Netherlands Journal of Sea Research
5 (*2*)*: 197–226* (*1971*)

DISTRIBUTION AND ECOLOGY OF THE DECAPODA REPTANTIA OF THE ESTUARINE AREA OF THE RIVERS RHINE, MEUSE, AND SCHELDT*

by

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CONTENTS

* Communication nr. 90 of the Delta Institute for Hydrobiological Research, Yerseke, The Netherlands.

I. INTRODUCTION

The Delta Plan aims at the closure of several of the estuaries in the southwestern part of The Netherlands. These estuaries, at present containing tidal salt and brackish water, will become stagnant freshwater lakes. The Delta Institute for Hydrobiological Research was founded to study the biological changes accompanying these large-scale engineering projects (VAAS, 1961).

The basis of such studies is formed by descriptions of the situation before any changes occurred. This paper represents such a description, and concerns the distribution and ecology of the Decapoda Reptantia in the Delta area.

Acknowledgements.—We should like to thank Messrs. P. de Koeijer, W. J. L. Robër, C. de Rooy and L. de Wolf for their help in collecting the material for this study, as well as Mrs. C. H. Borghouts, Mr. L. Braber, Dr. C. den Hartog, Mr. G. R. Heerebout, Dr. K. F. Vaas, and Mr. W. J. M. Vader for making available the data on Decapoda Reptantia collected during their investigations. We are also greatly indebted to Dr. L. B. Holthuis, Leiden, for his help with the identification of various specimens and for the informations he provided about the species kept in the collection of the State Museum of Natural History, Leiden. Prof. Dr. J. H. Stock informed us about the collections of the Zoological Museum, Amsterdam. To many others too numerous to mention individually we are grateful for incidental data and information. We thank Miss E. C. Kanaar for her help in preparing the manuscript.

II. SHORT DESCRIPTION OF THE DELTA AREA AND ITS HYDROGRAPHY

The Delta area (Fig. 1) comprises the estuarine area of the rivers Rhine, Meuse, and Scheldt in the southwestern part of the Netherlands. We refer to the papers by DEN HARTOG (1963) and PEELEN (1967) for a description of the area and for all hydrographical information. In the vicinity of the mouth of the Nieuwe Waterweg, however, the situation seems to be more complicated than was indicated by the latter author.

The median grain-size of the sediments in the estuaries of the Delta area ranges from about 50 μ to about 300 μ and different types of sediment are found in close proximity. Outside of the inlets of the estuaries the median grain-size of the sediments increases in a seaward direction, reaching a value over 500 μ on the westernmost localities sampled during our investigations (JARKE, 1956; our observations). Muddy sediments do not occur subtidally in this area, except for some small patches near the inlets of the estuaries.

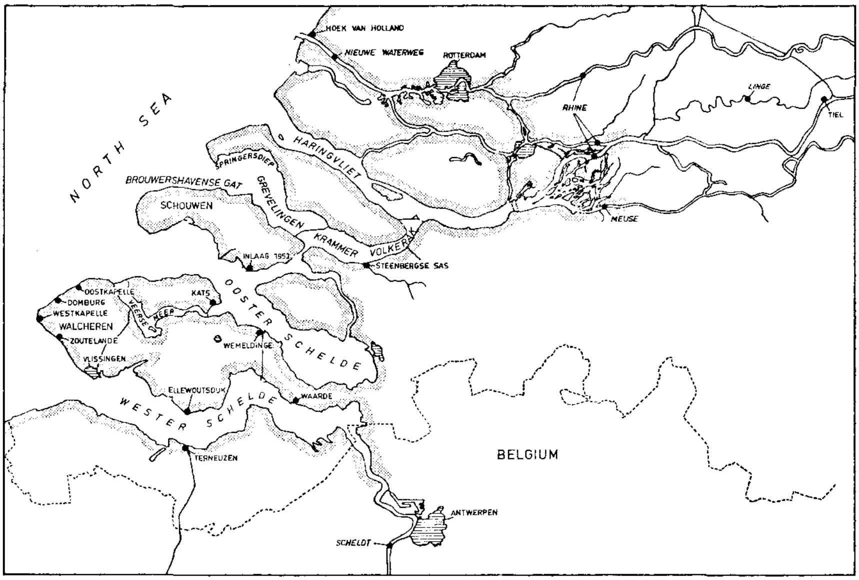

Fig.1. Map of the Delta area.

Rocky shores are lacking in the Delta area, and until recently the animals of such shores with them. Man, however, has created artificial rocky shores by constructing harbour moles, oyster basins, and—especially—by using bricks and stones to protect the many kilometres of dikes in the Delta area. This large-scale use of stones, in particular limestone and basalt, started in the beginning of the nineteenth century. Therefore, it is possible that within the relatively short time available, not all species capable of living in this type of habitat have yet been able to reach the newly created rocky shores of the Delta area.

III. METHODS

Our survey of the Decapoda Reptantia of the Delta area includes data from several sources. The bulk consists of a series of qualitative investigations of all places with artificial "rocks" in the intertidal zone since 1959, as well as many similar investigations of places with soft sediments in the intertidal zone since about the same time. Scattered all over the area we took some 2000 0.1 m^2 grab samples, together with over 100 0.2 m^2 grab samples taken offshore (Fig. 2). Data obtained from about 1500 hauls with a small shrimp-trawl, also spread over the larger part of the Delta area, are included as well. Off the islands of the Delta area a few observations were made on board commercial fishing cutters.

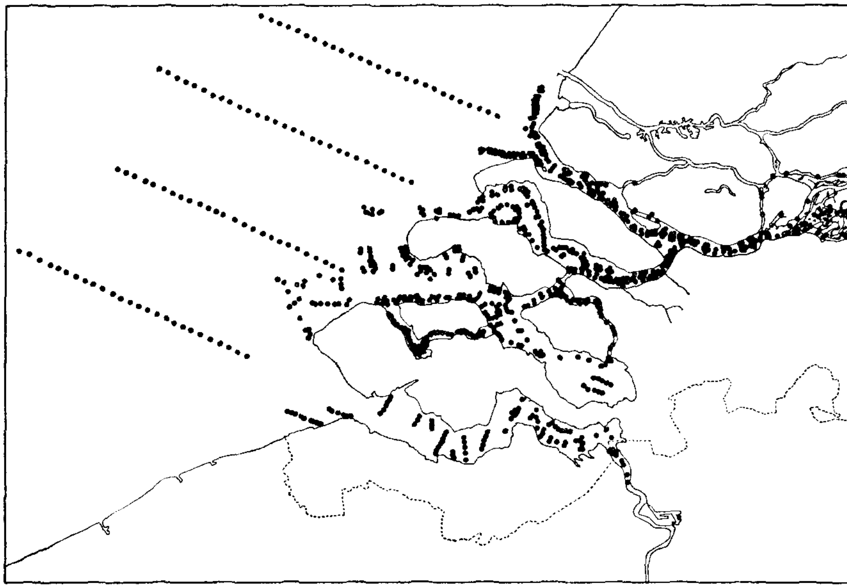

Fig.2. Localities where grab-samples have been taken.

Our survey also comprises data derived from the collections of the State Museum of Natural History, Leiden (RMNH), and the Zoological Museum, Amsterdam (ZMA). Data from the literature were added; the journal "Het Zeepaard" edited by the "Strandwerkgemeenschap van de N.J.N., K.N.N.V., en C.J.N." (Marine Working Group of three Dutch societies for nature studies), proved to be an especially rich source of information, as were the files of this group (quoted as S.W.G.).

A large number of specimens of various species were measured during 1967 to obtain information on growth, and the relationship between growth and various environmental factors. The width of the carapace was taken as a standard measure.

Sediment data were determined with a sieving apparatus having sieves of different mesh widths. The median grain-size was calculated as indicated by INMAN (1952).

IV. SYSTEMATIC PART

Nephrops norvegicus (Linnaeus, 1758)

HOLTHUIS, 1950: 95.

Remains of dead specimens of *Nephrops norvegicus* were occasionally washed ashore on the islands of Schouwen and Walcheren, but live specimens were never caught in the Delta area. Therefore, we presume that these remains originated from other areas and were brought to the Delta area by fishing boats returning from the fishing grounds.

Homarus gammarus (Linnaeus, 1758)
HOLTHUIS, 1950: 99.

The lobster established itself in the Delta waters at the end of the nineteenth century (HAVINGA, 1921), but how this happened has not been clarified sufficiently. Since then, *Homarus gammarus* has been an abundant species in the Delta area. However, the extremely cold winter of 1962–63, with water temperatures well below 0° C, apparently killed most of the specimens, and since then only an occasional specimen has been caught. From information supplied by local fishermen, it was, however, possible to reconstruct its former area of occurrence fairly well (Fig. 3a). HAVINGA (1921) published a similar map, but he does not record any lobster fishery from the entrances of the estuaries. It appears that in his time the fishing boats were too small to operate successfully in this area with considerable wave-action. Lobsters were found only in tidal waters of a high and stable salinity. From the map of HAVINGA and our Fig. 3a it can be deduced that they did not occur at salinities below about 15‰ Cl′. Nevertheless, the species may be able to endure much lower values. In a non-tidal brackish pool, the Inlaag 1953 near Ouwerkerk, with a salinity varying between 10 and 12‰ Cl′, a local fisherman illegally stored lobsters unsuitable for sale. Although the animals may not have moulted again, they nevertheless remained alive for more than a year. In the Veerse Meer a specimen was caught at a salinity of about 9.5‰ Cl′. Although this specimen possibly entered the lake via the locks at Kats, it nevertheless was able to remain alive at this low salinity. In the winters of 1965–66, 1966–67, and 1967–68, salinity in the Oosterschelde dropped to values as low as 9‰ Cl′, 9.6‰ Cl′, and 11.2‰ Cl′ respectively, but live lobsters were caught during and after these periods of low salinity. Hence, it may be concluded that *Homarus gammarus* is able to survive temporary reductions in salinity to as low as 9‰ Cl′. However, it seems very probable that it is not able to complete its life cycle at salinities much below 15‰ Cl′; especially the larval stages are probably affected by such low values, as has been shown for *H. americanus* (SCARRAT & RAINE, 1967).

In the Delta area lobsters are restricted to the oysterbeds and drowned peat-banks and to those places where subtidally an artificial rocky shore is formed by the stone-covered slopes of the dikes. There the lobsters live in holes between the boulders. These places are kept free of silt and mud by the fairly strong tidal currents.

Before the severe winter of 1962–63 the yearly catch in the Delta area amounted to 6816 kg and 7283 kg in 1960 and 1961, respectively. After

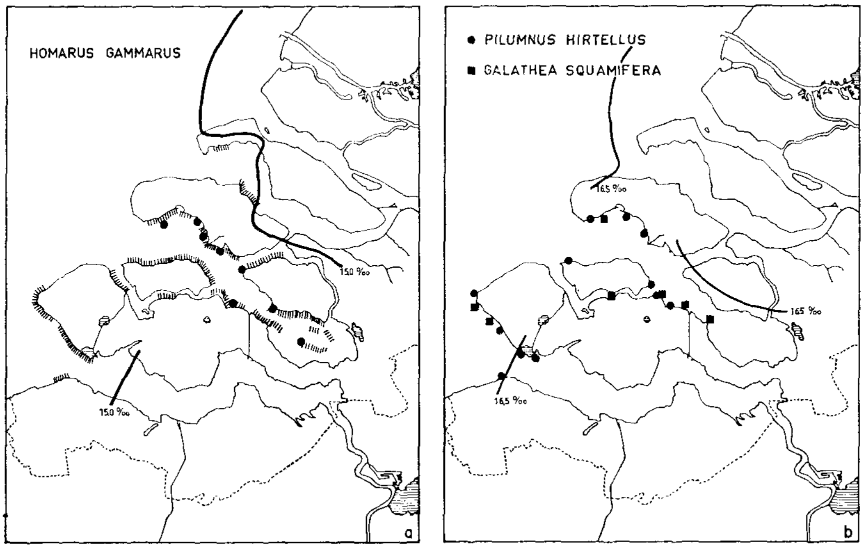

Fig.3. a. Distribution of *Homarus gammarus* after 1963, and areas of commercial fishing before 1963 (hatched). Surface isohaline of 15.0‰ Cl′ at mid-tide during average discharge. b. Distribution of *Galathea squamifera* and *Pilumnus hirtellus*. Surface isohaline of 16.5‰ Cl′ at mid-tide during average discharge.

that winter this figure dropped to 93 to 288 kg in the years between 1963 and 1967.

The Delta plan will cause the disappearance of the lobsters from the greater part of the area. Only the entrance of the Westerschelde may remain a suitable environment for this species.

Astacus astacus (Linnaeus, 1758)

Holthuis, 1950: 103.

Holthuis (1950) records this crayfish from the river Linge near Tiel Since this observation was made in 1890, and the quality of the water in this locality, as everywhere else, has dropped considerably since then, it is almost certain that *A. astacus* is absent now from the Delta area. It is also very improbable that it will colonize the future Delta lakes.

Galathea squamifera Leach, 1815

Holthuis, 1950: 118.

Since the Delta Institute started its investigations in 1959, not a single specimen of this species has been found in the Delta area. Our map (Fig. 3b) has been derived from Holthuis (1950) and a find of one specimen near Wemeldinge (RMNH).

The small number of observations limits what can be said about the ecology of the species. Probably it is restricted to waters of high salinity, since all records pertain to waters with an average salinity over 16.5‰ Cl′. The apparent absence of the species from the Delta area for long periods is probably related to similar phenomena in *Macropipus puber* and *Portumnus latipes* (see below).

Pisidia longicornis (Linnaeus, 1767)

HOLTHUIS, 1950: 125 (sub nom. *Porcellana longicornis*).

Pisidia longicornis is a fairly common species in the Delta area. Nevertheless, it was only found at places where the average salinity of the water is over 15‰ Cl′ (Fig. 4a). In accordance with its filter-feeding mode of life (NICOL, 1967), *P. longicornis* only occurs at places with fairly strong tidal currents. The animals often prefer sponges (*Halichondria panicea*) as a substrate, but also use egg capsules of the whelk, polyzoans, and hydroids. The species is also often found crawling on the boulders along the dikes. Although the number of subtidal observations is rather small, it seems that *P. longicornis* may be found at every depth in the estuaries of the Delta area, whose maximal depth is about 60 m. In the intertidal zone it was only found near the lower fringe.

Although *P. longicornis* is found together with *Porcellana platycheles* alongthe coast of the island of Walcheren, it was not possible to discover any kind of habitat differentiation.

Porcellana platycheles (Pennant, 1777)

HOLTHUIS, 1950: 128.

Porcellana platycheles has a somewhat remarkable pattern of distribution in the Delta area (Fig. 4a). Since as early as 1883, the species has been known from the southwestern and southern coasts of the island of Walcheren, where it may be quite abundant. Outside this area there are only two records of single individuals from the Oosterschelde. The Delta area forms the easternmost occurrence in the distributional area of this species (BOUVIER, 1940; HOLTHUIS, 1950). Because its distribution is probably limited by climatic factors, its occurrence almost exclusively on the island of Walcheren may be explained by the fact that this island has the mildest climate of The Netherlands. Frost and ice are not often registered at the meteorological station at Vlissingen. However, the climatic divergence from the other parts of the Delta is only slight, and makes it improbable that *P. platycheles* is restricted to such a small part of the Delta area solely by differences in climate. Salinity, normally varying between 15 and 17‰ Cl′, is most probably not the cause as almost identical salinities occur in the inlet of the Westerschelde, in the Oosterschelde, and in the Brouwershavense Gat. An important differ-

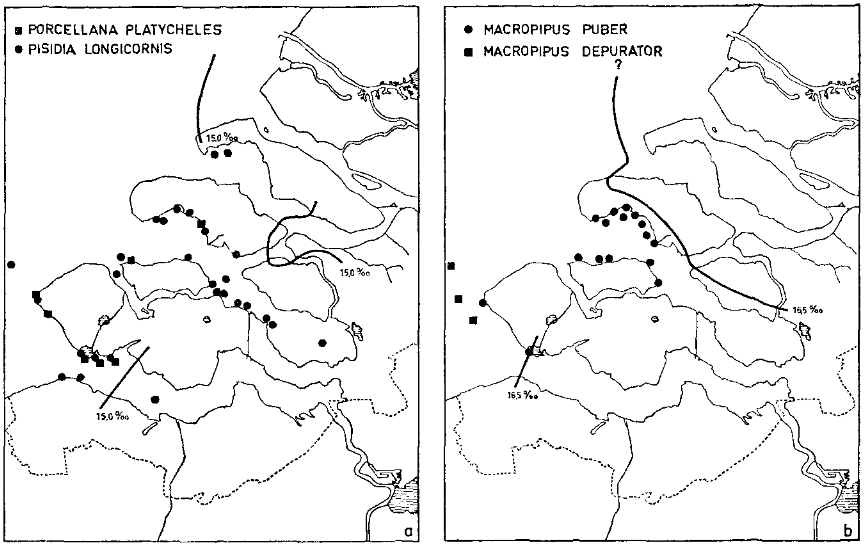

Fig.4. a. Distribution of *Pisidia longicornis* and *Porcellana platycheles*. Surface isohaline of 15‰ Cl′ at mid-tide during average river discharge for the situation the Grevelingen dam has been closed. b. Distribution of *Macropipus puber* and *Macropipus depurator*. Surface isohaline of 16.5‰ Cl′ at mid-tide during average discharge.

ence between the inlet of the Westerschelde and the other waters of high salinity concerns the amount of muddy particles in suspension. At the mouth of the Westerschelde about 200 mg/l dry weight is normal, due to erosion of Miocene clay beds in this area; whereas in the other waters of high salinity a value over 50 mg/l is seldom reached (TERWINDT, 1967). Since reference is sometimes made in the literature to a relation between the occurrence of *P. platycheles* and muddy situations (EALES, 1952; YONGE, 1959), it seems possible that the occurrence of *P. platycheles* in the Delta area is related in some way to the amount of suspended mud.

The species was only observed near the lower fringe of the intertidal zone, nearly always on large boulders along the dikes.

Diogenes pugilator (ROUX, 1828)

HOLTHUIS, 1950: 130.

Diogenes pugilator also is a species of southern origin, reaching its northeastern boundary in the Southern Bight of the North Sea (PIKE & WILLIAMSON, 1959). HOLTHUIS (1950) mentions a number of finds of animals washed ashore on the beaches between Katwijk and Hoek van Holland, all between 1937 and 1942. Since that time the species has

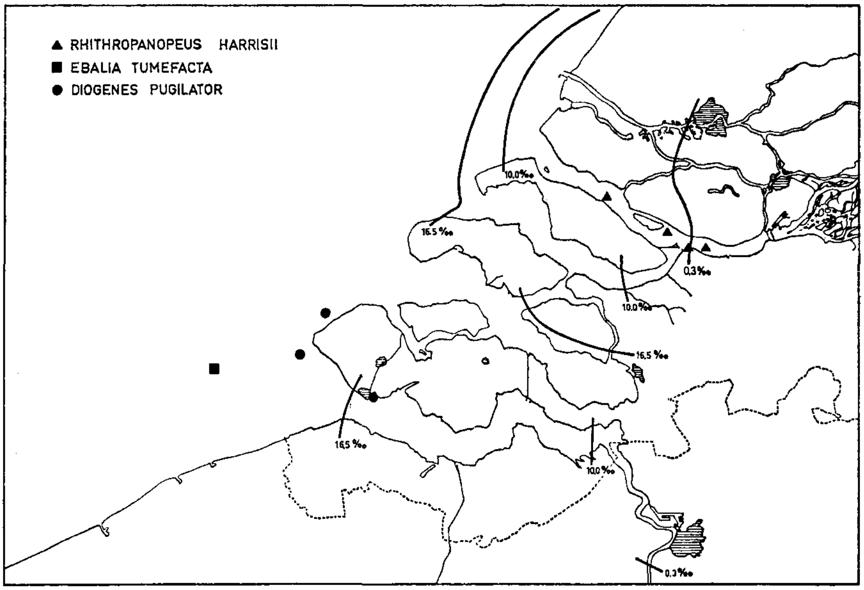

Fig.5. Distribution of *Diogenes pugilator*, *Rhithropanopeus harrisii*, and *Ebalia tumefacta*. Surface isohalines of 0.3, 10.0, and 16.5‰ Cl′ at mid-tide during average river discharge.

only been found in the Delta area in 1950 (Fig. 5). It seems that *Diogenes* is able to colonize the coastal waters in favourable years, but that it does not succeed in maintaining itself in that area.

Pagurus bernhardus (Linnaeus, 1758)

HOLTHUIS, 1950: 133.

The Hermit Crab is a very common species in the Delta area and the adjacent part of the North Sea (Fig. 6). Since our sampling was done mostly in the Delta area proper, it might suggest that this species is less common in the North Sea, but our data do not permit either this conclusion or the opposite.

In the Delta area the Hermit Crab inhabits especially the Grevelingen and the Oosterschelde, but is less common in the Westerschelde. From the intertidal zone only two records from Ellewoutsdijk and Terneuzen at about 14‰ Cl′ are available. Subtidal finds were only made at the entrance of the estuary. It may be argued that the lowered salinity in this estuary inhibits the occurrence of *P. bernhardus*, but from Fig. 6 it may be deduced that the species is able to reach the isohaline of about 13‰ Cl′ at high tide during average river discharge and even lower. Moreover, BOOKHOUT (1964) was able to rear the larvae, usually the

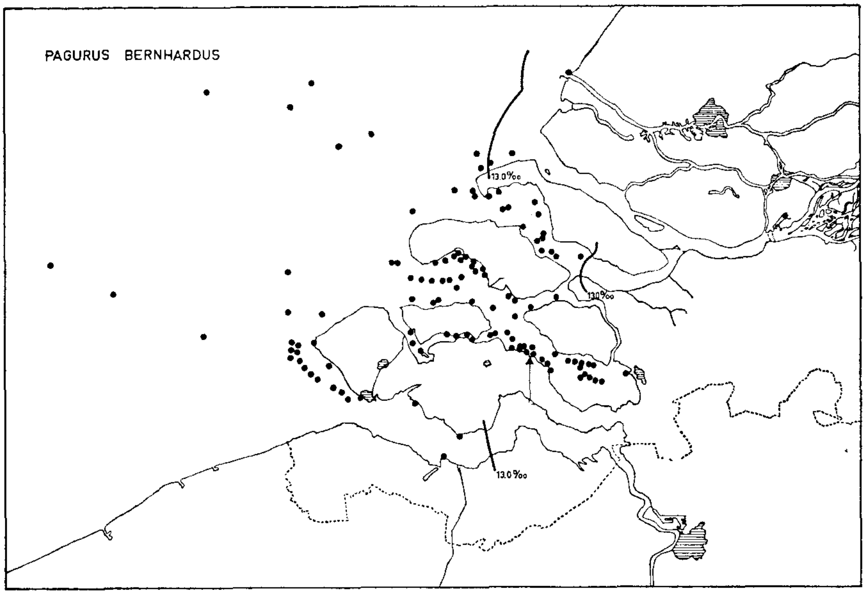

Fig.6. Distribution of *Pagurus bernhardus*. Surface isohaline of 13.0‰ Cl′ at mid-tide during average river discharge.

most sensitive developmental stage, at a temperature of 10° C and a salinity of about 11‰ Cl′, although the development was rather slow. At a salinity of nearly 14‰ and a temperature of 10° C, development was normal. This is in good general agreement with the distribution of the adults in the Delta area. Therefore, the absence of *P. bernhardus* from the western part of the Westerschelde estuary is not explained by the small range of its salinity tolerance. Also the nature of the sediment and the velocity of the tidal currents in the Westerschelde are not very different from conditions elsewhere in the Delta area. It seems possible that the high amounts of suspended matter mentioned (page 204) inhibit the occurrence of *P. bernhardus*, but it is difficult to see how. In any case we do not have a better explanation for our failure to catch Hermit Crabs in this area.

In the Delta area *P. bernhardus* was observed to inhabit the shells of the following species of gastropods: *Littorina littorea*, *L. obtusata*, *Thais lapillus*, *Buccinum undatum*, *Nassarius reticulatus*, and *Polinices polianus*. STOCK (1966) recorded a specimen living in the shell of *Neptunea contraria*, a sinistral fossil gastropod. No other large species of shell-bearing gastropods occur in the area of study.

Our only observation on the breeding of *Pagurus* was that females carrying eggs were found from February to May which fits well within the period mentioned by PIKE & WILLIAMSON (1959) for breeding around the British Isles.

Callinectes sapidus Rathbun, 1896

CHRISTIANSEN, 1969: 72.

HOLTHUIS (1969) summarizes the finds of *Callinectes sapidus* in Dutch waters. So far, no live specimens of this American species have been recorded from the Delta area. Remains (legs, *etc.*) however, have been washed ashore on the beaches of the island of Walcheren (G. R. HEEREBOUT, personal communication). Presumably, such remains originate from ships heading for the port of Antwerpen. Certainly, the species is not yet autochthonous in the Delta area.

Macropipus puber (Linnaeus, 1767)

BOUVIER, 1940: 239 (sub nom. *Portunus puber*);
CHRISTIANSEN, 1969: 55.

The occurrence of *Macropipus puber* in the Delta area is irregular. Observations along the coast of The Netherlands in each year (Fig. 7) are derived from two sources, *viz.* the records made by the Netherlands Institute for Sea Research concerning specimens caught by fishermen in the vicinity of Den Helder, and the observations recorded in the files of the S.W.G. Because the latter society was not founded until 1940 and because observations were difficult or impossible during the years of the Second World War, the most reliable data are those collected after 1945. Many observations are from 1948 to 1949, 1951 to 1953, and 1957 to 1962, and each observation often comprises several specimens. In the years in between only very few observations of single specimens are recorded. Apparently, periods of absence and of fairly abundant occurrence alternate in *M. puber*. It could be possible that these numerical changes reflect the normal fluctuations of the population level in the North Sea, and that in the years when *M. puber* was not observed, it was too scarce to be detected by our methods. The fact, however, that *M. puber*, like *Diogenes pugilator*, *Porcellana platycheles*, and *Portumnus latipes*, reaches the northeastern boundary of its area of distribution in the southern North Sea, offers another explanation. We suppose that the population in the coastal waters of the North Sea is not able to reproduce succesfully every year, but depends also on regular supply of larvae or migrating adults from the populations further away. In some years this supply is apparently insufficient, and consequently the population in the coastal waters becomes extinct. The population does not seem to be wiped out mainly by severe winters, because the species was already absent before the cold winters of 1946–47, 1955–56, and 1962–63. In 1962, for instance, the last specimens were observed on 6 March.

On the other hand, it seems very probable that *M. puber*, having a southern area of distribution, would not be able to tolerate the low temperatures occurring in the North Sea during these winters. Therefore, we are almost certain that *M. puber* is completely absent from the coastal waters of the North Sea in some years.

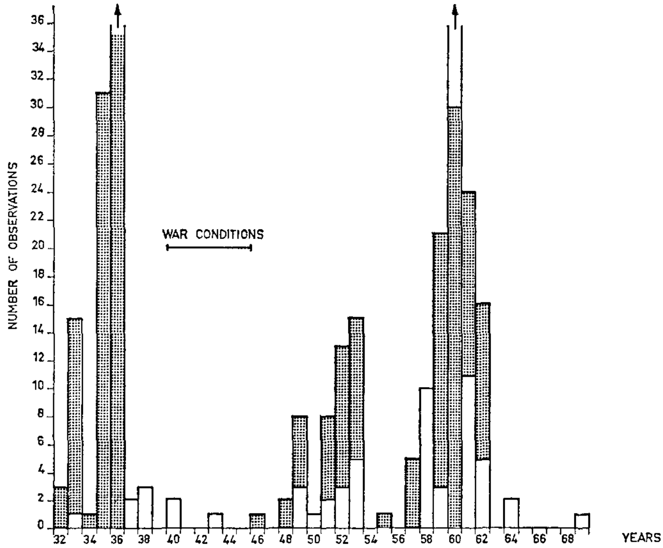

Fig.7. Yearly number of observations of *Macropipus puber* in the Netherlands. Dotted columns represent observations by the Netherlands Institute for Sea Research, white columns by SWG.

It is difficult to ascertain whether it is the larvae or migrating adults that recolonize the coastal waters of the southern North Sea. Larvae have not been recorded from the North Sea plankton (REES, 1952; B. SCHRIEKEN, personal communication), but after the very severe winter of 1962–63, when all adults of *M. puber* had certainly disappeared from the coastal waters of the North Sea, G. R. HEEREBOUT (personal communication) found in the spring of 1964 two juvenile specimens with carapaces of 8 mm and 17 mm near Vlissingen. These specimens consequently have arrived at this locality as larvae. It seems possible, that these larvae originated from a more southerly living population and were transported by the net northward flow of the coastal water masses (LAEVASTU, 1963). On the other hand, it is also possible that the adults migrate into the coastal waters of the North Sea, and are able to reproduce there. In any case, adults are caught in the offshore waters by trawl-fishers from Den Helder throughout the year (Fig. 8). Although the peak occurring in this curve in March to May is not significant (P = 0.537) and the one in November is only barely significant (P = 0.0233), we do not want to exclude the possibility that these peaks result from migratory movements: inshore in March to May, offshore in November. However, this point must be investigated more thoroughly.

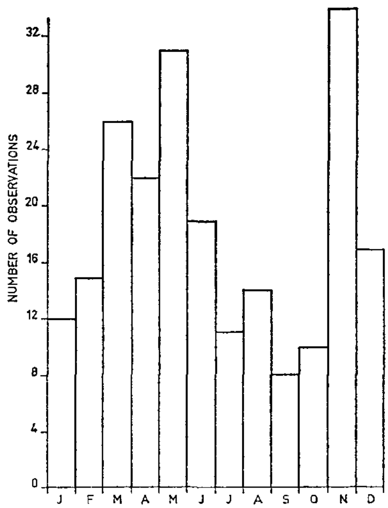

Fig.8. Average number of catches in each month of *Macropipus puber* according to the files of the Netherlands Institute for Sea Research.

In the years in which *M. puber* occurred in the Delta area, it was only found in waters of high salinity (over 16.5‰ Cl') (Fig. 4b). However, this may be partly due to other environmental requirements, because in accordance with its preference for rocky shores (Christiansen, 1969), this species was only found in localities where large quantities of stones were deposited in the sublittoral zone to protect the dikes. Its distribution resembles that of *Cancer pagurus* to some extent. Females in berry were never observed in the Delta area (G. R. Heerebout, personal communication).

Macropipus depurator (Linnaeus, 1758)

Bouvier, 1940: 242 (sub nom. *Portunus depurator*);
Christiansen, 1969: 64.

Only three observations of *Macropipus depurator* are available, all concerning specimens kept at the Leiden Museum (Fig. 4b). Apparently, this species does not penetrate into the estuaries of the Delta area.

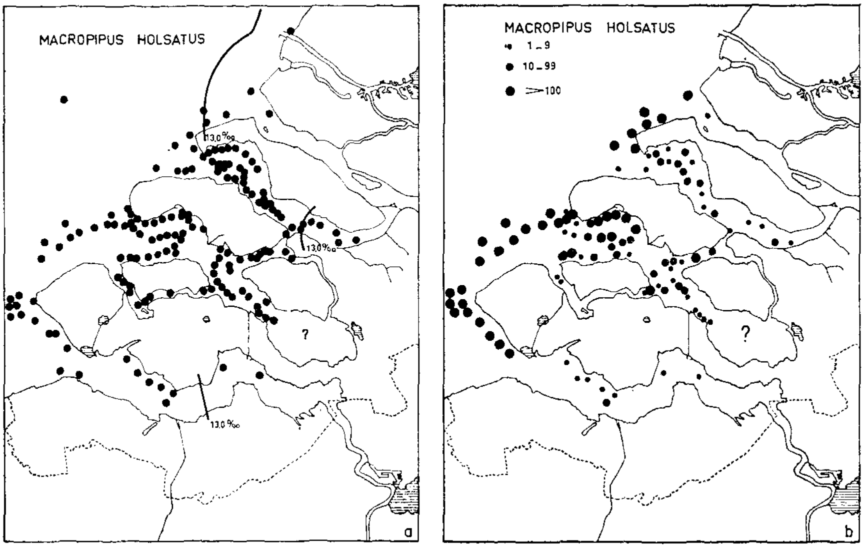

Fig.9. a. Distribution of *Macropipus holsatus*. Surface isohaline of 13.0‰ Cl′ at mid-tide during average river discharge. b. Quantitative distribution of *Macropipus holsatus*. The question-mark stands for an area with no quantitative observations. Quantitative observations are also lacking from the North Sea area.

Macropipus holsatus (Fabricius, 1798)
BOUVIER, 1940: 243 (sub nom. *Portunus holsatus*);
CHRISTIANSEN, 1969: 62.

Macropipus holsatus is a common species in the Delta area during a large part of the year (Fig. 9a). Fig. 10 gives information on the abundance of this species based on hauls with a shrimp-trawl within the estuaries. It is evident that the species is usually almost absent until May, when the numbers slowly start to rise. The average temperature of the estuaries is then over 10° C. Maximal numbers are encountered in August and September, but it is already November when the last specimens are caught in the estuaries. The water temperature in the estuaries falls below 10° C in the course of November. From observations of local fishermen and from our own investigations it appears that these variations in number are caused by migratory movements, on which a reproduction effect is superimposed in August. According to the local fishermen, the spring immigration has a very rapid character, the animals occurring all over the area within a few days. As indicated by VERWEY (1958) and MORGAN (1967), it seems very probable that the crabs perform these migratory movement by making use of the tidal currents. It is evident that in the summer period the species occurs wherever the salinity is fairly high (Fig. 9a). *M. holsatus*, also found offshore in the North Sea, is most common at the entrances of the estuaries (Fig. 9b). Further inland the numbers gradually decrease, but

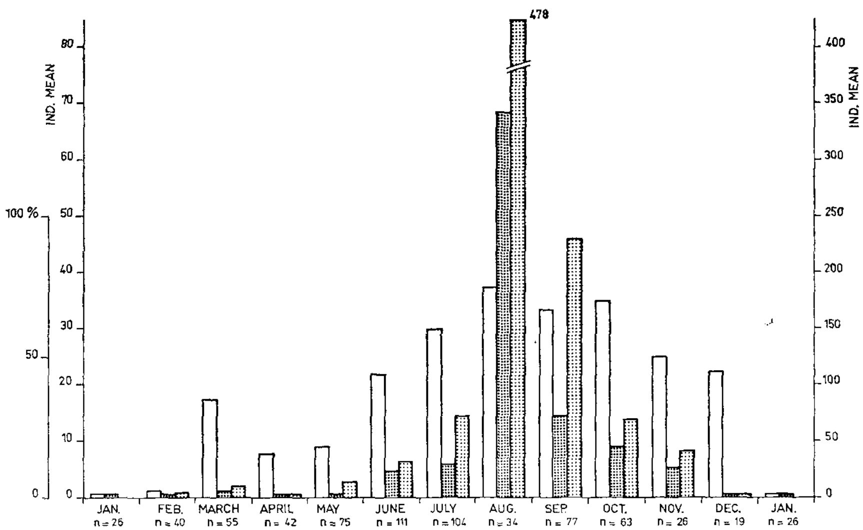

Fig. 10. Monthly occurrence of *Macropipus holsatus*. The white columns represent the percentage of the shrimp-trawl hauls containing *M. holsatus*, the coarse hatched columns represent the mean number of *M. holsatus* per haul, the finely hatched columns the maximum number; n denotes the total number of hauls.

single specimens are found as far as the Steenbergse Sas in the Krammer, and Waarde in the Westerschelde. In summer, the average salinity at these localities is usually not far under 15‰ Cl′. Although in the Kattegat area *M. holsatus* was still found at 11–13‰ Cl′ (Poulsen, 1922, 1949), it is clear that *M. holsatus* occurs especially in waters of high salinity.

For several decapod species it was shown that the juveniles live nearer to the shore or in shallower water than the adults, *e.g.* *Crangon crangon* (Hartsuyker, 1966; Pike & Williamson, 1959) and *Pagurus bernhardus*. For this reason we determined for *M. holsatus*, males and females separately, whether there is a correlation between the average size of the carapace in a sample, and the distance from the entrance of the estuary to the place where this sample was taken. No correlation was found ($r = -0.0004$). This probably means that the population arriving in the spring at the entrances of the estuaries spreads at random over the estuaries, and that growth rate is the same everywhere. In this population, however, the males are significantly larger than the females. Furthermore, the sex ratio of the samples varied greatly, but it was not possible to relate this variation to certain environmental factors.

Carcinus maenas (Linnaeus, 1758)

Bouvier, 1940: 234;
Christiansen, 1969: 49.

The Shore Crab is certainly the commonest crab of the Delta area. Offshore, however, this species soon becomes rare and has already vanished a few kilometres from the inlets of the estuaries, exactly as described by Broekhuysen (1936) for the tidal channels of the Wadden Sea area. Therefore *Carcinus maenas* is a typical species of the estuarine environment. Here it occupies a fairly large number of habitats: it is found in the small creeks of salt marshes, all over the tidal flats, on the mussel- and oysterbeds in shallow water, along the artificial "rocky shores" of the dikes, in the deeper part of the main tidal channels, and in non-tidal brackish inland waters. This variation of habitats points to a certain euryhalinity, and this is confirmed by the horizontal distribution over the estuaries.

It is difficult, however, to relate the distribution of *Carcinus* to the salinity distribution as the species shows migratory movements. In general the following picture can be sketched. In summer, *Carcinus maenas* does not reach the isohaline of 5.5‰ Cl′ at high tide during low river discharge (Fig. 11a and b). Moreover, large concentrations of the species were only noted in salinities of at least 10‰ Cl′ (Fig. 11b). According to Poulsen (1922, 1949) *C. maenas* was still found at salinities of about 4‰ Cl′ in the Baltic. Broekhuysen (1936) mentions a similar limit for the former Zuiderzee. It is, however, a common phenomenon that marine species are able to penetrate further into the stable brackish water of the Baltic than into the unstable brackish waters of estuaries (Den Hartog, 1964). In winter, when high river discharges prevail, *Carcinus* is pushed back over a large distance in seaward direction. For instance, no *Carcinus* can be caught in this period in the Haringvliet, or in the Krammer-Volkerak area.

In brackish non-tidal waters *Carcinus* also occurs, though not abundantly. It was found in some canals connected with estuaries, where salinity is fairly high, and in the Veerse Meer, which lake has a salinity varying between about 9 and 11‰ Cl′. These lake specimens are apparently in a rather bad condition since they only make slow movements when caught, unlike the specimens from the tidal waters which are always very lively. Most remarkable, however, is the occurrence in the brackish non-tidal creek near Schelphoek on the island of Schouwen. This large creek was closed off from the sea in 1953, after the flood disaster early in that year. Owing to seepage of salt water it remained

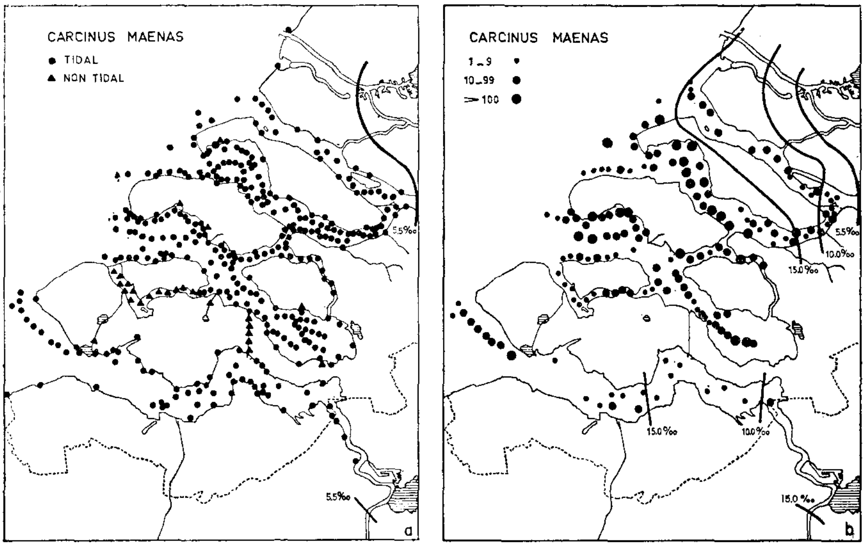

Fig. 11. a. Distribution of *Carcinus maenas*. Surface isohaline of 5.5‰ Cl′ at mid-tide during low river discharge. b. Quantitative distribution of *Carcinus maenas*. Surface isohalines of 5.5, 10.0, and 15.0‰ Cl′ at mid-tide during low river discharge.

brackish and the salinity fluctuated between about 10‰ Cl′ and 15‰ Cl′. *Carcinus* must have been able to tolerate the low salinities accompanied by low temperatures in the winter months, and even to reproduce in this body of water. The lowest salinity measured in winter was 10.79‰ Cl′; although the temperature of the water was not measured at the same time, it is estimated to have been about 2° to 3° C, and at least under 5° C. In the extremely cold winter of 1962–63, temperatures fell below 0° C; in this period the salinity was about 13‰ Cl′. In the other brackish non-tidal inland waters *Carcinus* does not occur, at least not continually. More extreme salinity conditions are probably the reason for this absence.

The migratory movements of *Carcinus* in both the horizontal and the vertical directions are well known (BROEKHUYSEN, 1936; EDWARDS, 1958; NAYLOR, 1962). As pointed out above, *Carcinus* shows migratory behaviour in the upper reaches of the estuaries of the Delta area under the influence of salinity conditions. There is also a vertical migration: in summer the adults of the species colonize the extensive tidal flats and leave these flats again in the autumn. It seems that horizontally the males do not migrate as far out to sea as do the females. When the lower values are omitted, the data in the tables given by BROEKHUYSEN (1936), point in this direction. We tested the hypothesis that males and females do not differ in the distance they migrate in a seaward direction, and hence, that the ratio between females and males does not differ along the main axis of an estuary. For this purpose we used material caught in the Grevelingen in May of 1967. It was found, however, that the proportion of males became significantly larger in an inshore direction ($0.05 > P > 0.02$). Such a difference in the month of May could, however, also be caused by a more rapid inshore migration of the males than of the females, when both have wintered at an equal distance offshore. Therefore, this hypothesis was tested again for samples caught in February 1969. Owing to technical difficulties, it was only possible to obtain samples of crabs from the central and inner parts of the Grevelingen, and from the outer and central parts of the Oosterschelde estuary, the boundaries being arbitrary. These samples were combined and a χ^2-test was applied to see whether the distribution of the crabs was the same for the 82 males and the 70 females catched. Males predominated in the inner parts, females in the outer parts, and this difference in distribution proved to be highly significant ($P < 0.005$). It may therefore be concluded that in the estuaries of the Delta area, female Shore Crabs move in winter further out to sea than the males. This brings the females into warmer as well as saltier water. It is, however, impossible to distinguish between the effects of these two factors. As according to BROEKHUYSEN (1936) there is no correlation between sex and salinity, this difference may be the result of temperature.

According to BROEKHUYSEN (1936) there is also no correlation between size and salinity. During our investigations we got the impression that the average size of carapace of a sample of crabs declined with declining salinity, but there was no significant decrease in size along the main axis of an estuary, at least not at salinities over 10‰ Cl′.

Carcinus maenas can be found on all types of substrate, with the possible exception of very soft muds.

Portumnus latipes (Pennant, 1777)

BOUVIER, 1940: 231;
CHRISTIANSEN, 1969: 52.

Portumnus latipes, too, is a southern species reaching its northern boundary in the North Sea. In this region it is known from the coasts of Belgium and The Netherlands, and from Helgoland (BOUVIER, 1940). Although this species is considered common in The Netherlands, not a single specimen has been observed in the Delta area during investigations by the Delta Institute since 1959. Apparently, this species is currently absent from the Delta area.

To clarify this point, we collected all the observations of *Portumnus* along the coast of The Netherlands, mainly from the files of the S.W.G. (Fig. 12). The number of specimens may be much higher because each

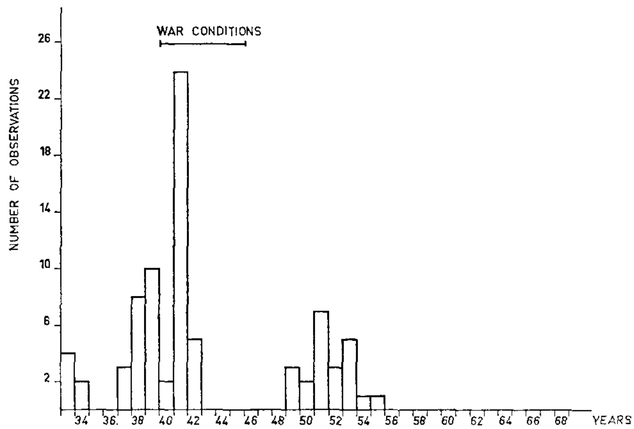

Fig. 12. Yearly number of observations of *Portumnus latipes*.

record can represent the findings of several specimens, tens or hundreds, and in one known case even thousands of specimens. Most of these observations are of individuals washed ashore after storms, but some concern specimens dug up on beaches. It is evident that the species was absent during the years between 1946 and 1948 and from 1956 to now (1969). The records before 1945 should be regarded with some reservation, because the beaches were largely inaccessible during the Second World War, and because the S.W.G. filing system was set up in 1940. In the years of absence from the beaches after 1956 single specimens were caught by trawlfishers from Den Helder (I. Kristensen, personal communication), but these crabs have apparently not been able to recolonize the beaches of The Netherlands. The number and the nature of the observations do not permit any definite conclusion about the factors responsible for the irregular occurrence, but presumably it is due to the climate. *P. latipes*, like *Macropipus puber*, seems to colonize the coastal waters of the southern North Sea in a favourable year, is then able to thrive for a couple of years, and ultimately disappears again, due to a cold winter or some other cause. From the data in the literature, the collections of Dutch museums, and the files mentioned above, it was possible to reconstruct the area of distribution (Fig. 13a). *P. latipes* seems to have been confined to the coastal waters and did not penetrate into the estuaries. It has been found only in sandy beaches or swimming in the offshore waters.

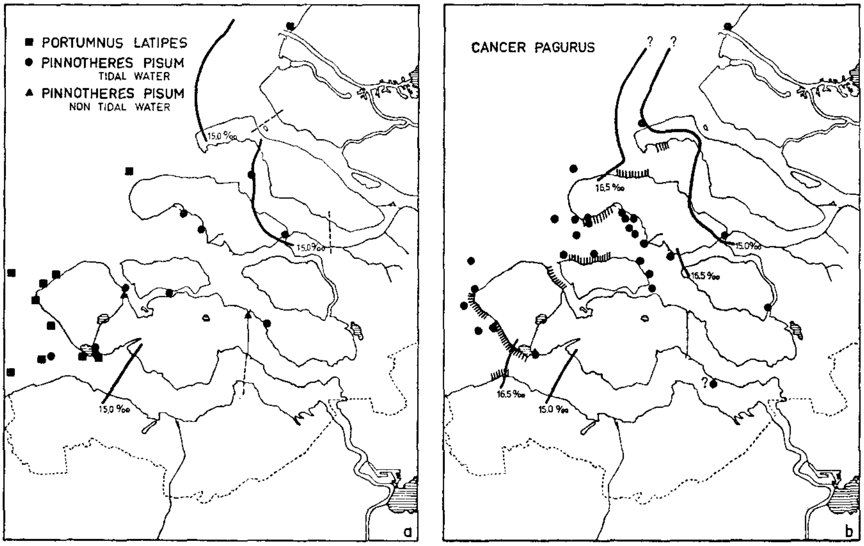

Fig. 13. a. Distribution of *Portumnus latipes* and *Pinnotheres pisum*. The dashed line represents the boundary of the occurrence of mussels. Surface isohaline of 15.0‰ Cl′ at mid-tide during average river discharge. b. Distribution and commercial fishing grounds (hatched) of *Cancer pagurus*. Surface isohalines of 16.5 and 15‰ Cl′ at mid-tide during average river discharge.

Cancer pagurus Linnaeus, 1758
Bouvier, 1940: 223;
Christiansen, 1969: 42.

During most of the period of our investigations *Cancer pagurus* was a rare species, owing to the effects of the very cold winter of 1962–63. In this icy winter, with water temperatures under 0° C, the local population almost died off entirely. Gradually, however, some new finds were made. Together with the available older data, and the areas where *Cancer* was fished commercially, they form a reliable picture of the distribution of the species (Fig. 13b). The majority of the observations are located at the entrances of the estuaries. In these entrances, fishing for the species was done only in localities where in the course of centuries large amounts of stone have been dropped to protect the subtidal parts of the dikes against the attack of the tidal currents. Observations of single specimens at a greater distance from the shore probably concern individuals involved in migratory movements. Williamson (1900, 1904) and Mason (1965) describe inshore and offshore migrations connected with seasonal variations in temperature.

According to Korringa (1969) the Edible Crab prefers a bottom of sand or shingle with occasional patches of rocks. Its normal habitat in the Delta area seems to be the subtidal parts of stone-covered dikes. Though this type of habitat can be found all along the Oosterschelde, the species is found only in the western part of this estuary. Salinity is not responsible for this type of distribution, because in the years previous to the winter of 1962–63 the salinity in the Oosterschelde was nearly always over 16.5‰ Cl′, whereas the commercial fishing grounds in the Brouwershavense Gat and Springersdiep had a salinity below 16.5‰ Cl′. Below 15‰ Cl′ the species did not occur, as is also the case in Danish waters (POULSEN, 1949). Consequently, it is supposed that the distribution of *C. pagurus* in the Delta area is governed by temperature, provided that salinity is not too low. At the entrances of the estuaries, temperature conditions are buffered by the North Sea, and are therefore less extreme than in the inner land-locked parts of the estuaries. It is, however, difficult to determine whether the absence of *Cancer* here is the result of the high summer temperatures, the low winter temperatures, or the relatively rapid daily changes in temperature. The find in the Westerschelde near Waarde (LELOUP, 1941) seems improbable, and may possibly be attributed to a labelling error.

Thia scutellata (Fabricius, 1793)
BOUVIER, 1940: 222 (sub nom. *Thia polita*);
CHRISTIANSEN, 1969: 40.

Thia scutellata has never been found in the Delta area proper. Nevertheless, it is common about 30 km offshore, where the species was found in the majority of the samples (Fig. 14). The differences between this area and the Delta area proper are:

(*a*) In the region where *Thia* occurs, the so-called "Channel-water" is found (LAEVASTU, 1963), whereas closer to the shore the "continental coastal water" occurs. The differences between these water masses concern turbidity, salinity, minimum temperatures in winter, maximum temperatures in summer, and so on. The finds of *T. scutellata* probably all fall within the area of Channel water.

(*b*) With increasing distance from the shore, the coarseness of the sediments also increases. Almost all finds of *T. scutellata* were made in sands with a median grain-size over 250 μ. Such sands are rare in the Delta area proper (Fig. 14).

(*c*) With increasing distance from the shore, the depth increases. All finds of *Thia* were made in depths of over 25 m. Inshore such depths only occur in the deepest tidal channels.

(*d*) During our sampling the salinity of the water above the sediment in the van Veen grab was determined. At all localities where *Thia* was found, salinity was over 18.5‰ (Fig. 14). Salinity in the Delta area rarely exceeds 17.0‰ Cl′.

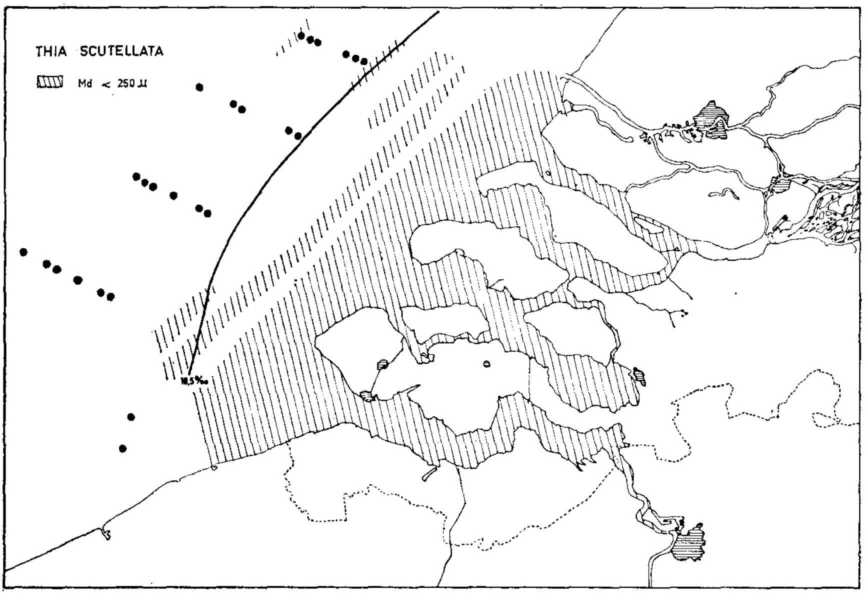

Fig.14. Distribution of *Thia scutellata*. Bottom isohaline of 18.5‰ Cl′ at mid-tide during average river discharge. The area with sediments with a median grain-size under 250 μ is hatched (except for the freshwater parts of the rivers).

(*e*) Turbidity in the offshore waters is considerably lower than in the Delta area.

Depth in itself cannot be important as it only governs the other environmental factors. Bouvier (1940), Schellenberg (1928), and Christiansen (1969) state that the species is able to live in sand as well as in mud, so the nature of the sediment does not seem to be very important either. Thus, the occurrence of *Thia* seems to be connected with the presence of the "Channel water" with its high salinity and low turbidity. In this study it was not possible to judge which of these two factors is the most important, or whether still another factor is involved. The assumption that the Channel water determines the distribution of *T. scutellata* is strengthened by the observations made by Rees (1952), who found the larvae of this species almost exclusively in the area where the Channel water predominates.

Pilumnus hirtellus (Linnaeus, 1767)

Bouvier, 1940: 255;
Christiansen, 1969: 75.

Pilumnus hirtellus is a rather rare species in the Delta area (Fig. 3b). It has been encountered most frequently in the vicinity of Vlissingen, and most of the specimens were juveniles. The species has only been found along the artificial "rocky shores" formed by the stone-covered dikes. It penetrates into the estuaries up to a salinity of about 16.5‰ Cl′. We feel that the record from the Westerschelde near Waarde (LELOUP, 1941) is an error, most probably due to a mistake in the labelling of the material (compare *Cancer pagurus*).

Rhithropanopeus harrisii (Gould, 1841)
BOUVIER, 1940: 259 (sub nom. *Heteropanope tridentatus*);
BUITENDIJK & HOLTHUIS, 1949: 95;
CHRISTIANSEN, 1969: 81.

Although the species *Rhithropanopeus harrisii* has been known for almost a hundred years from The Netherlands, and was extremely common in the former Zuiderzee and its surrounding waters, it appeared to be rare in the Delta area. We possess only four observations of this species, all in the oligohaline Haringvliet-Hollands Diep region (Fig. 5). It is remarkable that this species is so scarce in the Delta area with its large quantities of brackish waters.

Eriocheir sinensis H. Milne Edwards, 1854
BOUVIER, 1940: 296;
CHRISTIANSEN, 1969: 96.

The first specimens of *Eriocheir sinensis* in the Delta area were caught in 1931 in the vicinity of Rotterdam and at the entrances of the Nieuwe Waterweg, Brielse Maas, and Haringvliet (Kamps, 1937). As early as 1932, the species was found all over the Haringvliet-Hollands Diep estuary and in the river Waal, a branch of the Rhine. In the other estuaries of the Delta area Mitten Crabs were found for the first time in 1935 and 1936, and since then the species has become common all over the Delta area. The adjoining part of Belgium was also colonized in the same period (LESTAGE, 1935). Now the species (Fig. 15) is common in most of the fresh inland waters in the provinces of Zuid-Holland, Utrecht, Gelderland, and Noord-Brabant, and also in Belgium. It occurs abundantly in the large rivers and in the freshwater tidal area of the Biesbosch. In the brackish non-tidal inland waters of the provinces of Zuid-Holland and Zeeland, however, the species is absent.

In September–October and possibly as early as in August, migratory movements of adult specimens towards the sea are seen in the Hollands Diep and the Oude Maas. In the winter, fairly large numbers of adults are caught at the entrance of the Haringvliet and in the Krammer-Volkerak. In these areas salinities fluctuate strongly in the winter period, but on the average they are between 5 and 10‰ Cl′ (Fig. 15 shows the isohalines at half tide during average river discharge). The Weste

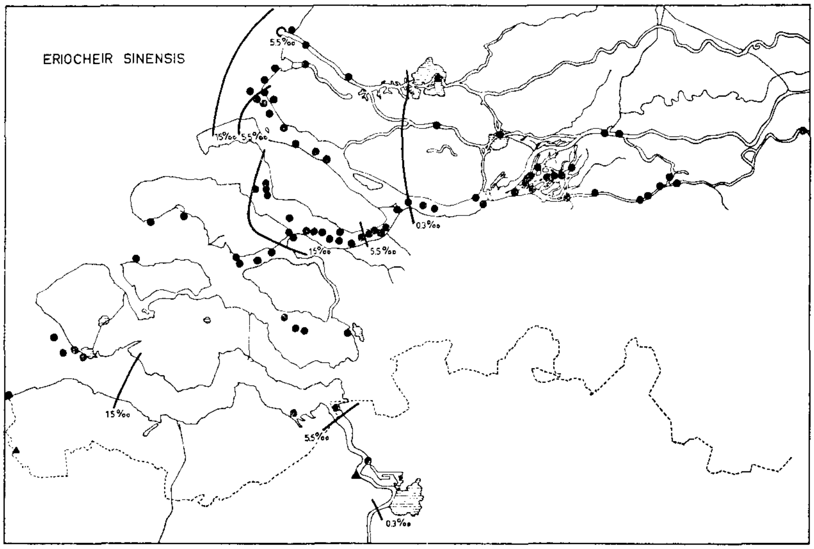

Fig.15. Distribution of *Eriocheir sinensis*. Surface isohalines of 0.3, 5.5, and 15‰ Cl′ at mid-tide during average river discharge. Triangles denote non-tidal localities.

schelde probably shows a similar distribution, but our data are not sufficiently numerous to be conclusive. In the seaward reaches of the estuaries, notably the western part of the Grevelingen and the whole Oosterschelde area, only occasional specimens of *E. sinensis* are caught. Apparently, the majority of the population does not penetrate so far. The Mitten Crab can be caught in the estuaries until June–July. At that time many dead specimens are washed ashore. By September, however, a new invasion of adult specimens occurs.

Unfortunately, we do not have any other information on the occurrence of this interesting species in the Delta area, but it seems almost certain that *E. sinensis* will be important in the future freshwater lakes.

Pinnotheres pisum (Linnaeus, 1758)
Bouvier, 1940: 301;
Christiansen, 1969: 88.

Although *Pinnotheres pisum* is a well-known inhabitant of *Mytilus edulis* in the Delta area, it proved to be rather scarce. Its numbers seem to show a certain fluctuation; minimal numbers were present after the extremely cold winter of 1962–63 when temperatures in the estuaries fell below 0° C. Since then, the population has apparently increased very slowly. It is rather difficult to determine whether a specimen has completed its development at a certain place, since the mussels are repeatedly moved by the mussel-growers. Fig. 13a concerns only specimens originating from mussels for which it was known with certainty that they had not been displaced. It is clear that *P. pisum* has a fairly wide distribution in the Delta area, probably coinciding roughly with that of *Mytilus*.

The density of *P. pisum* always seems to be low, the rate of infestion of *Mytilus* being under 1% and usually even under 0.1%. We have never heard of a case with more than one specimen within a mussel. In the Delta area the species is not known from other species of lamellibranchs. A few free-swimming specimens have been caught.

Ebalia tumefacta (Montagu, 1808)
BOUVIER, 1940: 209;
CHRISTIANSEN, 1969: 29.

Ebalia tumefacta was collected only once, 30 km off Zoutelande on the island of Walcheren (Fig. 5).

Hyas coarctatus Leach, 1815
BOUVIER, 1940: 335;
CHRISTIANSEN, 1969: 118.

Only two immature specimens of *Hyas coarctatus* were observed in the Delta area, both in the same week (Fig. 16b). The material was identified by Dr. L. B. Holthuis. In all probability these finds concern a temporary colonization.

Hyas araneus (Linnaeus, 1758)
BOUVIER, 1940: 334;
CHRISTIANSEN, 1969: 116.

Hyas araneus is a common species in the Delta waters (Fig. 16b). It is confined to areas with a rough bottom formed either by stones used for the protection of the dikes, beds of mussels and oysters, or the like. At the foot of dikes it may especially be abundant, but it seldom penetrates into the intertidal zone. HARTNOLL (1963), however, found the species mainly on the sandy bottoms in the sublittoral zone of rocky areas. Its absence from other types of bottom near the Isle of Man is probably due to competition with *H. coarctatus*.

Its tolerance to lowered salinity seems to be rather low, because it was only found in the Grevelingen and the Oosterschelde, both normally having a salinity of over 15.0‰ Cl′. Nevertheless, POULSEN (1949) records 8‰ Cl′ as the lower limit of tolerance of this species. According to SANKARANKUTTY (1968), *Hyas araneus* lives in Hardangerfjorden, Norway, at a depth of 0 to 10 m, being replaced by *H. coarctatus* in deeper water. In the Delta area *H. araneus* is also abundant at depths

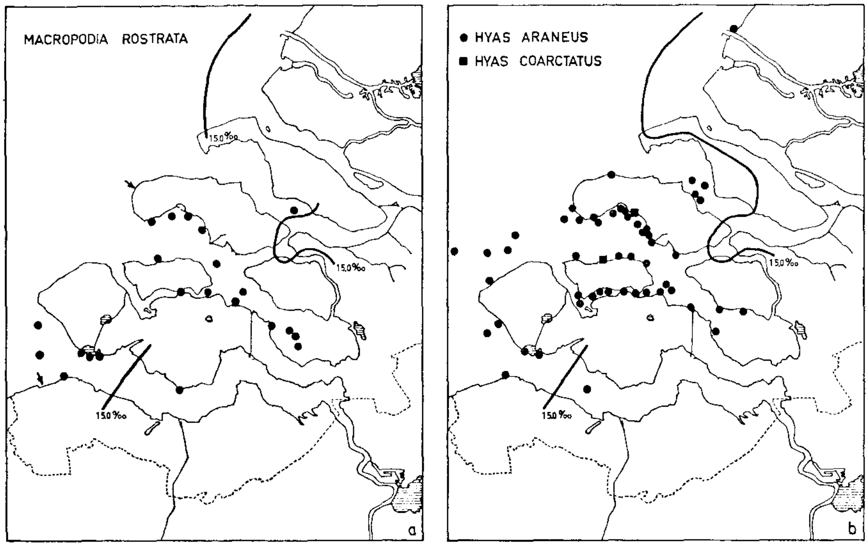

Fig. 16. a. Distribution of *Macropodia rostrata*. The arrows indicate places where specimens washed ashore have been found. Surface isohalines of 15.0‰ Cl′ at mid-tide during average river discharge and closed Grevelingen dam. b. Distribution of *Hyas coarctatus* and *H. araneus*. Surface isohalines of 15.0‰ Cl′ at mid-tide during average river discharge and closed Grevelingen dam.

between 0 and 10 m, but occasional specimens may also be found at depths down to 30 to 40 m. But as *H. coarctatus* is nearly absent from the Delta area, competition can be excluded. Also temperature stratification which may cause the pattern of distribution in Hardangerfjorden, hardly occurs in the Delta area.

H. araneus is especially abundant in places sheltered from wave-action. Strong tidal currents, however, do not seem to hinder it, since most of our observations are from places with maximal current velocities of about 1 m/sec.

In the easternmost part of the Oosterschelde *H. araneus* must be able to withstand summer temperatures of over 20° C and winter temperatures of under 2° C. HARTNOLL (1963) also found that *H. araneus* has a "markedly inshore distribution".

Macropodia rostrata (Linnaeus, 1761)
BOUVIER, 1940: 362;
CHRISTIANSEN, 1969: 110.

Macropodia rostrata is a rather scarce species in the Delta area (Fig. 16a). During the initial years of the Institute's investigations a few finds were made up to 1962. After the extremely cold winter of 1962–63, the species was not found until 1967. Since then, the number of observations has gradually increased.

All observations were made at places where a noticeable current passes over a rough substratum consisting for instance of mussel beds, fields of *Sertularia cupressina* and other hydroids, or stones used to protect the dikes. HARTNOLL (1963) reported the species especially from sandy bottoms, contrary to *M. longirostris*, which lives predominantly on muddier bottoms.

M. rostrata was mainly found in waters of high salinity, usually over 15.0‰ Cl′. Only the find in the Westerschelde originates from an area with a salinity of 13–14‰ Cl′. POULSEN (1949) reports 10‰ Cl′ to be the limit in Danish waters.

Since the species still occurs in the easternmost part of the Oosterschelde, it may be assumed that it is able to withstand summer temperatures higher than 20° C. Winter temperatures are sometimes under 2° C in this area. According to HARTNOLL (1963), this species also shows an inshore distribution near the Isle of Man.

V. DISCUSSION

The evidence shows that 8 species of Decapoda Reptantia occur abundantly within the estuaries of the Delta area: *Homarus gammarus, Pisidia longicornis, Pagurus bernhardus, Macropipus holsatus, Carcinus maenas, Cancer pagurus, Eriocheir sinensis,* and *Hyas araneus.* The pea crab, *Pinnotheres pisum*, forms the transition to another group of species that may be considered rare in the Delta waters: *Porcellana platycheles, Galathea squamifera, Macropipus puber, Portumnus latipes, Pilumnus hirtellus, Rhithropanopeus harrisii, Hyas coarctatus,* and *Macropodia rostrata.*

Offshore, the common species are: *Pagurus bernhardus, Macropipus holsatus, Cancer pagurus* (during part of the year), and *Thia scutellata.*

Lastly, there are a few species that do not occur in the estuaries and are rare offshore: *Nephrops norvegicus, Diogenes pugilator, Macropipus depurator,* and *Ebalia tumefacta.*

Of the species occurring within the estuaries, *Cancer pagurus, Portumnus latipes, Macropipus puber,* and possibly *Hyas coarctatus* are confined to the entrances, probably in dependence on water temperature. The other species occur all over the estuaries, up to roughly the isohaline of 15‰ Cl′, except for the species *Carcinus maenas, Rhithropanopeus harrisii* and *Eriocheir sinensis. Carcinus* is a typically estuarine species, occurring between salinities of 17‰ Cl′ and about 5‰ Cl′. *Rhithropanopeus* and *Eriocheir* are alien species, imported respectively from America and from China. They inhabit the parts of the estuary not occupied by the other local species: *Rhithropanopeus* in the meso- and oligohaline zones and

Eriocheir in the freshwater areas, although the latter migrates periodically into the seaward reaches of the estuaries. Thus, it is clear that in the area with a salinity above 15‰ Cl′ a number of decapod species live together, apparently by the achievement of a certain niche- and habitat diversification. Under 15‰ Cl′, down to about 5‰ Cl′, only one species, *Carcinus*, occurs, apparently occupying a very large niche. Under 5‰ Cl′, originally no species of crab occurred in the Dutch estuaries, but these empty niches have been occupied by *Rhithropanopeus* and *Eriocheir* during the last few centuries. In the freshwater of the rivers the crayfish *Astacus astacus* originally occurred, but this species has disappeared owing to pollution of the rivers.

The species curve given by REMANE (1958) for the brackish water is evidently also applicable to the Decapoda Reptantia of the Dutch estuaries. Because the empty niches in the brackish and fresh parts of these estuaries have only very recently been occupied by alien species, this species curve has been even more distinct in fairly recent times. This means that in the west European estuaries no species of crab capable of living under these conditions has developed in the course of evolution.

Species of interest for further investigation during the Delta closure program prove to be *Carcinus maenas*, *Rhithropanopeus harrisii* and *Eriocheir sinensis*, because these three are able to tolerate brackish or even fresh water.

VI. SUMMARY

The distribution and ecology of 24 species of Decapoda Reptantia in the estuarine part of the rivers Rhine, Meuse, and Scheldt, in the southwestern part of The Netherlands, is discussed.

A few species are common offshore, but a larger number are abundant in the seaward reaches of the estuaries at salinities over 15‰ Cl′. Below this value, only *Carcinus maenas* is abundant down to salinities of about 5‰ Cl′. In still lower salinities the alien brackish-water species *Rhithropanopeus harrisii* and the similarly alien freshwater species *Eriocheir sinensis* occur. This two species apparently occupy niches that were empty before the present inhabitants were imported from abroad.

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