. De Vos (1936) found the species abundant in the former Zuiderzee and reported a minimal salinity of $3.7^0/_{00}$ Cl′; Horst (1910) mentions about $1.4^0/_{00}$ Cl′. Filice (1958) reported it from San Francisco Bay in 0.6 to $14^0/_{00}$ Cl′. Apparently, the adults tolerate a extremely wide range of salinities. This was also shown by the experiments of Oglesby (1965, 1965a), who found that osmoregulation in this species failed only below $1.2\text{-}4^0/_{00}$ Cl′. Nevertheless, the ecological distribution of *N. succinea* is not so wide as that of *N. diversicolor*, which species is able to osmoregulate at much lower salinities (Hohendorf, 1963; Oglesby, 1965). A further explanation for this difference may be found in the lower tolerance of low salinities of the larvae (Banse, 1954; Kinne, 1954). This is confirmed by the observations of Muus (1967) who found

N. succinea only rarely in shallow mesohaline ($<10^0/_{00}$ Cl′) localities. These waters may not be reached by the larvae owing to the absence of stronger currents.

N. succinea has been found on many different types of substrates: sand and mud (Md: 1.38-4.00 φ), peat, stiff fossil clay layers, between shells, on mussel-beds, and on piles and harbour constructions. Banse (1954) found it under stones lying on fine sand with a very high content of organic detritus; Caspers (1951) and Muus (1967) mention it from mussel-beds and "meadows" of *Zostera, Potamogeton,* and *Chara.* Filice (1958) showed that it has a preference for mud-bottoms. Korringa (1951) found it rarely on oysters, but frequently on oyster-beds. In the brackish Lake Veere *N. diversicolor* inhabits soft sediments, whereas *N. succinea* also lives in these sediments, but is found especially on all types of solid substrates.

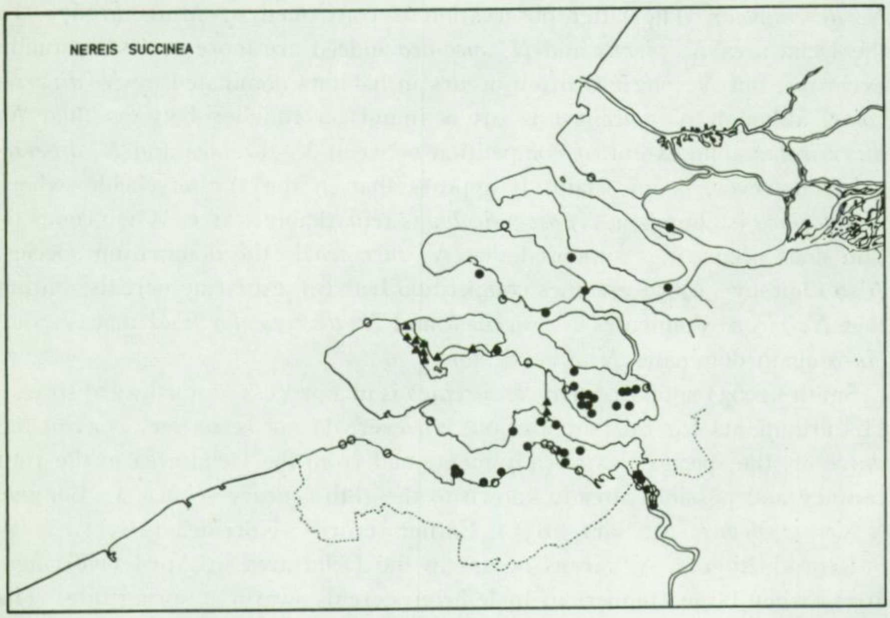

Fig. 28. Distribution of *Nereis succinea.* Symbols as in fig. 26. The Veerse Meer area has been shown in the situation after 1961.

Its vertical distribution ranges from about mid-tide level in the intertidal zone down to a depth of 21 m.

According to Filice (1958) and Wass (1967) *N. succinea* is an indicator of pollution. Its distribution over the Delta area does not confirm this completely. The species reaches its highest abundance in the eastern part of the Westerschelde, where pollution indeed is important, but it occurs also in many clean habitats. Possibly it has a preference for habitats with large amounts of organic detritus (compare Banse, 1954). Such habitats are polluted areas, but so are oyster- and mussel-beds.

Also the ecological relationship to *N. diversicolor* and *N. virens* has to be considered. Smith (1963) found that the species was found at the shoreward limit of the zone of *N. virens,* and that it did not occur together with *N. diversicolor.* The latter observation is confirmed by Muus (1967). In the Delta area *N. virens* and *N. succinea* indeed are more or less mutually exclusive, but *N. succinea* often occurs in habitats dominated by *N. diversicolor,* although *N. succinea* is often found on rougher bottoms than *N. diversicolor.* The extent of competition between *N. succinea* and *N. diversicolor,* however, is uncertain. It appears that in the Westerschelde, where *N. succinea* is abundant, *N. diversicolor* is remarkably scarce. When competition does occur, it is supposed that *N. succinea* is the dominating species. Also Oglesby (1965) assumes competition between estuarine nereids, stating that *N. virens* dominates *N. succinea* and *N. diversicolor,* and that *N. succinea* again dominates *N. diversicolor.*

Smith (1963) supposed that *N. succinea* is in a process of northward spread. His arguments for this supposition, however, do not seem very convincing. Anyhow, the species was already mentioned from the Delta area in the 19th century and possibly already known to the 18th century scholar L. Bomme.

Nereis virens (M. Sars, 1835). Earlier records: Korringa (1951).

Reproduction in *N. virens* occurs in the Delta area in April (Korringa, 1951) when large numbers of male heteronereids swarm at spring tides. The females spawn inside their burrows (Bass & Brafield, 1972). Thorson (1946) supposed that the larvae are not pelagic, but Bass & Brafield (op. cit.) found in laboratory cultures a planktonic phase of only 15 hours or less. About 5-6 days before and after this phase the developing larvae remain in the bottom waters close to the substratum, where they are liable to transport by the currents. When settled the worms take two years (or sometimes three years) to reach sexual maturity (Brafield & Chapman, 1967; Khlebovich, 1963). The food of *N. virens* consists of detritus, live and dead animals, as well as of pieces of algae (Copeland & Wieman, 1924; Sveshnikov, 1963; Lewis & Whitney, 1968).

The ecological distribution below LW-mark of *N. virens* may be summarized as:

$$\begin{array}{lll} \alpha_1 = 4.52 & \alpha_7 = 0.00 & \beta_1 = 0.00 \\ \alpha_2 = 5.78 & \alpha_8 = 4.26 & \beta_2 = 0.03 \\ \alpha_3 = 0.00 & \alpha_9 = 9.03 & \beta_3 = 0.09 \end{array}$$

$\alpha_4 = 0.00 \qquad \alpha_{10} = 2.44 \qquad \beta_4 = 0.31$
$\alpha_5 = 0.00 \qquad \alpha_{11} = 0.00 \qquad \gamma_1 = 0.37$
$\alpha_6 = 0.00 \qquad \alpha_{12} = 0.10 \qquad \gamma_2 = 1.00$

N. virens is absent from the brackish and fresh parts of the estuaries, as it has not been found below salinities of about $10^0/_{00}$ Cl′ (fig. 29). Also Muus (1967) found it only rarely at salinities below $10^0/_{00}$ Cl′. This is in partial accordance with the experimental data. Topping & Fuller (1942) found that *N. virens* is active and shows volume regulation down to $9^0/_{00}$ Cl′. but Sayles (1935) and Jørgensen & Dales (1957) found survival and complete volume adjustment down to $2.3^0/_{00}$ Cl′. However, this occurred only when the animals were transferred slowly; a rapid change was tolerated down to $7\text{-}8^0/_{00}$ Cl′. Oglesby (1965) stated that in European waters the following series of nereids with decreasing ability for osmoregulation exists: 1) *N. diversicolor*; 2) *N. succinea*; 3) *N. virens*; 4) *N. pelagica*. Indeed this is reflected perfectly in the lower limits of distribution of these species in the Delta area, where *N. diversicolor* and *N. succinea* penetrate much farther into the brackish water than does *N. virens*.

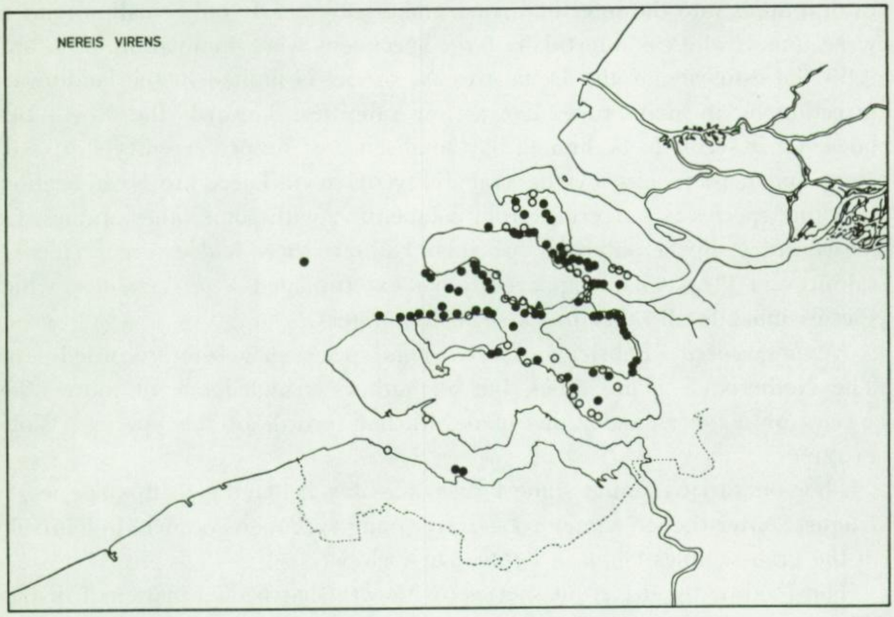

Fig. 29. Distribution of *Nereis virens*. Symbols as in fig. 26.

N. virens has a preference for the muddier types of sediment as is evident from the β-values. Its preference for sediments with high sorting coefficients may be explained by its preference for muddy sediments with large amounts of shells and shell debris.

The vertical distribution of *N. virens* ranges from the lower part of the intertidal zone down to a depth of 48 m. The vertical distribution of the various size-classes in the Delta area does not contradict the hypothesis of Bass & Brafield (1972) who postulate migration of juveniles from the sublittoral areas into the intertidal zone. Subtidally, nearly only small specimens were found, whereas intertidally large specimens were dominating.

In the estuaries of the Delta area *N. virens* is limited in the landinward direction by its inability to live at low salinities. Towards the North Sea, however, it seems to be limited by the absence of its preferred type of sediment and perhaps also by the availability of food. There are no indications that this species is suffering from competition with some other species. On the contrary, in the only brackish inland water where it does occur (median salinity: $11.3^{0}/_{00}$ Cl′), it apparently has exterminated *N. diversicolor*, which species inhabits all other brackish inland waters.

Nephtys caeca (Fabricius, 1780). This species has been recorded from The Netherlands many times, but all authors included one or more other species of *Nephtys* under this name. Earlier records of this species: Wolff (1971).

Thorson (1946) found some larvae, possibly belonging to this species, in August. After the ice-winter 1962-1963 young specimens occurred plentifully in the grab-samples taken in September-October.

The food of the different species of *Nephtys* has been a matter of dispute (Sanders, 1956; 1960; Clark, 1962). It seems that *N. cirrosa* and *N. hombergii* are true predators. Mainly because the density of *N. caeca* is not higher than that of these two species, it is assumed that it is also principally a predator on other soft-bottom organisms.

The ecological distribution of *N. caeca* in the Delta area below LW-mark may be represented as 1):

$$\begin{array}{lll}
\alpha_1 = 1.36 & \alpha_7 = \text{—} & \beta_1 = 0.14 \\
\alpha_2 = 1.74 & \alpha_8 = 0.56 & \beta_2 = 0.24 \\
\alpha_3 = 0.13 & \alpha_9 = 3.20 & \beta_3 = 0.13 \\
\alpha_4 = 0.00 & \alpha_{10} = 1.36 & \beta_4 = \text{—} \\
\alpha_5 = \text{—} & \alpha_{11} = 1.00 & \gamma_1 = 0.90 \\
\alpha_6 = \text{—} & \alpha_{12} = \text{—} & \gamma_2 = 1.00
\end{array}$$

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1) For some classes with no or very few observations of animals no indices have been calculated.

N. caeca does not occur beyond the isohaline of 12$^0/_{00}$ Cl′ at high tide during average river discharge (Wolff, 1971). Banse & Lefevere (1954) record it from 10-11$^0/_{00}$ Cl′ in the Baltic.

Its distribution in the area with a suitable salinity seems to be governed principally by the nature of the sediment. It shows a preference for fine sands, but also occurs in medium sand and in muddy sands. The degree of sorting does not seem to be very important.

N. caeca is remarkable for being absent from the intertidal zone. Of 262 samples containing *N. caeca,* not a single one originated from this habitat. Also Amoureux (1968), Clark & Haderlie (1960) and Clark, Alder & McIntyre (1962) record only very few *N. caeca* from the intertidal zone. In the Delta area the vertical distribution of *N. caeca* ranges from LW-mark down to 48 m, being the greatest depth sampled.

N. cirrosa Ehlers, 1868. Earlier record: Wolff (1971).

Hamond (1966) records breeding in March and August. Presumably the species has planktonic larvae. It is a predator on other soft-bottom animals (Clark, 1962).

The ecological distribution of this species below LW-mark may be represented as:

$$\begin{array}{lll}
\alpha_1 = 8.03 & \alpha_7 = \text{—} & \beta_1 = 0.12 \\
\alpha_2 = 2.19 & \alpha_8 = 0.16 & \beta_2 = 0.10 \\
\alpha_3 = 1.70 & \alpha_9 = 1.61 & \beta_3 = 0.04 \\
\alpha_4 = 0.00 & \alpha_{10} = 1.67 & \beta_4 = \text{—} \\
\alpha_5 = \text{—} & \alpha_{11} = 1.00 & \gamma_1 = 1.73 \\
\alpha_6 = \text{—} & \alpha_{12} = \text{—} & \gamma_2 = 1.00
\end{array}$$

It has to be noted that the species was absent from the Delta area in the periods that the Westerschelde (α_{11}, α_{12}) and the larger part of the Krammer (α_8) were sampled. This absence most probably was due to the very severe winter 1962-'63; it was absent until 1966.

Nevertheless, on the basis of the observations at the mouth of the Haringvliet and some occasional data from the Westerschelde, it may be concluded that *N. cirrosa* does not occur beyond the isohaline of 12$^0/_{00}$ Cl′ at high tide during average river discharge.

Also the distribution of *N. cirrosa* appears to be strongly influenced by the nature of the sediment. Clark & Haderlie (1960), Clark, Alder & McIntyre (1962) and Amoureux (1968) all stressed the fact that *N. cirrosa* lives in clean sandy beaches contrary to *N. hombergii,* which occupies the muddier types of sediment. This is also true in the Delta area. Clark & Haderlie (1960) reported *N. cirrosa* from sediments with median grain-sizes ranging from about 1.60 to about 2.30 φ. In the Delta area it occurs in sediments with median grain-sizes ranging from 0.90 to nearly 3.00 φ, but judging from the β-values it prefers the range 1.00-2.00 φ, meaning medium sands. *N. cirrosa* shows a preference for the better sorted types of sediment.

The vertical distribution ranges from the upper part of the intertidal zone down to a depth of 35 m, deeper places having been sampled only rarely.

Nephtys hombergii (Savigny, 1818). Earlier records: Korringa (1951); Wolff (1971).

Smidt (1951) assumes main spawning in May-June, because he found large numbers of pelagic and newly settled larvae in June-August. This is in accordance with the observations made in the Delta area. *N. hombergii* is a predator on soft-bottom organisms (Clark, 1962). Its ecological distribution below LW-mark may be represented as:

$\alpha_1 = 2.37$
$\alpha_2 = 3.60$
$\alpha_3 = 0.46$
$\alpha_4 = 0.08$
$\alpha_5 = —$
$\alpha_6 = —$
$\alpha_7 = —$
$\alpha_8 = 0.28$
$\alpha_9 = 1.34$
$\alpha_{10} = 2.80$
$\alpha_{11} = 1.00$
$\alpha_{12} = —$
$\beta_1 = 0.03$
$\beta_2 = 0.32$
$\beta_3 = 0.58$
$\beta_4 = —$
$\gamma_1 = 0.68$
$\gamma_2 = 1.00$

Also *N. hombergii* does not penetrate beyond the isohaline of $12\,^0/_{00}$ Cl′ at high tide during average river discharge.

Clark & Haderlie (1960) recorded the species from sediments with median grain-sizes of 1.70-2.50 φ, but in this investigation it occupied the range 1.05-3.45 φ. Nevertheless, a distinct preference for the fine and muddy sands (2.00-4.00 φ) appears from the β-values. Clark & Haderlie (1960), Clark, Alder & McIntyre (1962) and Amoureux (1968) recorded the species from muddy intertidal sandflats. Kirkegaard (1969) records a preference for sand mixed with mud and clay.

The sediment preference of *N. hombergii* is clearly different from those of *N. cirrosa* (1.00-3.00 φ) and *N. longosetosa* (1.00-3.00 φ), but less from that of *N. caeca* (2.00-3.00 φ). *N. hombergii,* however, prefers the less well-sorted types of sand, contrary to *N. caeca* which does not seem to have a distinct preference.

The vertical distribution of *N. hombergii* ranges from the upper half of the intertidal zone down to a depth of 33 m, deeper places having been sampled only rarely. Thamdrup (1935) recorded that in the intertidal zone the species is absent in places with immersion times less than 30% of the tidal cycle. This is confirmed by this study.

In an earlier paper (Wolff, 1971) it was demonstrated that ecologically

N. hombergii differs only slightly from *N. caeca,* but greatly from *N. cirrosa* and *N. longosetosa.* The differences with *N. caeca* are especially the absence of this species from the intertidal zone and a slight difference in the range of sediment inhabited.

With the likelihood ratio test mentioned in section 2.4 for $\alpha_1 = \alpha'_1 \ldots\ldots \ldots\ldots \gamma_2 = \gamma'_2$, it was tested whether the calculated ecological distributions of *N. caeca* and *N. hombergii* were similar. This proved to be very improbable ($P < 0.0001$) and, hence, in accordance with the previous findings, this hypothesis has been rejected.

Nephtys longosetosa Oersted, 1833. Earlier records: Horst (1883-'84) (this species?); Wolff (1971).

Nothing is known about the reproduction of this species, but probably it has planktonic larvae. Chiefly on account of its low density, it is assumed to be a predator on other soft-bottom organisms.

The ecological distribution of this species below LW-mark may be shown as:

$\alpha_1 = 0.95$ $\alpha_7 = 0.00$ $\beta_1 = 0.46$
$\alpha_2 = 0.25$ $\alpha_8 = 0.00$ $\beta_2 = 0.41$
$\alpha_3 = 0.23$ $\alpha_9 = 0.07$ $\beta_3 = 0.08$
$\alpha_4 = 0.00$ $\alpha_{10} = 0.24$ $\beta_4 = 0.00$
$\alpha_5 = 0.00$ $\alpha_{11} = 0.25$ $\gamma_1 = 1.39$
$\alpha_6 = 0.00$ $\alpha_{12} = 0.01$ $\gamma_2 = 1.00$

This species does not penetrate into the estuaries beyond approximately the isohaline of $12\,^0/_{00}$ Cl′ at high tide during average river discharge. *N. longosetosa* has been found in sediments with median grain-sizes ranging from 0.90 to 2.60 φ. Its preferred type of sediment apparently also lies in the range 1.00-3.00 φ. Also Kirkegaard (1969) records a preference for fine sands. Hence, it inhabits the same types of sediments as does *N. cirrosa.* Like *N. cirrosa,* it shows a preference for the better sorted types of sands.

N. longosetosa occurs in the intertidal zone, but apparently only in the parts flooded during at least 85% of each tidal period. Subtidally it has been found down to a depth of 36 m, very few deeper places having been sampled.

Earlier, it was stated that *N. longosetosa* differs clearly from *N. caeca* and *N. hombergii* with respect to sediment preference. Differences with *N. cirrosa,* however, could not be found (Wolff, 1971). This cannot be maintained, because the likelihood ratio test for $\alpha_1 = \alpha'_1 \ldots\ldots\ldots \gamma_2 = \gamma'_2$, mentioned in section 2.4, showed that it is very improbable that *N. cirrosa* and *N. longosetosa* have the same ecological distribution ($P < 0.001$). Moreover, the vertical distribution in the intertidal zone also is markedly different, *N. longosetosa* only occurring near low water mark, whereas *N. cirrosa* also occurs high on the beach.

Glycera capitata Oersted, 1843. This species has not been recorded before from Dutch waters.

In Norway it reproduces in summer (Hartmann-Schröder, 1971); probably it has pelagic larvae like *G. convoluta* (Cazaux, 1967). Possibly it is a selective deposit-feeder (Hartmann-Schröder, op. cit.), but Michel (1970) records that the closely related *G. convoluta* is a predator.

G. capitata only has been found in the North Sea proper; it has a distribution resembling that of *Corymorpha nutans*. Although the species is not restricted to the area of Channel water, it has been found only at salinities over $18^0/_{00}$ Cl′. Dörjes et al. (1969), however, found the species in the Jadebusen at salinities of 12-$18^0/_{00}$ Cl′.

The sediments inhabited by *G. capitata* have median grain-sizes in the range of 0.92-2.30 φ with sorting coefficients in the range of 0.25-0.80 phi-units. The weight percentage of the particles $<75\,\mu$ usually is 0.01-0.32%, although a value of 1.39% has been found once. Other samples with similar contents of mud, however, did not contain this species. Dörjes et al. (1969) and Kirkegaard (1969) also record this species as typical for the coarser grades of sand, but Hartmann-Schröder (op. cit.) mentions also mixed bottoms and muddy sediments. The vertical distribution of *G. capitata* ranges from 12 to 36 m.

Goniada maculata Oersted, 1843. This species has not been recorded before from Dutch coastal waters.

Thorson (1946) supposes that this species has a non-pelagic development, but Clark & Milne (1955) state that it has pelagic larvae. Southward (1957) supposes that this species is a predator.

G. maculata was found in only three samples from the North Sea proper. The salinity at these localities was over $18^0/_{00}$ Cl′. The median grain-size of the sediment was 1.80-1.92 φ with sorting coefficients of 0.37-0.54 phi-units. The depth was 25-29 m.

Lumbrineris latreilli Audouin & Milne Edwards, 1834. This species has not been recorded before from Dutch coastal waters.

Probably *L. latreilli* has a non-pelagic development (Hartmann-Schröder, 1971). Judging from its buccal armature, it is supposed to be a predator.

L. latreilli has been found in four samples from the North Sea proper. In all cases salinity was over $19^0/_{00}$ Cl′. Accordingly, the species was only found in the Channel water.

The median grain-size of the sediment is 1.23-1.87 φ with sorting coefficients of 0.36-0.44 phi-units. The depth was 29-32 m. According to Southward (1956, 1957) and Hartmann-Schröder (1971) the range of sediments and depths inhabited by this species is much larger and therefore it is concluded that it is restricted by the quality of the water.

Protodorvillea kefersteini (McIntosh, 1869). This species was not known before from Dutch coastal waters. Data about its reproduction or its food have not been found. Probably it is a predator. Only one find has been made of this species, viz. in the North Sea proper in the area of Channel water at a depth of 29 m. The salinity at this locality was $19.3^0/_{00}$ Cl′. The median grain-size of the sediment was 1.23 φ with a sorting coefficient of 0.43 phi-units.

Orbinia sertulata (Savigny, 1820). This species was not known before from Dutch coastal waters.

Thorson (1946) records that *O. sertulata* has a non-pelagic development in the East-Greenland fjords, but is in doubt whether this is also true in European waters. *O. sertulata* is a non-selective deposit-feeder.

The species was found only in five samples originating from the area of Channel water in the North Sea proper. The salinity at these localities was over $18.6^0/_{00}$ Cl′. The depth was 18-32 m. The sediment was medium sand with a median grain-size of 1.23-1.78 φ and a sorting coefficient of 0.25-0.48 phi-units, but, according to Southward (1957) and Eliason (1962), this species inhabits a much larger variety of sediments. Apparently it is not the nature of the sediment which restricts the distribution of this species.

Competition with its near relative *Scoloplos armiger* also does not seem very probable, because there exists an area without orbiniids between the areas of occurrence of both species. Therefore, it is assumed that some characteristic of the water governs the distribution of *O. sertulata.*

Scoloplos armiger (Müller, 1776). Earlier records: Baster (1765) (egg-capsules); Korringa (1951). Together with *Macoma balthica* it is the commonest soft-bottom species of the Delta area.

Thorson (1946), De Groot (1907) and Gibbs (1968) report on the reproduction and development of *S. armiger.* Their findings together with some data collected in the Delta area, may be summarized as follows. The reddish egg-cocoons may be found on the tidal flats — and probably also on the bottom of the tidal channels — of the Delta area in early spring. In 1966 the period with egg-cocoons on the tidal flats lasted from the second week of February to the last week of March, but in 1967 from the first week of March to the second week of April. In both years maximum numbers of egg-cocoons were observed in the first two weeks. No breeding was observed before the temperature of the overflowing water was above 5°C. This value is also recorded by Gibbs (1968) from Whitstable. He found that *Scoloplos* breeds for the first time in its second year and that a female most probably produces one egg-cocoon during the breeding season, the size of which and the number of eggs it contains depending on the age of the female. Thorson (1946) and De Groot (1907), however, state that *Scolophos* is able to spawn more than one cocoon. The larvae remain in the cocoons until three weeks after fertilization, and then hatch in the crawling stage. These stages are able to start a burying mode of life at once, but, apparently, they may also be whirled up and transported by the currents.

There also seems to exist a second breeding period. Giere (1968) found the larvae in autumn in the river Elbe, and Smidt (1951) found them in December in the Danish Wadden Sea, whereas Mr. Jan van de Kam (pers. comm.) found egg-cocoons in December 1968 in the Delta area.

Scoloplos armiger is a non-selective deposit-feeder. Its ecological distribution below LW-mark in the Delta area may be represented by:

$$\begin{array}{lll}
\alpha_1 = 1.77 & \alpha_7 = 0.00 & \beta_1 = 0.49 \\
\alpha_2 = 1.07 & \alpha_8 = 0.25 & \beta_2 = 1.07 \\
\alpha_3 = 0.03 & \alpha_9 = 1.58 & \beta_3 = 0.87 \\
\alpha_4 = 0.01 & \alpha_{10} = 2.13 & \beta_4 = 0.34 \\
\alpha_5 = 0.00 & \alpha_{11} = 0.33 & \gamma_1 = 0.86 \\
\alpha_6 = 0.00 & \alpha_{12} = 0.01 & \gamma_2 = 1.00
\end{array}$$

S. armiger principally inhabits the areas of high salinity. A few young specimens have been found in the transitional parts of the areas with brackish water, but in general *Scoloplos* does not occur beyond the isohaline of $10^0/_{00}$ Cl′ at high tide during average river discharge. Muus (1967) also found the species to be very rare in shallow, mesohaline localities. In the Baltic, however, the species occurs still at $4.5^0/_{00}$ Cl′ (Mulicki, 1957), but it is difficult to explain this difference. The tolerance of the larvae to lowered salinities is quite high (Lyster, 1965), although they died at $6^0/_{00}$ Cl′. Probably, an important role is played by temperature.

From the β-values it appears that the species inhabits a fairly large range of sediments, but that it prefers fine and muddy sands. This appears also from a slight preference for less well-sorted sediments, which often means sandy sediments with a certain amount of mud. Smidt (1951), who summarized the findings of many others, Jepsen (1965), Hamond (1966) and Kirkegaard (1969) also state that *S. armiger* prefers sandy bottoms. Mulicki (1957) found that in the Baltic *S. armiger* inhabits very different types of bottom, but that it shows a preference for sandy mud and fine sand. On the basis of not more than about 100 samples Reineck et al. (1968) concluded that this species did not show any specific relationship to the sediment.

The vertical distribution of *Scoloplos armiger* ranges from the upper part of the intertidal zone down to a depth of 48 m, being the deepest place sampled.

Aricidea minuta Southward, 1956. This species has not been recorded before from Dutch coastal waters.

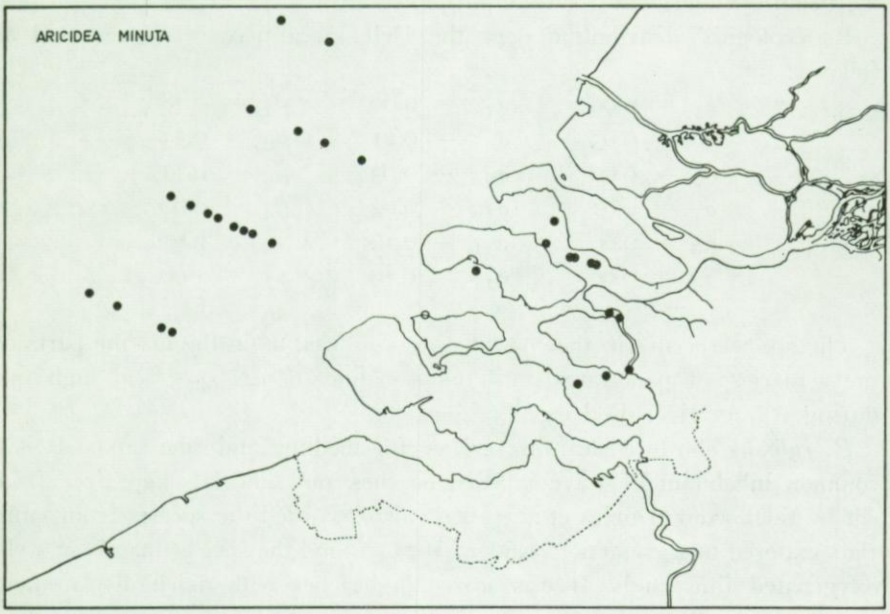

Fig. 30. Distribution of *Aricidea minuta.* Symbols as in fig. 22.

Gibbs (1965) suggested that spawning occurs between October and January. Mature females usually have less than 100 ova, thus suggesting a non-pelagic development. Information about the food of this species is not available, but judging from its anatomy it does not seem to be a suspension-feeder.

A. minuta has not been found beyond the isohaline of 15‰ Cl′ at high tide during average river discharge (fig. 30).

In the estuaries *A. minuta* lives in fine and muddy sands, with median grain-sizes of 2.52-2.98 φ and sorting coefficients of 0.28-0.46 phi-units. In the North Sea, however, it inhabits clean medium sands with median grain-sizes of 1.42-2.04 φ and sorting coefficients of 0.26-0.41 phi-units. Southward (1957), Eliason (1962) and Gibbs (1965, 1969) record the species from muddy sand with shell gravel, muddy sand and clean sand.

The species has been found in the lower part of the intertidal zone and down to a depth of 32 m.

Paraonis fulgens (Levinsen, 1883). This species has not been recorded before from The Netherlands.

Data about its reproduction are wanting, but the small number of large ova suggests a non-pelagic development. It is a selective deposit-feeder on the meioflora and -fauna (Röder, 1971).

Its ecological distribution over the Delta area may be represented as follows:

$\alpha_1 = 0.00$ $\alpha_7 = 0.00$ $\beta_1 = 0.48$
$\alpha_2 = 0.03$ $\alpha_8 = 0.21$ $\beta_2 = 0.53$
$\alpha_3 = 0.00$ $\alpha_9 = 0.05$ $\beta_3 = 0.11$
$\alpha_4 = 0.01$ $\alpha_{10} = 0.02$ $\beta_4 = 0.00$
$\alpha_5 = 0.00$ $\alpha_{11} = 0.10$ $\gamma_1 = 2.67$
$\alpha_6 = 0.00$ $\alpha_{12} = 0.10$ $\gamma_2 = 1.00$

The species occurs in the coastal waters as well as in the marine parts of the estuaries; it penetrates until the isohaline of $12\,^0/_{00}$ Cl′ at high tide during average river discharge.

P. fulgens shows a clear preference for medium and fine sands. It is a common inhabitant of wave-exposed beaches and sandflats kept free from silt by tidal scour. Dörjes et al. (1969) also recorded the species from sandflats exposed to wave-action. Röder (1971) found the species mainly in well-oxygenated fine sands. It was scarce in beaches with much displacement of sand.

Remarkable is the strong preference of this species for the better sorted types of sand. This preference possibly determines to a large degree its abundance in the more or less brackish Krammer area.

The vertical distribution of this species ranges from the lower part of the intertidal zone down to a depth of 28 m.

Aonides paucibranchiata Southern, 1914. This species was not recorded before from Dutch waters.

Hannerz (1956) found larvae, probably belonging to this species, in October. Further details on the reproduction are lacking. Most probably it is a selective deposit-feeder.

A. paucibranchiata was found only in the North Sea. Most finds were made rather far offshore, but it was also found 3 miles off the mouth of the Haringvliet and 4-5 miles off the mouth of the Westerschelde. The lowest salinity in which the species was found, was $16.5\,^0/_{00}$ Cl′.

Hannerz (1956), Southward (1957), Hartmann-Schröder & Stripp (1968) and Kirkegaard (1969) record the species always from coarse sand and fine gravel, one time from muddy sand mixed with fine gravel. These specimens, however, originated largely from fairly well-sorted medium sands (median grain-size 1.13-1.71 φ). Moreover, two finds were even made in fine sands with median diameters of 2.42 and 2.11 φ. The latter value was caused by 6.36% of mud in the sample; the former one consisted of very well-sorted clean sand.

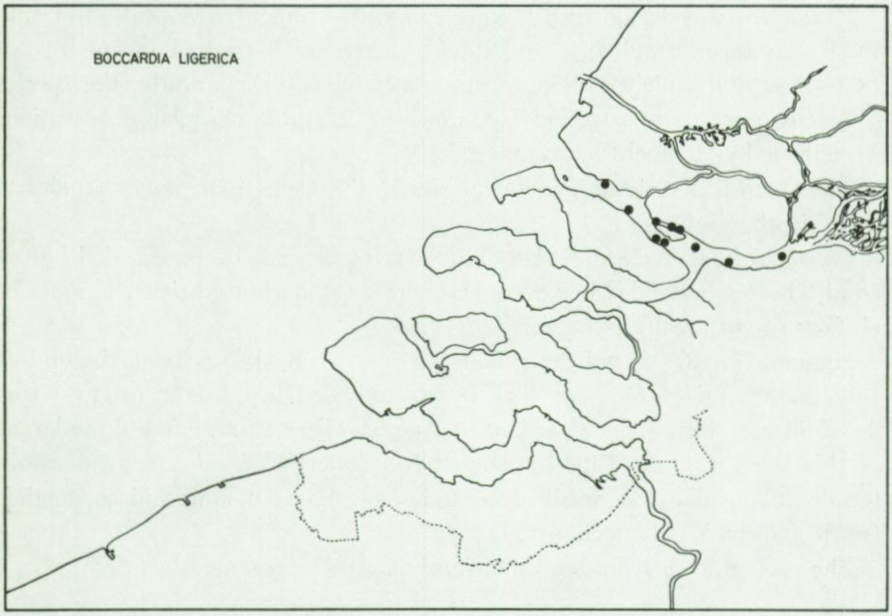

Fig. 31. Distribution of *Boccardia ligerica*. Symbols as in fig. 21.

The vertical range of *A. paucibranchiata* in the area studied is 10-34 m.

Boccardia ligerica Ferronière, 1898. The species has not been recorded before from the Delta area. *B. redeki* Horst, 1920, described from The Netherlands, is a junior synonym (Blake & Woodwick, 1971).

In Normandy spawning occurs in the period June-September (Rullier, 1960). In Germany sexually ripe specimens were found in July-October. The fertilized eggs are retained in the tubes of the females and the larvae usually stay there until the three-setiger stage is reached. The further planktonic development until metamorphosis takes at least several days. *B. ligerica* is a suspension-feeder and takes planktonic organisms under 600 μ (Hempel, 1957). *B. ligerica* was found exclusively in brackish waters between the isohalines of 0.3 and $10^0/_{00}$ Cl′ at high tide during average river discharge (fig. 31). During periods of small river discharge *B. ligerica* apparently is able to colonize temporarily areas more landinward. In the literature, summarized by Eliason & Haahtela (1969), the species is recorded from salinities of 1.2-6.2 $^0/_{00}$ Cl′, but these authors seem to have overlooked the data of De Vos (1936, 1954), who found the species in the former Zuiderzee most abundant in salinities of 4.3-6.8 $^0/_{00}$ Cl′. The highest salinity met with by her was 8.3 $^0/_{00}$ Cl′; the species disappeared from the Zuiderzee when salinity dropped below 0.15 $^0/_{00}$ Cl′.

B. ligerica was found in different types of sediment, viz. peat, stiff subfossil clay-layers, and fine and muddy sands with median grain-sizes of 1.03-3.99 φ and widely varying sorting-coefficients. Apparently, the species primarily needs a substratum for attaching its tubes. Similar observations were made by Hempel (1957a).

The vertical distribution of *B. ligerica* in the Delta area ranges from 2 to 15 m depth.

Polydora ligni Webster, 1879. This species has not been recorded before from The Netherlands; however, Hannerz (1956) showed that *P. ciliata* of Hofker (1930) really is *P. ligni*.

Hannerz (1956) found the pelagic larvae of this species from the end of July to the end of October. The larvae recorded by Hofker (1930) from the Zuiderzee were most abundant in August. Giere (1968) found the larvae of this species in the Elbe in August-November. *P. ligni* is a suspension-feeder, taking diatoms, small algae and semi-pelagic nauplii and copepodids (up to 0.6 mm) (Hempel, 1957).

The ecological distribution of *P. ligni* may be represented by:

$$\begin{array}{lll}
\alpha_1 = 0.00 & \alpha_7 = 0.00 & \beta_1 = 0.01 \\
\alpha_2 = 2.85 & \alpha_8 = 3.13 & \beta_2 = 0.02 \\
\alpha_3 = 4.83 & \alpha_9 = 2.72 & \beta_3 = 0.05 \\
\alpha_4 = 1.41 & \alpha_{10} = 1.15 & \beta_4 = 0.25 \\
\alpha_5 = 4.68 & \alpha_{11} = 0.85 & \gamma_1 = 0.80 \\
\alpha_6 = 0.00 & \alpha_{12} = 0.10 & \gamma_2 = 1.00
\end{array}$$

P. ligni tolerates a large range of salinities. It was found in salinities of about 1-3 $^0/_{00}$ Cl′, but also in a salinity of 16.5 $^0/_{00}$ Cl′. From the α-values it may be concluded that the species meets with optimal conditions in more or less brackish waters. Cory (1967) found it abundantly in salinities over about 3 $^0/_{00}$ Cl′.

P. ligni occurs on various substrates, but it has a preference for the muddier types with median grain-sizes over 4.00 φ. This was also observed by Wohlenberg (1937), Hempel (1957a) and Muus (1967). This species was not found in shells.

The vertical distribution of *P. ligni* ranges from the upper part of the intertidal zone down to a depth of 48 m, the deepest place sampled.

Wass (1967) mentions *P. ligni* as an indicator of pollution, but this is hardly confirmed by this study.

Polydora ciliata (Johnston, 1838). Earlier records: Korringa (1951).

The species has two spawning periods in the North Sea area, viz. March-June and September-December (Hannerz, 1956; Dorsett, 1961). Korringa (1951) found the larvae in May-June in the Oosterschelde. The eggs are deposited in egg-capsules in the tubes of the adults and the larvae leave these capsules in the three-setiger stage. After a pelagic stage of about 6 weeks the larvae settle. Dorsett (1961a) and Kiseleva (1967) demonstrated experimentally that the larvae preferred sands with a median grain-size over 2.00 φ. The settled larvae survived best in sands in the range 2.00-2.30 φ. The nature of the grains was not important, because the larvae settled equally well on sand, ground shells, glass and pumice. After settling the larvae build a primary tube, and only when this tube has been finished they are able to bore in shells and limestone. When they settle upon shells, they nevertheless first complete their primary tube before they start boring. Settling is not influenced by the chemical nature of the sediment, but it is positively influenced by the presence of a bacterial film and the presence of other individuals of the same species.

P. ciliata is a suspension-feeder as well as a selective deposit-feeder (Korringa, 1951; Dorsett, 1961a; Hempel, 1957). In general particles smaller than 30-50 μ are selected, and pass through the gut, irrespective of their further nature (Dorsett, 1961a).

P. ciliata occurs abundantly in the Oosterschelde in salinities over $16.5^0/_{00}$ Cl′. It penetrates the estuaries in an upstream direction until a salinity of $10\text{-}12^0/_{00}$ Cl′. At this salinity also several species of molluscs have their limit and for that reason *P. ciliata* may be limited by the absence of suitable substratum. Another factor at lower salinities is the large deposition of silt which according to Dorsett (1961), is deleterious to the larvae. *P. ciliata* has been found abundantly in Lake Veere in salinities of $9\text{-}11^0/_{00}$ Cl′ and also in the Gat van Ouwerkerk in a salinity of $10\text{-}11^0/_{00}$ Cl′. In inland waters with lower salinities the species has not been found, contrary to *P. ligni*. *P. ciliata* lives mainly in shells of molluscs, for instance *Ostrea edulis, Mytilus edulis* and *Littorina littorea* (Korringa, 1951), although occasional specimens may be found in loose sediments, a fact also recorded by Hempel (1957a).

The vertical distribution of *P. ciliata* ranges from the lower part of the intertidal zone down to a depth of 22 m.

Pseudopolydora pulchra (Carazzi, 1895). This species has not been recorded before from Dutch coastal waters.

Hannerz (1956) found the pelagic larvae in the period May-December; Rullier (1963) captured them in June-September. The metamorphosis, which depends very slightly on the nature of the substratum, can take place as early as the 10-12 segment stage, but it can also be postponed considerably. The worms build erect tubes extending far above the surface of the substratum. It is a suspension-feeder, taking plankton and detritus (Eleftheriou, 1970), although some deposit-feeding should not be ruled out.

P. pulchra has been found commonly in the marine parts of the estuaries, but not beyond the isohaline of $15^{0}/_{00}$ Cl′ at high tide during average river discharge. Eleftheriou (1970) mentions a minimal salinity of $12.2^{0}/_{00}$ Cl′ for the adults but records that the larvae are killed by salinities below $16.5^{0}/_{00}$ Cl′.

The sediments inhabited by the species had median grain-sizes of 2.22-3.15 φ with sorting coefficients of 0.25-0.71 phi-units. Eleftheriou (1970), Hartmann-Schröder & Stripp (1968), Eliason (1962) and Hannerz (1956) record the species from mud or muddy sand.

In the Delta area the vertical distribution of *P. pulchra* ranges from 2 to 25 m depth.

Malacoceros fuliginosus (Claparède, 1868). This species has not been found earlier in The Netherlands.

The species reproduces in summer and the pelagic larvae have been found in July-December (Hannerz, 1956: Sweden), June (Rasmussen, 1956: Denmark) and June-October (Gierę, 1968: Germany). The pelagic stage takes at least a month. Day & Wilson (1934) found that the species prefers sandy mud for metamorphosis. On the other hand Gray (1971) states that the settling larvae prefer certain species of bacteria as a coating of the sand-grains, and that the size of the grains seems to be relatively unimportant. *M. fuliginosus* probably is a selective deposit-feeder.

It is a rare species in the Delta area. Only two specimens are available, one from the entrance to the Oosterschelde, and another from the North Sea. Salinity at these localities is about $17^{0}/_{00}$ Cl′, but this factor cannot be limiting because the species tolerates much lower values in the Isefjord, Denmark (Rasmussen, 1956).

The sediment consisted of fine sand in both localities (Md = 2.17 φ), a very common type in the Delta area. The depth was 8 and 25 m, respectively. It is not clear why this species is so rare in the Delta area.

Nerinides tridentata Southern, 1914. This species was not reported before from The Netherlands.

The species has pelagic larvae (Hannerz, 1956; Bhaud, 1967), occurring in July-November at the western coast of Sweden. Most probably it is a selective deposit-feeder.

This species was found only once, viz. in the entrance to the Oosterschelde at a salinity over 16.5$^0/_{00}$ Cl′. The nature of the bottom is not known, but it has been found on mud and muddy sand bottoms (Hannerz, 1956; Southward, 1956, 1957).

The species was found at 7 m depth.

Scolelepis squamata (Müller, 1806). Earlier records: Den Hartog (1961, sub nom. *Nerine cirratulus*).

The larvae of this species have been recorded from March to January, but maximal numbers of trochophores occur in May-July. The length of the pelagic stage is over one month (Smidt, 1951; Hannerz, 1956; Joyner, 1962; Giere, 1968). Metamorphosis occurs rapidly in clean mineral sand (Hannerz, 1956). *S. squamata* behaves as a suspension-feeder as well as a selective deposit-feeder (Jepsen, 1965; Retière, 1967a).

The ecological distribution of *S. squamata* in the Delta area below LW-mark may be represented as:

$\alpha_1 = 0.01$
$\alpha_2 = 0.24$
$\alpha_3 = 0.33$
$\alpha_4 = 0.00$
$\alpha_5 = 0.00$
$\alpha_6 = 0.00$

$\alpha_7 = 0.00$
$\alpha_8 = 0.43$
$\alpha_9 = 0.23$
$\alpha_{10} = 0.00$
$\alpha_{11} = 0.04$
$\alpha_{12} = 0.10$

$\beta_1 = 0.26$
$\beta_2 = 0.07$
$\beta_3 = 0.03$
$\beta_4 = 0.00$
$\gamma_1 = 4.45$
$\gamma_2 = 1.00$

In the intertidal zone *S. squamata* is common in all intertidal sandflats and beaches along the North Sea and in the marine parts of the estuaries (fig. 32). It penetrates until the isohaline of 15$^0/_{00}$ Cl′ at high tide during average river discharge. Subtidally, however, its distribution is completely different. It is common just off the beaches along the coast of the North Sea, and also in those parts of the estuaries where during a tidal cycle salinity varies between 10$^0/_{00}$ and 15$^0/_{00}$ Cl′. The occurrence in the latter area resembles the "Brackwassersubmergenz", but it seems that the reason for this pattern of distribution is not salinity, but the type of sediment. From the β-values it appears that *S. squamata* inhabits sandy sediments with a strong preference for medium sands, which fact, however, does not explain the remarkable distribution of the species.

A better explanation probably may be found in the γ-values. *S. squamata* shows a very strong preference for well-sorted sediments. Its areas of subtidal abundance coincide exactly with the areas of well-sorted sands, viz. off the North Sea beaches where the waves are the sorting agency, and in the far inland parts of the estuaries where the sorting has been accomplished by the inshore transport of sediment by the strong tidal currents.

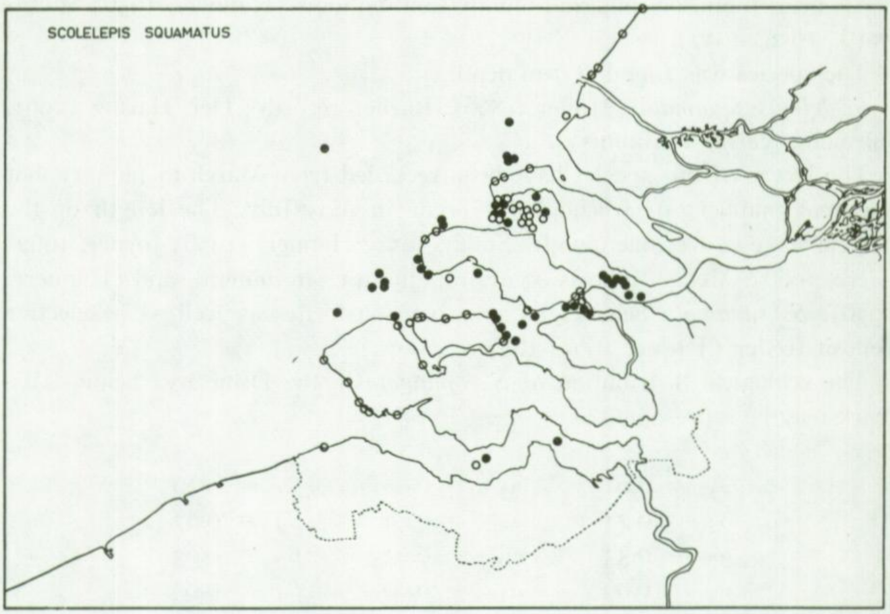

Fig. 32. Distribution of *Scolelepis squamata*. Symbols as in fig. 22.

The vertical distribution of *S. squamata* ranges from the upper part of the intertidal zone down to a depth of 25 m.

The intertidal distribution of this species has been investigated earlier by Joyner (1962), Amoureux (1966) and Retière (1967a). Joyner (1962) found the species to be concentrated in a narrow zone just below mean high water mark of neap tides. He states that it is improbable that the pattern of distribution of *S. squamata* is correlated either with the inclination of the beach, with the texture of the substratum, or with the amount of organic matter in the sediment. Also Amoureux (op. cit.) and Retière (op. cit.) found *S. squamata* living in a narrow zone on the beach. These authors assume a close correlation between the occurrence of *S. squamata* and the location of the "zone de rétention" (= zone of capillary water) and the "zone de résurgence" (= zone of outflowing water), *S. squamata* living approximately at the boundary between these zones. These authors also note the possibility of a correlation with very well-sorted sediments.

In the Delta area most beaches consist of very well-sorted sands, but nevertheless the distribution of *S. squamata* varies very much from one locality to another. Apparently, small differences in sorting of the sediment do not influence the distribution of this species in well-sorted beach sands. Nor is it possible to correlate the distribution of *S. squamata* with the zones distinguished by Amoureux and Retière. Neither can correlations be found with the inclination of the beaches, with the amount of organic matter in the sediment, or with the absolute height on the beach. It has to be concluded that the differences in microdistribution of *S. squamata* on well-sorted beaches cannot be explained by one of the factors investigated.

Scolelepis foliosa (Audouin & Milne Edwards, 1833). This species has not been recorded before from The Netherlands.

In German and Scandinavian waters the youngest larval stages were met with in December-February. After April no larvae were found. The larvae metamorphose readily in pure mineral sand from localities exposed to waves (Thorson, 1946; Hannerz, 1956; Giere, 1968). The young bottom stages range freely in the sediment; they feed on young molluscs (Hannerz, op. cit.). Jepsen (1965) describes how the adults live in a vertical burrow lined with mucus — as was observed in this study — and records that *S. foliosa* is a selective deposit-feeder, mainly on cyanophyceans. Hartmann-Schröder (1971), on the other hand, mentions it as a predator.

S. foliosa has been found in the nearshore parts of the North Sea as well as in the marine parts of the estuaries. No specimens have been found beyond the isohaline of $13^0/_{00}$ Cl′ at high tide during average river discharge.

S. foliosa has been found in medium and fine sands with median grain-sizes of 1.80-2.91 φ and sorting coefficients of 0.24-1.10 phi-units. Remarkably, many of the sands containing this species have a fairly large mud fraction (up to 23.5%). This is also recorded by Holme (1949a).

The vertical distribution of *S. foliosa* ranges from about half-tide level down to 30 m depth.

Scolelepis bonnieri (Mesnil, 1896). This species has not been recorded earlier from The Netherlands.

Data on its reproduction or its food have not been found.

The species has been found in the offshore parts of the North Sea, as well as in the marine parts of the estuaries of the Delta area. It has not been found beyond the isohaline of $15^0/_{00}$ Cl′ at high tide during average river discharge.

Its ecological distribution in the Delta area may be described as:

$$
\begin{array}{lll}
\alpha_1 = 1.05 & \alpha_7 = 0.00 & \beta_1 = 0.11 \\
\alpha_2 = 0.41 & \alpha_8 = 0.11 & \beta_2 = 0.17 \\
\alpha_3 = 0.00 & \alpha_9 = 0.02 & \beta_3 = 0.00 \\
\alpha_4 = 0.00 & \alpha_{10} = 0.04 & \beta_4 = 0.01 \\
\alpha_5 = 0.00 & \alpha_{11} = 0.00 & \gamma_1 = 2.32 \\
\alpha_6 = 0.00 & \alpha_{12} = 0.01 & \gamma_2 = 1.00
\end{array}
$$

S. bonnieri apparently prefers well-sorted medium and fine sands. It has been found at median grain-sizes ranging from 1.46 to 2.90 φ. It appears on comparison that the species prefers somewhat finer sands than *S. squamata.* On the other hand *S. bonnieri* occurs also in the offshore parts of the North Sea where coarser types of sand predominate. However, these coarser sands are also less well-sorted. Kirkegaard (1969) records it from fine and coarse sands.

Its vertical distribution is from just below LW-level down to a depth of 32 m.

Spio martinensis Mesnil, 1896. This species has not been recorded before from the Delta area.

Hannerz (1956) described two different types of larvae which perhaps both belong to this species, although he did not exclude the possibility that they are sibling species. One type occurs in June-February with a maximum in September-October, the other type was found in May-October with a maximum in July. He cites Mesnil, who found that there exist also two different types of eggs, viz. one mainly in April, and another especially in late summer. Both types of larvae give rise to the same type of bottom-living stage. Both larval types metamorphose in clean mineral sand, and somewhat less readily in mud. The worms build tubes, protruding above the surface of the substratum. *S. martinensis* is a suspension-feeder as well as a selective deposit-feeder.

Its ecological distribution over the subtidal parts of the Delta area may be represented as:

$$
\begin{array}{lll}
\alpha_1 = 1.54 & \alpha_7 = 0.00 & \beta_1 = 0.67 \\
\alpha_2 = 0.40 & \alpha_8 = 0.20 & \beta_2 = 0.77 \\
\alpha_3 = 0.17 & \alpha_9 = 0.25 & \beta_3 = 0.40 \\
\alpha_4 = 0.02 & \alpha_{10} = 0.29 & \beta_4 = 0.00 \\
\alpha_5 = 0.00 & \alpha_{11} = 0.00 & \gamma_1 = 1.80 \\
\alpha_6 = 0.00 & \alpha_{12} = 0.01 & \gamma_2 = 1.00
\end{array}
$$

S. martinensis is abundant in the offshore parts of the North Sea and it penetrates far into the estuaries. The limit of its occurrence is formed by the isohaline of $10^0/_{00}$ Cl′ at high tide during average river discharge.

The types of sediment inhabited range from medium to muddy sand with a preference for medium and especially fine sand. The species prefers the better sorted types.

The vertical distribution of *S. martinensis* ranges from the lower part of the intertidal zone down to a depth of 35 m.

Remarkably this species is nearly absent from the Westerschelde estuary. Perhaps this may be attributed to the very high load of suspended sediments of this estuary.

Spiophanes bombyx (Claparède, 1870). This very common species has not been recorded before from Dutch coastal waters.

The pelagic larvae of this species have been observed in the period April-December with maximal numbers in May-June and August-September (Maghraby & Perkins, 1956; Hannerz, 1956; Giere, 1968). Hannerz (1956) induced metamorphosis in sand as well as in mud. Probably it is a selective deposit-feeder (Hartmann-Schröder, 1971). The ecological distribution of this species over the Delta area may be represented as:

$$\begin{array}{lll}
\alpha_1 = 2.42 & \alpha_7 = 0.00 & \beta_1 = 0.63 \\
\alpha_2 = 0.54 & \alpha_8 = 0.04 & \beta_2 = 1.33 \\
\alpha_3 = 0.07 & \alpha_9 = 0.21 & \beta_3 = 0.61 \\
\alpha_4 = 0.01 & \alpha_{10} = 0.23 & \beta_4 = 0.00 \\
\alpha_5 = 0.00 & \alpha_{11} = 0.06 & \gamma_1 = 1.09 \\
\alpha_6 = 0.00 & \alpha_{12} = 0.01 & \gamma_2 = 1.00
\end{array}$$

The distribution of this species is very similar to that of *Spio martinensis*. It also is most abundant in the offshore parts of the North Sea and penetrates far into the estuaries. However, it has not been found beyond the isohaline of about $13^0/_{00}$ Cl′ at high tide during average river discharge. Like *Spio martinensis* it is also rare in the Westerschelde, probably for the same reason.

Spiophanes bombyx also prefers about the same type of sediment as does *Spio martinensis*. It has been found in medium, fine, and muddy sands with a distinct preference for fine sand. Reineck et al. (1968) concluded that the species did not show any specific relationship with the sediment, but this observation is invalidated by their small number of data. Kirkegaard (1969) observed it in fine and muddy sands.

From the γ-values it appears that *S. bombyx* hardly has a preference for sands with a certain sorting coefficient. This is not in accordance with the findings of Retière (1967) who found that this species was governed in its distribution by the sorting of the sediment.

The vertical distribution of *S. bombyx* ranges from the lower part of the intertidal zone down to a depth of 48 m, being the deepest place sampled.

Pygospio elegans Claparède, 1863. This abundant and well-known species has, remarkably enough, not been recorded before from the Delta area.

Sexual reproduction takes place in the period February-September with a maximum in July-August (Hannerz, 1956; Hempel, 1957). The eggs are laid in up to 16 capsules, each with 50-60 eggs, deposited in the tubes of the mother-animals. Maximally, 7 to 9 eggs in each capsule develop into embryos, while the remaining eggs serve as nourishment for the developing larvae. Depending on the number of developing embryos in a capsule and thus on the amount of available food, the larvae hatch at an earlier or later stage of development, which governs the length of the planktonic phase (Thorson, 1946). Perhaps development without a planktonic stage is also possible, namely when only one embryo develops in a capsule. Smidt (1951), on the other hand, found in the Danish Wadden Sea that all eggs developed into pelagic larvae. Hannerz (1956) solved this puzzle to some extent by the observation that in spring the larvae soon leave the capsules, thus having a long pelagic life, and remain in the capsules for a long time and have a short pelagic life in summer. The larvae may be found during all months of the year, but they show a maximum in spring and summer (Smidt, 1951; Giere, 1968). The larvae remain photopositive during their complete development (Thorson, 1946). Their settling is favoured by the presence of a natural sediment; without such a substratum they may prolong their pelagic life for over two months (Smidt, 1951). Besides sexual *P. elegans* also shows asexual reproduction (Muus, 1967; Hobson & Green, 1968). When a specimen is damaged or lives under unfavourable conditions, it fragmentates into 2-4 pieces, each of which regenerates a new individual within a few days. Hobson & Green (1968) observed in Barnstable Harbour (U.S.A.) that fragmentation was most intense in April-May; this process increasing the population tenfold.

Pygospio elegans is a selective deposit-feeder, also capable of some suspension-feeding (Thamdrup, 1935; Hempel, 1957a). Small green algae and diatoms, gathered during flood- as well as ebb-tide, when the tidal flats are still moist, are the most important food. The major part of the individuals of *Pygospio elegans* lives in the intertidal zone, which fact is in accordance with the photopositive behaviour of the larvae. Not a single observation is available from the subtidal part of the Westerschelde, and only three records from the subtidal part of the Oosterschelde. The species has a somewhat greater abundance in the subtidal parts of the Grevelingen—Krammer—Volkerak estuary, especially in the area with salinities fluctuating between 5 and 15$^0/_{00}$ Cl′. It is rare again in the subtidal parts of the Haringvliet, where it reaches apparently the limit of its salinity tolerance. On the tidal flats, however, it is extremely common all along the estuaries, except for the Hollands Diep—Haringvliet area where it is rather patchy in its distribution. This is in good accordance with its salinity tolerance as reported in the literature.

De Vos (1936) found it in the former Zuiderzee in salinities down to 4.5$^0/_{00}$ Cl′. Bagge et al. (1965) and Laakso (1968) report it from Finnish waters in salinities of 3-3.5$^0/_{00}$ Cl′. Hempel (1957a) mentions it from the Nord-Ostsee-Kanal down to 2.1$^0/_{00}$ (Cl′?). Green (1968) records that it is able to tolerate values down to 1.2$^0/_{00}$ Cl′ for short periods. In the Delta area it reaches the isohaline of 3$^0/_{00}$ Cl′ in the Haringvliet area. It was also found in brackish inland waters, but not in salinities below about 10$^0/_{00}$ Cl′. Muus (1967) reports that *P. elegans* is still reproducing in mesohaline waters. However, *P. elegans* is certainly not a brackish water species because it occurs also in the Oosterschelde and on the beaches along the North Sea in salinities over 16.5$^0/_{00}$ Cl′. In the latter localities, however, it is exterminated by wave action in autumn and winter.

The largest part of the population lives on fine and muddy sands with median grain-sizes in the range 2.00-4.00 φ. The species, however, has a much larger range and also occurs in low numbers in sediments with a median grain-size over 4.00 φ.

The vertical distribution ranges from near the high water mark down to a maximal depth of 25 m. Its occurrence high in the intertidal zone is favoured by its large temperature tolerance (up to 30°C; Thamdrup, 1935).

Streblospio shrubsolii (Buchanan, 1890). Earlier records: Korringa (1951, sub nom. *S. dekhuyzeni*).

Reproduction takes place in June-July (Faune marine de Roscoff, 1967); the larvae may occur in the plankton in large numbers (Hofker, 1930).

The food is unknown.

The maximum abundance of *S. shrubsolii* lies in the brackish area of the Haringvliet (fig. 33). This is in accordance with the literature data. Hempel (1957a) recorded the species from the Nord-Ostsee-Kanal in salinities between 2.4 and 11.7$^0/_{00}$ (Cl′?); De Vos (1936) records that it was the commonest polychaete species in the brackish former Zuiderzee and that it did not occur in salinities over 6.9-10.3$^0/_{00}$ Cl′. Nellen (1967) found it to be abundant in salinities over 6$^0/_{00}$ Cl′. Muus (1967) mentions it as a characteristic brackish water species and Kosler (1969) records it from

4.1-7.7$^0/_{00}$ Cl′. On the other hand, Korringa (1951) mentions two finds in the Oosterschelde, where salinity is high (over 16.5$^0/_{00}$ Cl′) and in this study a specimen was found in the offshore parts of the North Sea at still higher salinity. Apparently *S. shrubsolii,* although having its centre of abundance in brackish waters, is also able to live under marine conditions.

S. shrubsolii was found on fine and muddy sands with median grain-sizes of 2.47-3.35 φ and sorting coefficients of 0.26-0.75 phi-units. In several cases the sand was mixed with debris of peat, wood, and other organic matter.

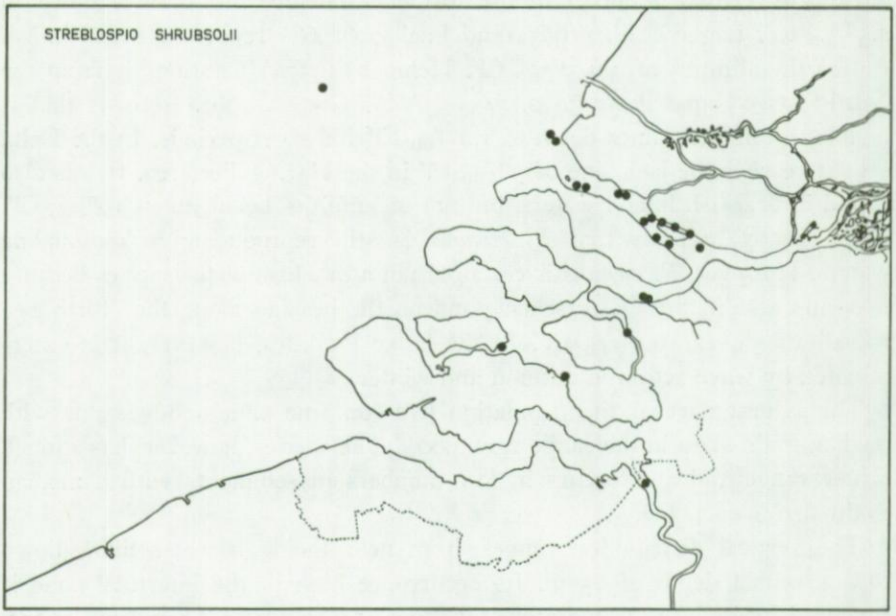

Fig. 33. Distribution of *Streblospio shrubsolii.* Symbols as in fig. 21.

The vertical distribution of this species ranged from the lower fringe of the intertidal zone down to a depth of 15 m.

Magelona papillicornis Müller, 1858. Earlier records: Horst (1919).

The larvae of this species occur in the North Sea from April-May to August and perhaps even to October (Hofker, 1922; Thorson, 1946; Hamond, 1966; Giere, 1968). The food consists of diatoms and all kinds of detritus. *M. papillicornis* behaves as a suspension-feeder as well as a selective deposit-feeder (McMahon & Jones, 1967; Jones, 1968).

The ecological distribution of *M. papillicornis* in the subtidal parts of the Delta area may be represented by:

$\alpha_1 = 0.41$ $\alpha_7 = 0.00$ $\beta_1 = 0.13$
$\alpha_2 = 0.72$ $\alpha_8 = 0.15$ $\beta_2 = 0.37$

$\alpha_3 = 0.26$ $\alpha_9 = 0.32$ $\beta_3 = 0.08$
$\alpha_4 = 0.00$ $\alpha_{10} = 0.27$ $\beta_4 = 0.00$
$\alpha_5 = 0.00$ $\alpha_{11} = 0.28$ $\gamma_1 = 4.79$
$\alpha_6 = 0.00$ $\alpha_{12} = 0.01$ $\gamma_2 = 1.00$

M. papillicornis occurs in the North Sea as well as in the marine parts of the estuaries, where it penetrates to the isohaline of $13^0/_{00}$ Cl′ at high tide during average river discharge in the Krammer and to $14^0/_{00}$ in the Westerschelde. From the β-values it appears that *M. papillicornis* prefers fine sands, but occurs also in medium and in muddy sand. Southward (1957) found the species in "clean sand", but Reineck et al. (1968) consider this species an inhabitant of muddy sand. Kirkegaard (1969) mentions it from fine sand. Remarkable is the strong preference of *M. papillicornis* for well-sorted sediments.

The vertical distribution ranges from the lower fringe of the intertidal zone down to a depth of 33 m.

Poecilochaetus serpens Allen, 1904. This species has not been recorded before from The Netherlands.

P. serpens has larvae with a very long pelagic stage; they have been observed in the months June-November (Thorson, 1946; Hannerz, 1956; Hamond, 1966). The metamorphosis is induced by pure mineral sand. *P. serpens* is a suspension-feeder on small algae and diatoms (Allen, 1904).

P. serpens only has been found in the offshore parts of the North Sea in salinities over $18^0/_{00}$ Cl′. The distribution is similar to that of *Corymorpha nutans*.

The species is not completely restricted to the Channel water, but occurs also in the Continental coastal water.

P. serpens lives in medium and fine sands with median grain-sizes of 1.25-2.30 φ and sorting coefficients of 0.27-0.80 phi-units. The amount of particles $<75\,\mu$ varies between 0.01 and 1.39%. Such sediments occur also nearer to the shore, hence *P. serpens* is not restricted to the offshore waters by the type of sediment. Kirkegaard (1969) records it from sand and sand mixed with clay or mud.

The vertical distribution in the area studied ranges from 21 to 39 m depth.

Psammodrilus balanoglossoides Swedmark, 1952. This species has not been recorded before from The Netherlands.

Reproduction occurs in Brittany throughout the year, but shows a maximum in May-July. The larvae do not possess a pelagic stage, although in November some larvae able to swim to some extent were observed. The food consists of benthic diatoms (Swedmark, 1955).

The species was met with in 7 different localities, scattered over the Delta area. The salinities at these localities were 12-16.5$^0/_{00}$ Cl′ at high tide during average river discharge. Swedmark (op. cit.) mentions the species from the Baltic at salinities varying between 7 and 9.5$^0/_{00}$ Cl′ as well as from Roscoff at a salinity of 19.5$^0/_{00}$ Cl′.

The type of sediments inhabited by *P. balanoglossoides* in the Delta area is fine sand with a median grain-size of 2.07-2.70 φ and a sorting coefficient of 0.23-0.38 phi-units. The amount of particles $<75\,\mu$ amounted maximally to 1.49%. Swedmark (op. cit.) only remarks that the species lives in fine sands, but Boaden (1963) and Westheide (1966) record it from sands with median grain-sizes ranging from 0.30 to 2.30 φ.

P. balanoglossoides was found mainly in the upper part of the intertidal zone, just as was recorded by Swedmark (op. cit.). It was not encountered below LW-mark.

Chaetozone setosa Malmgren, 1867. This species has not been recorded before from the coastal waters of The Netherlands.

Females with ripe eggs have been observed in May and July (Hartmann-Schröder, 1971); probably the species has non-pelagic larvae like all cirratulids (Dales, 1951a). Possibly, it is a selective deposit-feeder.

The ecological distribution of this species may be represented by:

$\alpha_1 = 1.68$
$\alpha_2 = 0.28$
$\alpha_3 = 0.00$
$\alpha_4 = 0.00$
$\alpha_5 = 0.00$
$\alpha_6 = 0.00$
$\alpha_7 = 0.00$
$\alpha_8 = 0.00$
$\alpha_9 = 0.00$
$\alpha_{10} = 0.03$
$\alpha_{11} = 0.00$
$\alpha_{12} = 0.01$
$\beta_1 = 0.18$
$\beta_2 = 0.28$
$\beta_3 = 0.00$
$\beta_4 = 0.00$
$\gamma_1 = 1.33$
$\gamma_2 = 1.00$

The species is abundant in the North Sea and penetrates into the western part of the Oosterschelde, where a few finds have been made. All observations originate from salinities over 16.5$^0/_{00}$ Cl′.

From the β- and γ-values it may be concluded that the species prefers medium and fine sands with a slight preference for the well-sorted types. Also Gibbs (1969) considers *C. setosa* to be characteristic for sands. Southward (1956, 1957) mentioned the species from muddy sand as well as clean sand with median grain-sizes between about 2.30 and 3.30 φ. Schulz (1969) mentions it from muddy sand and sandy mud.

The vertical distribution ranges from about LW-mark down to a depth of 32 m.

Tharyx marioni (Saint Joseph, 1894). Earlier records: Korringa (1951; sub nom. *T. multibranchiis*).

In the estuary of the River Thames the large eggs were shed in the sand in April. After 10 days the non-pelagic larvae hatch from those eggs. Each female bears 1000-1500 oöcytes (Dales, 1951a). Gibbs (1971) describes another population at Plymouth spawning a maximum of 540 eggs in October-November. *Tharyx marioni* is a selective deposit-feeder.

The ecological distribution of this species in the subtidal parts of the Delta area may be represented by:

$\alpha_1 = 1.61$
$\alpha_2 = 0.23$
$\alpha_3 = 0.00$
$\alpha_4 = 0.00$
$\alpha_5 = 0.00$
$\alpha_6 = 0.00$
$\alpha_7 = 0.00$
$\alpha_8 = 0.53$
$\alpha_9 = 4.18$
$\alpha_{10} = 0.52$
$\alpha_{11} = 1.07$
$\alpha_{12} = 1.00$
$\beta_1 = 0.00$
$\beta_2 = 0.08$
$\beta_3 = 0.30$
$\beta_4 = 0.30$
$\gamma_1 = 0.44$
$\gamma_2 = 1.00$

In the Krammer area *T. marioni* does not penetrate beyond the isohaline of $14^{0}/_{00}$ Cl′ at high tide during average river discharge. In the Westerschelde, however, it has still been found at a salinity of 7-$8^{0}/_{00}$ Cl′ under similar circumstances. It also has been found in the brackish Lake Veere at salinities of 9-$11^{0}/_{00}$ Cl′, as well as in two brackish inland waters with salinities of 10-$13^{0}/_{00}$ Cl′ and 11-$14^{0}/_{00}$ Cl′, respectively, but not in other inland waters with lower salinities. The difference between Krammer and Westerschelde probably may be explained by the fact that this species without a pelagic stage is limited by the largest extension of brackish water. During high river discharge and low tide the most landinward occurrence of this species is near the isohalines of $1^{0}/_{00}$ Cl′ in the Westerschelde and $2^{0}/_{00}$ Cl′ in the Krammer.

It appears from the β-values, as well as from the preference of this species for the less well-sorted sediments, that *T. marioni* mainly inhabits muddy types of sediment. Also Southward (1956, 1957) and Gibbs (1969) found that the species is typical of mud and muddy sand. Hartmann-Schröder & Stripp (1968), however, recorded the species also from coarse sands with stones.

The vertical distribution of *T. marioni* ranges from the upper part of the intertidal zone down to a depth of 25 m.

Scalibregma inflatum (Rathke, 1843). This species has not been recorded before from The Netherlands.

The larva probably has a pelagic stage of a few hours (Thorson, 1946). *S. inflatum* is a non-selective deposit-feeder (Hartmann-Schröder, 1971).

The species has been found at the entrance to the Oosterschelde and in the nearshore waters of the North Sea. The salinity at these localities was always over $16.5^0/_{00}$ Cl′. In the Baltic the species reaches a salinity of about $5^0/_{00}$ Cl′ (Hartmann-Schröder, op cit.).

The bottom consisted of fine and, especially, of muddy sand. In four cases the median grain-size was determined: 1.73-2.21 φ with sorting coefficients of 0.50-1.10 phi-units. The amount of particles $<75\ \mu$ maximally amounted to 8.54%. This preference for muddy sediments was also observed by Southward (1957), Eliason (1962), Reineck et al. (1968) and Schulz (1969).

The vertical distribution ranges from 3 to 30 m depth.

Possibly the species is limited to the seaward part of the estuaries and the North Sea by temperature, and to the nearshore waters by the absence of muddy sediments from the offshore waters.

Ophelia borealis Quatrefages, 1865. Earlier records: Horst (1922).

Thorson (1946) observed females with ripe eggs in April. It does not seem improbable that this species has pelagic larvae (compare Wilson, 1948). *O. borealis* is a typical non-selective deposit-feeder.

The ecological distribution of this species may be represented by:

$$\begin{array}{lll}
\alpha_1 = 4.46 & \alpha_7 = 0.00 & \beta_1 = 0.19 \\
\alpha_2 = 0.46 & \alpha_8 = 0.00 & \beta_2 = 0.03 \\
\alpha_3 = 0.00 & \alpha_9 = 0.00 & \beta_3 = 0.00 \\
\alpha_4 = 0.00 & \alpha_{10} = 0.20 & \beta_4 = 0.00 \\
\alpha_5 = 0.00 & \alpha_{11} = 0.29 & \gamma_1 = 1.45 \\
\alpha_6 = 0.00 & \alpha_{12} = 0.10 & \gamma_2 = 1.00
\end{array}$$

It inhabits the North Sea, penetrating into the estuaries only in small numbers (fig. 34). Nevertheless, occasional specimens have been found in the eastern part of the Oosterschelde. The species hardly occurs beyond the isohaline of $16.5^0/_{00}$ Cl′ at high tide during average river discharge. However, very juvenile specimens have been encountered floating in the water — this may be an argument in favour of a pelagic development — at salinities down to $13^0/_{00}$ Cl′.

From the β-values it appears that *O. borealis* prefers medium sands and becomes rarer in fine sands. From muddy sediments it is completely absent as was also found by Tebble (1952), Eliason (1962), Hamond (1966), Kirkegaard (1969) and Schulz (1969). It seems to prefer the better sorted types of sand. In the Delta area *O. borealis* occurs from just above LW-mark down to a depth of 36 m.

Ophelia rathkei McIntosh, 1908. Earlier records: Den Hartog (1961).

Thorson (1946) records breeding in April and September, but Westheide (1967) observed spawning in winter and early spring. The species does not possess pelagic larvae (Remane, 1952), but, nevertheless, Hamond (1966) records post-larval stages from the plankton in March, April and May. In the sediment the maximum numbers of this species occur in summer (Westheide, 1967; Schmidt, 1969). The adults of *O. rathkei* are non-selective deposit-feeders.

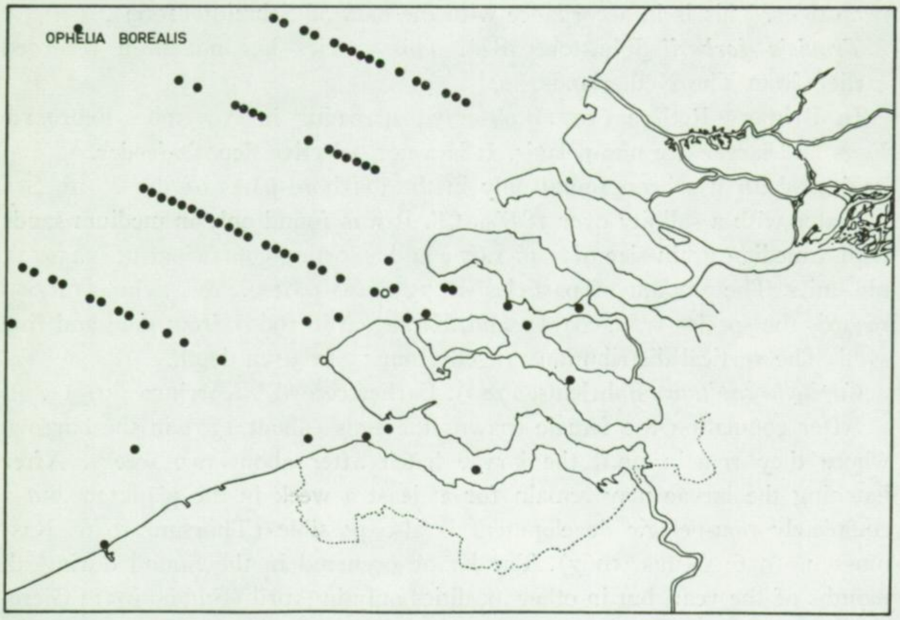

Fig. 34. Distribution of *Ophelia borealis.* Symbols as in fig. 22. Some data have been derived from Tebble (1952).

In the Delta area *O. rathkei* exclusively occurs in the intertidal zone, where it is abundant in many places. The same is true for Sylt, Germany (Westheide, 1967; Schmidt, 1969) and Roscoff, Brittany (Chassé & Picard, 1968). Tebble (1952), however, mentions some finds from the vicinity of the Isle of Man at a depth of 33 m, but his other records are all from the intertidal zone. Hartmann-Schröder (1971) records that in the Kieler Bucht it does not occur above 6-8 m depth.

O. rathkei occurs in every patch of sand along the North Sea and the marine parts of the estuaries of the Delta area. The limit of its occurrence is formed by the isohaline of $15^{0}/_{00}$ Cl′ at high tide during average river discharge. Remane (1952a) records this species from the Kieler Bucht where the salinity is about $10\text{-}12^{0}/_{00}$ Cl′ (Banse & Lefevere, 1954).

In the Delta area the species has been found only in sandy sediments with a median grain-size of 1.65-2.54 φ and a sorting coefficient of 0.20-0.75 phi-units. The amount of particles $<75\ \mu$ varied between 0.01 and 0.65%. Westheide (1967) and Schmidt (1968, 1969) record the species from sands with a median grain-size of 0.30-1.00 φ. Chassé & Picard (1968) record it from 1.85-2.15 φ.

The vertical range of *O. rathkei* is about the same as the tidal range at neap tides. This is in accordance with the data of Schmidt (1969).

Travisia forbesii Johnston, 1840. This species has not been recorded earlier from The Netherlands.

In Brittany Retière (1971) observed spawning in November-February. Eggs and larvae are non-pelagic. It is a non-selective deposit-feeder.

T. forbesii has been found only in the offshore parts of the North Sea in water with a salinity over $18^{0}/_{00}$ Cl′. It was found only in medium sands with a median grain-size of 1.46-1.97 φ and a sorting coefficient of 0.25-0.72 phi-units. The amount of particles $< 75\ \mu$ was 0.01-0.26%. Schulz (1969) records the species from coarse sand, Kirkegaard (1969) from sand and fine sand. The vertical distribution ranged from 15 to 30 m depth.

Capitella capitata (Fabricius, 1780). Earlier records: Korringa (1951).

After copulation the female spawns the eggs (about 130) in the burrow, where they remain until the larvae hatch after about two weeks. After hatching the larvae may remain for at least a week in the plankton, but a completely non-pelagic development is also possible (Thorson, 1946; Rasmussen, 1956; Muus, 1967). The larvae occurred in the Sound during all months of the year, but in other localities only in April (Smidt, 1951; Giere, 1968).

C. capitata is a non-selective deposit-feeder.

The ecological distribution of *C. capitata* may be described as:

$$\begin{array}{lll}
\alpha_1 = 0.00 & \alpha_7 = 0.00 & \beta_1 = 0.24 \\
\alpha_2 = 0.65 & \alpha_8 = 1.63 & \beta_2 = 0.49 \\
\alpha_3 = 0.04 & \alpha_9 = 1.83 & \beta_3 = 0.43 \\
\alpha_4 = 0.26 & \alpha_{10} = 0.36 & \beta_4 = 0.00 \\
\alpha_5 = 0.00 & \alpha_{11} = 0.34 & \gamma_1 = 1.27 \\
\alpha_6 = 0.00 & \alpha_{12} = 1.00 & \gamma_2 = 1.00
\end{array}$$

The species is absent from the offshore parts of the North Sea, but also from the brackish and fresh parts of the estuaries (fig. 35). During this investigation *C. capitata* was hardly found beyond the isohaline of $10^{0}/_{00}$ Cl′ at high tide during average river discharge, but Leloup & Konietzko (1956) found it in the Westerschelde down to the isohaline of $4^{0}/_{00}$ Cl′. Possibly, however, their record is due to confusion with *Heteromastus fili-*

formis, because they only mention *Heteromastus sp.* Muus (1967) records that *C. capitata* was scarce in Danish mesohaline (under $10^0/_{00}$ Cl′) bays and fjords, but abundant in the only locality investigated with a salinity over $10^0/_{00}$ Cl′.

Filice (1958) records the species from a salinity of about $13^0/_{00}$ Cl′, but also from about $0.3^0/_{00}$ Cl′. Probably the latter observation is a mistake, due to confusion with some other species. Moreover, Stone & Reish (1965) reported that *C. capitata* was killed by rainwater.

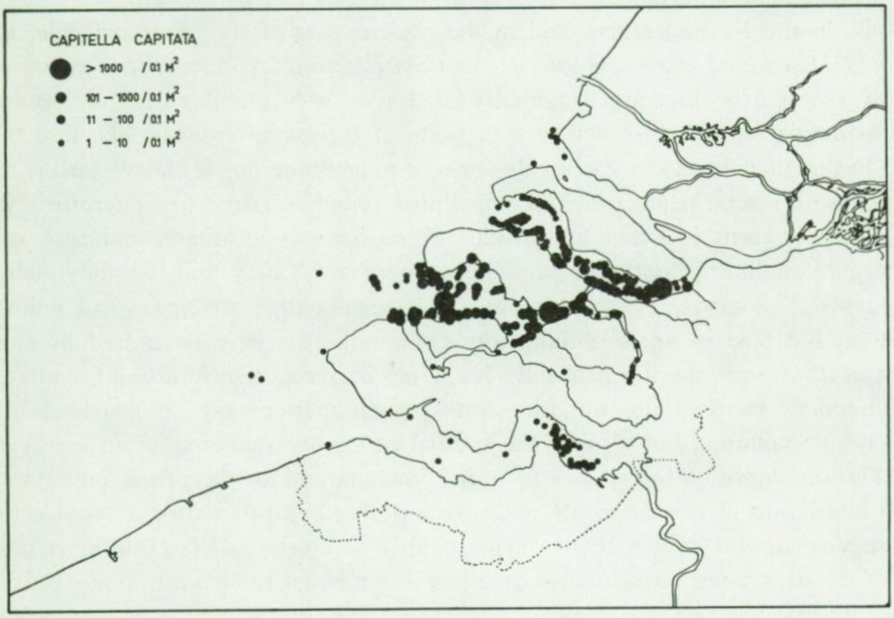

Fig. 35. Quantitative distribution of *Capitella capitata.* Only subtidal observations have been shown.

Judging from the β- and γ-values *C. capitata* prefers well-sorted fine and muddy sands. This is confirmed by Southward (1957), but Eliason (1962) mentions it also from muddy sediments. In the Delta area it may be quite abundant in the sandy beaches along the North Sea. Its vertical distribution ranges from the upper part of the intertidal zone down to a depth of 28 m.

C. capitata is frequently mentioned as an indicator of organic pollution (Filice, 1958; Reish, 1959a, 1960; Reish & Barnard, 1969; Wass, 1967; Henriksson, 1969). On the other hand, Muus (1967) was not able to find any correlation between the occurrence of *C. capitata* and pollution. However, nearly all localities investigated by him had salinities below $10^0/_{00}$ Cl′ and, hence, were probably not very suitable to study such a correlation for this species. Schulz (1969) who studied the species in the Baltic, also did not find any correlation with organic pollution. In the Delta area a correlation between the occurrence of this species and abundance of organic remains is also doubtful. The highest densities all occur in places were salinity is over $10^0/_{00}$ Cl′. It seems that the species is abundant where large amounts of organic material are deposited in areas of high salinity by the river discharge, viz. in the Krammer area and in the eastern part of the Westerschelde. It was also found that samples rich in *Capitella* contain innumerable remains of plants, for instance fragments of leaves, stems and rhizomes, seeds, sporangia of mosses, together with parts of terrestrial animals, like insects. On the other hand the species also proved to be numerous in the western part of the Oosterschelde, which is unpolluted (compare fig. 16). Therefore, it does not seem justified to consider *C. capitata* as a suitable indicator of organic pollution, not even at salinities over $10^0/_{00}$ Cl′ and in sandy sediments. The species is numerous indeed in areas with a strong organic pollution, but also in areas without any pollution. This may be caused by the fact that this species probably feeds on bacteria, which are, of course, abundant on decaying organic matter. Such matter may be provided by organic pollution but also by the normal processes occurring in an estuary. The resistence of the species to rather low amounts of oxygen is important when living in environments with decomposing organic matter. It is able to survive several days without oxygen and to complete its life cycle in values of about 3.5 mg oxygen/liter at 15-17°C or about 40% saturation (Reish & Barnard, 1960).

Heteromastus filiformis (Claparède, 1864). Earlier records: Korringa (1951).

Smidt (1951) describes a larva possibly belonging to this species. This larva was found in the plankton mainly in March-April and in October, with occasional specimens in August and December. Rasmussen (1956) describes spawning and development, but he is in doubt whether his animals really belong to *H. filiformis*. Spawning took place in April when the eggs are laid in globular capsules of jelly, anchored at the surface of the sediment. One such a egg-cocoon may contain several hundreds of eggs. The young trochophores hatch after two or three days and the pelagic stages may be found in the plankton in April and early May. Hamond (1966), however, ascribes the same type of egg-cocoon to *Eteone longa*. Giere (1968) records the larvae in spring from the River Elbe. It is assumed that the species has a pelagic larval stage. *H. filiformis* is a non-selective deposit-feeder.

The ecological distribution below LW-mark may be represented by:

$\alpha_1 = 0.13$ $\alpha_7 = 0.00$ $\beta_1 = 0.53$
$\alpha_2 = 0.12$ $\alpha_8 = 0.34$ $\beta_2 = 0.73$
$\alpha_3 = 0.10$ $\alpha_9 = 0.48$ $\beta_3 = 1.75$
$\alpha_4 = 0.11$ $\alpha_{10} = 0.23$ $\beta_4 = 0.91$
$\alpha_5 = 0.02$ $\alpha_{11} = 0.59$ $\gamma_1 = 0.71$
$\alpha_6 = 0.00$ $\alpha_{12} = 1.00$ $\gamma_2 = 1.00$

H. filiformis is able to withstand low salinities, as evidenced by the α-values and also by fig. 36. The limit of its occurrence is about the isohaline of $3^0/_{00}$ Cl′ at high tide during average river discharge, but it becomes rarer already beyond the isohaline of $10^0/_{00}$ Cl′ under similar conditions. Muus (1967) also states that in Danish waters the species is rare at salinities below $10^0/_{00}$ Cl′.

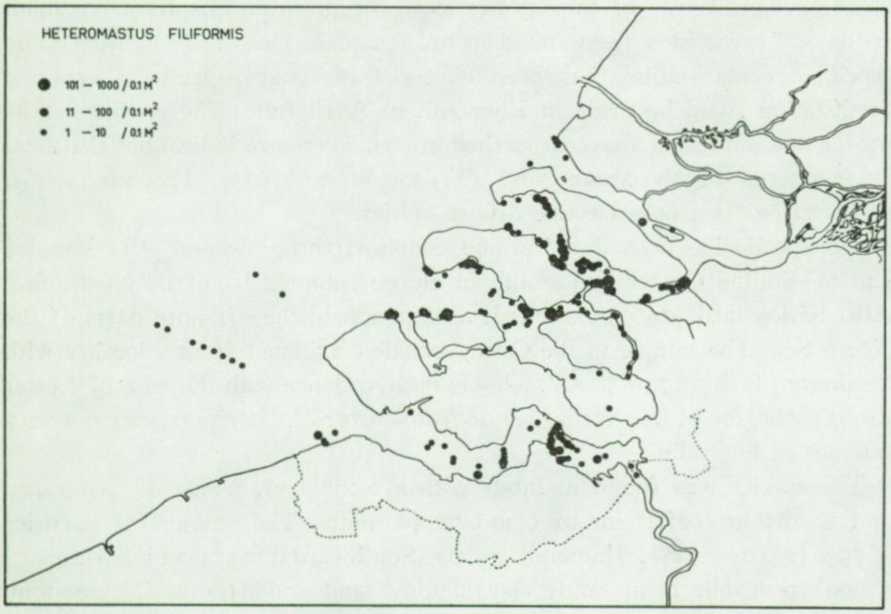

Fig. 36. Quantitative distribution of *Heteromastus filiformis*. Only subtidal observations have been shown.

From the α-values it appears that *H. filiformis* mainly inhabits the muddier types of sediment with a preference for the less well-sorted types. Nevertheless, it also occurs regularly in fine and median sands. A similar distribution was observed by Linke (1939), Smidt (1951), Korringa (1951), Filice (1958), Eliason (1962), Jepsen (1965) and Dörjes et al. (1969). Hence, *H. filiformis* constitutes more or less the ecological complement of *Capitella capitata* which lives primarily in sand.

The vertical distribution of *H. filiformis* ranges from high in the intertidal zone down to a depth of 48 m, being the maximal depth sampled.

H. filiformis has also been mentioned as an indicator of organic pollution (Wass, 1967). The impression arises, mainly from figs. 35 and 36, that *H. filiformis* is an indicator just as bad and just as good as *Capitella capitata*. Probably *H. filiformis* also is able to tolerate anaerobic conditions.

Notomastus latericeus M. Sars, 1851. This species has not been recorded from The Netherlands before.

The pelagic larvae of this species leave the plankton already after about 10 days. Larvae have been found in the Sound in December, February and April, whereas settling has been observed in August-October. Artificial fertilization could be made in Plymouth in April-June. The settling larvae prefer mud and sand above clean shell gravel. There are indications that mud is favoured slightly above sand (Wilson, 1932, 1937; Thorson, 1946). *N. latericeus* is a non-selective deposit-feeder.

The species has been found in one sample from the deepest place sampled (48 m) in the Oosterschelde and in eleven samples from the North Sea. Also Kirkegaard (1969) records it as common in the offshore parts of the North Sea. The sample in the Oosterschelde originated from a locality with a salinity of 16.5-17.0$^0/_{00}$ Cl′. This is in accordance with the data of Lyster (1965) who found that the larvae of *Notomastus* cf. *latericeus* were not very tolerant of low salinities.

The species was found in sands with a median grain-size of 0.92-2.45 φ and a sorting coefficient of 0.30-0.72 phi-units. The amount of particles $<75\,\mu$ is 0.01-0.32%. Hamond (1966), Southward (1957) and Kirkegaard (1969) record it from sandy clay, muddy sand, muddy gravel, fine stony gravel, and coralline gravel. Apparently, *N. latericeus* prefers the coarser types of sediment, sometimes with a certain amount of mud. Wilson (1937), however, stated that *N. latericeus* is generally confined to mud and very muddy sand and that it does not occur in clean coarse sand or gravel. Also Reineck et al. (1968) and Hartmann-Schröder (1971) state that *N. latericeus* prefers muddy bottoms.

The vertical distribution of *N. latericeus* is from 27 to 48 m depth.

Arenicola marina (Linné, 1758). Earlier records: Horst (1883-'84), Korringa (1951). In southern North Sea areas *A. marina* spawns in October-November (De Groot, 1907; Pirlot, 1933; Newell, 1948; Smidt, 1951).

In other areas, however, spawning also has been observed in April and August-September (Howie, 1959; Brenning, 1965). The eggs are spawned at the surface of the sediment and do not float. Nevertheless, they are transported by the currents and — by the same mechanism acting on small particles of sediment (Postma, 1961) — more landinward and to the higher parts of the shore. The suitability of this mechanism was demonstrated by the occurrence of lugworms all over the island of Walcheren (162 km^2), when this island was inundated from October 1944 to the end of 1945 (Bakker, 1950). The larvae hatch from these eggs after 4-5 days and penetrate into the sediment immediately. Here they live until their metamorphosis in the next spring (Newell, 1948). These post-larval stages are able to swim and have been observed in the plankton (Thorson, 1946; Newell, 1949), although not very frequently. In November-February the young worms, which then are in their second winter, migrate from the high shore level to lower intertidal areas, probably by swimming (own observation). Apparently, this is another mechanism for dispersal. Also the full-grown specimens are able to migrate by swimming (Werner, 1956). Thamdrup (1935) and Wells (1945) considered *A. marina* as a non-selective deposit-feeder, but Krüger (1959) postulated the occurrence of a filter-feeding mechanism also. Jacobson (1967), however, calculated that the latter mechanism is insufficient to cover the requirements of the worms. In a later paper Krüger (1971) demonstrated the filter-feeding mechanism experimentally, but admitted that its efficiency remains a matter of conjecture. For the time being, the lugworm has been considered as a non-selective deposit-feeder.

The major part of the observations on the lugworm in the Delta area originates from the intertidal zone. In this zone it reaches the isohaline of 10$^0/_{00}$ Cl′ at high tide during average river discharge in the Krammer area, whereas it nearly reaches that of 5$^0/_{00}$ Cl′ in the Westerschelde estuary. In both estuaries this more or less coincides with the isohaline of 0.3$^0/_{00}$ Cl′ at high tide during high river discharge. It may, however, be assumed that for *A. marina* the salinity conditions are buffered to some degree by its occurrence within the sediment. It has also been found in a non-tidal creek with a salinity of 11-13$^0/_{00}$ Cl′ and in the Veerse Meer in 9-11$^0/_{00}$ Cl′. *A. marina* lives in the Baltic in salinities of 5.1-9.0$^0/_{00}$ Cl′ (averaged 6.5$^0/_{00}$ Cl′) (Brenning, 1965) and 4.1-7.7$^0/_{00}$ Cl′ (averaged 5.4$^0/_{00}$ Cl′) (Kosler, 1969). Sveshnikov (1963) records 5.5$^0/_{00}$ Cl′ as the lower limit. Amoureux (1966) records the species from median grain-sizes of -0.20 to 3.65 φ with a strong preference for the finer sediments.

Longbottom (1970) has shown that the abundance of *A. marina* is correlated with the abundance of organic matter in the sediment. Since usually a linear correlation exists between the amount of organic matter and the median grain-size (log-scales; paragraph 3.3.5.), this means that normally the largest quantities of lugworms will be found in fine sediments. Longbottom (1970) records a median grain-size of 3.65 φ to be the limit, but at this value the biomass of the species is extremely low, because it has difficulties in maintaining its burrow.

In the Delta area *A. marina* occurs in fine and muddy sands with median grain-sizes varying between 2.30 and 3.30 φ, but the majority of the observations originates from the range 2.90-3.20 φ with sorting coefficients of 0.16-0.58 phi-units. Sediments in the latter range do occur below MLW-level, but in general they are rare. This seems the major reason for the scarce occurrence of *A. marina* in the subtidal zone. The species is very well capable to live permanently submerged, as it does in the Baltic (Brenning, 1965; Thorson, 1946), as well as in some non-tidal waters in the Delta area. Any relation between the occurrence of lugworms and the period of emersion (Callame, 1955) certainly does not exist, as evidenced by its occurrence in the Baltic and the Veerse Meer.

In the Delta area *A. marina* is most common in the intertidal zone, where it occurs from just below HW-mark down to the vicinity of the LW-mark. Occasional specimens have been found down to a depth of 18 m below MLW-level, but the lugworm is difficult to catch with a Van Veen grab. When SCUBA-diving, the characteristic cast may be observed regularly, though not abundant.

Owenia fusiformis Delle Chiaje, 1841. This species was not known before from the Delta area.

Ripe adult specimens occur near the British Isles from March to July. Main spawning takes place during a short period in June. The pelagic larvae remain in the plankton for at least four weeks (Wilson, 1932a). Smidt (1951), however, found the larvae already in May. *O. fusiformis* is a suspension-feeder as well as a selective deposit-feeder (Dales, 1957).

O. fusiformis has only been found in the North Sea and at the entrances of the estuaries. All observations were made in salinities over 16.0$^0/_{00}$ Cl′. It occurs in the Channel water as well as in the Continental coastal water.

The species has been found in medium and fine sands with median grain-sizes ranging from 1.45 to 2.90 φ and with sorting coefficients from 0.29-1.20 phi-units. The amount of particles $<75\ \mu$ ranges from 0.01 to 18.95%. Toulemont (1972) found the species in the range of about 0.50-3.25 φ.

Sediments in the range inhabited by *O. fusiformis* occur all over the Delta area, hence, the species is not restricted to the North Sea by a preference for a certain type of sediment. As salinity also does not seem to prevent its occurence in the Oosterschelde, it is supposed that temperature restricts the distribution of this species.

The vertical range of *O. fusiformis* is from 4 to 30 m.

Lagis koreni Malmgren, 1866. Earlier records: Korringa (1951); Eisma (1966).

The pelagic larvae have been found in the period May-August (Thorson, 1946; Smidt, 1951). *L. koreni* is a selective deposit-feeder, obtaining its food from a chamber dug out below the surface of the sediment (Watson, 1928; Wilcke, 1952). It takes Foraminifera, ciliates, copepods, algae, and faeces of echinoderms and molluscs. The large particles refused by the animal apparently form the mass of coarse material observed by König (1949).

The ecological distribution of *L. koreni* may be represented by:

$\alpha_1 = 0.82$
$\alpha_2 = 1.05$
$\alpha_3 = 0.03$
$\alpha_4 = 0.00$
$\alpha_5 = 0.00$
$\alpha_6 = 0.00$

$\alpha_7 = 0.00$
$\alpha_8 = 0.07$
$\alpha_9 = 0.15$
$\alpha_{10} = 0.43$
$\alpha_{11} = 0.10$
$\alpha_{12} = 0.01$

$\beta_1 = 0.21$
$\beta_2 = 0.81$
$\beta_3 = 1.56$
$\beta_4 = 2.14$
$\gamma_1 = 0.66$
$\gamma_2 = 1.00$

L. koreni does not occur beyond the isohaline of $15\,^0/_{00}$ Cl′ in the Krammer area as well as in the Westerschelde. In higher salinities it is fairly common in the estuaries, but it becomes abundant at the entrances to the estuaries and in the North Sea.

It appears from the β-values that *L. koreni* prefers the muddier types of sediment. Most probably, it requires especially stable sediments, in most cases identical with muddy ones. However, according to Hamond (1966) *L. koreni* avoids the muddiest type of sediment, and prefers clean and slightly muddy sand. On the other hand, Southward (1957), Schulz (1969) and Hartmann-Schröder (1971) record the species from fine and muddy sand, muddy sand mixed with shell gravel, and mud. Amoureux (1966) records it from the range 1.00-3.30 φ.

The calculated γ-values indicate a preference for the less well-sorted sediments. Perhaps this may be correlated with the nature of the grains needed for the construction of the tube, because juvenile stages take minute grains, and the size of the grains taken increases with the growth of the animal (Watson, 1928). It is also possible that this is the expression of a preference for sands with an admixture of mud.

The vertical distribution of *L. koreni* ranges from just above MLW-mark down to 48 m, being the greatest depth sampled.

Ampharete acutifrons (Grube, 1860). This species has not been recorded before from Dutch coastal waters.

The development of this species is non-pelagic. It seems that the eggs are shed in early spring (Thorson, 1946). *A. acutifrons* seems to be a selective deposit-feeder (Pearson, 1971).

A. acutifrons has been found in only six samples, originating from the eastern part of the Grevelingen, from the Eendracht—Krabbekreek area, and from the eastern part of the Oosterschelde. The salinity at these localities usually is over $15.0^0/_{00}$ Cl′.

The species lives on muddy sand bottoms, often paved with mussel shells (*Mytilus edulis*). The median grain-size was 2.96-3.31 φ with a sorting coefficient of 0.32-0.50 phi-units. Also Holme (1949) and Schulz (1969) recorded the species from muddy sand and various types of mud.

The vertical distribution ranges from LW-mark down to 5 m depth.

Neoamphitrite figulus (Dalyell, 1853). Earlier records: Horst (1898); Korringa (1951).

Korringa (1951) supposed that the species reproduces in early spring. Other details on its reproduction are not available, nor is it known whether it has a pelagic development. *N. figulus* is a selective deposit-feeder, taking diatoms and other small food particles (Dales, 1955). *N. figulus* is common, though not abundant, in the Delta area. It has been found until the isohaline of $12^0/_{00}$ Cl′ at high tide during average river discharge, but also at the most seaward part of the entrance to the Oosterschelde.

N. figulus is usually found in muddy sediments. The median grain-size of the samples containing *N. figulus* is 2.55-3.10 φ with a sorting coefficient of 0.29-1.10 phi-units. Also Schulz (1969) reports it from muddy sand and sandy mud. The vertical distribution ranges from the lower part of the intertidal zone down to a depth of 45 m.

Lanice conchilega (Pallas, 1766). Earlier records: Baster (1765); Korringa (1951).

L. conchilega reproduces in summer, and the pelagic larvae occur from April to October (Thorson, 1946; Smidt, 1951; Newell, 1954; Kessler, 1963; Giere, 1968). In Dutch waters the larvae were observed in May-June (Hofker, 1922; Korringa, 1951). The species is a selective deposit-feeder, also capable of some suspension-feeding (Ziegelmeier, 1952). The ecological distribution of *L. conchilega* below LW-mark may be represented by:

$\alpha_1 = 16.51$ $\alpha_7 = 0.00$ $\beta_1 = 0.03$
$\alpha_2 = 7.01$ $\alpha_8 = 0.22$ $\beta_2 = 0.10$
$\alpha_3 = 0.00$ $\alpha_9 = 2.78$ $\beta_3 = 0.13$
$\alpha_4 = 0.00$ $\alpha_{10} = 4.35$ $\beta_4 = 0.00$

$\alpha_5 = 0.00$ $\alpha_{11} = 1.11$ $\gamma_1 = 0.56$

$\alpha_6 = 0.00$ $\alpha_{12} = 0.10$ $\gamma_2 = 1.00$

L. conchilega is very abundant in the North Sea proper and in the estuaries it is also one of the common species. In the Westerschelde as well as in the Krammer area it reaches the isohaline of $14^0/_{00}$ Cl′ at high tide during average river discharge. De Vos (1936) reported it from the former Zuiderzee at a minimal salinity of $13.6^0/_{00}$ Cl′.

From the literature (Hartmann-Schröder, 1971) and from the β-values it appears that *L. conchilega* inhabits sandy sediments with a preference for medium and fine sands. It seems to prefer the less well-sorted types.

Its vertical distribution ranges from the lower part of the intertidal zone down to a depth of 48 m.

Nicolea zostericola (Oersted, 1844). This species has not been found before in Dutch coastal waters.

The development of *N. zostericola* is non-pelagic; reproduction takes place in March-June (Thorson, 1946; Hamond, 1966). It is a selective deposit-feeder (Hartmann-Schröder 1971). *N. zostericola* has been found in three samples from the eastern part of the Oosterschelde, taken before the severe winter 1962/'63. Since then, no other specimens have been found.

The salinity at these localities was over $16.5^0/_{00}$ Cl′ at that time. The bottom consisted of peat. The depth was 4½ to 13 m.

Manayunkia aestuarina (Bourne, 1883). This species has not been observed before in the Delta area.

Reproduction takes place in spring from March onwards (Schütz, 1965). *M. aestuarina* is a suspension-feeder, taking detritus, bacteria, flagellates, ciliates, cyanophytes, and especially diatoms (Schütz, op. cit.).

M. aestuarina occasionally has been found in the salt-marshes of the Delta area, but according to the observations of De Vos & Redeke (1941) and Schütz (1965), it probably is abundant there. The species was also found in the brackish Haringvliet, viz. once on a mudflat and once at a depth of 8 m on a bottom of stiff, subfossil clay. The salinity at the latter two localities varied between 0.3 and $10.0^0/_{00}$ Cl′. Indeed, *M. aestuarina* is considered a typical brackish water species (Schütz, op. cit.).

Nerilla antennata O. Schmidt, 1848. This archiannelid has not been recorded before from The Netherlands.

N. antennata does not have pelagic larvae. The food consists of small organisms like ciliates and diatoms (Remane, 1932). Of this species only two finds have been made in the beaches along the North Sea. The salinity at these localities was over $16.5^0/_{00}$ Cl′. The median grain-size was 1.95 and

1.99 φ with sorting coefficients of 0.25 and 0.36 phi-units and a percentage of particles <75 μ under 0.17%.

Trilobodrilus axi Westheide, 1967. This archiannelid has not been recorded earlier from The Netherlands.
Its period of reproduction seems to be between the end of May and July (Schmidt, 1969); its development apparently is non-pelagic. Its food consists possibly of benthic diatoms.

This species was found only once in a sandflat at the entrance to the Westerschelde at a salinity of 15.0-16.0‰ Cl′. The median grain-size was 1.52-1.78 φ. Until now, this species only has been recorded from the intertidal zone.

Protodriloides chaetifer (Remane, 1926). This species has not been reported before from The Netherlands.

P. chaetifer has a non-pelagic development (Swedmark, 1964). The reproduction occurs in early summer. Data on the food have not been found.

P. chaetifer has been found in beaches and sand-flats along the North Sea as well as in the central part of the Oosterschelde. All localities are along waters with salinities over 15.0‰ Cl′. The median grain-size of the sand inhabited by *P. chaetifer* ranges from 1.56 to 2.35 φ with sorting coefficients of 0.23-0.75 phi-units. The percentage of grains <75 μ never rose above 0.43%. Maximum numbers (>1000/0.03 m^2) were found in sands with median grain-sizes of 2.12 and 2.13 φ. All other samples contained only small (<10) numbers. This is confirmed by an interesting experiment by Boaden (1962) who found that *P. chaetifer* colonized sands with grain diameters between the limits of -0.50 and 2.70 φ, but that the animals had a preference for a median grain-size of 2.45 φ over one of 1.50 φ.

P. chaetifer only has been found in the middle and lower parts of the intertidal zone.

Protodriloides symbioticus (Giard, 1904). This species has not been recorded before from The Netherlands.

P. symbioticus has a non-pelagic development (Swedmark, 1964). Reproduction occurs in spring, because Schmidt (1969) found juveniles from June onwards. The food of *P. symbioticus* probably consists of diatoms.

In the Delta area *P. symbioticus* has been found in a large number of localities scattered along the beaches of the North Sea as well as over the marine parts of the estuaries. It has not been found beyond the isohaline of 15‰ Cl′ at high tide during average river discharge. Although Gray (1966) was able to show that *P. symbioticus* tolerates salinities of about 10‰ Cl′ during 12 hours, the species apparently is not able to live permanently in such situations.

Specimens of *P. symbioticus* have been found in sands with median grain-sizes ranging from 1.65 to 2.95 φ and sorting coefficients of 0.20-0.54 phi-units. The amount of particles $<75\ \mu$ maximally was 2.69%, but usually was below 1%.

Very large numbers of specimens (500-3000/0.03 m^2) occurred in sands with median grain-sizes of 1.95-2.35 φ. This is in agreement with Gray (1966a) who found experimentally that *P. symbioticus* prefers sands with median grain-sizes of 1.75-2.33 φ. *P. symbioticus* is certainly not a typical wadden species as was stated by Schmidt (1969). The distribution found by that author seems to be due to the nature of the sediments and not to the amount of exposure to waves.

P. symbioticus only was found in the intertidal zone, but at high as well as at low levels. The only difference with *P. chaetifer* seems to be the nature of the sediments inhabited, as the impression arose that *P. chaetifer* on the average lives in coarser sediments than does *P. symbioticus*. However, there exists apparently a very large overlap.

Glossiphonia complanata (Linné, 1758), *Glossiphonia heteroclita* (Linné, 1761), *Haemopis sanguisuga* Linné, 1758, *Erpobdella octoculata* (Linné, 1758), *Erpobdella monostriata* (Gedroyć, 1913), *Trocheta bykowskii* Gedroyć, 1913. The leeches of the Delta area will be treated in a future paper by Dr. C. den Hartog. Their ecology will not be discussed here, but data on these species have been incorporated in the chapters 6 and 7.

5.5 CRUSTACEA

Pandalus montagui Leach, 1814, *Pandalina brevirostris* (Rathke, 1837), *Processa parva* Holthuis, 1951, *Pontophilus trispinosus* Hailstone, 1835, *Crangon crangon* (Linné, 1758), *Crangon allmanni* Kinahan, 1857, *Diogenes pugilator* (Roux, 1828), *Pagurus bernhardus* (Linné, 1758), *Macropipus holsatus* (Fabricius, 1798), *Carcinus maenas* (Linné, 1758), *Portumnus latipes* (Pennant, 1777), *Thia scutellata* (Fabricius, 1793), *Rhithropanopeus harrisii* (Gould, 1841), *Eriocheir sinensis* H. Milne Edwards, 1854, *Ebalia tumefacta* (Montagu, 1808).

The ecology and distribution in the Delta area of these soft-bottom species have been discussed in papers by Heerebout (1973) and Wolff & Sandee (1971).

Gastrosaccus spinifer (Goës, 1864), *Neomysis integer* (Leach, 1814). Mysids are more or less pelagic animals and as such they are investigated by my colleague Mrs. C. H. Borghouts. Several species have been found a few times in grab samples, but only the two mentioned were so numerous that they may be considered to have more intimate relationships with the sediment. Mrs. Borghouts therefore made some data available to report briefly on their distribution.

G. spinifer occurs in the offshore parts of the North Sea as well as in the lower reaches of the estuaries. In bottom-samples it has been found upstream to about the isohaline of 10$^0/_{00}$ Cl′ at high tide during average river discharge. *G. spinifer* is a typical inhabitant of sandy sediments and it has been found mainly on well-sorted medium and fine sands. It was observed from the lower part of the intertidal zone down to a depth of 36 m.

The ecological distribution below LW-mark of *N. integer,* as far as appears from grab samples, may be represented as:

$\alpha_1 = 0.00$ $\alpha_7 = 0.00$ $\beta_1 = 0.13$
$\alpha_2 = 0.00$ $\alpha_8 = 0.21$ $\beta_2 = 0.15$
$\alpha_3 = 0.59$ $\alpha_9 = 0.04$ $\beta_3 = 0.20$
$\alpha_4 = 0.36$ $\alpha_{10} = 0.00$ $\beta_4 = 0.00$
$\alpha_5 = 1.36$ $\alpha_{11} = 0.16$ $\gamma_1 = 0.72$
$\alpha_5 = 0.19$ $\alpha_{12} = 1.00$ $\gamma_2 = 1.00$

N. integer is a typical brackish-water species (Kinne, 1955; Kühl, 1964). Roughly, the species has been found between the isohalines of 0.3 and 10$^0/_{00}$ Cl′ with occasional specimens up to 15$^0/_{00}$ Cl′. It has been found on bottoms of medium, fine, and muddy sand, without showing any evident preference. It has not been found on muddy bottoms, however. It shows a slight preference for the less well-sorted types of sediment. Its vertical distribution ranges from about mid-tide level in the intertidal zone down to a depth of 25 m.

Cumopsis goodsirii (Van Beneden, 1851), *Bodotria scorpioides* (Montagu, 1804), *Iphinoe trispinosa* (Goodsir, 1843), *Lamprops faseiata* G. O. Sars, 1863, *Pseudocuma longicornis* (Sp. Bate, 1858), *Pseudocuma similis* G. O. Sars, 1900, *Diastylis bradyi* Norman, 1879, *Diastylis rathkei* Krøyer, 1841.

The cumaceans of the Delta area are the subject of a paper by Vader & Wolff (1973).

Tanaissus lilljeborgi (Stebbing, 1891). This small species has not been recorded before from the Delta area.

Holthuis (1956) records egg-bearing females in June, but further data on its reproduction, or on its food have not been found.

T. lilljeborgi only has been found in a number of samples taken for the study of the interstitial fauna. It occurs all over the Oosterschelde; the minimal salinity endured by this species was $16.5^{0}/_{00}$ Cl′. The sediments inhabited were sands with a median grain-size of 1.87-2.60 φ. It was only found in subtidal samples.

Paragnathia formica (Hesse, 1864). Earlier records: Holthuis (1956).

The first larval stages of this species occur in spring and early summer. In the course of summer and autumn two other larval stages are passed until metamorphosis towards the adult stage takes place in spring or summer of the next year (Stoll, 1962; Amanieu, 1963). The larvae are blood-sucking ectoparasites on various species of fishes, but free-swimming larvae may also be observed. After having collected a sufficient amount of blood they return to their original habitat and live, like the adults, in burrows in the hard clay along the creeks in salt-marshes. It is not known whether the adults take any food.

Animals in burrows have been encountered in salt-marshes along the Zandkreek, the Eendracht and the Krammer. Free-swimming larvae have been observed in various localities along the Oosterschelde. All localities normally have flood-water with a salinity over $10^{0}/_{00}$ Cl′. Those along the Zandkreek even have a salinity over $16.5^{0}/_{00}$ Cl′.

All specimens in burrows were found in fairly hard clay bottoms, at a level not far below MHW-mark.

Cyathura carinata (Krøyer, 1848). Earlier records: Holthuis (1956); Den Hartog (1961).

The reproduction takes place in April-July (Gruner, 1965; Amanieu, 1969); the juveniles leave the marsupium of the mother animal without a pelagic stage. The species of *Cyathura* are omnivorous; they take especially diatoms and detritus (Burbanck, 1967).

C. carinata is a typical brackish-water species. In the Delta area it has been found in salinities of $3\text{-}15^{0}/_{00}$ Cl′ at high tide during average river discharge, but with maximum numbers in salinities of $3\text{-}10^{0}/_{00}$ Cl′. According to Gruner (op. cit.) it lives at a minimal salinity of $5^{0}/_{00}$ Cl′ in the Baltic, whereas experimentally a salinity range of $4.5\text{-}19.5^{0}/_{00}$ Cl′ could be observed. In the former Zuiderzee, however, it became abundant after the closure in the period the salinity of the water was between 0.5 and $2.0^{0}/_{00}$ Cl′. It does not seem impossible, however, that the muddy sediments inhabited by *Cyathura* retained a higher salinity for some time. Salvat (1962, 1967) records the species from a salinity over $17^{0}/_{00}$ Cl′ and of $14.8\text{-}17.4^{0}/_{00}$ Cl′.

C. carinata occurs especially in muddy sediments. The median grain-size of samples containing *Cyathura* was minimally 2.98-3.31 φ, but often much higher.

A high oxygen requirement as found by Burbanck (1962) for the closely related species *C. polita*, might well explain the absence of *C. carinata* from the brackish inland waters of the Delta area, and its scarcity in the strongly polluted brackish part of the Westerschelde.

Its vertical distribution ranges from about mid-tide level down to a depth of 12 m.

Eurydice pulchra Leach, 1815. Earlier records: Holthuis (1956); Wolff (1966).

E. pulchra is a predator and scavenger, taking living, dead and injured animals. It alternates free-swimming and burrowing periods. In the Bassin d'Arcachon a spring generation develops in the marsupium of the females from March to July, and is liberated in June-July. The females of this generation produce juveniles again in August-September, but some do not reproduce before the next spring (Salvat, 1966).

E. pulchra occurs all over the marine parts of the estuaries of the Delta area and also in the beaches along the North Sea. The species penetrates to about the isohaline of $10^0/_{00}$ Cl′ at high tide during average river discharge. Its landward limit is subject to shifting due to the varying amount of river discharge.

It has been found in medium and fine sands with a median grain-size of 1.46-2.90 φ. The majority of the animals, however, were found in a median grain-size of 2.00-2.25 φ. The sorting coefficient varied from 0.26 to over 1.00 phi-units. The vertical distribution of *E. pulchra* ranges from just below MHW-level down to a depth of 15 m. It shows, however, a distinct preference for the intertidal zone, and possibly also for a certain intertidal level. This could be caused by a reliance upon wave-action to wash the animals out of the sand for the start of their active feeding phase (Jones, 1970), but Fish & Fish (1972) demonstrated a semi-lunar rhythm in their swimming behaviour resulting in the same type of distribution on sheltered beaches nearly without wave-action.

Eurydice affinis Hansen, 1905. Earlier records: Wolff (1966).

E. affinis is a predator and scavenger, taking living, dead and injured animals. Incubating females occurred in the Bassin d'Arcachon from the end of April onwards. The first juveniles are liberated at the end of June and it is possible that this population is able to reproduce again in the same season (Salvat, 1966).

E. affinis has been found only along the Oosterschelde and its branches and in the beaches along the North Sea. It has not been found in salinities below $15^0/_{00}$ Cl′. The median grain-size of the sediments inhabited by *E. affinis* is 1.56-2.33 φ, but the majority of the observations lies between

2.00 and 2.25 φ. Jones (1970), however, observed that *E. affinis* prefers finer sands than does *E. pulchra.*

The species has only been found in the intertidal zone, perhaps with a preference for the upper part, contrary to *E. pulchra,* which species has its maximum at about mid-tide level. This was also stated by Salvat (op. cit.), but contested by Jones & Naylor (1967). Indeed the differences in vertical distribution often are very slight, but this may be caused by the climatic conditions, because according to Salvat (op. cit., 1967) the differences are caused by different tolerances to high temperatures.

Sphaeroma rugicauda Leach, 1814. Earlier records: Holthuis (1956); Den Hartog (1961).

The young animals are released from the marsupium of the females in August. Females carrying eggs and embryos are observed in May-July (Harvey, 1969). The very closely related *S. hookeri* is omnivorous, but takes chiefly benthic diatoms and filamentous algae (Gruner, 1965). Probably the food of *S. rugicauda* is very similar.

S. rugicauda has an extensive distribution over the Delta area. It is very abundant in the salt-marshes and reed-beds of the Haringvliet area between the isohalines of about $3^0/_{00}$ and $10^0/_{00}$ Cl′ at high tide during average river discharge. On the other hand it lives also in salt-marshes all along the Oosterschelde under marine conditions. For instance, it was abundant in a salt-marsh without any influence of fresh water, situated at the confluence of Oosterschelde and Veerse Gat, where the salinity of the flood water was nearly always over $16.5^0/_{00}$ Cl′. Also along the Westerschelde the species occurs in the salt-marshes all along the estuary from a salinity of about $16^0/_{00}$ Cl′ down to about $3^0/_{00}$ Cl′ at high tide during average river discharge. It is certainly not a typical brackish water species, but rather a very euryhaline one, finding optimal conditions of substrate or nourishment in the brackish part of estuaries. Jansen (1970) found experimentally that the species was better adapted to both survival and reproduction in a higher range of salinities ($9\text{-}18^0/_{00}$ Cl′) than it encountered in the southern part of the Baltic, where it often was abundant. Harris (1972) found experimentally a range of survival from 0.4 to $36.4^0/_{00}$ Cl′.

S. rugicauda occurs nearly always just around MHW-level, sometimes descending to slightly lower levels. It occurs underneath stones, between the vegetation of salt-marshes and nearly always in situations with a certain amount of mud deposition.

Trichoniscoides albidus (Budde-Lund, 1880), *Metatrichoniscoides leydigii* (Weber, 1881), *Haplophthalmus mengei* (Zaddach, 1844). Earlier records: Holthuis (1956); Heyligers (1965).

No information on the reproduction and the food of these species is available. They have been found a few times in the osier-beds of the freshwater tidal area, where they lived buried in a fairly well aerated clayey soil (Heyligers, 1965).

All finds were made at or just above MHW-level.

Armadillidium album Dollfus, 1887. Earlier records: Holthuis (1956); Vader (1965a).

Information on the food or the reproduction of this species has not been found. *A. album* lives on the sandy beaches along the North Sea above MHW-level. It is mostly found under driftwood high on the beach (Vader, 1965a).

Gammarus crinicornis Stock, 1966, *G. locusta* (Linné, 1758), *G. salinus* (Spooner, 1947), *G. zaddachi* Sexton, 1912, *G. pulex* (Linné, 1758), *Cheirocratus sundevalli* (Rathke, 1843). Den Hartog (1964) reported on the occurrence and ecology of these species in the Delta area, whereas Vader (1966) made a few comments on *G. crinicornis* (sub nom. *G. plumicornis*).

Nototropis swammerdami (Milne-Edwards, 1830). Earlier records: Vader (1966).

This species with a partly pelagic mode of life was reported especially from the entrances of the estuaries in salinities over $15^0/_{00}$ Cl′. It has a very similar distribution in the Elbe estuary (Movaghar, 1964). Vader (1966) considers it as a characteristic inhabitant of subtidal sand-bottoms.

Talitrus saltator (Montagu, 1808), *Talorchestia deshayesii* (Audouin, 1826), *T. brito* (Stebbing, 1891), *Orchestia gammarellus* (Pallas, 1766), *O. cavimana* (Heller, 1865), *O. mediterranea* (A. Costa, 1857). Den Hartog (1963a) reported on the distribution and ecology of these species in the Delta area, whereas Vader (1968) discussed the occurrence of *T. brito*.

Urothoe grimaldii poseidonis Reibisch, 1905, *U. brevicornis* Sp. Bate, 1862, *Bathyporeia guillamsoniana* (Sp. Bate, 1862), *B. pelagica* (Sp. Bate, 1856), *B. elegans* Watkin, 1938, *B. pilosa* Lindstrom, 1855, *B. sarsi* Watkin, 1938, *Haustorius arenarius* (Slabber, 1769). The distribution and ecology of these species were described by Vader (1965, 1966, 1969). Salvat (1967) studied the reproduction of several of the above-named species.

The species of *Urothoe* and *Bathyporeia* may be considered as selective deposit-feeders. They feed by cleaning sandgrains from adhering microorganisms and detritus (Nicolaisen & Kanneworff, 1969). *H. arenarius* is a suspension-feeder, taking its food from the interstitial water (Dennell, 1933).

Pontocrates altamarinus (Bate & Westwood, 1862) sensu Schellenberg, *P. arenarius* (Sp. Bate, 1858) sensu Schellenberg.

Vader (1966) reported on the occurrence and ecology of these species in the Delta area. Data on the reproduction or the food of these species have not been found.

P. altamarinus lives in coastal waters and at the entrances to the estuaries; it does not penetrate beyond the isohaline of $16.5^0/_{00}$ Cl′ at high tide during average river discharge. *P. arenarius* only occurs in the coastal water and in the beaches along the North Sea; it does not penetrate into the estuaries (Vader, op. cit.).

P. altamarinus occurs in fine sand, *P. arenarius* seems to prefer medium sand (Vader, op. cit.). The former species occurs nearly exclusively subtidally, the latter also intertidally.

Leptocheirus pilosus Zaddach, 1844. Earlier records: Den Hartog (1963c).

It is a selective deposit-feeder reproducing in summer (Goodhart, 1939; Schütz, 1969).

L. pilosus has been found only at two localities along the Haringvliet, where salinity at high tide during average river discharge amounted to about $3^0/_{00}$ Cl′. Depending on the amount of river discharge the salinity may vary between about 0.3 and $10^0/_{00}$ Cl′. The animals lived on muddy sediments in the intertidal zone, although Schütz (op. cit.) considers it as a species inhabiting mainly plants and hydroids.

Microprotopus maculatus Norman, 1867. Earlier records: Vader (1966).

It is a scarce inhabitant of sandy bottoms in the marine parts of the estuaries, where salinity is over $16.5^0/_{00}$ Cl′ (Vader, 1966).

Corophium acherusicum Costa, 1857, *C. arenarium* Crawford, 1937, *C. insidiosum* Crawford, 1937, *C. multisetosum* Stock, 1952, *C. volutator* (Pallas, 1766). The taxonomically difficult genus *Corophium* has only been investigated superficially. Only the specimens from grab-samples have been identified; the remaining data derive from some incidental identifications of specimens from intertidal localities, and from a survey of the literature.

All species have non-pelagic larvae; they are selective deposit-feeders.

The brackish-water species *C. multisetosum* is only known from a single find in the nearly fresh part of the Spui at a depth of 2.70 m (Stock, 1952).

The brackish water species *C. insidiosum* was found abundantly in some inland brackish waters with salinities between 8 and $15^0/_{00}$ Cl′, but remarkably enough, also in two grab-samples from the Oosterschelde at salinities of 16-$17^0/_{00}$ Cl′. The specimens obtained originated from fine and muddy sands.

C. acherusicum proved to be the principal species in the marine parts of the estuaries; it was regularly observed in grab-samples from the Oosterschelde and the western part of the Grevelingen—Krammer estuary, thus in salinities not below $15^0/_{00}$ Cl′ at high tide during average river discharge.

One find originated from about 35 km offshore in the North Sea. This distribution is in agreement with the observations of Crawford (1937), who considered this species as characteristic of waters of high salinity.

The species was found on medium, fine and muddy sand with a preference for the latter two categories. Some specimens originated from peat and subfossil clay-layers.

C. volutator occurred in some grab-samples from the marine Oosterschelde (16-17$^{0}/_{00}$ Cl′), but was much more numerous in the brackish Krammer—Volkerak area, the Eendracht and the Haringvliet. A single specimen even was found in the Hollands Diep, where usually very low salinities prevail. This is in good agreement with the salinity preferences of this species, which tolerates a minimal salinity of about 1.2$^{0}/_{00}$ Cl′ and a maximal value of 30$^{0}/_{00}$ Cl′, but prefers salinities from 3 to 12$^{0}/_{00}$ Cl′ (McLusky, 1967, 1968, 1970). Nearly all specimens originated from mud and muddy sand.

C. arenarium was found a few times among *C. volutator*, but it did not occur at the riverward side of the isohaline of 10$^{0}/_{00}$ Cl′ at high tide during average river discharge. The specimens obtained lived in fine and muddy sand.

From the North Sea to the freshwater the following series of soft-bottom corophiids probably occurs: *C. acherusicum-C. arenarium-C. volutator* together with *C. insidiosum-C. multisetosum*.

It seems that in the intertidal zone of the Delta area *C. volutator* and *C. arenarium* are the most important species.

Phtisica marina Slabber, 1769. Earlier records: Vader (1966).

It is a partly pelagic species, living over sandy bottoms in the marine parts of the estuaries in salinities over 16.5$^{0}/_{00}$ Cl′ (Vader, 1966).

5.6. ECHINODERMATA AND CHORDATA

Astropecten irregularis (Pennant, 1777), *Asterias rubens* (Linné, 1758), *Ophiura texturata* Lamarck, 1816, *O. albida* Forbes, 1839, *O. affinis* Lütken, 1859, *Spatangus purpureus* (Müller, 1776), *Echinocardium cordatum* (Pennant, 1777), *Echinocyamus pusillus* (Müller, 1776). The distribution and ecology of these species were discussed in an earlier paper (Wolff, 1968a).

All these species have pelagic larvae. The asteroid and ophiuroid species are predators, taking chiefly molluscs. The echinoids are non-selective deposit-feeders.

The ecological distribution of *Echinocardium cordatum* has been calculated with the method described in section 2.4. It may be represented as:

$\alpha_1 = 1.41$ $\alpha_7 = 0.00$ $\beta_1 = 0.40$
$\alpha_2 = 0.20$ $\alpha_8 = 0.00$ $\beta_2 = 0.56$
$\alpha_3 = 0.03$ $\alpha_9 = 0.04$ $\beta_3 = 0.64$

$$\begin{array}{lll} \alpha_4 = 0.00 & \alpha_{10} = 0.12 & \beta_4 = 0.02 \\ \alpha_5 = 0.00 & \alpha_{11} = 0.00 & \gamma_1 = 1.43 \\ \alpha_6 = 0.00 & \alpha_{12} = 0.01 & \gamma_2 = 1.00 \end{array}$$

Apparently *E. cordatum* is not very selective with regard to the type of sediment; only muddy soils are avoided. It prefers well-sorted sands.

Branchiostoma lanceolatum (Pallas, 1778). Earlier records: Eisma & Wolff (1970).

It has pelagic larvae and is a suspension-feeder. It has been found offshore in the Channel water on bottoms of coarse and medium sand. The depth varied between 23 and 34 m (Eisma & Wolff, op. cit.).

6. THE ESTUARY AS A HABITAT

6. 1. Introduction

Among the brackish habitats the estuary occupies a special position. Rochford (1951), Dahl (1956), and Caspers (1967) stressed that the short-term fluctuations of the hydrographical factors caused by the tides form a very distinct character of estuaries as opposed to all other large brackish waters, and proposed to reserve the term "estuarine" for the former category of brackish waters. In this study, however, the term "estuarine" also includes the freshwater tidal area. The term "brackish" has been used in this study as a collective name for all water with a salinity between that of the coastal North Sea and of fresh water.

In the following sections biological boundaries of the estuarine environment of the Delta area will be sought in the first place. Than it is tried to find some general trends in the distribution of species over the estuarine environment in relation to environmental factors. On this basis a biological subdivision of the estuarine environment, such as the Venice system (Anonymous, 1959), will be considered for the estuaries of the Delta area. After this the fauna of these estuaries will be compared with those of other estuaries in Europe and other parts of the world. Finally, a common feature of the European estuaries, viz. a species minimum in the brackish parts, will be investigated in more detail.

6.2. Biological limits of the estuarine environment

Vertically, the biological limit of the estuarine environment is marked by the upper limit of the occurrence of species bound to estuarine or tidal conditions.

On the beaches near the entrance of the estuaries such species are *Talitrus saltator, Talorchestia deshayesii, Armadillidium album,* and perhaps some species of insects. On the salt-marshes along the marine parts of the estuaries this upper limit is marked by *Littorina littorea, L. saxatilis, Hydrobia ulvae, Assiminea grayana, Ovatella myosotis, Orchestia gammarellus* and beetles of the genus *Bledius.*

In the brackish reaches of the estuaries only *Assiminea* and *Orchestia* are left. In the freshwater tidal area the upper limit is indicated by *Potamopyrgus jenkinsi, Pseudamnicola confusa, Limnaea peregra, L. palustris, Perforatella rubiginosa,* and *Orchestia cavimana.*

Horizontally, the seaward limit of the estuarine area is not marked by the disappearance of estuarine species — they have already vanished earlier — but by the appearance of marine species. Near or at the point where the estuarine environment, as defined in paragraph 3.4.12. ends, quite a number of marine species makes its appearance. Such species are *Corymorpha nutans, Polinices polianus, Spisula elliptica, Nereis fucata, Glycera capitata, Aonides paucibranchiata, Processa parva, Crangon allmanni, Pontophilus trispinosus, Ophiura affinis,* and *Echinocyamus pusillus.* The abiotic limit of the estuarine environment thus is accompanied by a clear faunal break, which may be called the biological limit of the estuarine environment. It has to be noted that nearly all the above named species probably are limited by temperature conditions. Further it has to be stressed that this faunal break is so evident, because the change in the abiotic environment is rapid at this place (compare section 6.4).

Den Hartog (1961, 1968, 1971) paid ample attention to the riverward limit of the estuarine environment, and arrived at the conclusion that this limit is not accompanied by any biological change. The fluviatile fauna more or less merges into the fauna of the freshwater tidal area and the major changes are of a quantitative nature. If a biological boundary has to be indicated, it may be set at about the place where regularly alternating tidal currents are no longer observed. According to Den Hartog (op. cit.) it may be characterized for hard-bottom species by the replacement of the fluviatile *Ancylus fluviatilis* by *Acroloxus lacustris,* and of the fluviatile *Plumatella fungosa* by *Cordylophora caspia* and *Ephydatia fluviatilis,* as well as by several changes of a quantitative nature.

It is hardly possible to characterize this boundary by any change in the soft-bottom macrofauna. In the major channel of the river such a fauna is nearly absent, and in the shallow water along the banks only very few differences have been observed. Only *Gammarus zaddachi* has been observed to disappear near this boundary. The typically fluviatile species of *Pisidium* accompany the river Meuse into the tidal area until they reach the polluted water of the Rhine or the brackish water of the Haringvliet. They do not seem to be influenced by the change from fluviatile to tidal watermovements.

6.3. The influence of various environmental factors on the distribution of species

6.3.1. Salinity

Pora (1969) indicated the possible importance of the rhopic factor, i.e. the ratio between the various ions, in brackish water. In his opinion many distributional data can be explained by differences in the ionic composition of the water, even when the total salinity is comparable. This factor might have influenced the distribution of species in the Delta area, but it was far beyond the technical possibilities available to determine the ionic composition of the many thousands of water samples needed for a good hydrographical description of the estuaries of the Delta area. Therefore, only Cl′ readings have been used.

The species enumerated in chapter 5 show a number of distributional patterns. The following general types may be distinguished (compare Table 5):

1. offshore species, e.g. *Corymorpha nutans* (fig. 21);
2. offshore species penetrating into the entrances of the estuaries, e.g. *Anaitides groenlandica* (fig. 24) and *Ophelia borealis* (fig. 34);
3. species living offshore as well as in the estuaries in water with a salinity over about $15^{0}/_{00}$ Cl′, e.g. *Aricidea minuta* (fig. 30);
4. species living in a narrow zone along the shore as well as in the estuaries in water with a salinity over about $10^{0}/_{00}$ Cl′, e.g. *Cardium edule* (fig. 22), *Anaitides maculata* (fig. 25) and *Capitella capitata* (fig. 35), or species living mainly intertidally in water with a salinity over about $10^{0}/_{00}$ Cl′, e.g. *Arenicola marina*;
5. species living in a narrow zone along the shore as well as in the estuaries in water with a salinity over about $3^{0}/_{00}$ Cl′, e.g. *Macoma balthica* (fig. 23) and *Heteromastus filiformis* (fig. 36).
6. species with their main occurrence in the brackish parts of the estuaries, e.g. *Nereis diversicolor* (figs. 26, 27), *Boccardia ligerica* (fig. 31), and *Streblospio shrubsolii* (fig. 33);
7. species occurring in the tidal brackish and freshwater parts of the estuaries, e.g. *Pseudamnicola confusa* and *Gammarus zaddachi*;
8. species with their main occurrence in the freshwater tidal area, e.g. *Perforatella rubiginosa*;
9. freshwater species occurring in the rivers as well as in the freshwater tidal area, e.g. the species of *Pisidium, Sphaerium,* and *Unio*;
10. the migratory species, e.g. *Crangon crangon, Macropipus holsatus,* and *Eriocheir sinensis.*

Moreover, several intermediate or aberrant patterns occur. These ten

TABLE 5

Distribution of soft-bottom species over the salinity gradient from the North Sea to the rivers.

<table>
<tr><th>A
North Sea</th><th>B
Lower reaches of estuaries</th><th>C
Middle reaches of estuaries</th><th>D
Upper reaches of estuaries</th><th>E
Rivers</th></tr>
<tr><td>Very stable, high salinity
Exposed</td><td>Stable, high salinity
Sheltered</td><td>Unstable, medium salinity
Sheltered</td><td>Stable low salinity
Sheltered</td><td>Stable low salinity
Sheltered</td></tr>
<tr><td>Restricted to A (types 1, 2)
44 species</td><td>Restricted to B (type 4)
17 species</td><td rowspan="2">Restricted to C (type 6)
Boccardia ligerica
Rhithropanopeus harrisii
Cyathura carinata
Leptocheirus pilosus
Corophium multisetosum</td><td rowspan="2">Restricted to D (type 8)
Perforatella rubiginosa
Erpobdella monostriata
Haemopis sanguisuga
Glossiphonia heteroclita</td><td rowspan="2">Restricted to E (type 9)
4 species</td></tr>
<tr><td colspan="2">Restricted to A and B (types 2, 3, 4)
104 species</td></tr>
<tr><td colspan="3">Restricted to A, B and C (type 5)
(Talitrus saltator)
(Talorchestia deshayesii)
Macoma balthica
Mya arenaria
Eteone longa
Heteromastus filiformis
Crangon crangon
Carcinus maenas</td><td colspan="2">Restricted to D and E (type 9)
22 species</td></tr>
<tr><td></td><td colspan="2">Restricted to B and C (types 5, 6)
Nereis succinea
Polydora ligni
Pygospio elegans
(Orchestia gammarella)
Assiminea grayana
Limapontia depressa
Alderia modesta
Streblospio shrubsolii
Manayunkia aestuarina
Neomysis integer
Sphaeroma rugicauda
Gammarus salinus
Corophium volutator</td><td colspan="2"></td></tr>
<tr><td></td><td colspan="3">Restricted to B, C and D (type 6)
Nereis diversicolor</td><td></td></tr>
<tr><td colspan="2"></td><td colspan="2">Restricted to C and D (type 7)
Gammarus zaddachi
Pseudamnicola confusa</td><td></td></tr>
<tr><td colspan="2"></td><td colspan="3">Restricted to C, D and E (types 7, 8)
Potamopyrgus jenkinsi
Limnaea peregra
Trocheta bykowskii
(Orchestia cavimana)</td></tr>
<tr><td colspan="5">Migrating species (type 10)
Eriocheir sinensis</td></tr>
</table>

groups in general agree with the estuarine faunal components of Day (1964).

When Table 5 and the distribution data in chapter 5 are inspected, it appears that the number of species decreases when going from the North Sea in the direction of the brackish water and then rises again in the direction of the freshwater. In the North Sea and along the sandy North Sea beaches about 157 soft-bottom macrofauna species have been observed. In the Oosterschelde, with a high and stable salinity of over $16.5\,^{0}/_{00}$ Cl′, at least 144 soft-bottom macrofauna species occur. In the centre of the brackish area, the Haringvliet, however, only 34 such species have been observed. In the freshwater tidal area of the Biesbosch 34 species were found, but the oligochaetes and chironomids, nearly absent from the brackish Haringvliet but abundant in the fresh Biesbosch, have not been considered. The abundance of species along the rivers probably is similar to that in the Biesbosch area. It may be concluded that the brackish water curve of Remane (1934, 1958) is also valid for the estuaries of the Delta area.

In table 5 the salinity gradient from the North Sea to the fresh water of the rivers has been divided into five sections, viz. 1) the North Sea with a very stable high salinity and exposed beaches; 2) the lower reaches of the estuaries with a stable high salinity and sheltered shores (for instance the Oosterschelde); 3) the middle reaches of the estuaries with an unstable salinity of medium height and sheltered shores (for instance the Haringvliet); 4) the upper reaches of the estuaries with fresh water — thus a stable low salinity — and sheltered shores (for instance the Biesbosch); and 5) the rivers with a stable low salinity.

Only 17 out of 144 species occurring in the sheltered areas of high salinity, are restricted to such areas. Certainly, this is due to the shelter, and not to salinity, because most of these species are inhabitants of muddy substrates and salt-marshes.

Only five soft-bottom macrofauna species are restricted, at least in the Delta area, to waters of rather low and varying salinity, such as the Haringvliet. The total number of soft-bottom macrofaunal species inhabiting this type of waters amounts to 34. Most of these usually are designated as brackish water species. However, 23 of these species occur under normal circumstances also in the Oosterschelde with its stable high salinity. Of these, *Macoma balthica, Mya arenaria, Eteone longa, Nereis succinea, Polydora ligni, Heteromastus filiformis, Crangon crangon, Carcinus maenas* and *Corophium volutator* are normal and often abundant members of the fauna living in the tidal channels and flats of the Oosterschelde. *Nereis diversicolor, Pygospio elegans* and *Manayunkia aestuarina,* living intertidally as well as subtidally in the brackish area, occur, often abundantly, only in the intertidal zone along the Oosterschelde. *Assiminea grayana, Limapontia depressa, Alderia modesta, Sphaeroma rugicauda* and the three talitrid species occur exclusively in the intertidal zone, along the Haringvliet as well as along the Oosterschelde. *Streblospio shrubsolii, Gammarus salinus,* and *Neomysis integer* are abundant in the brackish part of the estuaries, but occasional specimens also may be found in the Oosterschelde at high salinities.

Four species common in freshwater biotopes, also occur in the brackish Haringvliet, viz. *Potamopyrgus jenkinsi, Limnaea peregra, Trocheta bykowskii* and *Orchestia cavimana,* whereas *Pseudamnicola confusa* and *Gammarus zaddachi* occur abundantly in fresh as well as in brackish tidal water. *Gammarus zaddachi* occurs also at much higher salinities than in the Haringvliet, viz. in the creek "Schelphoek" where salinity never falls below 11.0$^0/_{00}$ Cl′ and sometimes rises over 15.0$^0/_{00}$ Cl′. Hence, it may probably be considered as a very euryhaline species of marine origin. *Pseudamnicola confusa* is most common in the freshwater tidal area, so it probably cannot be considered as a brackish water species. *Eriocheir sinensis* is a katadromous animal. Of the five remaining species *Leptocheirus pilosus, Corophium multisetosum* and *Rhithropanopeus harrisii* have been found only very rarely, and consequently are left out of further consideration. Only *Cyathura carinata* and *Boccardia ligerica* seem to be restricted entirely to the brackish Haringvliet. However, *C. carinata* occurs also in the non-tidal Canal through Zuid-Beveland and there tolerates salinities varying between 11.0 and 15.0$^0/_{00}$ Cl′, which is much higher than in the Haringvliet. Salvat (1967) records this species even from 14.8-17.4$^0/_{00}$ Cl′. *Boccardia ligerica* is the only fairly common species occurring exclusively in brackish water of low salinity.

Hence, if "true", stenohaline brackish water species do exist, they are at least very rare. Remane (1969) also arrived at this conclusion. He considered as such only *Gammarus duebeni, Cordylophora caspia* and some rotifers of the genus *Notholca.* None of these can be classified as a soft-bottom organism. Also the physiological data are not in favour of the existence of brackish water species. Nearly all species designated as such proved to be very euryhaline and many of them even capable of living and reproducing in seawater and hypersaline water (Kinne, 1964; Jansen, 1970; T. Harris, 1970; R. R. Harris, 1972). Stenohaline brackish water species only have been observed in the Caspian Sea (Zenkevitch, 1963). Of the brackish water species of the Delta area not a single one has been shown experimentally only to be able to live in a limited range of brackish water. It is concluded, therefore, that all or nearly all of the so-called brackish water species of the estuaries of the Delta area are in fact very euryhaline marine or freshwater species restricted to brackish water by some factor other than salinity. Probably, in many cases this factor will prove to be competition.

For instance, *Nereis diversicolor,* as explained before, is an euryhaline species forced into extreme habitats by a stronger competitor, viz. *N. virens.* For *Macoma balthica* it could be shown already that it meets optimal conditions at high salinities and not in brackish water. Its frequent dominance in the latter type of water should be explained by its preference for areas of fine and muddy sand with an abundant supply of food. The same explanation probably does hold for *Mya arenaria.* Hence, the latter two species, generally considered as brackish water species, are typical instances of very euryhaline marine species, finding optimal substrate and nourishment conditions in the brackish parts of estuaries. Because these species do not show any sign of "brackish water submergence", they probably have no strong competitors forcing them into extreme habitats in the marine parts of the estuaries.

Nevertheless, it is possible to enumerate a series of species with predominance of their distribution in the brackish part of the estuaries, meaning here the Haringvliet and the eastern part of the Westerschelde. These species are listed in column C of Table 5. The prawn *Palaemon longirostris,* formerly common in the upper reaches of the Rhine-Meuse estuary (De Man, 1923; Redeke, 1932, 1937) probably may be added. The species nowadays is nearly absent, probably owing to water pollution.

To this list some species inhabiting hard bottoms, plants, and hydroids may be added, viz. *Cordylophora caspia, Garveia franciscana* (Vervoort, 1964), *Embletonia pallida* (Swennen, 1961) (Roginskaya (1970) suggests that the correct name for this nudibranch is *Tenellia adspersa* (Nordmann, 1845)), *Membranipora crustulenta, Victorella pavida* (Heerebout, 1969), *Balanus improvisus, Jaera albifrons ischiosetosa* (Prud'homme van Reine-De Jager, 1965) and *Gammarus duebeni* (Den Hartog, 1964). These 25 species appear to be characteristic of estuarine brackish water areas in The Netherlands, although the species themselves may be considered as euryhaline marine species.

In the Delta area a number of other species is restricted to stagnant brackish waters. These are *Laomedea loveni, Conopeum seurati, Hydrobia stagnorum* (= *H. ventrosa*), *Congeria cochleata, Cardium glaucum* (= *C. lamarckii*), *Mercierella enigmatica, Palaemonetes varians, Sphaeroma hookeri, Idotea chelipes* (= *I. viridis*) and *Corophium insidiosum* (Heerebout, 1970; Wolff, 1969b). *Alkmaria romijni, Heterotanais oerstedii* and *Coro-*

phium lacustre, found in The Netherlands (Redeke, 1937) but not yet in the Delta area, probably also belong to the latter group of species. This group of about 38 brackish water species occurring in The Netherlands and for a considerable part already mentioned by Redeke (1932), appears to be very similar to the group of genuine brackish water animals as distinguished by Segerstråle (1957) for the Baltic.

6.3.2. TEMPERATURE

In chapter 5 some influences of climate and especially temperature have been met with. Firstly, very cold winters are able to exterminate some species completely. This was observed for *Brachystomia scalaris, Lithoglyphus naticoides, Sthenelais boa*, and *Nephtys cirrosa* after the very severe winter of 1962/1963. For some of these species it took several years before they were found again in the Delta area. In general, southern species reaching the limit of their distribution near the area investigated, are most seriously affected by such cold winters. Other species also suffer from important losses, but these regain the area lost very soon.

In chapter 5 it has been shown that species occurring only in the offshore parts of the North Sea, for instance, *Corymorpha nutans, Polinices polianus, Spisula elliptica, Anaitides groenlandica, Nereis fucata, Glycera capitata, Aonides paucibranchiata, Poecilochaetus serpens, Owenia fusiformis, Pontophilus trispinosus, Astropecten irregularis, Ophiura albida*, and *Echinocyamus pusillus*, probably are restricted in their distribution by differences in temperature. In many cases it is difficult to ascertain whether such a species is susceptible to the high summer temperatures or to the low winter temperatures prevailing in the estuaries. For *Polinices polianus*, however, it was found that the species becomes inactive and dies above 20°C.

Several of these offshore species show the limit of their distribution in the narrow transitional zone between the area with an estuarine topography and that with a marine character. Others and especially the semi-pelagic species, such as *Portumnus latipes, Pontophilus trispinosus, Bathyporeia guillamsoniana, Pontocrates arenarius*, and *P. altamarinus* are able to penetrate a small distance into the entrances of estuaries. Probably they are only able to do this in periods when temperature conditions are favourable.

The conclusion is that the fauna of the Delta area and the adjacent part of the North Sea may be divided in a relatively stenotherm component, occurring only offshore, and a relatively eurytherm component occurring offshore as well as inshore. Estuarine faunas, therefore, are not only euryhaline, but also eurytherm. Moreover, many of the most euryhaline species, e.g. *Bathyporeia pilosa, Nereis diversicolor*, and *Manayunkia aestuarina*, occur in the intertidal zone, where only very eurytherm species may find suitable conditions.

6.3.3. DEPTH AND INTERTIDAL LEVELS

The only factor related definitely with depth is hydrostatic pressure. Many other factors also change in a way suggesting a relationship with depth, but such relationships only have local value. For instance, the general trend in the relationship sediment-depth is that the muddier sediments are found at greater depths. In the Delta area, however, the coarsest sediments occur at the greater depths. Therefore, many apparent relationships between depth and the vertical distribution of species, are better explained by an ecological factor other than depth. This was also possible in this study.

Mulicki (1957), studying the zoobenthos of the Baltic, arrived at a similar conclusion and stated that "depth and the high pressure connected with it, are not decisive in the distribution of benthos". It appeared also experimentally that relatively slight differences in pressure (0-10 atm.) had no noticeable effect on animals (Schlieper, 1963).

In the intertidal zone, however, very clear relationships exist between the vertical distribution of animals and either the length of the period of emersion (the complement of the period of immersion) or the frequency of immersion or emersion.

In most cases these parameters determine the upper limit of distribution of a species. The upper limit of *Cardium edule,* for instance, is determined by the average length of the period of immersion, which determines the quantity of food to be taken (Kristensen, 1957). These phenomena have been discussed extensively by Thamdrup (1935), Linke (1939), Smidt (1951), and Jepsen (1965).

The lower limit of distribution in the intertidal zone of many species has been related to mean low water, mean low water at spring tides, or mean low water at neap tides, which levels may be translated into period or frequency of emersion and immersion. However, during this study the greater part of these species was found frequently below these levels, and, therefore, it may be concluded that their lower limit in the intertidal zone is set by other factors that mean waterlevels. Possibilities are, for instance, the type of sediment, the vertical distribution of salinity, or the presence of predators or competitors.

Of the species living mainly or exclusively in the intertidal zone *Ovatella myosotis, Agriolimax reticulatus, Perforatella rubiginosa, Trichoniscoides albidus, Metatrichoniscoides leydigii, Haplophthalmus mengei, Armadillidium album, Talitrus saltator, Talorchestia deshayesii, T. brito, Orchestia* *gammarellus, O. cavimana* and *O. mediterranea* are ecologically essentially terrestrial organisms, with a preference for the supralittoral fringe (compare also Den Hartog (1968a)). Their lower limit is determined by the frequency or the duration of flooding or by the lower limit of organic material washed ashore.

Littorina saxatilis, Assiminea grayana, Pseudamnicola confusa, Limapontia depressa, Alderia modesta, Paragnathia formica and *Sphaeroma rugicauda* are ecologically aquatic species, bound to salt-marshes or similar habitats. Their lower level is governed by the presence of vegetation or by the amount of water movements.

The number of observations of *Antinoella sarsi* and *Psammodrilus balanoglossoides* is too low to draw any conclusions; moreover, the literature does not support a preference for intertidal habitats (Meunier, 1930; Swedmark, 1955).

Littorina littorea, Hydrobia ulvae, Pygospio elegans, and *Arenicola marina* seem to prefer areas with small water movements and little disturbance of the sediment, but not especially intertidal mudflats. Of course, intertidal flats have these characteristics, but these species may also occur subtidally in similar environments, as may be observed in the Baltic (Schulz, 1969; Kosler, 1969) as well as elsewhere in the Delta area.

The remaining species observed exclusively or mainly intertidally are *Ophelia rathkei, Protodriloides symbioticus, Eurydice affinis,* and *E. pulchra. O. rathkei* is a non-selective deposit-feeder and it is difficult to imagine what relation might exist between some water level and its lower distribution limit. Moreover, Tebble (1952) and Hartmann-Schröder (1971) record it from subtidal habitats.

Protodriloides symbioticus has symbiontic (?) green algae in its skin. Probably, this species is not able to live below a certain level on the shore, because the alga needs a certain amount of light. The species of *Eurydice* possibly are bound to beaches with wave-action because the animals would rely on the waves to wash them out of the sand (Jones, 1970), but Fish & Fish (1972) postulate a semi-lunar rhythm as mechanism.

Hence, of the soft-bottom fauna of the Delta area only three species, the terrestrial and salt-marsh species excluded, are strictly limited to the intertidal zone. Other species find very suitable living conditions in this zone, but these are not restricted to it.

These three species all have a direct development without a pelagic phase, which ensures that the juveniles remain in the very restricted habitat of the adults.

On the other hand it might be expected that all species with larvae remaining photopositive during their complete development (Thorson, 1946) are also typically littoral species. *Pygospio elegans* indeed has its optimum in the intertidal zone and, hence, this photopositive behaviour might be a good adaptation to such an environment. *Asterias rubens*, on the other hand, has its centre of abundance below LW-level.

6.3.4. SEDIMENTS

Wilson (1937, 1948), Hannerz (1956), Gray (1966, 1966a, 1971) and Gray & Johnson (1970) showed that the larvae of several benthic species are very discriminating in their choice of a substratum.

They have also shown that larvae and adults are able to test the grain-size of the sediment and the nature of populations of bacteria on the grains. Of course, this is very important for those species which have to make a choice once and for all of their life-time, viz. the completely sedentary species. The choice has far less importance for many predatory species firstly depending on the presence of their prey. Also species with a pelagic phase, such as many amphipods and mysids, do not need to be very discriminating in their choice of substrate.

Of course, these differences will be reflected in the distribution of the adults. There exist indeed typical sand-dwellers, like *Angulus tenuis, Scolelepis squamata,* and *Ophelia borealis,* but also characteristic inhabitants of muddy sediments, e.g. *Tharyx marioni, Polydora ligni,* and *Scrobicularia plana.* Several other species, however, are not restricted to a particular grade of sediment, but live in a fairly large range of sediments. Nevertheless, they always show a maximum of abundance in one or two grades of sediment. For instance, *Mytilus edulis* and *Lagis koreni* have been found on all grades of sediment, but they have an evident maximum in the muddier types. Similarly, *Heteromastus filiformis* shows a maximum abundance in muddy sand, *Scoloplos armiger* in fine sand. It has been tried to find some correlations between the sediment preference of a species and its mode of feeding (Table 6). In this Table the species preferring medium and coarse sands or mud are probably under-represented, because the number of samples containing such sediments was too low to calculate indices for most of the species living mainly in these sediments.

It seems that every mode of feeding occurs in all types of sediments, especially when it is realized that the differences between predators, scavengers and omnivores often are only slight and gradual. The very soft muds found by Rhoads & Young (1970) to be inhabited nearly exclusively by deposit-feeders, do not occur in the Delta area. Some very specialized types of feeding, such as suspension-feeding in the interstitial water by *Haustorius*

TABLE 6

Relationship between mode of feeding and preferred grade of sediment for 35 species for which β- and γ-indices have been calculated.

Type of sediment	medium sand		fine sand		muddy sand		mud	
Sorting (in phi-units)	$\leqslant 0.45$	> 0.45	$\leqslant 0.45$	> 0.45	$\leqslant 0.45$	> 0.45	$\leqslant 0.45$	> 0.45
Mode of feeding								
suspension-feeders	-	-	-	1	1	1	-	2
selective deposit-feeders	1	-	7	1	1	4	-	2
non-selective deposit-feeders	1	-	-	1	1	1	-	-
scavengers and predators	2	-	-	-	-	-	-	1
omnivores	-	-	-	3	1	1	-	1
unknown	-	-	1	-	-	-	-	-
total	4	0	8	6	4	7	0	6

arenarius and *Branchiostoma lanceolatum*, are possible only in the limited range of the sandier types of sediment.

Further, there seems to exist a relationship between the salinity preference of the species and their sediment preference. For five out of the about 34 species occurring in the brackish Haringvliet (Table 5) the sediment indices have been calculated (Table 7). All of these prefer mud or muddy sand.

TABLE 7

Sediment preferences of species occurring in the brackish Haringvliet. Shown are the values calculated for the indices β and γ; the maximum values have been underlined.

	β_1	β_2	β_3	β_4	γ_1	γ_2
Macoma balthica	0.07	0.23	$\underline{0.39}$	0.00	0.76	$\underline{1.00}$
Nereis diversicolor	0.24	0.31	$\underline{0.69}$	0.00	$\underline{1.12}$	1.00
Polydora ligni	0.01	0.02	0.05	$\underline{0.25}$	0.80	$\underline{1.00}$
Heteromastus filiformis	0.53	0.73	$\underline{1.75}$	0.91	0.71	$\underline{1.00}$
Neomysis integer	0.13	0.15	$\underline{0.20}$	0.00	0.72	$\underline{1.00}$

Also many of the other species occurring in brackish water have been shown to prefer muddy bottoms. Only *Boccardia ligerica, Pygospio elegans,* and *Crangon crangon* possibly do not favour muddy sediments, whereas *Nereis succinea, Gammarus salinus* and *G. zaddachi* inhabit a very large range of substrates. Nevertheless, the latter six species are capable of living in muddy sediment.

Apparently, it is a general trend that species inhabiting the brackish part of estuaries are also capable of living in muddy sediments or even prefer such sediments. For *Macoma balthica* it could be shown that for this reason it is wrongly considered as a typical brackish water species. It is believed that this is also the case for *Mya arenaria, Nephtys hombergii, Polydora ligni, Heteromastus filiformis,* and perhaps others.

6.3.5. SORTING OF SEDIMENTS

The sorting of a sediment is difficult to interprete in relation to the ecology of animal species. The degree of sorting influences the permeability of a sediment, and it is also a measure for the amount of very fine particles (sub-paragraph 3.3.4.1.). A high sorting coefficient usually means a sediment with a considerable amount of mud.

It appears that species preferring the sandier types of sediment, prefer also the well and very well sorted types of sediments (Table 6). Species preferring the muddier types of sediment, on the other hand, prefer also the less well-sorted types. Perhaps this may be interpreted in such a way that species of sandy sediments prefer sands without mud, — which hampers the watercirculation and thus the oxygenation within the sediment —, whereas species preferring muddy sediment are dependent in the first place on the mud fraction as a source of food.

6.3.6. EXPOSURE TO WAVE-ACTION

The degree of exposure to wave-action (fig. 18) firstly determines the nature of the sediment, and secondly it also may govern the distribution of animals directly.

Several species are confined to the sheltered parts of the shore, but in all cases this seems to be due either to the nature of the sediments or the presence of vegetation, because they are also absent from sandy sediments originating by tidal scour.

Talitrus saltator, Talorchestia deshayesii, T. brito and *Armadillidium album* are restricted to the semi-exposed beaches along the North Sea. However, it appears that these species are dependent on the nature of the sediment and on a certain amount of organic material washed ashore.

Thus, in the Delta area not a single soft-bottom species is directly dependent on a greater amount of wave-action. On the other hand it was found in paragraph 6.6.2. and also by Ledoyer (1969) that soft-bottom areas with strong wave-action are often poor in species.

6.3.7. TURBIDITY

Although it may be expected that turbidity, being a measure for the amount of suspended matter, will influence the distribution of benthic animals, there exists hardly any evidence for such an influence. The effects of turbidity possibly may be revealed by a comparison between the very turbid western part of the Westerschelde and the relatively clear Grevelingen area. The other conditions in these two areas are more or less similar.

It appears that a number of species occurring in the Grevelingen is absent, or at least rare in the Westerschelde, for instance, *Pagurus bernhardus, Spio martinensis,* and the sea-grasses *Zostera marina* var. *stenophylla* and *Z. noltii* (Beeftink, 1965). Because the influence of pollution is comparatively slight in the seaward part of the Westerschelde, it seems possible to ascribe the absence of these species to the high turbidity. Moreover, Howell & Shelton (1970) found that suspension-feeders did not occur in a large area affected by a suspension of China clay, whereas the deposit-feeders were positively affected. Only in a small area the deposition of clay apparently was too heavy to permit the occurrence of nearly any species. Rhoads & Young (1970) also found that turbidity affects suspension-feeders negatively.

6.3.8. POLLUTION

Wass (1967) enumerates several indicator species of organic pollution. Although many species are favoured by a tiny amount of pollution (Henriksson, 1969), only few species possibly may be considered as indicators of large-scale organic pollution in the Delta area. These are *Sphaerium corneum, Nereis succinea, Capitella capitata, Heteromastus filiformis* and unidentified oligochaetes. The other species mentioned by Wass (op. cit.) are brackish water species.

These species, which profit by increased amounts of bacteria, are indicative only of organic pollution. Inorganic pollution, as seen in the Nieuwe Waterweg, is indicated by absence or strong reduction of benthic species.

6.3.9. OXYGEN SATURATION

It seems probable that the water in the estuarine environment in NW-Europe normally is saturated with oxygen. Of course, there exists a day-night rhythm with low saturation values in the late night in shallow water, but in the main channels these fluctuations certainly will be much less.

In our century waste disposal into rivers and estuaries has lowered considerably their saturation values in many industrial areas. In the Delta area the waters of the Rhine and the Scheldt often show saturation values below 50% (paragraph 3.4.7.). These undersaturated waters are mixed in the estuaries with well-saturated marine waters and thus the saturation values gradually increase in a seaward direction. Nevertheless, low values may be encountered temporarily in the brackish parts of the estuaries.

Quite a number of estuarine species, e.g. *Nereis diversicolor, Arenicola* *marina, Capitella capitata, Heteromastus filiformis, Corophium lacustre, C. multisetosum,* and probably others are very tolerant to low oxygen values (Hecht, 1932; Reish & Barnard, 1960; Mulicki, 1957; Schütz, 1969) or even tolerate anaerobic conditions. Other species, for instance *Cyathura carinata* and *Leptocheirus pilosus,* seem to require high saturation values (Burbanck, 1962; Schütz, 1969) and this probably causes the absence of these and other species from the polluted eastern part of the Westerschelde.

6.3.10. FOOD

Large amounts of organic waste are carried by the rivers Rhine and Scheldt and emptied into their estuaries. This causes a permanent supply of organic detritus and bacteria, to which the freshwater plankton is added. In the rivers various species of oligochaetes depend on this source of food; in the estuaries these are replaced by *Heteromastus filiformis* and *Capitella capitata.* Because in The Netherlands large quantities or organic waste and bacteria are disposed of only in the fresh parts of the rivers and not in the estuaries themselves, the concentration of this type of food decreases in a seaward direction. Hence, marine species dependent on this source of food will be most abundant nearest to the source. This is exactly what has been found for *Heteromastus filiformis* and *Capitella capitata* which are abundant in the estuaries as soon as the salinity has risen high enough. Towards the North Sea their numbers gradually diminish (figs. 35 and 36).

This very pattern, — abundance in the estuaries and decrease towards the North Sea —, has been found for many species living in the estuaries of the Delta area, for instance *Mytilus edulis, Cardium edule, Macoma balthica, Mya arenaria,* and others. In many cases their distribution towards the North Sea will be limited by the quantity of food available, as was explained for *Mytilus* and *Cardium.*

6.4. BIOLOGICAL SUBDIVISION OF THE ESTUARIES OF THE DELTA AREA

It has been attempted many times to establish biological subdivisions of brackish waters and, more relevant to this study, of the estuarine environment. In 1958 these efforts resulted in the "Venice-system for the classification of brackish waters" (Anonymous, 1959). The subdivisions then proposed and the older Redeke-Välikangas-system are based on the distribution of species along the salinity gradient from sea to fresh water. Such a subdivision is based on the assumptions (1) that species are restricted to certain salinity intervals, and (2) that groups of species have their limits at about the same salinity. From the following lines, however, the conclusion may be drawn that especially the latter assumption does not hold.

Caspers (1955, 1958, 1959) and Den Hartog (1961, 1964a, 1968, 1971) have tried to fit these systems to the distribution of fauna and flora in the estuaries of the Elbe and of the Delta area, respectively. On the basis of the distribution of the flora and fauna the latter divides the area between the North Sea and the non-tidal rivers of the estuaries of the Delta area into no less than seven subareas.

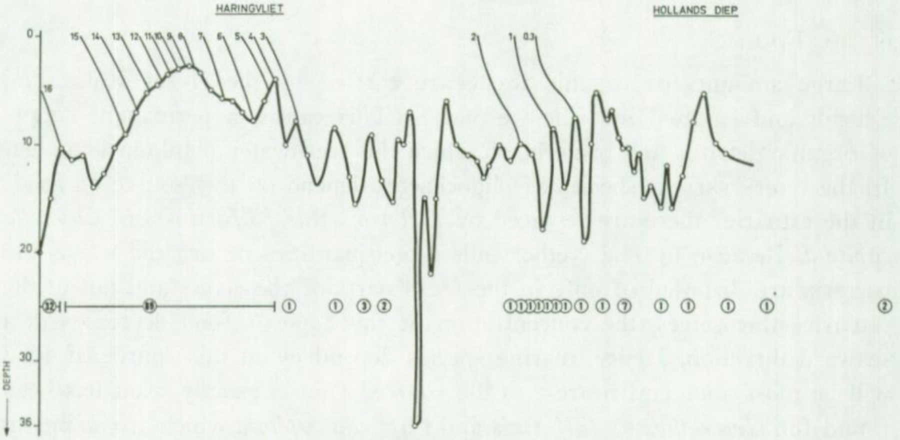

Fig. 37. Longitudinal section through the Haringvliet-Hollands Diep estuary with the position of the isohalines at low tide during an average river discharge. The solid line represents the depth of the bottom of the estuary. The figures at the base of the bottom line indicate the number of marine and brackish water species reaching their landward limit at that place.

Although it is agreed with Den Hartog that a subdivision is possible for the estuaries of the Delta area, it may be asked whether the cause of this phenomenon really is salinity. Den Hartog (1971) fixed the boundaries between the subareas at places with surface salinities of about 16.5, 10, 1.8, and 0.3$^0/_{00}$ Cl′. In the next lines this subdivision of Den Hartog will be compared with the results of this study.

In the Haringvliet-Hollands Diep estuary the following faunal breaks may be noticed. The border between the level sea bottom and the area with an estuarine topography forms the limit for a number of species occurring in the North Sea, but not in the estuaries. Den Hartog (1971) assumes that these species are restricted by their stenohalinity, but it is believed that stenothermy is the main cause (paragraph 6.3.2.). The border line between these areas lies in a zone with a fairly steep slope, and, hence, the transition also will be rapid (figs. 37, 38, 39).

The boundaries of Den Hartog between estuarine euhalinicum and polyhalinicum, and between polyhalinicum and mesohalinicum in the Haringvliet are found in a region characterized by an extremely unstable salinity, coinciding with the region where the semi-exposed character of the shore changes into a more sheltered one. The hydrographical instability is caused by a continuous bar with maximal depths of only 4 m across the mouth of the estuary. Because the penetration of salt water into an estuary is related to the third power of the depth of the main channel (Van der Burgh, 1968), such an area of very shallow water will cause a very steep horizontal salinity gradient and, hence, a clustering of isohalines (fig. 37). Due to this phenomenon species limited in their distribution by very different salinity values, have their limits clustered in the same region. Moreover, the instability of salinity in this area also may set a common limit to a large number of species. In fact, at least 90 soft-bottom macrofaunal species find their landward limit in the near vicinity of this bar.

The boundaries of Den Hartog between mesohalinicum and oligohalinicum and between oligohalinicum and the marginal zone of the freshwater tidal area both fall in an area with an extremely complicated hydrography (paragraph 3.4.5.; Peelen, 1970). It is very difficult to draw here any borderline based on the data of the soft-bottom macrofauna. The boundary between the marginal zone and the central part of the freshwater tidal area more or less coincides with the boundary between polluted Rhine water and cleaner Meuse water. The boundaries of the zones still further inland are difficult to assess, as was also pointed out by Den Hartog (op. cit.) himself.

In the Oosterschelde-Keeten-Krammer-Volkerak estuary (fig. 38) an evident faunal break occurs, just as in the Haringvliet, at the place where the level sea bottom changes into the estuarine channels; this is the boundary between marine and estuarine euhalinicum of Den Hartog (op. cit.). Further inland several species disappear one by one until the shallow area in the Krammer-Volkerak, where about 60 species have their landward limit. In this area, where Den Hartog (op. cit.) put his boundary between poly- and mesohalinicum as well as between meso- and oligohalinicum, again a dense cluster of isohalines, accompanied by an unstable hydrographical situation, is found. The borderline between the oligohalinicum and the marginal zone of the freshwater tidal area lies in the Hollands Diep and has already been treated.

The Westerschelde estuary (fig. 39) has a very broad shallow bar across its mouth, but inside the estuary large depths prevail over large distances. This causes a very slow and regular decline of salinity landinward. Upstream as far as investigated the marine species disappear one by one along this salinity gradient.

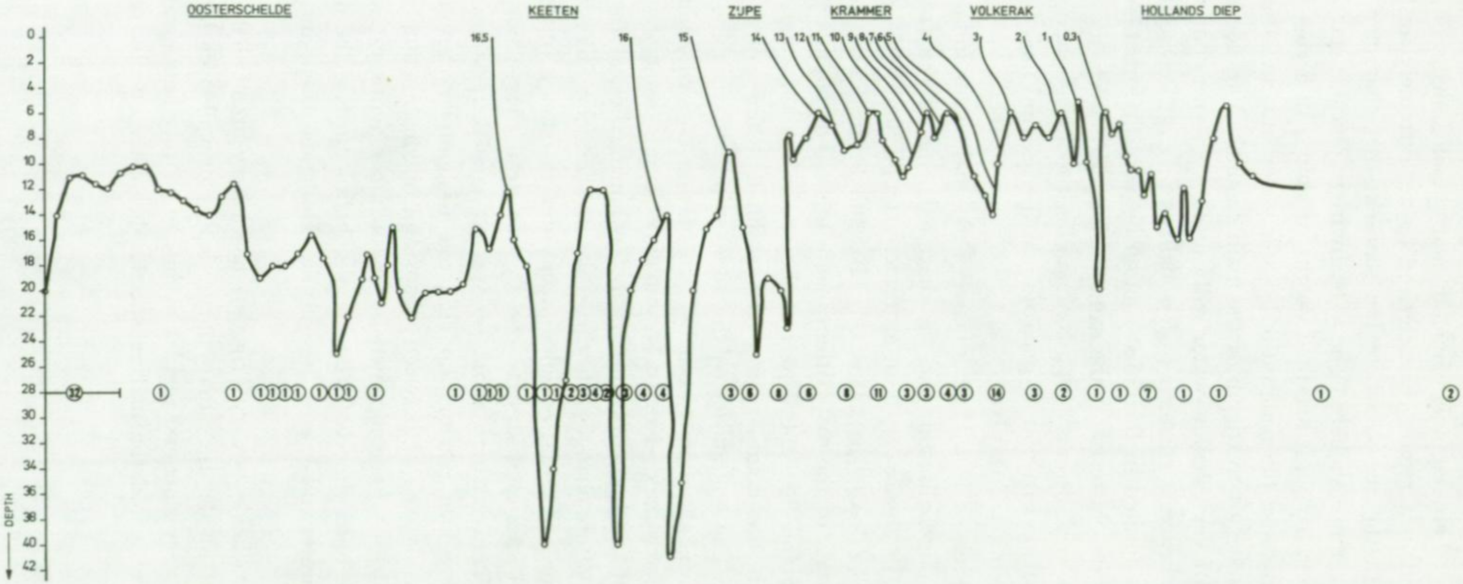

Fig. 38. As figure 37, but for the Oosterschelde—Keeten—Zijpe—Krammer—Volkerak—Hollands Diep estuary.

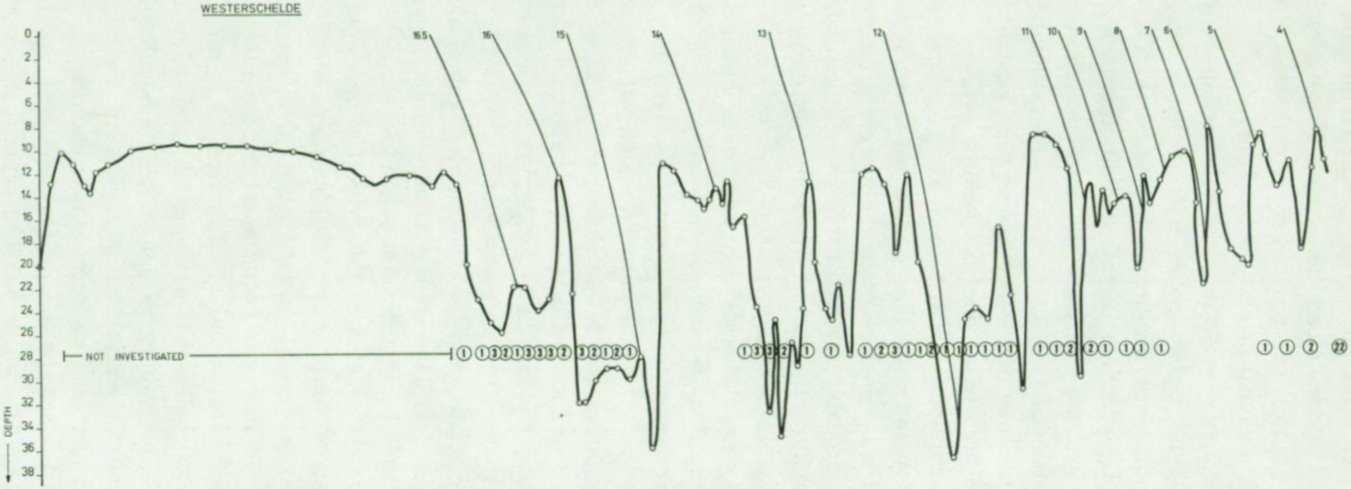

Fig. 39. As figure 37, but for the Westerschelde estuary.

Dahl (1956) presents a similar graph of the relationship between salinity and the number of species along the stretch North Sea-Skagerrak-Baltic. The smoothness of this curve is very remarkable. Nowhere a break, corresponding with a faunal break, can be observed.

Thus, when a graph representing the relationship between the number of marine and brackish water species and salinity is constructed there are only very faint indications for breaks in the curve. The breaks observed always occur at places with a complicated hydrographical structure, such as the confluence of two estuaries and shallow sills with steep salinity gradients. It is concluded that there exist no discontinuities in the species-salinity curve. Hence, one of the two assumptions on which brackish water classifications have been based does not hold.

The second assumption was that there exist groups of species typical of a certain salinity interval. This matter has already been discussed in paragraph 6.3.1. It was concluded that the marine offshore species and the freshwater species probably are characteristic for their salinity interval but that the distribution along the salinity gradient of estuarine species separately differs considerably. It is evident that a classification of brackish waters also cannot be based on the brackish water fauna, because this fauna does not behave as an entity in its reactions to salinity.

Although it is agreed with Den Hartog (op. cit.) that it is possible to divide the estuaries of the Delta area into a number of subareas characterized by their fauna, the places for this subdivision in all cases may be found at sharp discontinuities in the gradients of environmental factors.

On the other hand Khlebovich (1968, 1969) advocated the existence of a critical salinity value in the range of about 3-4.5$^0/_{00}$ Cl′ caused by important changes in the relative ionic composition of waters along the gradient from sea to fresh water. This critical salinity would separate marine and freshwater faunas and also be the cause of the low numbers of species living near this salinity. In the Delta area this critical salinity could not be studied because both instances were situated in hydrographically unstable areas. Moreover, there exist several species, such as *Pseudamnicola confusa, Nereis diversicolor, Gammarus zaddachi* and *Cordylophora caspia,* which occur on either side of this boundary. Apparently it is not a very strict one.

Therefore it is concluded that a biological subdivision of the estuarine environment based on salinity is impossible. Undoubtedly, in an ideal estuary with a perfectly smooth salinity gradient the number of species would decrease and increase in a very regular manner.

This conclusion also may be drawn when the evolution of estuarine and brackish water species is considered. The capacity for osmoregulation has to be acquired by each species or small group of species separately and there is no reason why the results should be the same for every species.

As a consequence it is concluded that it is better to avoid the terms of the Venice-system, and to use neutral terms as upper, middle and lower reaches for estuaries (Carriker, 1967). The freshwater tidal area of the Biesbosch can serve as an instance of the upper reaches, the Haringvliet of the middle reaches, and the Oosterschelde of the lower reaches.

6.5. COMPARISON WITH OTHER ESTUARIES

6.5.1. ESTUARIES IN N.W. EUROPE

Estuaries with similar physical and topographical characteristics as those of the Delta area, may be found all along the Atlantic coasts of Europe and N.W. Africa. Most Mediterranean river mouths, however, are different because of the general absence of tidal movements from this sea. In the next paragraph the brackish water areas of the estuaries of N.W. Europe, as far as they have been investigated, have been compared with those of the Delta area.

In Denmark Muus (1967) investigated 17 brackish waters but only three of these were considered to be estuaries. The Kysing Fjord estuary is inhabited by the same species as occur in the estuaries of the Delta area. Only *Cardium glaucum, Rissoa* sp., *Hydrobia neglecta, H. ventrosa* (= *H. stagnorum*), *Palaemon adspersus, Sphaeroma hookeri, Idothea viridis,* and *Fabricia sabella* are in the Delta area either absent (*H. neglecta*) or occur in sheltered brackish inland waters without tidal movements.

Thamdrup (1935) and Smidt (1951) both investigated the Danish Wadden Sea. The average salinity here is 14-15.5$^0/_{00}$ Cl′, falling as low as 10$^0/_{00}$ Cl′ in one place. The fauna proves to be essentially similar to that living in parts of the Delta estuaries with a salinity over 10-15$^0/_{00}$ Cl′, except for a small number of euryhaline marine species.

In the North Frisian part of the German Wadden Sea, adjacent to the Danish Wadden Sea, the principal investigations are those of Wohlenberg (1937) and Reineck et al. (1968). The tidal flats and channels investigated experience salinities permanently over 15$^0/_{00}$ Cl′. The fauna resembles closely that found in parts of the Delta area with salinities over 15$^0/_{00}$ Cl′, except for some marine species either showing a northern distribution or being dependent upon the occurrence of *Zostera.*

The Elbe estuary and adjacent waters have been investigated by Caspers (1949, 1952, 1953, 1955, 1958, 1959), Garms (1961), Schumacher (1961), Movaghar (1964), Jepsen (1965), Riemann (1966), Giere (1968) and

Michaelis (1969). It has an extended salinity gradient and the influence of the tides creates an extensive freshwater tidal area. The polyhaline zone of the river is bordered by large tidal flats. The only important difference with the estuaries of the Delta area lies in the presence of large areas of muddy sediments off the mouth of the Elbe, contrary to the sandy sediments in front of the estuaries of the Delta area.

A comparison between the fauna of the Elbe estuary and that of the Delta estuaries reveals that they are very similar, as is also the case with the distribution patterns of the various species. Unfortunately, most soft-bottom groups have only been treated in a general way by Caspers (op. cit), but the data presented are sufficient to make a close comparison possible. Some unimportant differences occur in the composition of the marine fauna of the lower reaches of these estuaries.

Of the 16 soft-bottom species considered as characteristic for estuarine brackish water areas (paragraph 6.3.1.; Table 5, column C) only *Alderia modesta, Limapontia depressa, Boccardia ligerica, Streblospio shrubsolii, Cyathura carinata,* and *Corophium multisetosum* have not been found in the Elbe estuary. The first two species are recorded from the vicinity by Seeleman (1968, 1968a). *Boccardia ligerica, Cyathura carinata,* and *Corophium multisetosum* occur in the Nord-Ostsee Kanal, connected with the Elbe estuary, and therefore certainly will also occur in the estuarine waters. The small and inconspicuous *Streblospio shrubsolii* very probably occurs also in the Elbe estuary because it has also been found in the Baltic further eastward.

Of the 34 species occurring in the brackish Haringvliet area (Table 5), at least 24 occur also in the Elbe estuary. The exceptions are the six species mentioned above, *Talitrus, Talorchestia, Pseudamnicola confusa* and *Trocheta bykowskii.* It seems very probable that the two last mentioned species have been overlooked until now in the Elbe estuary. *Talitrus* and *Talorchestia* are inhabitants of sandy beaches and not characteristic for estuarine brackish waters.

The conclusion has to be drawn that the similarity of the brackish water faunas of these estuaries is nearly complete, also because no other brackish-water species occur in the Elbe.

The Jadebusen has been investigated by Linke (1939), Schuster (1951, 1952), and Dörjes et al. (1969). Only the Vareler Rinne investigated by Schuster (1952) has a regular drainage of fresh and brackish water. The remaining part of the Jadebusen has a salinity varying between 12.2 and 17.7$^0/_{00}$ Cl′. Typical brackish water species have not been mentioned from the area.

The Ems-Dollard estuary has been investigated by a number of Dutch scientists; their papers have been edited by Van Voorthuysen & Kuenen (1960). The unpublished polychaete data were made available by Dr. S. van der Spoel (Amsterdam). The Ems-Dollard area is a typical estuary with a salinity gradient from fresh to entirely marine.

The only brackish-water species mentioned from this estuary, and not occurring in the Delta area, are *Gammarus oceanicus, Corophium sextoni* and *Corophium lacustre,* whereas in the Delta area *Hydrobia stagnorum* occurs only in stagnant inland waters. However, the specimens of *Gammarus* in fact were unidentifiable juvenile specimens (Den Hartog 1964). whereas the species of *Corophium* were studied insufficiently in the Delta area. Therefore, the main difference is the occurrence of *Hydrobia stagnorum* in tidal waters, which, however, may be ascribed to the extremely sheltered position of the shallow Dollard, an explanation corroborated by the abundant occurrence of the polychaete *Manayunkia aestuarina.*

Of the characteristic brackish water species of the Delta area several have not been found in the Ems-Dollard estuary, probably because the biological investigations in the latter were far less extensive. It is concluded, therefore, that the fauna of the Ems-Dollard estuary resembles very much that of the Delta area, except for the more sheltered nature of the Dollard area.

The most important descriptive studies of the Dutch Waddensea are those of Van Goor (1919) and of Van der Baan et al. (1958). From these two papers, together with many other data in the Dutch literature — not mentioned here — and personal observations, it is concluded that the fauna of the Dutch Wadden Sea does not differ qualitatively from that of the marine parts of the estuaries of the Delta area, except for some species with a distributional limit lying in between the two areas.

The former Zuiderzee has been the subject of a classical brackish water study (Redeke, 1922, 1936). It was hydrographically not quite comparable to the estuaries of the Delta area, owing to the very large and shallow southern part without strong currents and, hence, without rapid changes of temperature and salinity. The salinity in this large shallow area normally varied in the range 3 to 6$^{0}/_{00}$ Cl′. In the northern part of the Zuiderzee a salinity gradient towards the Wadden Sea (15-16$^{0}/_{00}$ Cl′) was found.

Owing to the relative stability of salinity as well as temperature, many species occurring in the Delta area only in stagnant brackish waters, were living in this part of the tidal Zuiderzee. Further differences between the soft-bottom macrofauna of the Zuiderzee and the Delta area concern a few euryhaline marine species and two species of *Corophium,* studied insufficiently in the Delta area. Nevertheless, it can be concluded that the brackish water faunas of the Delta area and the Zuiderzee were very similar.

The study of Leloup & Konietzko (1956) on the Belgian part of the Westerschelde has been integrated in this study.

Rullier (1959) published a study on the Aber near Roscoff. This small area (ca. 1 km^2) shows some estuarine characters, but owing to the small influx of fresh water, there is a very strong marine influence. Nevertheless, the trends in the distribution of the various soft-bottom species are similar to those in the Delta area. Also the brackish water species met with are the same as those occurring in the Delta area, viz. *Nereis diversicolor, Manayunkia aestuarina,* and *Cyathura carinata.*

The Bassin d'Arcachon has been studied by Davant & Salvat (1961), Boisseau (1962), Salvat (1962, 1967), Renaud-Debyser (1963) and Amanieu (1969a). The salinity of the larger part of the Bassin is over $15^0/_{00}$ Cl′, but lower salinities may be observed in the northeastern part of the area where several small rivers reach the Bassin. Unfortunately, the investigations mentioned above have been directed mainly to the seaward part of the bay, and the brackish water species have received relatively little attention. Only one brackish-water species absent from the estuaries around the North Sea, viz. *Gammarus chevreuxi,* has been recorded. Of the characteristic brackish water species (paragraph 6.3.1.) *Assiminea grayana, Limapontia depressa, Nereis diversicolor, Streblospio shrubsolii, Manayunkia aestuarina, Cyathura carinata, Sphaeroma rugicauda, Heterotanais oerstedii, Corophium insidiosum, Palaemonetes varians* and *Neomysis integer* have been observed.

The conclusion is that the brackish water fauna of the Bassin d'Arcachon probably is very similar to that of the Delta area.

The studies of Brun (1967) on the "estuary" of the Rhone and of Vatova (1963) on some river mouths near Venice are not detailed enough to permit a close comparison with this study. It seems that the brackish water fauna of these areas does not differ essentially from that of the Delta area, although it looks poorer.

The benthic fauna of the mouths of the Danube has some euryhaline marine species in common with the Delta area, but the brackish water species nearly all seem to be of Ponto-Caspian origin (Rudescu & Marinescu-Popescu, 1969).

In Britain a large number of estuaries has been investigated in some detail.

The fauna along the salinity gradient from the sea to the fresh water and in some cases to the tidal limit was investigated in the following estuaries: Afon Water (Goodhart, 1941: amphipods only), Exe estuary (Allen & Todd, 1902; Crawford, 1937; Holme, 1949), Tamar and Lynher estuaries (Percival, 1929; Crawford, 1937; Spooner & Moore, 1940), the Severn estuary (Bassindale, 1942: amphipods only), the Towy estuary, Carmathenshire

(Crawford, 1937; Howells, 1964), the Mersey estuary (Bassindale, 1938), the Aberdeenshire Dee (Milne, 1940), the Tay and the Tees estuaries (Alexander, Southgate & Bassindale, 1935) and some East Norfolk estuaries (Gurney, 1907). Crawford (1937) made a few observations in the brackish part of some other small estuaries, whereas Spooner (1947) corrected some identifications of several earlier authors. From these studies the following picture of the brackish water fauna in British estuaries can be given.

Species common in the brackish water area of these estuaries are: *Cordylophora caspia* (sub nom. *C. lacustris*), *Procerodes ulvae, Nereis diversicolor, Polydora ligni* (Percival (1929) records *P. ciliata* building tubes in mud), *Streblospio shrubsolii, Tubifex costatus, Clitellio arenarius, Potamopyrgus jenkensi, Carcinus maenas, Crangon crangon, Neomysis integer, Mesopodopsis slabberi, Heterotanais oerstedii, Cyathura carinata, Sphaeroma rugicauda, S. hookeri, Paragnathia formica, Orchestia gammarellus, Gammarus duebeni, G. salinus, G. zaddachi, G. chevreuxi, Melita pellucida, Leptocheirus pilosus, Corophium volutator,* and *C. insidiosum.* All these estuaries are much smaller than those of the Delta area. Hence, pelagic marine forms, such as *Mesopodopsis slabberi,* and *Crangon crangon,* are swept very easily into the brackish water area by the tidal currents. The small scale of these estuaries also makes it more difficult to distinguish between marine species tolerating brackish water, for instance, *Carcinus maenas, Paragnathia formica, Chaetogammarus marinus* and *Melita palmata* and the typical brackish water species. The oligochaetes have not been studied in the Delta area, but of the other species typical for the brackish water of the Haringvliet only *Garveia franciscana, Assiminea grayana, Embletonia pallida* (see Roginskaya, 1970), *Boccardia ligerica* and *Rhithropanopeus harrisii* have not been recorded in the studies mentioned above. However, *G. franciscana* and *R. harrisii* are recently introduced American species, whereas the small *E. pallida* and *B. ligerica* might have been overlooked. The absence of *A. grayana,* often living in enormous numbers in estuaries, is rather puzzling, although *A. grayana* is known from the English coast between the Thames and the Humber estuary (Anonymous, 1951a).

There exist, however, four other species which are characteristic for the brackish part of (some) English estuaries and which have not been found in the Delta area, viz. *Procerodes ulvae, Heterotanais oerstedii, Gammarus chevreuxi* and *Melita pellucida.* The two last mentioned species are restricted to the S.W. part of England and Wales and therefore, they may be absent from the Delta area for climatic reasons. *H. oerstedii* is known from stagnant brackish waters in The Netherlands (Holthuis, 1956), but may have been overlooked in this study owing to its small size.

The conclusion is that the brackish water fauna of the British estuaries is rather similar to that of the Delta area, but that some small differences exist.

The fauna of a freshwater tidal stretch has been investigated in the river Tay and the river Tees (Alexander et al., 1935), in the river Exe (Crawford, 1937) and in the river Towy (Howells, 1964). The following species have been mentioned: *Ephydatia fluviatilis, Planaria polychroa, Dendrocoelum lacteum, Tubifex tubifex, Limnodrilus hoffmeisteri, Erpobdella octoculata* (sub nom. *Herpobdella atomaria*), *Helobdella stagnalis, Glossiphonia complanata, Hemiclepsis marginata, Haemopis sanguisuga, Asellus aquaticus* (this species?), *Gammarus zaddachi, G. pulex, Potamopyrgus jenkinsi,* and *Limnaea peregra* (compare also Spooner, 1947). Except for the leech *Hemiclepsis marginata,* which is common in stagnant water in The Netherlands, all these species also have been found in the freshwater tidal areas of the estuaries of the Delta area. Just as in the Delta area, these species are not confined to the freshwater tidal areas of the British rivers investigated, but are part of the more widespread river fauna, except for *Gammarus zaddachi,* a brackish water species.

The final conclusion with respect to the estuaries of N.W. Europe is that the faunas of the brackish water areas as well as those of the freshwater tidal areas are very similar to one another. The differences observed arise either from insufficient research on the occurrence of species, or from insufficient taxonomical knowledge. They have to be considered as true differences in distribution in a few cases only. The fauna of the seaward reaches of the estuaries often is very similar to that of the shallow water along the neighbouring coast, and shows the same trends with respect to the occurrence of various species.

6.5.2. Other estuaries

Other areas where estuaries have been investigated extensively are S. Africa, S.E. Asia, New Zealand, the Pacific and the Atlantic coast of North America, and the Arctic coast of Siberia.

The group of species typical of brackish water areas in The Netherlands and N.W. Europe (paragraph 6.3.1., Table 5, column C), will be compared in the next lines with the species living under similar conditions (roughly between 1 and $10\,^{0}/_{00}$ Cl′) in other estuaries of the world.

In the South African estuaries such species are (Day, 1951, 1964; Day, Millard & Harrison, 1954; Day, Millard & Broekhuysen, 1953; Macnae, 1957; Millard & Harrison, 1954; Scott, Harrison & Macnae, 1952) the snail *Assiminea bifasciata,* the bivalve *Modiola capensis,* the crabs *Hy-*

menosoma orbiculare and *Varuna literata,* the isopods *Cirolana fluviatilis, Corallana africana, Exosphaeroma hylocoetes, Pseudosphaeroma barnardi, Dies monodi,* and *Cyathura carinata,* the tanaid *Leptochelia savignyi,* the amphipods *Melita zeylanica, Chiltonia capensis, Parorchestia rectipalma, Corophium triaenonyx* and *Grandidierella lignorum,* and the polychaetes *Ceratonereis hircinicola* and *Dendronereis arborifera.* It appears that the estuarine fauna of S. Africa is completely different from that of other parts of the world. The only species common to N.W. Europe and S. Africa seems to be *Cyathura carinata,* but according to Burbanck (1967) even this one may be different.

The extensive brackish waters of the estuaries and lagoons of India and adjacent S.E. Asia are inhabited by a rich brackish water fauna (Annandale, 1922; Annandale et al. 1915-1924; Pannikkar & Aiyar, 1937; Sewell, 1934). Nevertheless, species occurring in the estuaries of S.E. Asia as well as in those of N.W. Europe are very few and only comprise some groups easily transported by ships and, moreover, taxonomically difficult in many cases. These species are the entoproct *Barentsia gracilis,* the bryozoans *Alcyonidium mytili* and *Bowerbankia caudata,* the polychaetes *Mercierella enigmatica* and *Hydroides norvegica* (= *Mercierella*?), and the barnacle *Balanus amphitrite.* It is concluded that the brackish water faunas of N.W. Europe and S.E. Asia are very different and that all resemblance is caused by shipping traffic.

The characteristic brackish-water polychaetes of the Heathcote Estuary in New Zealand are completely different from the brackish-water species occurring in brackish-water areas elsewhere (Estcourt, 1967).

Filice (1958), Painter (1966), Ganssle (1966) and Hazel & Kelley (1966) found the following species to be characteristic of the brackish water of the upper reaches of the estuarine portion of San Francisco Bay: *Corophium stimpsoni, Balanus improvisus, Parapleustes pugettensis, Rhithropanopeus harrisii, Neomysis awatschensis, Nereis limnicola, Polydora uncata,* and perhaps *Synidotea laticauda.* Of these, only *Balanus improvisus* and *Rhithropanopeus harrisii* occur also in estuaries of N.W. Europe. The latter, however, was introduced from the Atlantic coast of America in Europe as well as on the Pacific coast of America. The former is so easily transported by ships that its original distribution is unknown. Therefore it is concluded that the oligo-mesohaline upper reaches of the San Francisco Bay estuary originally had no species in common with the estuaries of Europe. The same probably is true for the transitional area between brackish and fresh water in this estuary, where only *Limnodrilus hoffmeisteri, Manayunkia speciosa, Corbicula fluminea, Pisidium occidentalis, Corophium spinicorne* and *C.*

stimpsoni have been found. Only the first mentioned species occurs also in European waters. In the lower reaches of the San Francisco Bay estuary, however, several species occur living in the lower reaches of estuaries as well as in marine coastal waters and also occur in similar habitats in Europe. These are *Mya arenaria, Macoma balthica* (sub nom. *M. inconspicua*), *Nereis succinea, Capitella capitata, Heteromastus filiformis, Polydora ligni, Eteone longa* and *Corophium acherusicum*. Of these *Mya arenaria* and *Nereis succinea* have been introduced in recent times into this area. The number of species known to be introduced by man in recent years into the San Francisco Bay estuary is fairly high. Of the 53 species encountered by Filice (1958) not less than 8 are known to be introduced.

Haertel & Osterberg (1967) published a short account of the benthos in the Columbia River estuary. The species inhabiting the brackish part of this estuary are *Cordylophora lacustris, Nereis limnicola, Neomysis mercedis, Corophium salmonis, Anisogammarus confervicolus, Mesidotea entomon*, and *Crangon franciscorum*. There appears to be some relationship with the fauna of San Francisco Bay estuary, but, except for the easily transported *Cordylophora lacustris*, no relationship at all with the estuaries of N.W. Europe. The fauna of the lower reaches of the Columbia River estuary shares *Jassa falcata* and *Macoma balthica* with that of the estuaries of N.W. Europe.

The conclusion has to be drawn that the brackish water faunas of the estuaries of the Pacific Coast of N. America and of N.W. Europe originally were completely different. In the lower reaches of the estuaries of these regions, however, a number of mostly circumboreal species occurs which are common to both regions.

The fauna of some estuaries on the Atlantic and Gulf coast of America has been described by Pearse & Wharton (1938), Ladd (1951), Wells (1961), and Sanders, Mangelsdorf & Hampson (1965). Ladd (op. cit.) studied mainly the molluscan fauna of some bays of the Texas Gulf coast. In the oligo-mesohaline bays only *Rangia cuneata, Littoridina sphinctostoma*, and *Tellina texana* were found.

Pearse & Wharton (op. cit.) studied an estuarine area in Florida. The only characteristic brackish water species also occurring in Europe, is *Balanus improvisus*, an animal very easily transported by ships.

Wells (op. cit.) described the fauna associated with oyster beds in a North Carolina estuary. At the most characteristic brackish water station *Brachidontes recurvus, Nereis succinea, Nereis occidentalis, Polydora websteri, Streblospio benedicti, Eurypanopeus depressus, Rhithropanopeus harrisii, Callinectes sapidus, Cassidisca lunifrons, Cyathura polita* (sub nom.

C. carinata), *Corophium cylindricum, Victorella pavida* and *Electra crustulenta* occurred. Tenore (1972) mentions from the brackish area of another North Carolina estuary *Nereis succinea, Cyathura polita, Macoma balthica* and *Rangia cuneata.* Of these *Macoma balthica, Nereis succinea, Rhithropanopeus harrisii, Callinectes sapidus, Victorella pavida,* and *Electra crustulenta* are also found in European estuaries. However, the last two species are easily transported by ships, and *R. harrisii* and *C. sapidus* are known to be introduced into Europe from America. Hence, only *N. succinea* and *Macoma balthica* seem to occur naturally in both areas.

Soft-bottom species having their maximum numbers in the upper reaches of the estuary of Pocasset River, Massachusetts, where the daily variation of salinity surpasses $15^0/_{00}$ Cl′, are (Sanders, Mangelsdorf & Hampson, 1965) : *Hypaniola grayi, Almyracumi proximoculi, Gammarus tigrinus, Leptocheirus plumulosus, Leptochelia* spec., *Cyathura polita* and *Edotea triloba.* Only the amphipod *Gammarus tigrinus* occurs also in European waters, but is known to be introduced recently.

Therefore, the conclusion is reached that the brackish estuarine fauna of the Gulf and Atlantic coast of North America is nearly completely different from that of N.W.-Europe. There are some relationships, but these mainly seem to be caused by species introduced recently in Europe or by "fouling" species with a cosmopolitan distribution.

Investigations of the brackish water fauna of the large estuaries of the Dvina, the Pechora, the Ob, the Yenisey, and the Lena were made by various Russian investigators and summarized by Zenkevitch (1963). Along large parts of the Siberian shores a littoral fauna is wanting but permanently submerged, among others, the following species occur: *Mysis oculata, M. relicta, Mesidotea entomon glacialis, Pontoporeia affinis, Pseudalibrotus birulai, Gammaracanthus loricatus, Oediceros minor, Monoculodes minutus, Acanthostepheia incarinata, Brandtia fasciatoides, Ampharete vegae, Marenzelleria wireni, Laonice annenkovae, Portlandia arctica, P. aestuariorum, Cyrtodaria kurriana,* and *Macoma balthica.*

Apparently, this brackish cold-water fauna has very little in common with the estuarine brackish water fauna of N.W. Europe, although some of these species have been able to reach the brackish parts of the Baltic (Zenkevitch, 1963).

The main conclusions to be drawn from this and the previous paragraph are:

1. The fauna living in the brackish middle reaches of the estuaries of N.W. Europe forms an entity all over this area. The same species may be found again and again in many different rivers. The slight differences

in the faunal composition observed arise either from insufficient knowledge of the fauna of certain estuaries, from insufficient taxonomical knowledge, from species introduced recently, or from some "original" differences, probably partly due to differences in climate.

2. This fauna typical of N.W. Europe is completely different from comparable faunas along the coasts of Siberia, S. Africa, New Zealand and S.E. Asia, and the Pacific as well as the Atlantic states of N. America. The similarity of brackish water faunas all over the world, claimed by some authors (Carriker, 1967; De Lattin, 1967), is largely based on a number of species easily transported by ships, such as *Balanus amphitrite, B. improvisus, Corophium acherusicum,* and *Mercierella enigmatica* (compare also Hedgpeth, 1957). For several species it is even known that they have been introduced from other parts of the world (Fauvel, 1933: *Mercierella enigmatica*; Buitendijk & Holthuis, 1949: *Rhithropanopeus harrisii*).

6.6. HABITAT AND NICHE DIVERSIFICATION IN THE ESTUARINE ENVIRONMENT

6.6.1. INTRODUCTION

The main gradient in the estuary is that of salinity. For this reason habitats comparable as regards temperature, tidal movements and currents, sediments, and supply of food, but dissimilar with respect to salinity, and in some cases also pollution and turbidity, are inhabited by different assemblages of species. Moreover, the size of these assemblages also differs as a function of salinity. It may be wondered whether these different assemblages of animals utilize their environment to the same extent or whether in the parts of the estuary with a small number of species some resources will not be exploited.

This problem has been approached in various ways. The first method is based on the assumption that the number of species or the species diversity in a habitat reflects the extent of the utilization of the resources available, achieved either through the distribution of species over different microhabitats or over different niches. The niche is defined here as the position occupied by an animal in the food chain, whereas the habitat is the framework of physical, chemical and to some extent of biotic (vegetation!) factors surrounding the animal.

The use of species diversity as a means to characterize the fauna of an environment is a "macroscopic" method of approach of the ecosystem (Margalef, 1968). It will be tried, however, to investigate this problem also with a "microscopic" method by comparing the characters of the species themselves in the different environments (paragraphs 6.6.3.; 6.6.4.).

6.6.2. SPECIES DIVERSITY

Species diversity may be considered as a measurement for the subdivision of a habitat into microhabitats and niches by the species occurring. However, as was pointed out by Margalef (1968) and Odum (1969) species diversity is not the only measurement for the diversification of a habitat, because the distributional pattern of the species and the biochemical diversity also should be taken into account. This has not been done in this study, because it is assumed that in the cases investigated, the biochemical and pattern diversifications are correlated positively with the diversification achieved by a higher number of species.

The most simple measurement of the parameter diversity (D) is the number of species in the sample, but this measurement is strongly influenced by the size of the bottom-sample, as well as by the number of specimens in the sample. To a lesser extent this is also true for most other indices of diversity (Sanders, 1968). Indices only slightly affected by this inconvenience are obtained by Sanders' rarefaction method, presenting the number of species per number of individuals, and some indices derived from information theory (Margalef, 1968), for instance the Shannon-Wiener formula:

$$D = -\sum_{i=1}^{s} p_i \log_2 p_i$$

(p_i = the ratio between the number of individuals of ith species in the sample and the total number of individuals in the sample).

This formula has been used as a measurement of diversity. It denotes the average uncertainty in obtaining a certain species when randomly drawing an individual from a sample. Because Sanders (1968) has shown that his rarefaction method acts better at low numbers of individuals than do other methods, this method has also been used. Because Sanders' rarefaction method, like the methods derived from information theory, combines species diversity (= number of species per sample) and equitability diversity (= number of individuals per species) in one index, the number of species in the samples has been taken as a third index of diversity. The diversities computed by means of these three methods will be compared for the various parts of the Delta area.

As a measurement of diversity the number of species in a sample has been determined in the following way. The highest value for the number of species per sample in a series of 10 neighbouring samples (a few times

8 or 9 samples were used) was used as an index of diversity for the particular area from which these samples originated. These indices have been plotted on a map (Fig. 40).

This rather crude measurement already shows a differentiated pattern of diversity along the estuaries of the Delta area, with a high diversity in the marine and freshwater areas and low values in the brackish water areas. Outstanding are three areas of very low diversity, coinciding exactly with the areas of very large salinity changes in the course of a tidal cycle (Fig. 14). Interesting is the area of higher diversity in between two areas of very low diversity in the Haringvliet. The chief difference between these areas is in the rate of change of salinity (paragraph 3.4.5.); the area in between has a relatively stable salinity contrary to the other areas which are very unstable. In all of these brackish areas the average level of salinity is comparable. This shows that diversity is not only correlated with the level of salinity but also with the rate of change of salinity.

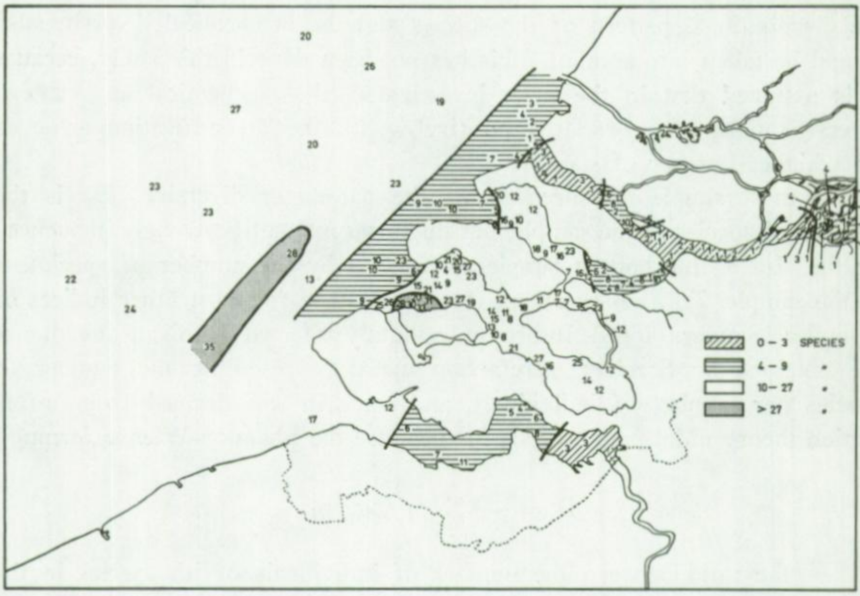

Fig. 40. Diversity of the soft-bottom macrofauna expressed as the maximum number of species occurring per sample for series of ten samples.

Remarkable is an area of low diversity along the North Sea coast. Apparently some factor, possibly the action of the surf, has a negative effect on the diversity in this area.

The species diversity reaches the same relatively high level in the offshore parts of the North Sea, in the Oosterschelde and in the Grevelingen, all regions with high and stable salinity. This is notwithstanding the fact that the annual temperature amplitude in the North Sea is much smaller than that in the estuaries.

With the rarefaction method of Sanders (1968) the number of species per number of individuals may be obtained (Fig. 41). In this way the disturbing effect of a varying number of specimens per sample is eliminated.

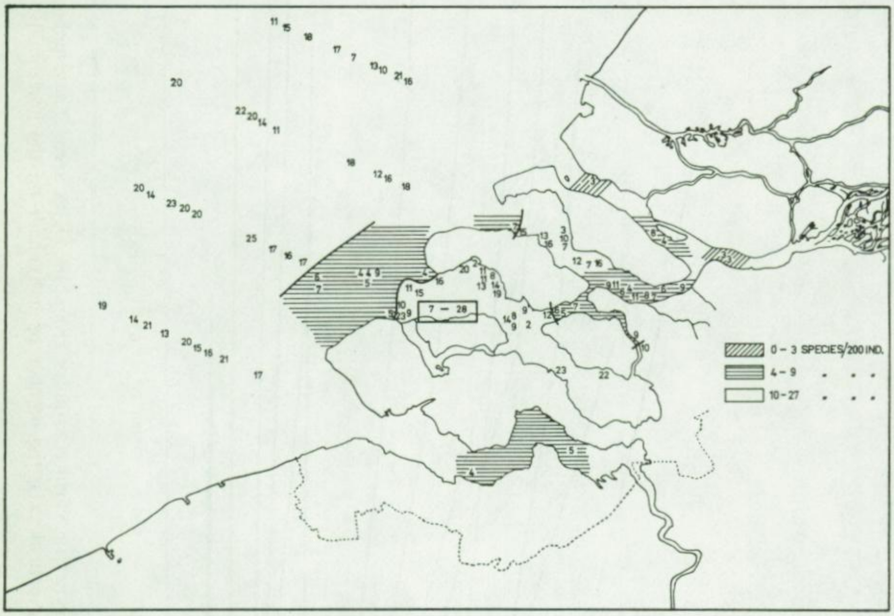

Fig. 41. Diversity of the soft-bottom macrofauna expressed as the number of species per 200 individuals for all samples containing 200 or more individuals.

The map with the (rounded) number of species per 200 individuals shows the same trends as the map representing the number of species per sample (fig. 40). Unfortunately, the number of samples containing over 200 individuals is very low in the brackish and freshwater areas, and this makes the number of species per 200 individuals or more not very suitable for comparison. Or course, more data may be obtained by using numbers of individuals under 200, but the results from such procedures become progressively less accurate. Nevertheless, the trends are similar for all numbers of individuals considered. Again the conclusion may be drawn that the diversity is low in brackish areas, and lowest in brackish areas with a strongly fluctuating salinity. Nearly equal diversities occur in the North

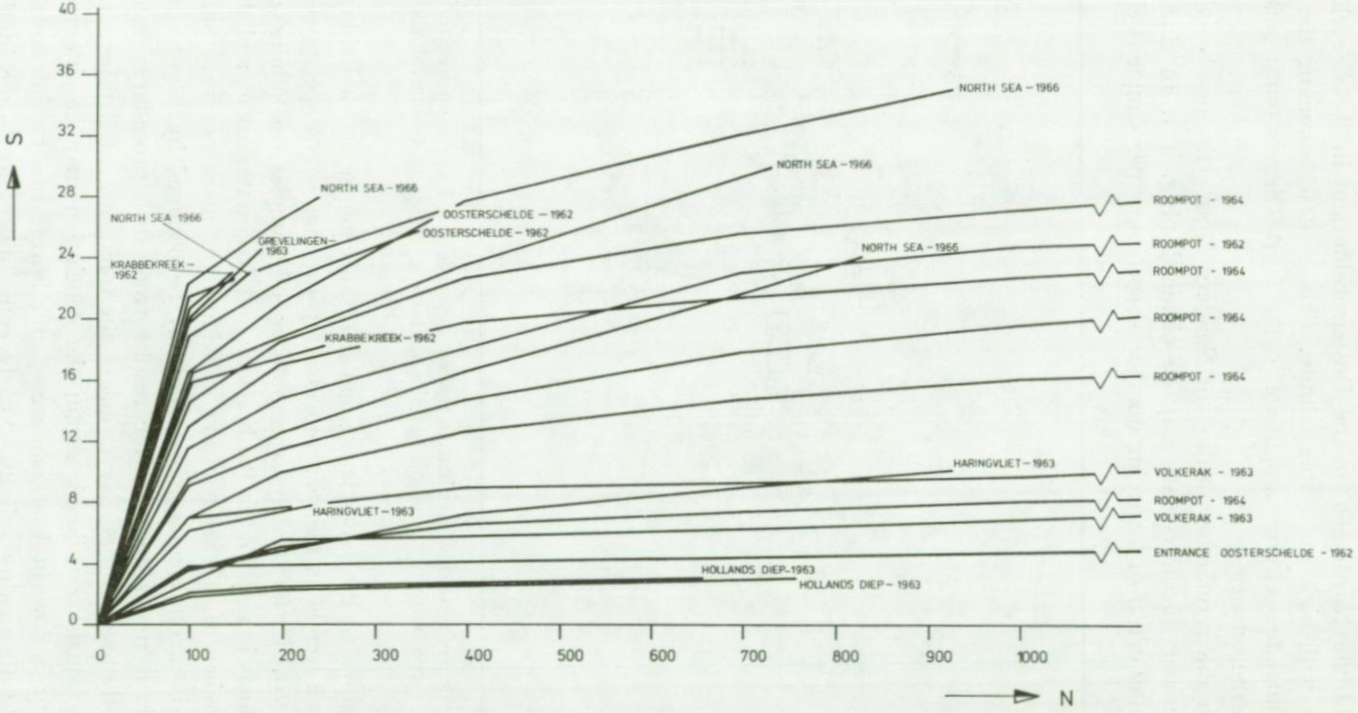

Fig. 42. Rarefaction curves for various samples from the Delta area. The number of species is shown on the vertical axis, the number of individuals on the horizontal axis.

Sea, and in the Grevelingen and Oosterschelde areas. However, it might be argued that this is only the case at the 200 individuals level, but that the ultimate numbers of species will be different in the three areas. Therefore, the complete rarefaction curves (fig. 42) have been drawn for a number of samples of maximal species abundance. The curve of samples from the brackish Haringvliet, Volkerak and Hollands Diep are on a much lower level than those from the other areas. The Roompot samples obtained in 1962 and 1964 seem to be on a lower level than those from the North Sea obtained in 1966, but it seems a matter of conjecture whether the North Sea samples really differ from the 1962 Oosterschelde samples and the samples from Grevelingen and Krabbekreek. Therefore, it is concluded, that the diversity in the North Sea is equal to that in the marine parts of the estuaries.

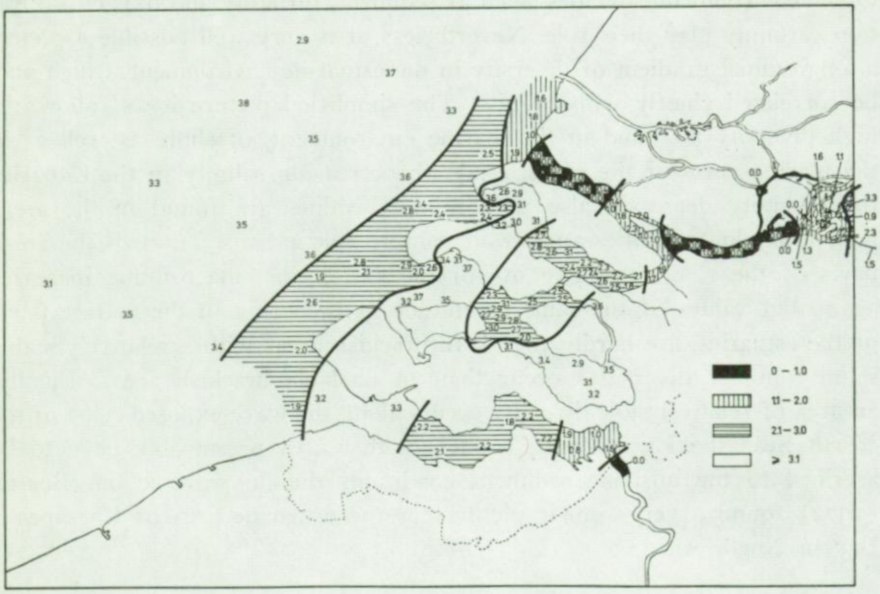

Fig. 43. Diversity of the soft-bottom macrofauna expressed as the maximum value of the Shannon-Wiener formula occurring in a series of ten samples.

Fig. 43 represents the diversity as obtained by the Shannon-Wiener formula. Although Pielou (1966) pointed out that this index is subject to a considerable sampling error, when used as in the present study, the picture is similar to that in the previous figures. High diversities (expressed as bits per individual; Margalef, 1968) occur in the North Sea and in the marine parts of the estuaries. Again apparently no difference in diversity exists between the North Sea and the with respect to temperature more unstable estuaries. Again a zone of low diversity is found along the North Sea coast and an area of relatively high diversity is situated in between two areas of very low diversity in the Haringvliet-Hollands Diep area. The diversity increases again in the direction of the fresh parts of the rivers.

Of course, diversity in an estuary is not only dependent on salinity. Other environmental factors, such as sediment, turbidity and oxygen saturation certainly play their role. Nevertheless, it is very well possible to detect a longitudinal gradient of diversity in the estuarine environment, which may be correlated chiefly with salinity. The simplified picture is as follows: a high diversity is found in the marine environment, offshore as well as in the marine parts of the estuaries. With decreasing salinity in the estuaries the diversity decreases also until minimal values are found in the areas with fairly low salinities and strong salinity fluctuations. Towards the fresh parts of the rivers the diversity of the soft-bottom macrofauna increases again, but values of the same magnitude as occurring in the marine parts of the estuaries, are hardly found. In brackish areas with a relatively stable salinity higher diversities occur than in unstable brackish areas. Finally, an area of relatively low diversity occurs along the wave-exposed coast of the North Sea; the low diversity values in that area presumably have to be ascribed to the unstable sediment conditions due to wave-action. Boesch (1972) found a very similar picture for the estuarine area of Chesapeake Bay in North America.

6.6.3. Distribution of various groups of species in the estuary

6.6.3.1. Taxonomical groups

The distribution of various taxonomical groups of the soft-bottom macrofauna in the estuaries in the S.W. Netherlands is shown in Table 8.

The brackish and freshwater tidal area are inhabited by species belonging to groups which have their centre of dominance either in the sea or in the freshwater. Taxonomical groups above family level with their centre of occurrence in brackish or freshwater tidal areas, do not occur.

6.6.3.2. Developmental types

The aspects of reproduction and larval development governing the dispersal of the species over the estuary are most interesting.

A series of juvenile stages with decreasing ability for dispersal may be distinguished as follows: planktotrophic pelagic larvae — lecithotrophic

TABLE 8

Distribution of various taxonomical groups over the estuaries of the Delta area.

Group	marine water	brackish water	tidal fresh water	river water	number of species considered
Hydrozoa	1	–	–	–	1
Anthozoa	1	–	–	–	1
Gastropoda prosobranchia	6	3	2	3	11
Gastropoda pulmonata	1	1	3	2	5
Gastropoda opisthobranchia	1	–	–	–	1
Gastropoda saccoglossa	2	2	–	–	2
Lamellibranchia	27	2	17	17	44
Echiurida	1	–	–	–	1
Polychaeta	73	9	1	–	76
Archiannelida	4	–	–	–	4
Oligochaeta	few	few	many	many	?
Hirundinea	–	1	4	6	6
Decapoda	13	4	1	1	15
Mysidacea	1	1	–	–	2
Cumacea	8	–	–	–	8
Tanaidacea	1	–	–	–	1
Isopoda	5	2	3	?	9
Amphipoda	24	9	3	2	31
Insecta	–	1–2	many	many	?
Echinodermata	8	–	–	–	8
Cephalochordata	1	–	–	–	1

pelagic larvae — semi-pelagic larvae depending on turbulence by currents — non-pelagic larvae. A general trend in this series is a decrease of the number of larvae per parent in the same sequence.

Another series of juvenile stages with mostly also decreasing numbers of offspring per parent may be distinguished among the species with non-pelagic development: species with eggs without brood-protection — species with eggs and brood-protection — viviparous species.

All these developmental types have been found in the estuaries of the Delta area (Table 9). Because the difference between lecithotrophic and semi-pelagic larvae is only gradual these two categories have been taken together.

The different types of development do not take the same share in all parts of the estuary. From the sea towards the rivers the share of the species with a pelagic development decreases whereas the non-pelagic developing species show the opposite behaviour. The decrease of the species with a pelagic development may be explained by the type of water movements.

TABLE 9

Distribution of soft-bottom macrofauna species with different types of larval development over the estuaries of the Delta area.

Type of development	Marine		Brackish	Tidal freshwater	Rivers
	North Sea	Delta area			
Planktotrophic pelagic	72	58	9	0	0
Lecithotrophic + semi-pelagic	1	5	1	1	0
Pelagic, but details unknown	15	10	7	0	0
Total pelagic	88 (56%)	73 (51%)	17 (50%)	1 (3%)	0 (0%)
Non-pelagic with eggs without brood-protection	11	15	0	6	5
Non-pelagic with eggs with brood-protection	20	26	14	12	10
Non-pelagic and viviparous	1	1	1	14	16
Non-pelagic, but details unknown	15	7	0	0	0
Total non-pelagic	47 (30%)	49 (34%)	15 (44%)	32 (94%)	31 (100%)
Development unknown	22 (14%)	22 (15%)	2 (6%)	1 (3%)	0 (0%)
Total	157 (100%)	144 (100%)	34 (100%)	34 (100%)	31 (100%)

In the offshore parts of the sea water movements in all directions occur. Pelagic larvae therefore form an efficient means of dispersal. In the marine parts of estuaries the water movements are chiefly in two directions, but here also pelagic dispersal may be effective. In the brackish parts of the estuaries an important difficulty is met with, because photopositive larvae are carried seaward and photonegative larvae riverward by the estuarine pattern of water circulation with a net seaward transport in the upper layers and a net riverward transport near the bottom. Any species maintaining itself in this part of the estuary must be very well adjusted to this circulation pattern and of course, to the prevailing salinity conditions in its larval development. Any species which fails to do so is either carried by the bottom flow in waters of too low salinity or by the surface currents towards the sea (Bousfield, 1955). This might be the reason for the very scarce occurrence of *Pygospio elegans*, which is very tolerant to low salinities, in the brackish Haringvliet area. *P. elegans* has larvae which remain photopositive during their complete development and such larvae will be transported back to the seaward reaches of the estuaries, when they do not become photonegative in brackish water (Thorson, 1964).

In the freshwater tidal area the water movements are still in two directions, but the salinity stratification characteristic of the brackish parts of the estuaries does not exist here. Due to the excess of river water, pelagic larvae are subject to a net downstream transport at all depths. Species with pelagic larvae thus only are able to disperse in the downstream direction (Sollas, 1883). Only one species with semi-pelagic larvae occurs in the freshwater tidal area, viz. *Nereis diversicolor*. This very tolerant species has large semi-pelagic larvae concentrated by their weight in the bottom layers. The distribution of this species suggests that its larvae are dispersed as far as the brackish bottom currents extend in the upstream direction.

The introduced hard-bottom species *Dreissena polymorpha* also has planktonic larvae and nevertheless seems able to maintain itself in the river and in the freshwater tidal area. Probably this population in running water is dependent on a constant supply of new larvae from stagnant waters, as well as from colonies transported by ships. No doubt, its permanent occurrence in the rivers is greatly facilitated by human activities.

When the passive transport of pelagic larvae falls short as a means of dispersal, other means have to be employed. In the freshwater of the rivers this difficulty has been encountered by transport of the larvae or adults by fishes (Unionidae, some leeches) or other free-swimming aquatic animals, by passive aerial transport either by birds or aquatic insects (*Pisidium*, Rees, 1965), by the wind (protozoans) or by active aerial dispersal (water insects). Insects with a flying adult stage form the freshwater counterpart of marine invertebrates with pelagic larvae.

Needham (1930) has pointed out that the difficulties in dispersal are accompanied by another problem, because the eggs of marine invertebrates need considerable amounts of inorganic ions from the seawater. Therefore, he supposes that there would be an important difficulty for the early stages of freshwater species in acquiring such minerals. Hatching at a late developmental stage therefore would be of considerable importance, because the individual then could rely at once on its mechanisms for uptake of these minerals. As Hutchinson (1967) remarked this hypothesis offers also a good explanation for the migrations of katadromous invertebrates (*Eriocheir, Carcinus*).

The brackish water species (paragraph 6.3.1.) meet with special difficulties, especially those with a non-pelagic development. It is supposed that many of these species only are able to disperse directly from one brackish-water area to another, without intermediate sojourn in sea water or freshwater. Hence, this group of species has considerably more difficulties in dispersal than the species of the marine parts of the estuaries which may disperse via the shallow coastal waters.

6.6.3.3. FEEDING TYPE

Alexander, Southgate & Bassindale (1935) showed the relationship between the numbers of suspension-feeders and non-suspension-feeders and the gradient of salinity in three British estuaries. They found that in these two groups the numbers more or less simultaneously decreased to zero, thus resembling the marine part of the brackish-water curve of Remane (1934). This is remarkable because it means that below a certain salinity the rich sources of food present in the estuary are not utilized. Therefore, the distribution of species with different modes of feeding in relation to the estuarine salinity gradient has been investigated again (Table 10).

TABLE 10

Distribution of species with different methods of feeding over the estuaries of the Delta area. The category of herbivores includes also diatom-feeders; scavengers take live as well as dead animal food, whereas omnivores employ at least two of the other feeding methods.

	Marine				
Type of feeding	North Sea	Delta area	Brackish water	Tidal freshwater	Rivers
Suspension-feeders	25 (16 %)	17 (11 %)	6 (18 %)	18 (53 %)	18 (58 %)
Non-selective deposit-feeders	11 (7 %)	8 (6 %)	2 (6 %)	0 (0 %)	0 (0 %)
Selective deposit-feeders	36 (23 %)	37 (26 %)	4 (12 %)	0 (0 %)	0 (0 %)
Predators	27 (17 %)	19 (13 %)	3 (9 %)	6 (18 %)	4?(13 %)
Scavengers	8 (5 %)	7 (5 %)	1 (3 %)	1 (3 %)	1 (3 %)
Herbivores	3 (2 %)	11 (8 %)	3 (9 %)	3 (9 %)	2 (6 %)
Omnivores	9 (6 %)	17 (12 %)	12 (35 %)	2 (6 %)	5 (16 %)
Unknown	38 (24 %)	28 (19 %)	3 (9 %)	4 (12 %)	1 (3 %)
	157 (100%)	144 (100%)	34 (101%)	34 (100%)	31 (99 %)

Suspension-feeders occur in all water types, contrary to the findings of Alexander et al. (op. cit.). Deposit-feeders seem to dwindle towards the freshwater, but it is important to notice that Oligochaeta and chironomids were not studied. The former are non-selective deposit-feeders, whereas several species of the latter are selective deposit-feeders.

The group of predators and scavengers shows a minimum in the brackish water area. The herbivores are represented in the area of the North Sea by a few species; these are diatom-feeders which live in shallow-water areas. They become much more abundant in the marine and brackish part of the estuaries, but seem to decrease towards the rivers.

The omnivores are relatively most abundant in the brackish water area. Therefore, it may be concluded that the widest niches are found in the brackish water area with the lowest number of species.

6.6.4. The utilization of the environment

6.6.4.1. Introduction

In an estuary the number of species strongly decreases from the sea towards the brackish parts, but increases again in the direction of the river.

Nevertheless, the same major sources of food, viz. plankton and organic matter in the sediment, are present all over the estuary. Therefore, it has been investigated how these sources of food are utilized by the fauna at different salinities. This has been done for the following habitats: 1) subtidal sandbottoms, 2) intertidal sandflats and beaches, and 3) intertidal mudflats and salt-marshes. Subtidal mud-bottoms are too scarce to make such an investigation possible.

To this end a comparison has been made of these habitats in a) the offshore area and the North Sea beaches (no muddy sediments), b) the inshore marine water, such as found in the Grevelingen, the Oosterschelde and the western part of the Westerschelde, c) the brackish waters (oligo-mesohaline) such as found in the Haringvliet and the Belgian part of the Westerschelde, d) the fresh waters with temporarily influxes of brackish water, such as found in the Hollands Diep, e) the tidal fresh water, such as found in the Biesbosch. Sand-bottoms have been defined as sediments with median grain-sizes of 1.30-2.30 φ; mud-bottoms with 3.00-3.50 φ.

6.6.4.2. Subtidal sand-bottoms

The faunas of subtidal sand-bottoms have been compared in Table 11. The North Sea and the Oosterschelde are more or less comparable with 20

TABLE 11

Niche differentiation of subtidal sandbottoms (Md: 1.50-2.30 φ) in areas with different salinities.

	suspension-feeders	non-selective deposit-feeders	selective deposit-feeders	herbivores	omnivores	predators	scavengers	unknown
North Sea very stable high salinity	10	7	20	-	5	19	1	20
Oosterschelde stable high salinity	9	4	17	1	9	15	2	12
Haringvliet unstable medium salinity	2	⩾ 2	1	-	4	1	-	-
Hollands Diep unstable low salinity	-	⩾ 1	-	-	-	-	-	-
Biesbosch stable low salinity (freshwater tidal area)	9	⩾ 1	-	-	2	-	-	-

and 17 predators and scavengers feeding on respectively, 37 and 30 suspension- and deposit-feeders.

In the Haringvliet these relationships are much simpler. One predator exploits 5 or slightly more (oligochaetes) suspension- and deposit-feeders and 4 omnivores.

In the Hollands Diep it is not possible to speak of a food-web. Only a few deposit-feeding oligochaetes inhabit the subtidal sand-bottoms in this area. Also Caspers (1952) records that the hydrographically comparable part of the Elbe estuary was a "tabula rasa" with regard to its fauna.

In the freshwater tidal area of the Biesbosch the number of suspension- and deposit-feeders again increases, but the next link in the food-web, the predators, are absent.

Thus, the rich source of food provided by the estuarine plankton and detritus, is badly exploited by the estuarine benthos, as far as the brackish part of these estuaries is concerned. Apparently, many niches and microhabitats are unoccupied in this area. Gerlach (1953) describes a similar phenomenon for the nematode populations inhabiting comparable types of subtidal sandbottoms in German waters of different salinity. On the other hand the relatively large numbers of omnivores in the brackish area probably means that some species inhabit a larger niche or microhabitat than they do in the more seaward reaches of the estuaries. Noodt (1969, 1970) described a similar phenomenon for copepods in the brackish parts of the Baltic. This means that in estuaries and brackish waters the "within-habitat" as well as the "between-habitat" diversity (MacArthur, 1965) are lower than elsewhere.

6.6.4.3. INTERTIDAL SAND-BOTTOMS

The fauna of sandy beaches may be split up into 1) the species living above or just below MHW-level, 2) those living at lower levels.

The first group consists mainly of selective deposit-feeders dependent on organic matter deposited on barren beaches. Such beaches, however, need to be swept clean by a regular occurrence of strong waves and thus are absent along the estuaries (Fig. 18). Hence, the species of the first group do not find their type of habitat in lower salinities and thus they are absent (Fig. 44).

The species of the second group, however, find similar habitats at all salinities down to freshwater. Nevertheless, their numbers also decrease very strongly with decreasing salinity. The lower part of the beaches along the North Sea and the sandflats along the lower reaches of the estuaries are inhabited normally by about 25 species (fig. 44). About four of these seem to invade the intertidal zone from deeper water, but the remaining species apparently are well established in the intertidal sandflats. The food-web is relatively simple, with 7 selective deposit-feeders, 3 non-selective deposit-feeders, 1 suspension-feeder, 1 scavenger, 4 omnivores, and 3 predators. The herbivores have not been shown in fig. 44, but these include some diatom-feeders. Although much more intricate relationships are imaginable, all major sources of food evidently are being exploited.

This is different in the brackish water of the Haringvliet, where 3 selective deposit-feeders, 2 omnivores, and 1 predator occur. Common species are, however, only the selective deposit-feeder *Macoma balthica* and the omnivores

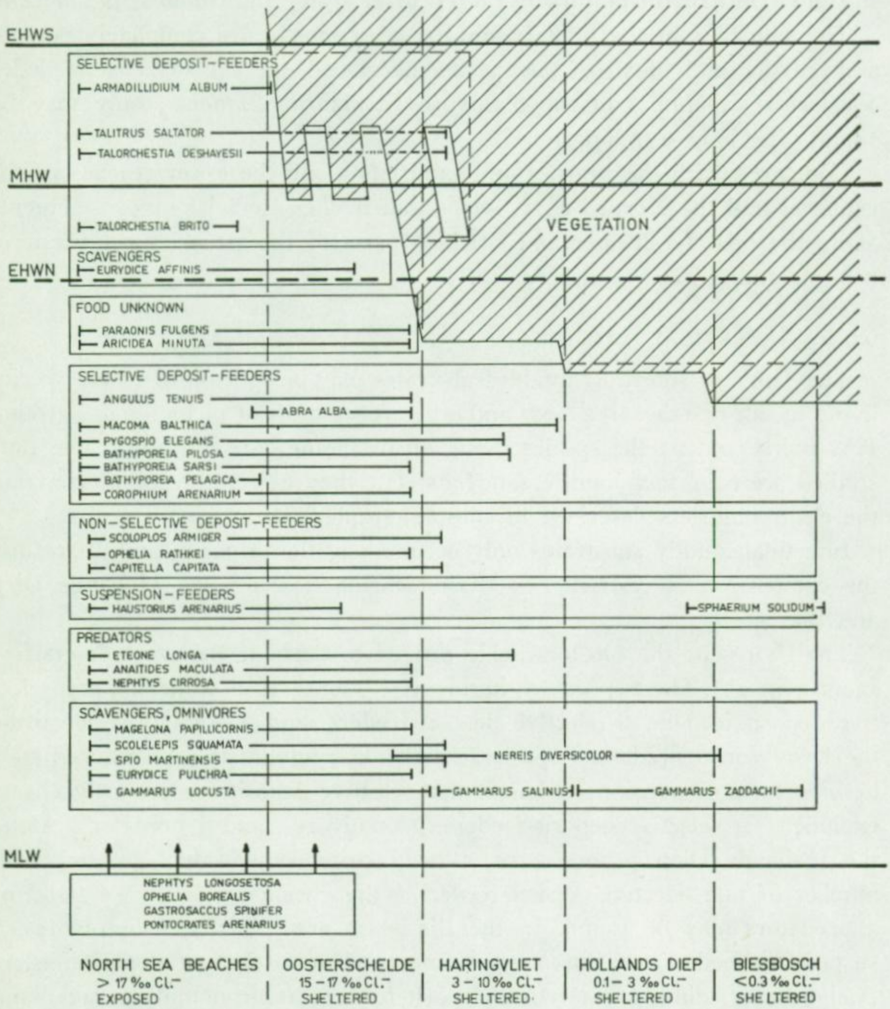

Fig. 44. Habitat and niche diversification in intertidal sand-bottoms.

Nereis diversicolor and *Gammarus salinus*. The potential sources of food thus are exploited much less thoroughly than in the more saline areas. It is interesting in this respect that *Macoma balthica* has been shown to be capable also of suspension-feeding and *Nereis diversicolor* of selective and non-selective deposit-feeding, of suspension-feeding and of predatory behaviour. Thus a large number of more or less specialized species is balanced to some extent by a low number of unspecialized species.

The freshwater area of the Hollands Diep with irregular influxes of brackish water, has only very few sandy intertidal areas; these seem to be inhabited only by the omnivores *Nereis diversicolor* and *Gammarus zaddachi*.

The sandflats in the tidal freshwater area mostly are completely barren, and the few individuals of the species mentioned, viz. the suspension-feeder *Sphaerium solidum* and the omnivore *Gammarus zaddachi*, only may be found after long searching.

Compared with the beaches and sandflats along the lower reaches of the estuaries and the North Sea, it seems that in the intertidal sandy sediments along the tidal freshwater and brackish parts of the estuaries many microhabitats and niches are unoccupied.

6.6.4.4. Intertidal mudbottoms

The fauna of intertidal muddy substrates may be split up in 1) the species living in salt-marshes, reedbeds and other vegetations of phanerogams around HW-mark, and 2) the species living on or in the bare mudflats. The flats studied were in fact muddy sandflats, but they differed very much from the clean sandflats described in sub-paragraph 6.6.4.3.

Intertidal muddy substrates only occur along the estuaries and, therefore, the comparison is restricted to Oosterschelde, Haringvliet, Hollands Diep and Biesbosch.

The shores of the Oosterschelde proved to harbour the most diversified fauna (fig. 45). The 7 species of herbivores, 5 suspension-feeders, 4 non-selective deposit-feeders, 9 selective deposit-feeders, and 2 omnivores constitute the basis for 6 predatory species. In the Haringvliet this is reduced to 3 herbivores, 2 suspension-feeders, 1 non-selective deposit-feeder (Oligochaeta excluded), 4 selective deposit-feeders, 2 omnivores, and 3 predators. Along the Hollands Diep 5 herbivores, 1 or 2 suspension-feeders, an unknown number of non-selective deposit-feeders (Oligochaeta), 1 omnivore and 2 or 3 predators may be found. In the Biesbosch area, finally, 6 herbivores, 7 suspension-feeders, an unknown number of non-selective deposit-feeders (Oligochaeta) and of selective deposit-feeders (chironomid larvae), and about 6 predators may be found.

Thus, a minimum of species occurs in the mudflats along the Haringvliet and Hollands Diep. This minimum is accompanied by a less pronounced minimum of the species living between the vegetation.

Along the salinity gradient species are replaced by others living in the same niche and habitat. For instance, in the salt-marshes along the Oosterschelde *Hydrobia ulvae* is abundant and *Assiminea grayana* is present.

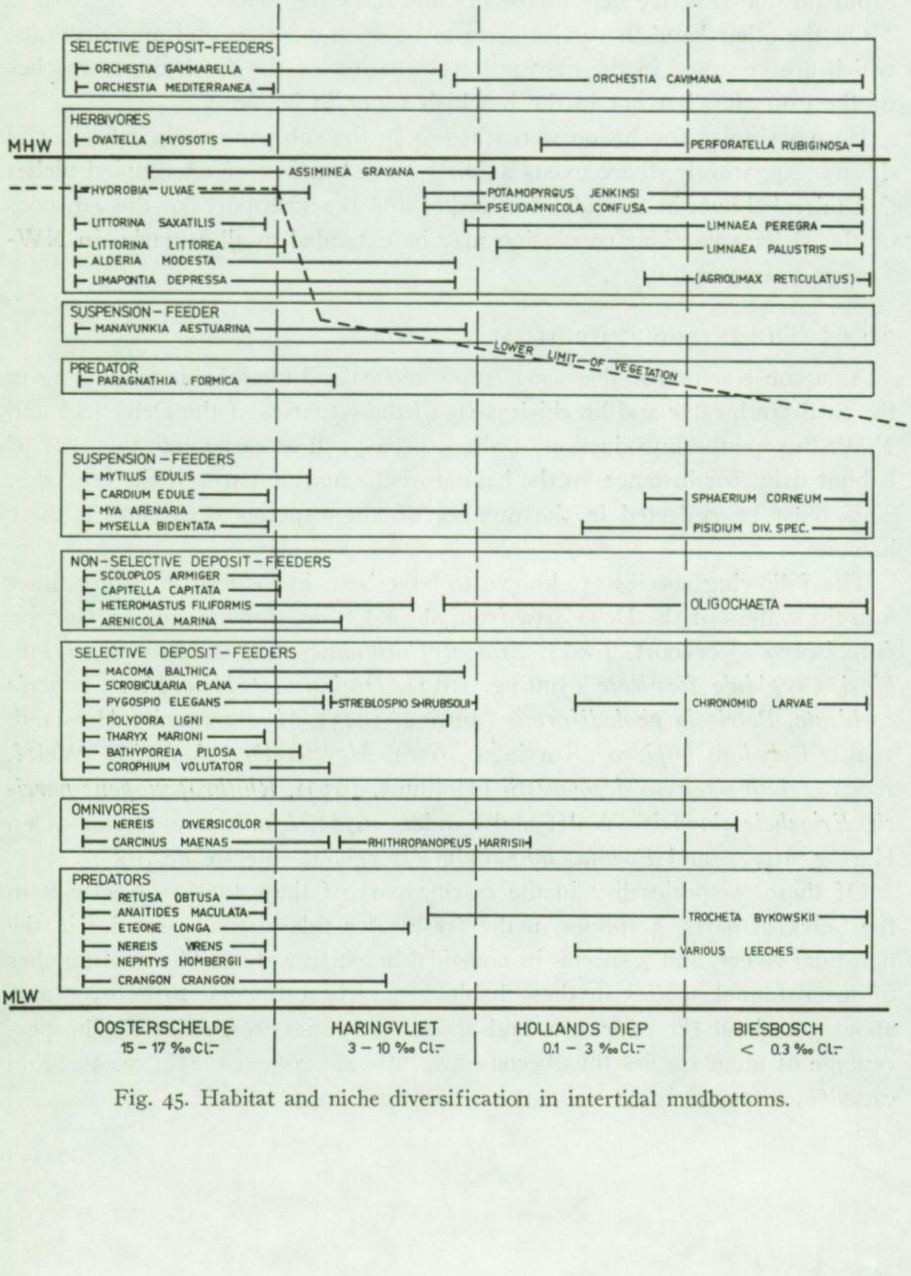

Fig. 45. Habitat and niche diversification in intertidal mudbottoms.

Along the Haringvliet *A. grayana* has become abundant and *H. ulvae* has dropped out. Now *Potamopyrgus jenkinsi* and *Pseudamnicola confusa* come to the fore and the latter two species completely take over when *A. grayana* disappears along the Hollands Diep. Hence, everywhere along the estuarine salinity gradient 1-3 little snails of the hydrobiid type live between the vegetation just around HW-mark.

Similar observations may be made for the species of *Orchestia,* the capitellid non-selective deposit-feeders and the Oligochaeta.

On the other hand there also seem to be several niches and microhabitats, which are occupied in the marine lower reaches or the fresh upper reaches of the estuaries, but not in the brackish water in between.

Here a similar conclusion is reached as in the sub-paragraphs 6.6.4.2. and 6.6.4.3. Apparently, there exists a fairly large number of unoccupied niches and microhabitats in the tidal freshwater and brackish parts of the estuaries of the Delta area. This conclusion may be extended to all estuaries in NW-Europe (paragraph 6.5.1.).

6.6.4.5. THE INTRODUCTION OF ALIEN SPECIES

As a consequence of the many empty niches and microhabitats existing in the tidal freshwater and brackish parts of the estuaries of the Delta area and N.W. Europe the introduction of alien species will be easier into this type of habitat than, for instance, in the habitat of the marine parts of the estuaries. This must be reflected in the number of alien species occurring in these habitats.

The following species are known to have been introduced in recent times into the waters of the Delta area from abroad: *Cordylophora caspia, Garveia franciscana* (Vervoort, 1964), *Lithoglyphus naticoides, Potamopyrgus jenkinsi, Crepidula fornicata* (Jutting, 1933), *Dreissena polymorpha, Congeria cochleata, Petricola pholadiformis* (Jutting, 1943), *Mya arenaria* (Hessland, 1945), *Polydora hoplura* (Korringa, 1951), *Mercierella enigmatica* (Wolff, 1969a), *Aethyaephyra desmarestii* (Holthuis, 1950), *Rhithropanopeus harrisii, Eriocheir sinensis* (Wolff and Sandee, 1971), *Elminius modestus* (Den Hartog, 1953), and *Balanus amphitrite (*Borghouts-Biersteker, 1969).

Of these, 5 species live in the marine part of the estuaries, 6 species in the brackish parts, 5 species in the freshwater tidal areas, 5 species in the non-tidal rivers, and 7 species in non-tidal brackish waters. The total number of macrofaunal species in these habitats may be estimated to be over 250, about 30, about 60, over 100, and about 25 species, respectively. The percentage of alien species thus becomes ca. 2%, ca. 20%, ca. 8%, ca. 5%, and ca. 28%, respectively.

Especially in brackish water, tidal as well as non-tidal, the percentage of alien species is high (20% and 28%, respectively) indicating that, compared with other habitats, immigration into the brackish water habitats of N.W. Europe is relatively easy. This notwithstanding the fact that the number of brackish water species available all over the world is low when compared with the number of freshwater and shallow-water marine species. Also in the brackish water of the San Francisco Bay estuary the number of introduced species is exceptionally high (about 15%; Filice, 1958).

These data indicate that the brackish water habitat in N.W. Europe (and on the Pacific Coast of America) is "undersaturated" with respect to its number of species.

7. POSSIBLE CAUSES FOR THE BRACKISH WATER MINIMUM OF SPECIES

7.1. INTRODUCTION

The low number of species in the brackish part of estuaries when compared either to the sea or the river, has been known for many years (Remane, 1934; Alexander, Southgate & Bassindale, 1935). Many different explanations have been forwarded for this phenomenon, but there does not seem to exist a communis opinio yet. In the following sections it is attempted to investigate the various explanations forwarded, with the main emphasis on the soft-bottom macrofauna of the Delta area.

7.2. POLLUTION

The Rhine and the Scheldt drain polluted water into the brackish parts of the estuaries of the Delta area (paragraph 3.4.9.). Consequently, these rivers, contrary to the Meuse, harbour a very poor freshwater fauna and it might be expected that this poverty extends into the brackish water area as far as the polluted water extends its influence. Indeed a number of anadromous fishes, affected primarily in their spawning areas, and the prawn *Palaemon longirostris* are known to have declined owing to water pollution (Heerebout, 1973). For other brackish water species this has not been found, although it has to be admitted that the information on earlier periods is very scanty.

However, the other estuaries discussed in paragraph 6.5.1., also the unpolluted ones, all show the same picture of a minimal number of species in the tidal freshwater and brackish areas.

Further, the freshwater tidal area of the Biesbosch contains fairly clean water and, nevertheless, its sand- and mudflats (sub-paragraphs 6.6.4.3. and 6.6.4.4.) are very poor in species. Lastly, the fauna of many unpolluted brackish inland waters in the Delta area is of about the same poverty as the fauna of the estuarine brackish waters.

It is concluded that water pollution is not the cause of the poverty of species in the tidal brackish and freshwater parts of the estuaries of the Delta area.

7.3. TURBIDITY

Turbidity is highest in the brackish parts of the estuaries (paragraph 3.4.8.). Unfavourable results of a high turbidity are deposition of silt and mud on all types of substratum, filling of the interstices of sandy sediments with mud and an unfavourable ratio between the amounts of food and other particles for suspension-feeders. Moreover some species probably will meet with difficulties in keeping clean their respiratory apparatus. Therefore, it seems possible that high turbidity inhibits the occurrence of many marine and freshwater species in the estuarine environment. It is, however, usually very difficult to distinguish between the influence of turbidity and the influence of salinity in the same area. In the Delta area, however, this happens to be possible.

It appeared (paragraph 6.3.7.) that a high turbidity of estuarine waters may inhibit the occurrence of certain species, but that a large number of other species is able to thrive under such conditions. Therefore, turbidity does not explain why there are so few brackish water species in the brackish parts of estuaries.

7.4. INSTABILITY OF SALINITY

Attempts to explain differences in species diversity by differences in stability of the environmental factors were made by Klopfer (1959), Fischer (1960), Dunbar (1960) and Connell & Orias (1964), whereas Sanders (1968) integrates their ideas in his stability-time theory (compare section 7.8.). The former three authors especially considered climatic instability on a world-wide scale, but this does not provide an explanation for differences in species diversity along the main axis of an estuary. Connell & Orias (op. cit.) argue that in environments where the physical factors in general are more stable, less energy is required for regulatory activities, and so more energy becomes available for the further chains in the food web. Such a stable production of food would allow a farreaching subdivision of the environment, thus a high species diversity. Sanders (op. cit.) also thinks that stability of the physical environment plays an important role in the determination of species diversity and states that in environments where the species must adapt continually to changes in the physical factors, the biological interrelationships, and thus the species diversity, will not be allowed to develop very far. Slobodkin & Sanders (1969) speak of the predictability of the physical environment and conclude that regions characterized by high species diversity also tend to be characterized by high environmental predictability and low variability. Moreover they show that species living in predictable environments theoretically are prone to speciation in the course of evolution, whereas species in unpredictable environments easily may become extinct.

Van Leeuwen (1965, 1966) followed another line of reasoning. He formulated a Relation Theory based on a cybernetical approach to analysis of terrestrial vegetations. This theory relates the number of species to be found in an area with the variety in space and the stability in time of the environmental factors in this area. It predicts that relatively stable environments with no or only slow changes of the environmental factors tend to be rich in species, whereas relatively unstable environments are poor in species. Beeftink (1965, 1966) tested this theory for the salt-marsh vegetation of the Delta area. He was able to demonstrate a minimal number of species in those areas where salinity was most unstable.

Margalef (1960, 1967, 1968) developed similar ideas based on his plankton studies.

The unstable brackish estuarine environment with its low number of species, in between the stable marine and freshwater environments with their high number of species, can be fitted in this theory, as was done by Beeftink (op. cit.). This is also possible for the results of this study.

Moreover, Den Hartog (1960a, 1964a) showed that many brackish water species penetrate to lower salinities in the stable Baltic than in the unstable estuaries of the Delta area, another fact in agreement with this theory.

On the other hand Remane (1934, 1958) stressed that the middle and inner Baltic, with a relatively stable low salinity, are much poorer in species than the western Baltic (Belt Sea) with an unstable high salinity.

It could also be shown in the sub-paragraphs 6.6.4.2. and 6.6.4.3. that the subtidal and intertidal sandbottoms of the freshwater tidal area with its stable low salinity, are much poorer in species than the comparable habitats in the unstable brackish parts of the estuaries.

These observations apparently form exceptions to the rules formulated by Van Leeuwen (op. cit.) and Margalef (op. cit.). Moreover, it has to be noted that, although their theories are in accordance with a large part of the observations, they do not give an evolutionary explanation for the fact that so few species have evolved in habitats with unstable environmental factors. If a few species have done so, why have not many others?

Thus it appears that the hypotheses on the relation between species diversity and environmental predictability indeed may be used to explain part of the differences in species diversity along the main axis of the estuaries of the Delta area, but that they fail to do so especially for the situation in the Baltic and that in the freshwater tidal area of the Biesbosch. Therefore other explanations have to be looked for.

7.5. INSTABILITY OF TEMPERATURE

Compared with the sea and the freshwater of the river the estuarine environment is not only unstable with respect to salinity, but also to temperature. However, against instability of temperature of the estuarine environment as a cause of the reduced number of species, it also may be objected that, if a few species have been able to adapt, why have not many others? Moreover, in the brackish Haringvliet as well as in the marine Oosterschelde the instability of temperature is of the same magnitude, but the number of species occurring in the latter is at least 10 times that in the former.

7.6. SIZE OF BRACKISH WATERS

Chislenko (1964) — whose paper could not be studied in detail — believed that marine animals have difficulties in passing into brackish and freshwater, because they must adapt to life in relatively small areas, and, consequently, in relatively small numbers. This would be the reason for the relative paucity of the brackish water fauna.

Although this difficulty indeed may exist, the following objections can be made against this theory. Firstly, brackish seas, like the Baltic, the Black Sea, and the Caspian Sea, are also poor in species when compared to normal seas, despite their large size. Secondly, the same difficulty more or less exists for the freshwater fauna, but this does not appear from the number of freshwater species. Lastly, this hypothesis does not explain why the brackish waters have not been colonized from the fresh water.

7.7. THE CRITICAL SALINITY HYPOTHESIS OF KHLEBOVICH

Khlebovich (1968, 1969) demonstrated that in the salinity range of about 3-4.5$^0/_{00}$ Cl′ the relative ionic composition of nearly all brackish waters changes considerably. This salinity range, therefore, would constitute an important boundary between marine and freshwater faunas. This hypothesis is confirmed by data from the Delta area. However, Khlebovich (1969) also ascribed the poverty of species of brackish waters to the presence of this boundary, called horohalinicum by Kinne (1971).

There exists, however, a number of species occurring on either side of this boundary, for instance *Assiminea grayana* and *Gammarus zaddachi*. Apparently it is possible to cross it, so the question arises why not many other species have done the same in the course of evolution. Also this hypothesis does not explain why the number of species between, for instance, 5 and $10^0/_{00}$ Cl′ is much lower than in normal seawater.

When Khlebovich (op. cit.) meant that the poverty of species will be caused by a continually changing position of this boundary, his argument becomes identical to those discussed in section 7.4.

7.8. THE TIME-STABILITY HYPOTHESIS OF SANDERS

7.8.1. THE TIME-STABILITY HYPOTHESIS

Based on earlier theories of Klopfer (1959), Dunbar (1960), Fischer (1960) and Simpson (1964), Sanders (1968) developed a time-stability hypothesis to explain differences in the diversity of the soft-bottom fauna of estuaries, shallow seas and and the deep-sea. The part of this hypothesis based on stability was placed on a better theoretical basis by Slobodkin & Sanders (1969).

They distinguish between two types of environments, forming the two ends of a gradual transition. One is the unpredictable environment with widely and irregularly fluctuating environmental factors; in the other, predictable environment these factors remain constant and uniform for long periods. They argue, that according to genetical and ecological theory, the amount of environmental predictability dictates to some degree the properties of the organisms in an environment. Species living in areas of low predictability therefore will be subject to more probable extinction and less probable speciation than species in high predictability areas. Moreover, the invasion of areas of low predictability by species from areas of high predictability is less probable than the reverse process. When invasions occur, it is less probable that an invasion of a species from an area of low predictability into an area of high predictability eliminates a resident population, but this may be expected in the case of the reverse process. Therefore, Slobodkin & Sanders (op. cit.) conclude that species diversity tends to become greater in areas of high predictability.

So far, their arguments are related to the cybernetical and information-theoretical hypotheses of Van Leeuwen (1965, 1966) and Margalef (1968).

The important addition by Sanders (op. cit.), however, is that he takes over Fischer's (1960) suggestion that the geological time-scale also has to be considered. The evolution of a highly diverse fauna requires not only a predictable environment, but also the existence of this environment during a considerable amount of time. Of course, time will also favour the development of a more diverse fauna in an unpredictable environment.

Although it is recognized that the low number of species in the brackish parts of the estuaries of N.W. Europe may partly be attributed to the low predictability of this environment with respect to salinity and temperature (compare paragraphs 6.3.1., 6.3.2., and sections 7.4., and 7.5.), it appears also that the influence of time has to be investigated, especially with regard to the exceptions mentioned in section 7.4. Indeed, Hedgpeth (1953), Dahl (1956, 1959), and Muus (1967) already stressed that, geologically speaking, most brackish waters are short-lived. This also implies that brackish water species always must be disappearing and that new forms always must be recruted. Also Zenkevitch (1959, 1963) stressed the importance of the geological history for brackish water faunas.

7.8.2. THE GEOLOGICAL HISTORY OF THE ESTUARIES OF THE DELTA AREA

Estuaries exist only in periods of rising sea level (Russell, 1967). Although this may be true from the hydrographical and geological point of view, it is nevertheless assumed that also in periods of falling sea level brackish water areas with estuarine characteristics exist at the mouths of large rivers (Hedgpeth, 1966). Therefore, it may be concluded that the estuarine brackish water environment exists already a very long time in N.W. Europe.

On the other hand, this environment has experienced many changes, especially during the Pleistocene glaciations. This may be illustrated by the history of the estuaries of the Delta area during the last glaciation.

At the maximum of the Würm or Weichselian glaciation, about 18-20.000 years ago, the sea level was 100-120 m below the present day sea level (Emery, 1967; Emery & Garrison, 1967), although recently levels of even -150 to -175 m have been mentioned (Veeh & Veevers, 1970; Jongsma, 1970). Over Scandinavia, the northern part of the North Sea and Scotland an ice-cover existed (Fig. 46), causing all rivers of the North Sea basin to run jointly to the Atlantic Ocean through the English Channel (Valentin, 1957; Jelgersma, 1961; Veenstra, 1965; De Jong, 1967; Woldstedt, 1967). Smith & Hamilton (1970) indeed found that the Hurd Deep north of Normandy — the deepest part in the English Channel — was eroded by currents within a river mouth.

The large N.W. European river running through the Channel reached the Atlantic Ocean somewhere to the west of the present entrance to the English Channel. Certainly a large brackish water area has existed at the mouth of this river, where the environment probably was comparable to the present conditions at the mouths of the large Siberian rivers.

Similar brackish water environments probably have existed off the mouths of the Loire and the Garonne-Gironde in France (Lapierre, 1970) and off the rivers at the western side of the Iberian peninsula. However, in between, along the northern coast of the Iberian peninsula, a stretch of 600 km of steep rocky coast nearly without possibilities for the development of estuarine environments, occurred.

After the maximum of the last glaciation the sea level started to rise and

Fig. 46. Topography of Western Europe at the maximum of the Weichselian or Würm glaciation (after Valentin, 1957). The thick lines surround the glaciated areas; the thin lines denote coastlines and rivers. The hatched area represents a hypothetical freshwater lake (Veenstra, 1965).

showed a rapid rise up to about 4-7000 years ago. Since that time the rising gradually proceeded slower, but it did not yet come to an end (Jelgersma, op. cit.; Emery, op. cit.; Bird, 1969). With the rising sea level the coast lines and the estuarine environments at the mouth of the rivers shifted in a landward direction. In this way the estuary at the mouth of the large river through the Channel was displaced upstream into the direction of the Strait of Dover. But at the same time the connection across the North Sea between the ice-covers of Scotland and Scandinavia became disrupted and the sea water invaded the North Sea area also from the North. The inspection of the depth contours in the southern North Sea, however, makes it probable that the area of the Southern Bight was reached first by the sea invading from the South through the Strait of Dover (Jelgersma, op. cit.). This means that the estuary of the large river through the Channel was able to displace upstream as far as the present estuaries of the Thames, and of the rivers of the Delta area (fig. 47). The Ems, the Weser, and the Elbe, however, were reached by the sea from the North.

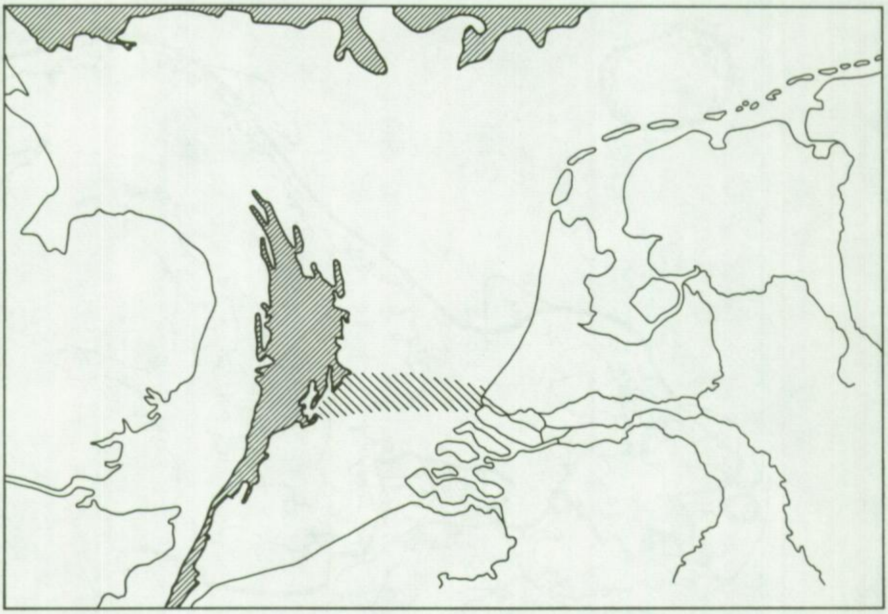

Fig. 47. Topography of the southern North Sea about 9300 years ago (after Jelgersma, 1961). Areas covered by water are finely hatched; the supposed course of Rhine and Meuse is widely hatched.

About 7500 years ago the rising North Sea invaded the present Delta area and the present estuarine environment started its development (De

Jong, Hageman & Van Rummelen, 1960; Jelgersma, op. cit.; De Jong, op. cit.).

During the displacement of the estuary mentioned above from the Atlantic shore to the shores of the North Sea the concomitant climatic conditions changed from arctic to warm-temperate and then again became slightly colder.

The series of events sketched above for the period between the maximum of the last glaciation and to-day, of course, occurred every time during the period between the maximum of a glaciation and that of the following interglacial, whereas the reverse process must have occurred between the maximum of an interglacial and the maximum of the following glacial. Especially during the period from the maximum of the Riss or Saale glaciation to that of the warm Eemian interglacial the change must have had a large amplitude.

7.8.3. THE HISTORY OF THE ESTUARINE AND BRACKISH WATER FAUNA OF N. W. EUROPE

It does not seem impossible that during the Tertiairy in the western Mediterranean a brackish water fauna, comparable to the present rich Caspian fauna, has evolved (Ekman, 1953). When at the beginning of the Pliocene the connection between the Mediterranean and the Atlantic was re-established, such a fauna may have spread along the neighbouring European coasts. Hence, it is possible that before the start of the Pleistocene glaciations a rich fauna inhabited the brackish water habitats along the European coasts.

During the development of the first glaciation this largely hypothetical fauna will have been exterminated in its northernmost localities, but climatic conditions suitable for this fauna will have originated further to the south. Owing to the fact that probably many representatives of that brackish water fauna will have possessed non-pelagic larvae (Needham, 1930; sub-paragraph 6.6.3.2.), it will have been difficult for many species to colonize brackish waters more southerly, owing to the discontinuous nature of the estuarine and brackish water habitat. Hence, the greater part of this hypothetical Pliocene brackish water fauna had to endure the climatic change in the estuaries and brackish water areas where it occurred before the first glaciation or else it had to become extinct.

During the first interglacial, the remaining brackish water fauna had to shift again to the North because the southernmost localities probably became unsuitable for many species, owing to the rising temperature and the decreasing river discharge.

Similar events will have occurred during each glaciation. Also at the onset of the last glaciation the brackish water fauna inhabiting the brackish waters of N.W. Europe will have been exterminated in all habitats east of the line Brittany-Britain (fig. 46). A shift to areas further south for most species probably was very difficult because the very inhospitable northern coast of Spain will have offered an important barrier for species with a non-pelagic development. So, the remaining species had to survive the arctic climate in the brackish habitats on the western coast of France. If there existed warm-adapted brackish water species in N.W. Europe during the preceding warm Eemian interglacial, it seems very improbable that these have survived the Weichselian glaciation on the western coast of France, and many of them will have become extinct.

After this glaciation the species which had survived in this area, were able to migrate along with the displacing estuarine environment towards the North Sea and the estuaries of the Delta area (paragraph 6.5.1.). When the southern North Sea had been reached, the coastal topography will have made it possible to migrate further eastward via the brackish margins of the North Sea and Wadden Sea towards the rivers Ems, Weser, and Elbe, and eventually to the Baltic. This also explains the similarity of the brackish water fauna all over N.W. Europe (paragraph 6.5.1.), because the fauna of all estuaries can be traced back to a common ancestral area at the western coast of France. However, the species which possibly survived the last glaciation further south, had to cross the inhospitable coast of northern Spain in the first place. When this met with success they probably arrived in N.W. Europe when the estuaries already were displaced upstream and when the estuarine environment was already split up into numerous estuaries at the many rivermouths. Their further dispersal thus was hampered by the discontinuous nature of their habitat. It is not impossible that this is the cause of the restricted distribution of species like *Melita pellucida* and *Gammarus chevreuxii*, not found east of the English Channel.

Burbanck (1959) supposes that comparable events have acted on the populations of *Cyathura polita* along the Atlantic coasts of N.W. America.

The hazards sketched above for a brackish-water fauna during the Pleistocene, exist also for a fauna adapted to the conditions in a freshwater tidal area. Because it is probable that during a glaciation such an area would be frozen during a very large part of the year, it may be assumed that such a fauna has met with even more difficulties during the various glacial and interglacial stadia. This probably explains why the freshwater tidal area of the Biesbosch is so poor in species inhabiting the intertidal zone.

Of course, it is very well possible that at the height of the last glaciation arctic brackish water species occurred in the brackish areas at the western coast of France. However, they apparently have not been able to adapt to the high summer temperatures of the N.W. European estuaries. Only in the colder Baltic such species have been able to maintain themselves after they had reached this area (Ekman, 1953).

It may be concluded that the series of glaciations and interglacial stadia will have been very difficult to survive for a fauna with partly a non-pelagic development and a discontinuous habitat along the coasts of N.W. Europe. Therefore, it is assumed that the Pleistocene glaciations are mainly responsible for the poverty of the present estuarine and brackish water fauna of this area. A rich brackish water fauna in the Pliocene has been assumed to illustrate this hypothesis more clearly, but such a rich Pliocene fauna of course is no prerequisite. Also when the brackish water fauna of N.W. Europe was already poor in species in the Pliocene owing to a similar geological instability in earlier periods, the Pleistocene glaciations would have been a negative factor for the further development of this fauna.

Since the last glaciation took place not more than 18-20,000 years ago, time probably has been too short for the evolution of new brackish water species as a result of geographical isolation (Mayr, 1963).

7.8.4. GEOLOGICAL HISTORY AS AN EXPLANATION FOR THE POVERTY OF BRACKISH WATER FAUNAS

In the preceding paragraph it was concluded that the Pleistocene glaciations had a strong negative effect on the development of a brackish water fauna in N.W. Europe. The same hypothesis may be defended for the brackish water faunas of the Pacific and Atlantic coasts of N. America, although the latter fauna probably found better possibilities for survival in the southern part of its range, where a coherent series of estuaries and lagoons extends down to the Caribbean area.

Other brackish water faunas have been affected much less by the Pleistocene glaciations and the concomitant climatic changes, for instance the Ponto-Caspian fauna. This fauna dates back to long before the Pleistocene glaciations (30 million years? — Ekman, 1953; Zenkevitch, 1963). The result of an uninterrupted development in roughly the same area was a highly diversified brackish water fauna with some 700 species of which not less than 222 are endemic to the Ponto-Caspian area.

The S.E. Asian brackish water areas probably have been displaced slightly by sea level changes in the Pleistocene period, but a very long and uninterrupted existence of such an area under comparable climatic conditions seems very probable. This would explain sufficiently the rich development of the S.E. Asian brackish water fauna (paragraph 6.5.2.).

Von Martens (1857) presented another explanation for the rich development of this brackish water fauna, extending his conclusion to all tropical brackish faunas. He assumed that the absence of freezing and the stable temperature conditions in the tropics made the invasion of fresh and brackish waters by stenotherm marine organisms easier. Although this hypothesis cannot be rejected, Pelseneer (1905) remarked that the greater part of the species mentioned by Von Martens came from the S.E. Asian area, thus pointing to a local character of the phenomenon observed by von Martens.

Also Panikkar (1951) based part concerning his hypothesis on the richness of the S.E. Asian brackish water fauna on climatic conditions. On the base of physiological work he concluded that osmoregulation is easier at high temperatures and that therefore tropical brackish water faunas are richer in species than temperate ones. Hutchinson (1967) added that for species with an imperfectly developed ionic uptake mechanism it will be easier to penetrate brackish and fresh waters at high temperatures. This hypothesis, also defended by Den Hartog (1971), may be true to some extent, but it meets with the same objections as can be made against Von Martens' hypothesis. Moreover, many other species show better capacities for osmoregulation at low temperatures (Remane, 1969; Kinne, 1971).

Caspers (1967) holds that the relative richness of the tropical brackish water fauna may be explained as a matter of chance. He argued, that since the marine tropical fauna is much richer than the marine temperate fauna, it is logical that a comparable rate of invasion of brackish waters creates a much richer brackish water fauna in the tropics than in the temperate zone.

Summarizing, the hypotheses of Von Martens (op. cit.), Panikkar (op. cit.), Caspers (op. cit.) all may contribute to the explanation of the richness of the brackish water fauna of S.E. Asia, but they also do not contradict Sanders' time-stability hypothesis.

Therefore, it has to be maintained that, besides the predictability of the environment, the geological history is very important for the explanation of the differences of the numbers of species occurring in brackish waters. Southwood (1961) forwarded a very similar hypothesis to explain the differences in the numbers of phytophagous insects on various British species of trees and Briggs (1970) assumes that similar events have caused the relative poverty of the Atlantic marine fauna.

It seems useful to investigate also the influence of geological history on the speciation in brackish water faunas.

It has to be emphasized that brackish water faunas have to evolve in brackish habitats, because marine and freshwater species cannot give rise to brackish water species as long as such invading populations remain in contact with the main population in the sea or in fresh water. This is because a gene-combination suited to life in estuaries or other brackish waters would be broken up every time there was an exchange of genes with the main population (Mayr, 1963).

Two possibilities for the origin of brackish water species can be distinguished. The first one has been described by Hutchinson (1967) and Slobodkin & Sanders (1969). They postulate a species occurring in the coastal sea as well as along the seaward part of the estuarine salinity gradient. When this species comes into contact with a more stenohaline, but competitively superior species, the former species will be driven out of the seaward part of its range and become restricted to the estuarine part. Competition in the border zone between these species will result in a recombination of the available gene material, causing a shift of the optimum of both species away from the border zone. This will result in a shift to lower salinities of the optimum of the first species. Of course, such events may occur repeatedly, causing a series of species with different salinity optima along the estuarine salinity gradient. In N.W. Europe such events may have occurred in the genera *Nereis, Gammarus, Corophium, Jaera,* and *Sphaeroma,* for instance. Theoretically, such a phenomenon is also possible for freshwater species, but in N.W. Europe no instances are known. Hutchinson (1967) means that this type of evolution will have occurred especially in groups with a relatively impermeable body wall, such as crustaceans. The influence of the Pleistocene glaciations on the frequency of this mode of evolution of brackish water species could not be estimated, but it is clear that this may happen in any estuary at any moment. The Pleistocene glaciations possibly favoured that closely allied species, required for this type of evolution, came into contact, but on the other hand they formed a negative factor for the species forced into the estuary.

A second possibility for the evolution of brackish water species can be found in isolated and gradually freshening seas. Rygg (1970) assumes this to have happened in the case of *Cardium glaucum,* and the Ponto-Caspain fauna shows another instance. Hutchinson (op. cit.) thinks that that type of evolution especially will have occurred in groups with a large semipermeable surface area, such as molluscs. The frequency of this type of evolution is probably very low, but when it occurs, it may act on a large number of species at the same time. Runnegar & Newell (1971) give a beautiful illustration of this possibility for a Permian brackish-water fauna in South-America. During the Pleistocene glaciations the geological changes probably have been too rapid for this type of evolution. The period since the last glaciation has been too short for this way of evolution (paragraph 7.8.3.).

For existing brackish water species the discontinuous nature of their habitat forms a strongly positive factor for further speciation by geographical isolation, although this is counteracted by the regularly occurring stress-situations in this type of habitat (Slobodkin & Sanders, 1969). During the Pleistocene glaciations, however, the duration of the periods of isolation was probably not long enough to give rise to specific differences. On the other hand, Stock & Pinkster (1970) were able to demonstrate subspecific differences between two populations of *Gammarus duebeni* probably arisen during the last two glaciations. It is concluded that although the geographically discontinuous habitat of brackish water faunas seems to favour speciation, this has been counteracted in N.W. Europe by the Pleistocene glaciations.

Remane (1958) stressed that individual bodies of fresh water are of the same geological instability as brackish waters, but nevertheless contain much more species. Although this is true, the major difference is that bodies of fresh water always are connected to a fresh drainage system, thus permitting an escape and a continuous existence of their fauna when they disappear. Brackish waters, however, nearly always are isolated, either by land, by seawater or by fresh water and their disappearance thus often will result in the extinction of their fauna.

Conclusions to be drawn from this and the preceding paragraphs are that the Pleistocene glaciations in N.W. Europe most likely have caused the extermination of many earlier occurring brackish water species, and that they probably counteracted the evolution of new species.

Hence, the estuarine and brackish-water fauna of N.W. Europe and its history form a beautiful illustration of Sanders' stability-time theory, which requires a stable habitat with constant and uniform environmental conditions during a very long period of time for the evolution of a rich and diversified fauna.

8. SUMMARY

During the years 1958-1970 a study has been made of the soft-bottom macrofauna (Coelenterata, Mollusca, Echiuroidea, Polychaeta, Archiannelida, Crustacea Malacostraca) of the estuaries of the rivers Rhine, Meuse, and Scheldt in the southwestern part of The Netherlands and of the adjacent part of the North Sea.

1751 samples were taken with 0.1 and 0.2 m^2 Van Veen grabs; in the intertidal zone several hundreds of samples were dug out, whereas further samples were taken for the analysis of interstitial polychaetes and archiannelids. Of the environmental factors especially salinity, sediment composition, current velocity, water temperature, oxygen saturation, turbidity, water pollution, exposure to waves, and the influence of ice have been investigated. Salinity shows a gradient from over 19.0‰ Cl' in the offshore waters to below 0.3‰ Cl' in the freshwater tidal area. Sediments mostly consist of medium, fine and very fine sands, but coarse sands, muds, and peat banks also occur.

Current velocity is in general below 1.5 m/sec., whereas water temperatures range between about 1 and 22°C in the course of the year. Oxygen saturation is low in the rivers (0-70%) and shows in the brackish water areas a gradient to values over 100% reached in the marine parts of the estuaries. Water pollution shows the reverse pattern, but turbidity is highest in the brackish parts of the rivers. The larger part of the shores of the estuaries is sheltered against wave-action, but the beaches along the North Sea may be considered as semi-exposed. The influence of ice is most severe in the freshwater tidal area.

Food is abundant in the estuaries, but less in the offshore parts of the North Sea.

Taxonomical remarks have been made on, among others, *Polinices polianus, Venus gallina striatula, Eteone foliosa, Nereis virens, Nephtys caeca, Aricidea minuta, Spio martinensis, Streblospio shrubsolii, Tharyx marioni,* and *Ophelia borealis.*

For 2 coelenterates, 19 gastropods, 44 lamellibranchs, 1 echiurid, 76 polychaetes, 4 archiannelids, 6 leeches, 15 decapod crustaceans, 2 mysids, 8 cumaceans, 1 tanaid, 9 isopods, 31 amphipods, 8 echinoderms, and 1 species of *Branchiostoma* the distribution is compared with the environmental data mentioned above or earlier papers treating this have been enumerated. For many species this comparison was carried out by means of a maximum-likelihood method.

The following general trends in the distribution of the species studied over the estuarine area were observed.

The biological limit of the estuarine environment at the seaward side could be placed where the level sea-bottom changes into a topography of tidal channels and shallows. At the landward side no clear-cut limit could be demonstrated.

The brackish-water minimum in the species distribution demonstrated first by Remane (1934) could be confirmed for the estuaries of the Delta area. It appears that nearly all species occurring in the brackish water area also live or may live in either the more marine parts of the estuaries or in fresh water. Hence, nearly all may probably be considered as euryhaline marine or freshwater species.

The fauna investigated could be divided in a relatively stenotherm component occurring only offshore and a relatively eurytherm component occurring offshore as well as in the estuaries.

Below low water level no species could be demonstrated to be restricted by hydrostatic pressure to a certain depth range. Only three species could be shown to be restricted to the intertidal zone.

Several species proved to be restricted to a certain sediment range. Of the species occurring in the brackish water area most appeared to prefer muddy sediments. Therefore, species considered as brackish-water species probably often are really euryhaline inhabitants of mud-bottoms.

No species could be shown to be governed directly in its distribution by the exposure to wave-action, but many proved to be so indirectly by the nature of the sediment.

Some species probably were inhibited in their occurrence by a high turbidity. Pollution and low values for the oxygen saturation could be shown to be inhibiting for several species in the freshwater tidal area, but for only very few in the brackish tidal area.

Shortage of food probably is the reason for the absence from the offshore waters of some species common in the seaward parts of the estuaries.

It proved to be impossible to apply any biological brackish water subdivision to the estuaries of the Delta area. The subdivisions proposed earlier could be correlated to hydrographical irregularities of the estuaries.

The species characteristic for the brackish water stretch of the estuaries of the Delta area are demonstrated to occur in nearly all estuaries and brackish waters along the Atlantic coasts of Europe. Some species also occur in the western part of the Mediterranean. This European estuarine brackish-water fauna, however, is nearly completely different with regard to species composition from similar brackish water faunas in South-

Africa, S.E. Asia, New Zealand, and N. Siberia, and along the Pacific as well as along the Atlantic and Gulf coasts of N. America. Hence, a similarity of brackish-water faunas all over the world does not exist.

The species diversity proved to be lowest in the brackish parts of the estuaries and in the intertidal zone of the freshwater tidal area. Especially intertidal sand-bottoms show a gradient from a high number of species in the beaches along the North Sea to nearly no species in the sand flats of the freshwater tidal area; intertidal mud bottoms and subtidal sand bottoms show a comparable pattern. Because the brackish water areas lodge a relatively high number of species introduced from other parts of the world, they are supposed to be undersaturated with regard to the number of species occurring.

Omnivores are relatively abundant in the brackish parts of the estuaries, so the few species occurring apparently occupy wide niches.

The percentage of species with pelagic larvae decreases strongly from the sea to the river, whereas the number of species with a non-pelagic development shows the reverse pattern.

Pollution, turbidity, size of brackish waters and the critical salinity hypothesis of Khlebovich are ruled out as an explanation for the species minimum in brackish waters. Instability of temperature and salinity partially explain this phenomenon, but a satisfactory explanation for the exceptions only is provided by the time-stability hypothesis of Sanders.

It is shown that the history of the N.W. European estuaries during the Pleistocene glaciations sufficiently explains the poverty of brackish water species in these estuaries. Also for other brackish water faunas, geological history probably forms a reasonable explanation for their poverty.

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