The Mollusca of the estuarine region of the rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area. I. The Unionidae

by
W. J. WOLFF
(Communication No. 6 of the Hydrobiologisch Instituut, afd. Delta-onderzoek, Yerseke, Netherlands)

INTRODUCTION

Several of the estuaries in the southwestern part of the Netherlands (fig. 1) will be closed in the near future. These tidal areas, usually indicated collectively with the name Delta area, now contain salt or brackish water, but after the closure will be changed into stagnant freshwater lakes. The Delta Reseach Division of the Hydrobiological Institute of the Royal Netherlands Academy of Sciences was founded to investigate the biological changes caused by these large works (VAAS, 1961).

During these studies much attention will be paid to the molluscs; many marine species will certainly disappear, some brackish-water species may show a temporary increase and many freshwater species will colonize the new lakes.

To investigate these processes adequately, it is necessary to have detailed information of the situation before changes occur. Starting with this paper, we intend to publish a series of descriptions of the original distribution of various groups of molluscs. In many cases useful ecological information may be derived from the distribution data, especially concerning the anticipated reactions to future changes of environment.

ACKNOWLEDGEMENTS

We are grateful to the many people who helped us during our investigations. Dr. C. DEN HARTOG, Mrs. C. H. BORGHOUTS-BIERSTEKER and Mr. W. J. M. VADER presented the material collected on their excursions in the Delta area. Messrs. P. DE KOEIJER, W. J. L. ROBER, L. DE WOLF and especially A. J. J. SANDEE assisted in the field-work. The navigational skill of Mr. C. DE ROOIJ, captain of the institute's vessel 'Jan Verwey', made it possible to collect material in almost inaccessible places. Mr. J. A. NIEUWENHUIJZE determined the grain-size distributions of sediments. Mr. D. W. FEY collected interesting data on unionids and their predators in the Biesbosch area (see map). Mr. H. E. COOMANS, Dr. C. O. VAN REGTEREN ALTENA and Mr. A. W. JANSSEN made it possible for me to study the collections of their respective museums. Ir. A. E. HOFSTEDE supplied us with data on the occurrence of freshwater fishes. Mr. S. BAR-EVEN has corrected the English of the present paper.

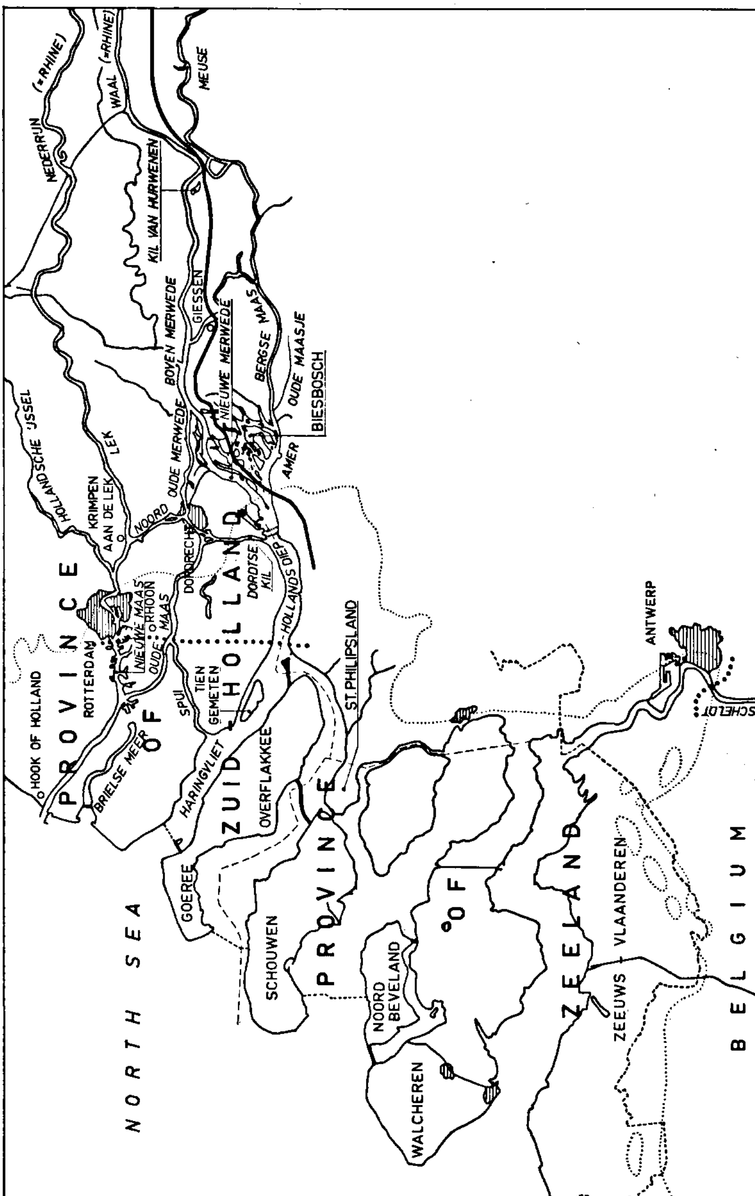

Fig. 1. Map of the Delta area. The dotted thin line indicates the landward limit of Sub-Atlantic marine deposits according to De Jong (1960). The solid line forms the southern boundary of the area with more than 10% Rhine-water. The dotted line indicates the mean annual isohaline of 0.3‰ Cl′.

HISTORY OF THE AREA INVESTIGATED

During the Holocene the Delta area was a border region between the land, the rivers Rhine, Meuse and Scheldt, and the North Sea (DE JONG, 1960). In fig. 1 the landward limit of Sub-Atlantic marine deposits is indicated (DE JONG, l.c.). During the sedimentation of these deposits (from 700 B.C. until now) large parts of the area were of course not suitable for land- and freshwater molluscs. These groups could only survive on the more elevated Pleistocene soils in the south and east of the area, in and near those parts of the rivers containing fresh water, and in the peat area in the north. BUTOT (1962) also supposes that certain land molluscs survived during the transgression periods in the dune areas of the islands of Walcheren, Schouwen and Goeree. It is, however, nearly certain that, at least in some periods, no land and freshwater molluscs could have survived in the area between the regions mentioned above. The last time that the whole low-lying Delta area was flooded by the sea, was during the so-called Post-Karolingian transgression period in the 10th century. Marine sediments from that period may be found over nearly the whole area (VAN DER SLUIS, STEUR & OVAA, 1965). Afterwards Man began to construct dikes, and it seems probable that only since then a few areas in the general region remained dry when the major part of the latter was flooded (TRIMPE BURGER, 1960). So it is evident that the land and freshwater molluscs could only have started colonizing the Delta area in the Middle Ages. Many times, however, they must have been exterminated by inundations of salt and brackish water. For the freshwater molluscs this disadvantage has probably been most serious; their habitat is destroyed even by minor inundations, as they live in the lowest places of the polders. Land molluscs, however, during short periods of inundation can probably survive on elevated structures, e.g. dikes, large buildings and trees. The survival of *Laciniaria biplicata* is perhaps an example of this phenomenon (DEN HARTOG, 1965). Some of the islands of the Delta area were not available for occupation by non-marine molluscs until a few centuries ago. The island of Noord-Beveland was flooded in 1530 and remained covered with salt water until 1598 (DE BRUIN & WILDEROM, 1961). St. Philipsland was inundated in 1530 and became inhabitable again in 1645 (WILDEROM, 1964). The first polders of Overflakkee and of Tiengemeten were reclaimed in the first half of the 15th century and in the second half of the 18th century respectively (TEXEIRA DE MATTOS, 1925, 1941). The last important inundations were in 1944/45 and in 1953. The influence of these is still clearly seen in the distribution pattern of several species of molluscs. Fig. 2 represents the extension of the inundations of salt and brackish water caused by

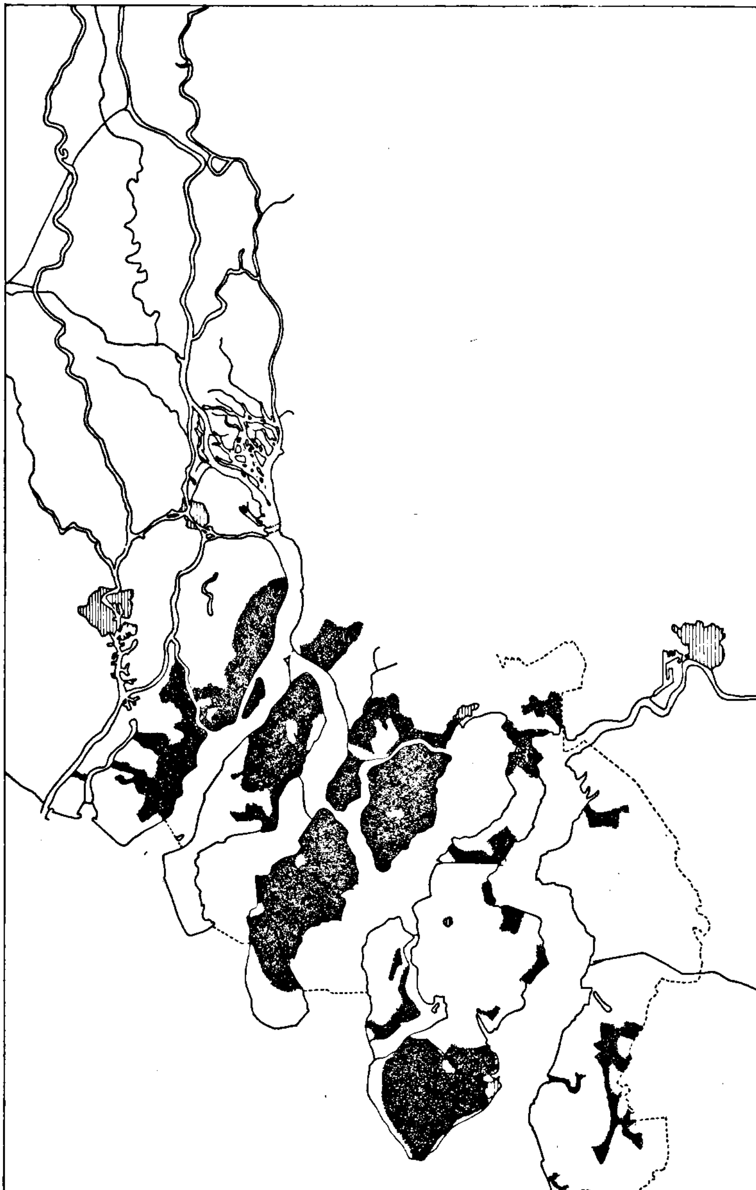

Fig. 2. Extension of the inundations of salt and brackish water in 1944/45. Slightly flooded areas are also included.

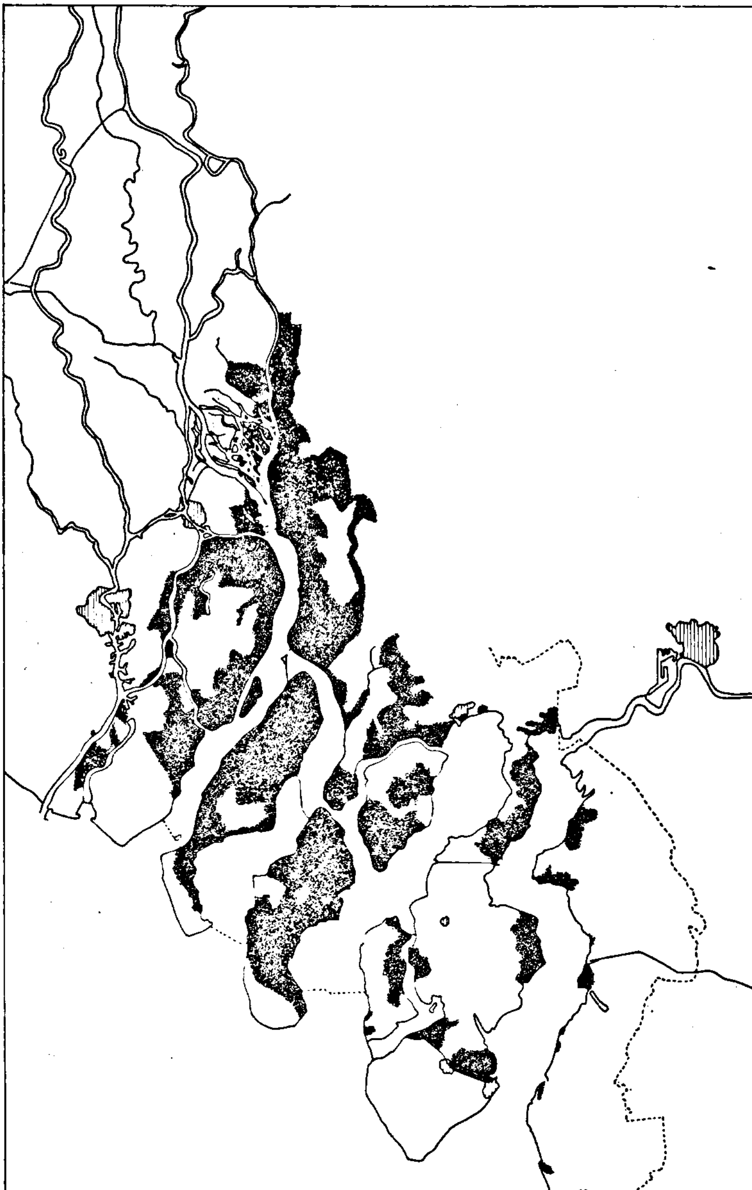

Fig. 3. Extension of the inundations of salt and brackish water in 1953.
Slightly flooded areas are also included.

military action during the Second World War (WESTERHOFF, 1947). On most islands these inundations lasted for several months. Fig. 3 shows the inundations after the flood disaster of February 1st, 1953 (unpublished data of the Rijksdienst Landbouwherstel; ANONYMOUS, 1961). The duration of these inundations varied from a few days to about eleven months.

HYDROGRAPHY OF THE DELTA AREA

For a general description of the hydrography of the tidal waters we may refer to DEN HARTOG (1961, 1963) and PEELEN (1967). PARMA (1966) gave a detailed account of the hydrography of the Biesbosch, a freshwater tidal area. Some remarks on the waters within the enclosure of the dikes may be made here. Such inland waters include the ditches, pools, ponds and 'wielen'. 'Wielen' are deep pools just behind a dike, which are formed during dike breaks by the water rushing in through the breach; after the repair of the dike these holes dug by the current remain as pools. The water inside the dikes is generally shallow (less than 3 m), but some 'wielen' may be rather deep (up to 15 m) (VAN HEUSDEN, 1945). These 'wielen' often show a distinct thermocline with anaerobic conditions in the deeper layers (LEENTVAAR, 1958).

The salinity of the inland waters varies greatly. Fig. 4 shows the area where the salinity of the inland water never rises above $0.3^0/_{00}$ Cl'; fig. 5 shows the area where it never rises above $1.0^0/_{00}$ Cl'. The data are derived from maps in a series of reports of the C.O.L.N.-T.N.O. (KOUWE & VRIJHOF, 1958; VAN 'T LEVEN, VAN DER WEERD & LINDENBERGH, 1958; STOL & VRIJHOF, 1958; VISSER, 1958). Obviously, nearly all freshwater molluscs are restricted to the areas shaded in black.

METHODS OF INVESTIGATION

In the province of Zeeland all the larger inland waters were checked for the presence or absence of unionids. The same was done on the islands of the province of Zuid-Holland; east of the town of Dordrecht we investigated only the rivers and the polder area bordering them. Most collecting in the small inland waters was done with small hand-operated nets and grabs. In the freshwater tidal area and in the rivers however, we collected from the institute's vessel 'Jan Verwey' with an 0.1 m^2 Van Veen grab and with an oyster-dredge (fig. 6). The latter apparatus with a width of 1 m, proved to be very effective in dredging for unionids. It can be used at various depths and can be towed over considerable distances. It digs a few centimeters into the substrate.

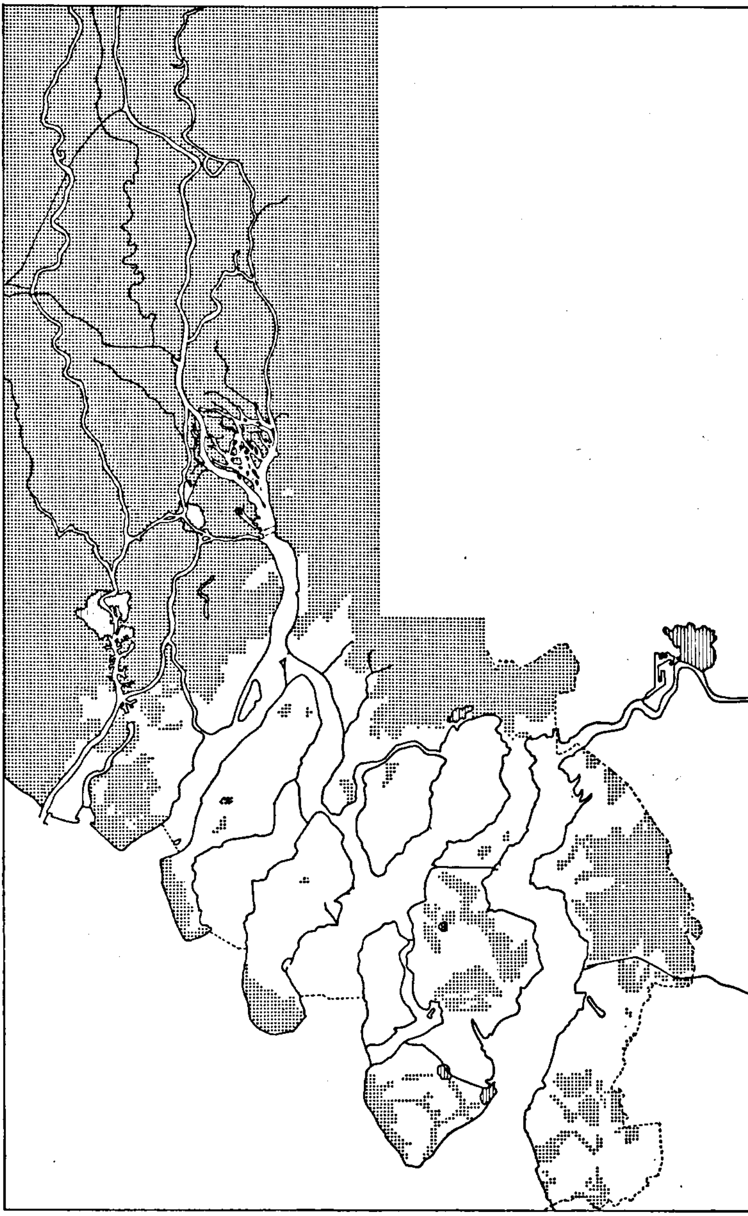

Fig. 4. Extension of the area where the salinity of the inland water never rises above 0.3‰ Cl'.

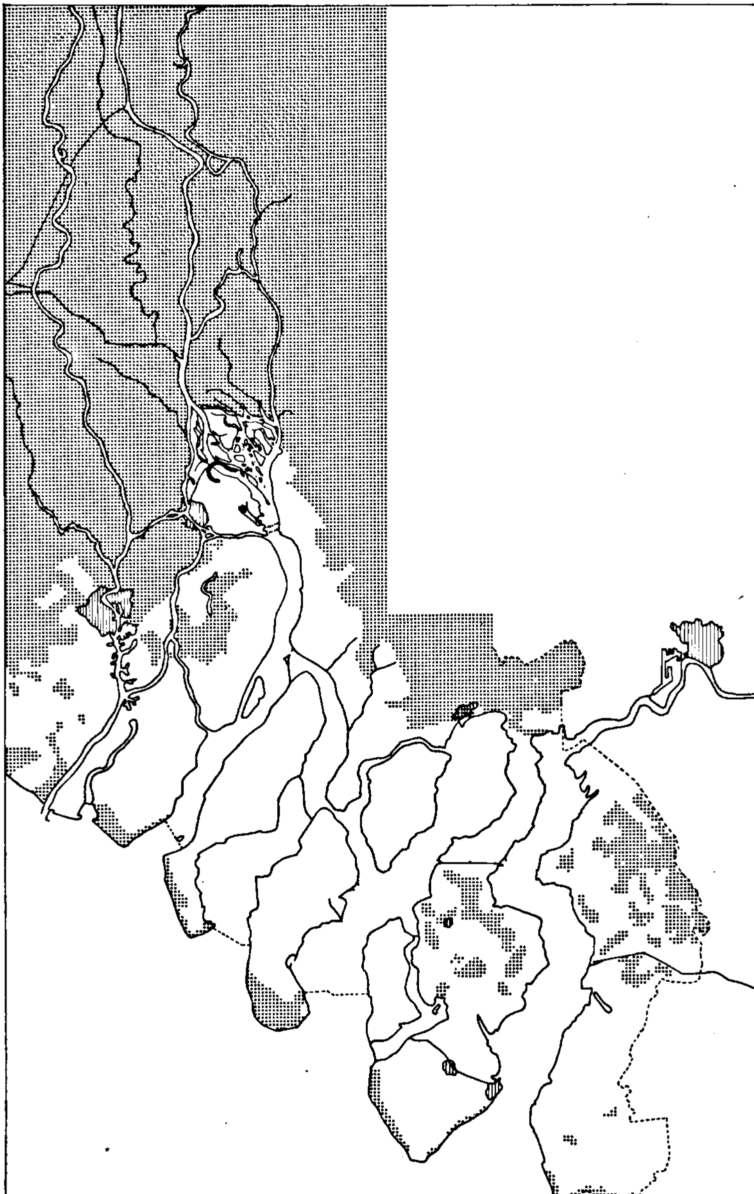

Fig. 5. Extension of the area where the salinity of the inland waters never rises above 1.0‰ Cl'.

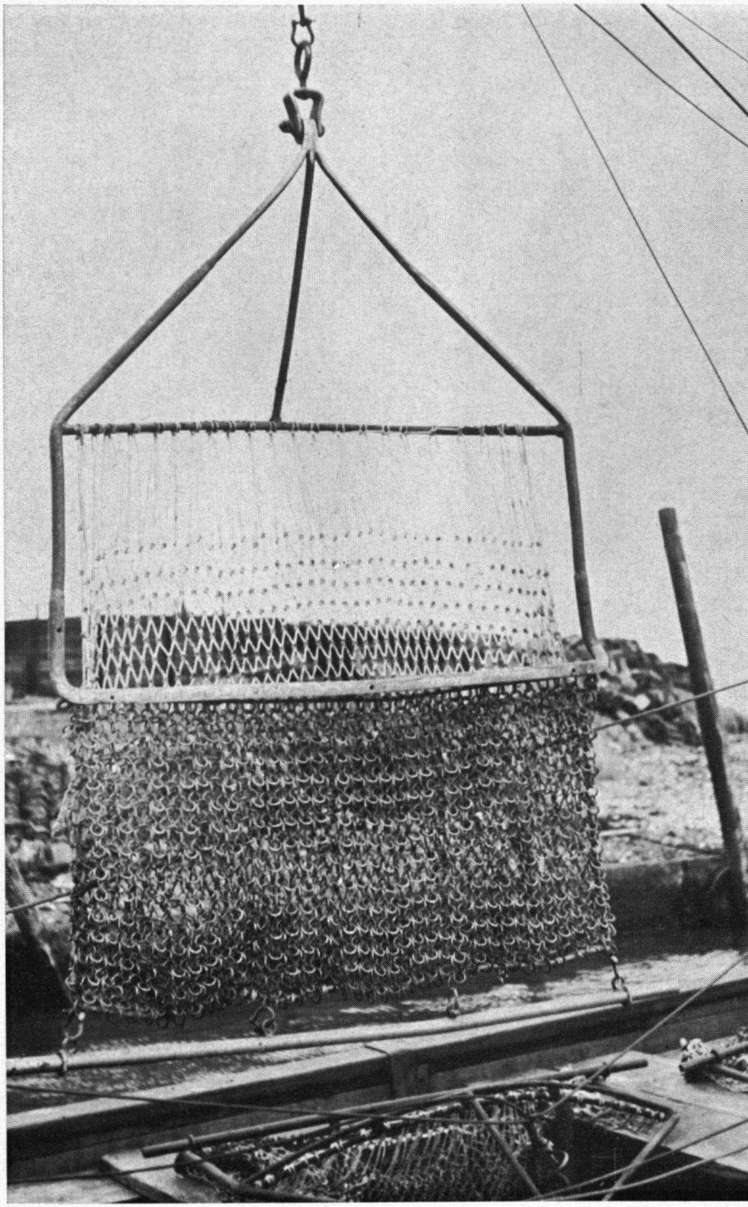

Fig. 6. Oyster-dredge used for dredging unionids.

Data from the literature are only incorporated when it could be ascertained that the records originated from live animals taken in situ, because many unionids are transported by the rivers to brackish areas and even to the North Sea (KRUIZINGA, 1936). Live specimens have even been washed ashore on the beach at the Hook of Holland. Most places at which unionids have been recorded in the past, were visited by us. If we found no traces of their occurrence, we assumed that they had disappeared from those places.

Data on the grain-size distribution of sediments were determined with the aid of a sieving-apparatus with a number of sieves of different mesh size. From these data the median grain-size could be determined.

THE FAMILY UNIONIDAE FLEMING, 1828

According to VAN BENTHEM JUTTING (1943) six species of the family Unionidae occur in the Netherlands. All species have been found in the estuarine region of the rivers Rhine, Meuse and Scheldt, the so-called Delta area. Our data on the distribution of freshwater mussels have been derived from the literature (VAN BENTHEM JUTTING, 1943; KUIPER, 1944; HENRARD, 1946; VAN BENTHEM JUTTING, 1947; LEENTVAAR, 1955; JANSSEN, 1958; BUTOT, 1960a; BUTOT, 1960b; BUTOT, 1962; HIGLER, 1964), from the collection of the Rijksmuseum van Natuurlijke Historie (Leiden), the Zoölogisch Museum of the University of Amsterdam and of the Natuurhistorisch Museum (Rotterdam), from the card index of the 'Comité ter Bestudering van de Molluskenfauna van Nederland' and from our own investigations. Our identifications are based on VAN BENTHEM JUTTING (1943), ADAM (1960), ELLIS (1962) and JANSSEN & DE VOGEL (1965).

ECOLOGY OF UNIONIDS IN A FRESHWATER TIDAL AREA

Freshwater tidal areas are uncommon. The Biesbosch is such an area and with its large extension (about 100 sq. km) presents an ideal opportunity to study the ecology of freshwater molluscs in aberrant conditions. For a full description of the hydrography of the Biesbosch we already referred to PARMA (1966). The following are extracted from his study and that of ZONNEVELD (1960). The salinity of the water is less than 0.3‰ Cl' and often even less than 0.1‰ Cl'. The vertical tidal difference is about 2 m. From about mid-tide level upward the litoral zone is covered by rushes and reed, but below this level a large variety of sand-bars and mudflats is uncovered by the falling tide. Many creeks have a depth of only 0-50 cm at low tide, but in some gullies considerable depths (up to 8 m) may also be encountered during low tide. During normal meteorological conditions maximum current-velocities of 0.8 m/sec. are measured in the gullies. During storms the velocity is certainly higher, but there are also large areas where these speeds are never reached. Particularly, in some inundated polders the currents are always very slight.

Part of the Biesbosch is influenced by the polluted water of the Rhine (fig. 1), and thus has a relatively high salinity and a low oxygen content: another part is under the influence of the cleaner water of the Meuse, whereas between these two regions a third, intermediate, area is known to exist. Freshwater mussels are not found in the part of the Biesbosch most heavily influenced by the Rhine, but in the two remaining areas with less than 10 % Rhine-water they occur in substantial quantities in suitable places. Consequently our observations on the ecology of unionids in a freshwater tidal area were made in the sectors of the Biesbosch influenced by the Meuse.

Although freshwater mussels are fairly common in the clean parts of the Biesbosch area, they somehow do not occur in the intertidal zone. *Anodonta* spp. were never found above the low water line; the species of *Unio* were collected only at very low tides in the immediate vicinity of the edge of the water. It seems that unionids are not adapted to the extreme habitat of the intertidal zone of a freshwater tidal area. A possible explanation for this lies in the fact that they do not burrow sufficiently deep to be protected when the intertidal zone is exposed at low tide. In this respect it is interesting to mention the observation of MENTZEN (1926) who states that in normal rivers the unionids always remain below the lowest summer level of the river. We do not have information on temperatures inside the shells of unionids which lie upon the mud during low tide on warm, sunny days, but it is conceivable that these temperatures may be high and probably lethal for an aquatic organism (compare KONDRAT'EV, 1963, who records damage to cilia at 34° C). On the other hand during low tide the unionids are liable to be killed by frost in winter. Thus organisms which do not burrow during low tide have to stand all climatological extremes. Perhaps also the rapid changes of the temperature during falling and rising tides may have a harmful effect on unionids. Moreover, there exists another, indirect, influence of the climate. In winter, during periods with floating ice, the ice-floes are transported over the shallows by the tidal currents. During these movements of the ice the surface of the flats is thoroughly disturbed. Freshwater mussels, immobilized by the low temperature, are then in danger of being covered with mud. Moreover they may be carried off to the sea.

We consider herons, coots, waders, gulls, crows and rats possible predators of unionids in the intertidal zone. Otters have become extinct in the Biesbosch area. At various low tides during a period of frost Mr. D. W. FEY observed one or two Carrion Crows (*Corvus corone corone*) which devoured in about two weeks no less than 156 specimens of *Anodonta anatina*. They probably found these clams in shallow water during very low tides. The intensity of their searching may be demonstrated by the fact that we ourselves were able to find five or six specimens only in the same area before the arrival of the crows. It may be assumed that Carrion Crows and probably also Hooded Crows (*Corvus corone cornix*) are very destructive predators of unionids in the intertidal zones of freshwater tidal areas. We think that the same is true for various species of gulls, which visit the mudflats during low tide, although we do not have evidence of this. Waders, herons and coots (WOLFF, 1966) also possibly prey upon these clams, though we never observed this in the Biesbosch area. VAN DER VOO (1966) observed rats (*Rattus norvegicus*) devouring *Anodonta* and *Unio*—as did STEUSLOFF (1926). As these rats are very common in the Biesbosch area, we suppose that here they also act as predators on unionids, although VAN DER VOO (l.c.) made his observations in stagnant water.

Once again we may point out the disadvantage to the unionids in not resorting to burrowing during low tide, since this facilitates the activities of predators. From these observations it may be deduced that the intertidal zone of a freshwater tidal area in western Europe forms an environment which cannot be inhabited by unionids. Nor is there any other large species of filter-feeding molluscs which inhabits this environment. In the euhaline and polyhaline estuaries of western Europe, however, a similar environment is occupied by species such as *Cardium edule* and *Mya arenaria*. The unionids in western Europe clearly have been unable to develop a burrowing type of species adapted to the special conditions of the intertidal zone of a freshwater tidal area. We suggest that such an environment is too rare and, when it occurs, too ephemeral to cause the evolution of types adapted to its conditions.

INFLUENCE OF POLLUTION

The Rhine is a strongly polluted river (ANONYMOUS, 1956-1966). It has a high anthropogenic salinity and often suffers from low oxygen-contents. The water of the Meuse, however, is still fairly clean and has a high content of oxygen (WIBAUT-ISEBREE MOENS, 1956).

The water of the Rhine flows to the sea through the rivers Lek and Waal. In the branches Hollandse IJssel, Nieuwe Maas, Noord, Boven-Merwede, Oude Merwede, Nieuwe Merwede, Oude Maas, Spui, and Dordtse Kil only Rhine-water is transported. The water of the Meuse flows through the Bergse Maas and Amer, then unites with the water of the Nieuwe Merwede (= Rhine basin) to form the Hollands Diep. There is no other direct connection between Meuse and Waal. Since the annual discharge of the Amer into the Hollands Diep is only $^1/_5$—$^1/_6$ of that of the Nieuwe Merwede (PARMA, 1966), it is clear that the Hollands Diep may be considered as a branch of the Rhine with regard to the quality of its water. Rhine water is also found in the western part of the Biesbosch (fig. 1).

During our investigations we were unable to find unionids anywhere in the Rhine and its branches, although there are several earlier records. Only in some isolated, dead branches, which are influenced by the Rhine only during high river discharges in early spring, some individuals may be found, e.g. in the Kil van Hurwenen. In the part of the Biesbosch influenced by the Rhine we found only one specimen of *Unio tumidus*, at the end of a gully, where the biological self-purification of the water probably exerts its influence. We found another specimen of the same species in a comparable gully in the vicinity of the Oude Maas (= Rhine basin). In a similar gully, but influenced by the much cleaner Meuse, we obtained many hundreds of unionids.

Our conclusion is that the Rhine water is too much polluted to be suitable for unionids. As the water in the Biesbosch area is either highly polluted Rhine water or much cleaner Meuse water, almost without intermediate grades, we are not able to say much on the pollution tolerance of the various species. From the note by VAN BENTHEM JUTTING (1943) on *Unio crassus batavus* being found especially in the Meuse unlike the other species, it may be deduced that this species was the first to disappear from the Rhine and that it is the most susceptible to pollution. Since the pollution of the Rhine strongly influences the Hollands Diep, the Oude Maas and the Nieuwe Maas, it is now impossible to investigate the distribution of unionids in the interesting transitional zone of fresh and brackish water in these branches.

SYSTEMATIC PART

Unio crassus batavus (Maton & Rackett, 1807)

Van Benthem Jutting 1943, p. 117-121; Adam, 1960, p. 326-328; Ellis, 1962, p. 15-16.

Distribution: *Unio crassus* occurs from Spain to northern Russia, but the subspecies *U. c. batavus*, the one occurring in the Netherlands, is only known from the Atlantic region of Spain and France, Belgium, the Netherlands and western Germany. It is rather rare in the

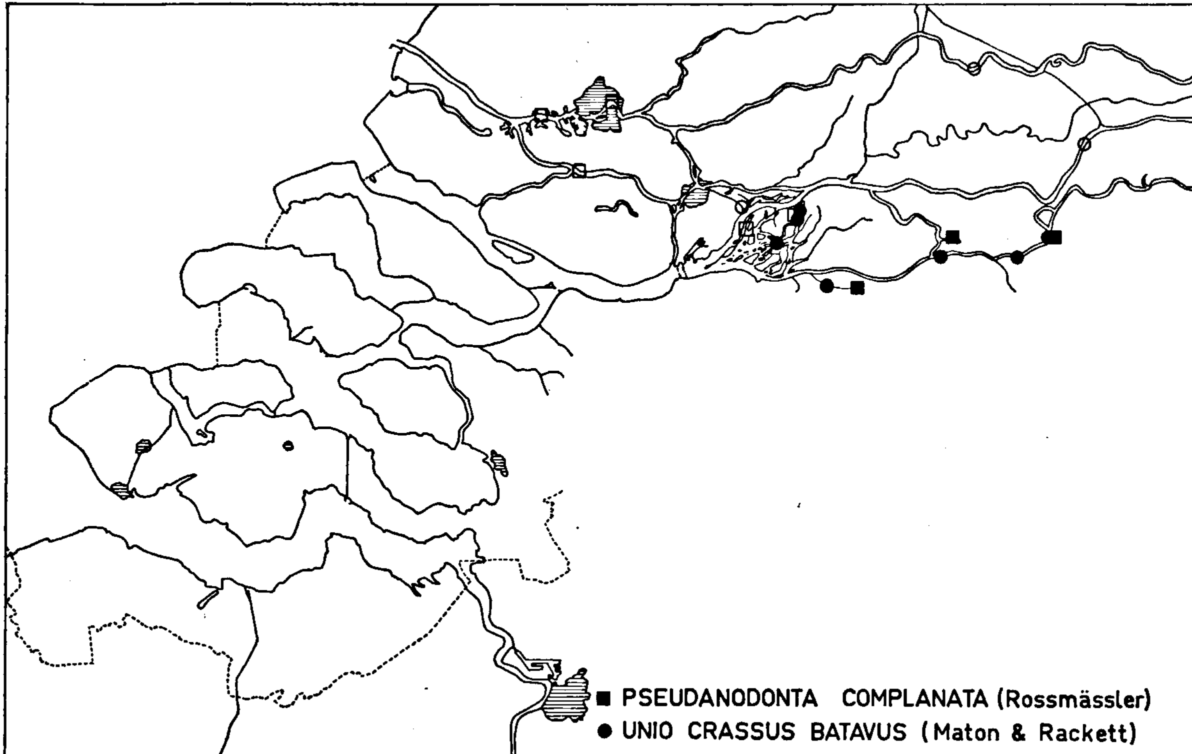

Fig. 7. Distribution of *Unio crassus batavus* and *Pseudanodonta complanata*. Black circles, squares and triangles represent observations of live specimens during our investigations; open symbols denote localities where living specimens were formerly observed, but not during our investigations. Circles represent localities inside and triangles localities outside the winterbed of the river.

Netherlands. The distribution in the area investigated is mapped in fig. 7.

Localities *): Province of Zuid-Holland: Wantij near Ottersluis (†, ZMA). Province of Gelderland: Lek near Culemborg (†, RMNH), Waal near Tiel (†, RMNH). Province of Noord-Brabant: Reugt, Brabantse Biesbosch (W), Steurgat, Brabantse Biesbosch (W), Oude Maasje near Waspikse Veer (W), Maas near Heusden (W), Maas near Empel (ZMA).

Ecology: It is generally agreed that *Unio crassus batavus* is a typically riverine species. Indeed all our observations are from localities in open connection with the rivers; we do not have any observation from inland waters. On the other hand *U. c. batavus* seems to avoid strong currents, as do all Dutch unionids, since we did not find any in the central part of the rivers, where coarse sands indicate high current-velocities. We therefore consider the statement of VAN BENTHEM JUTTING (1959) on *U. c. batavus* living fully exposed to the current not correct.

In sheltered places with muddy sediments it can, however, be fairly abundant. The species lives even in almost stagnant water, e.g. in the last part of blind-ending creeks. From our observations we have no indication that it is more tolerant to high current-velocities than *Unio tumidus*. Probably it is not the current itself which limits the occurrence of unionids in rivers, but the increased transport of sand. We did not find any preference for a certain kind of substrate, because *U. c. batavus* was met with in a fairly wide range of sediments, from soft muds to medium sands. Nevertheless it is possible that the very young stages do have a preference for a certain kind of substrate, as is indicated by MENTZEN (1926), who mentions a preference for fine sands and mud over pebbles and stones.

Considering its occurrence in parts of the rivers nearly without currents, it is remarkable that this species is not found in similar stagnant inland waters, a fact also mentioned by MENTZEN (l.c.). Possibly the species is only able to complete its larval development in a limited number of species of fish occurring exclusively in rivers, e.g. *Chondrostoma nasus, Leuciscus idus* and *L. grislagine* (REDEKE, 1941); this was shown by DAVENPORT & WARMUTH (1965) to be the case in *Anodonta implicata,* which can only develop on the fish *Pomolobus pseudoharengus.*

*) † = formerly occurring, nowadays absent; NHMR = collection Natuurhistorisch Museum Rotterdam; RMNH = collection Rijksmuseum van Natuurlijke Historie, Leiden; ZMA = collection Zoölogisch Museum, Amsterdam; W = own observations.

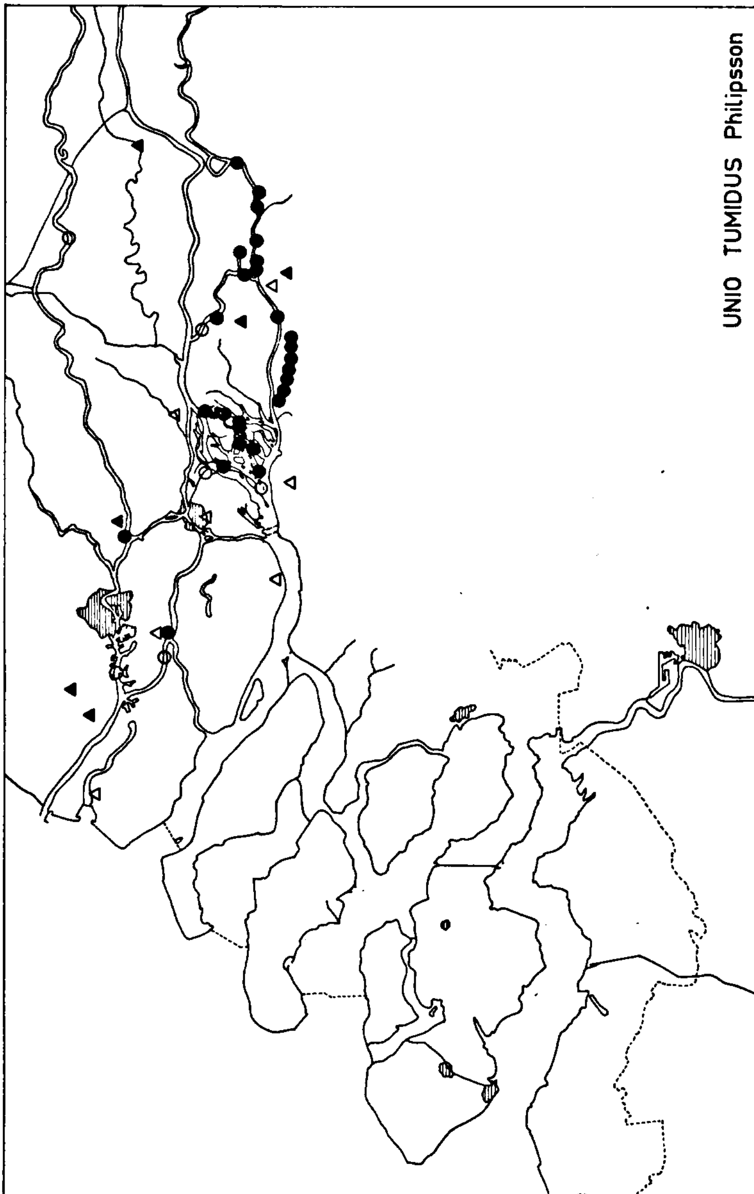

Fig. 8. Distribution of *Unio tumidus*. Symbols as in fig. 7.

From the observation of VAN BENTHEM JUTTING (1943), that *U. c. batavus* occurs more frequently in the Meuse than in the Rhine, one may assume that the species is susceptible to pollution. Whether this susceptibility and the consequent rarity of the species is due to the relatively high salinity of the polluted water, or to its low oxygen content, is at present a matter for conjecture. The statements of JAECKEL (1962), that the maximum salinity at which *Unio crassus* was observed is about 0.3°/oo Cl', indicates that salinity has a harmful effect on the species. However, HORVATH (1966) states that *U. crassus* needs a high oxygen content of the water. Presumably a combination of factors has caused the disappearance of the species.

We do not expect it to penetrate the future Delta lakes.

Unio tumidus Philipsson, 1788

Van Benthem Jutting, 1943, p. 124-126; Adam, 1960, p. 328-329; Ellis, 1962, p. 13-15.

Distribution: *Unio tumidus* occurs in western and central Europe as far east as southern Russia. It is a common species in the Netherlands. The distribution in the area investigated is given in fig. 8.

Localities: Province of Zuid-Holland: Boonervliet, Maasland (W), Vlaardingse Vlietlanden, Maasland (NHMR), Nieuwe Maas near Vijfsluizen (†, NHMR), Heindijksloot, Oostvoorne (†, Henrard, 1946), Oude Maas near Poortugaal (†, ZMA), Rhoon (†, ZMA), Kooigat near Rhoon (W), harbour of Strijen (†, W), Schuwachtse polder, Lekkerkerk (RMNH), Bakkerskil near Krimpen aan de Lek (W), Giessen near Giessen-Oudekerk (†, RMNH), Dordrecht (†, ZMA), Wantij near Ottersluis (†, ZMA), Nieuwe Merwede near Ottersluis (†, RMNH). Province of Gelderland: Linge near Wadenoyen (RMNH,) Afgedamde Maas near Nederhemert (W), Lek near Culemborg (†, RMNH). Province of Noord-Brabant: Lange Reeweg, Hooge Zwaluwe (†, W), Gat van de Kleine Hil, Brabantse Biesbosch (W), Boerenplaat, idem (†, ZMA), Gat van de Binnennieuwesteek, idem (W), Vlooiensloot, idem (W), Gat van de Noorderklip, idem (W), Reugt, idem (W), Steurgat from Pauluszand to Werkendam, idem (W), Alm near Veen (RMNH), Afgedamde Maas near Rijswijk (†, ZMA), Afgedamde Maas near Giessen (ZMA), Heusdens Kanaal (W), Oude Maasje from Keizersveer to Kapelse veer (W), Bergse Maas near Drongelen (W), Maas near Heusden (W), Maas near Well (W), Maas near Hedel (RMNH), Maas near Empel (ZMA), Doeveren near Heusden (†, W), Drunen (RMNH).

Ecology: *Unio tumidus* is usually characterized as a species occurring in sluggish rivers and canals. This is certainly true for the investigated area.

Regarding the tolerance to high current-velocities it appears that *U. crassus batavus* and *U. tumidus* have the same upper limit. *U. c. batavus* is nearly always found together with *U. tumidus* (tables 1 and 2), but the reverse is not true. The remark by VAN BENTHEM JUTTING (1959) (text in Dutch) that *U. tumidus* lives fully exposed to the current, does not seem to be correct. Both species may also be found together in areas of the rivers nearly without current. However, contrary to *U. c. batavus, U. tumidus* penetrates into the inland waters, since it can often be found in stagnant canals and pools.

Concerning the substratum it may be noted that we found specimens in very soft mud as well as on medium sand.

U. tumidus seems to have the largest resistance to pollution of all Unionidae. In the Biesbosch area it was the species found closest to the Rhine and the influence of its polluted waters (Gat van de Binnennieuwesteek). Moreover, it was the only species found living in three blind-ending creeks branching from the Rhine (Kooigat near Rhoon, Bakkerskil near Krimpen aan de Lek, Gat van de Kleine Hil in the Biesbosch). We suppose that the water in these creeks goes to a certain extent through a process of biological self-purification owing to the fairly long time that it stays in these creeks. On the other hand it apparently does not become sufficiently clean to support the other species of unionids occurring in the Netherlands.

According to JAECKEL (l.c.) the maximum salinity at which this species was found is 1.67‰ Cl′. We do not, however, have any observation of unionids occurring at higher values than about 0.3‰ Cl′, but it should be noted that in most areas with brackish water unionids may be absent for reasons of accessibility. Inside the dikes the species is only found in the area where fresh water from the Rhine and the Meuse exerts its influence (fig. 8). It is absent on the many islands of the Delta, probably because the fishes acting as 'vectors' were not able to cross the salt and brackish estuaries. According to THIEL (1929) and VAN BENTHEM JUTTING (1943) the glochidia of *Unio* are expelled in June, July and August and it is exactly at this time that the brackish water of the estuaries penetrates to its farthest distance in an upstream direction, thus preventing freshwater fishes, which may bear glochidia, from crossing those parts of the estuaries often filled with fresh water in winter, e.g. the Haringvliet (cf. PEELEN, l.c.). Some of the localities of *U. tumidus* on the islands no longer harbour the species, probably as a result of the inundations of 1944/45 and 1953.

From our observations we conclude that *U. tumidus* is the most euryokous unionid of the Netherlands. Therefore we certainly expect that it will colonize the future Delta lakes.

Unio pictorum (L., 1758)

Van Benthem Jutting, 1943, p. 121-124; Adam, 1960, p. 329-330; Ellis, 1962, p. 11-13.

Distribution: *U. pictorum* is found in north-western, northern and central Europe and North Africa. It is a common species in the Netherlands. Its distribution in the area investigated is shown in fig. 9.

Localities: Province of Zuid-Holland: Heindijksloot, Oostvoorne (†, Henrard, 1946), Brielle (†, Henrard, 1946), Brielse Meer near Nieuwersluis (NHMR), Boonervliet, Maasland (W), Vlaardingse Vlietlanden, Maasland (NHMR), Nieuwe Maas near Vijfsluizen (†, NHMR), Nieuwe Maas near Rotterdam (†, RMNH), Bergse plas, Rotterdam (RMNH), Rotterdam (RMNH), Gouda (RMNH), Koedood near Charlois (†, RMNH), near churchyard and near castle of Rhoon (†, ZMA), Oude Maas near Rhoon (†, RMNH), Oude Maas near Dordrecht (†, ZMA), Oud-Beyerlandse kreek, Oud-Beyerland (†, W), Oude Diep, Numansdorp (†, ZMA), Dordrecht (†, ZMA), Lek near Krimpen aan de Lek (W), Schuwachtse polder, Lekkerkerk (RMNH). Province of Gelderland: Duck-decoy near Asperen (RMNH), Linge near Wadenoyen (RMNH), Kil van Hurwenen, Hurwenen (W), Afgedamde Maas near Nederhemert (W) and Aalst (W). Province of Noord-Brabant: Lange Reeweg, Hooge Zwaluwe (W), Boerenplaat, Brabantse Biesbosch (†, ZMA), Gat van de Noorderklip, idem (W), Reugt, idem (W), Steurgat from Pauluszand to Werkendam, idem (W), Afgedamde Maas near Rijswijk (†, ZMA), Oude Maasje from Keizersveer to Kapelse veer (W), Maas near Heusden (W), Maas near Hedel (ZMA), Maas near Empel (ZMA), Oude Maasje, Heusden (†, RMNH), Orthen (RMNH). Province of Zeeland: Axelse Sassing, Axel (†, W).

Ecology: In the region under consideration *U. pictorum* has about the same ecological range as *U. tumidus*, but in general the former is more often found in stagnant waters and the latter more in running waters. Figs. 8 and 9 show 13 inland localities for *U. tumidus* and 21 for *U. pictorum* respectively. As the total number of localities is 49 and 47 respectively, the difference is not significant ($P > 0.05$), so that we cannot conclude with certainty that *U. pictorum* inhabits the more stagnant waters. In inland localities where both species occur together, *U. pictorum* is usually more numerous, but we do not have quantitative data to give statistical proof of this. It is evident from table 1 that in river localities *U. tumidus* is the most numerous species, but in the very slow running Oude Maasje (table 2) *U. pictorum* is almost as abundant as *U. tumidus*. VAN BENTHEM JUTTING (1959) probably is mistaken when she states that *U. pictorum* lives fully exposed to the current, because in the Dutch summary she reports this to be the case for *U. tumidus*. *U. pictorum* was mostly encountered on

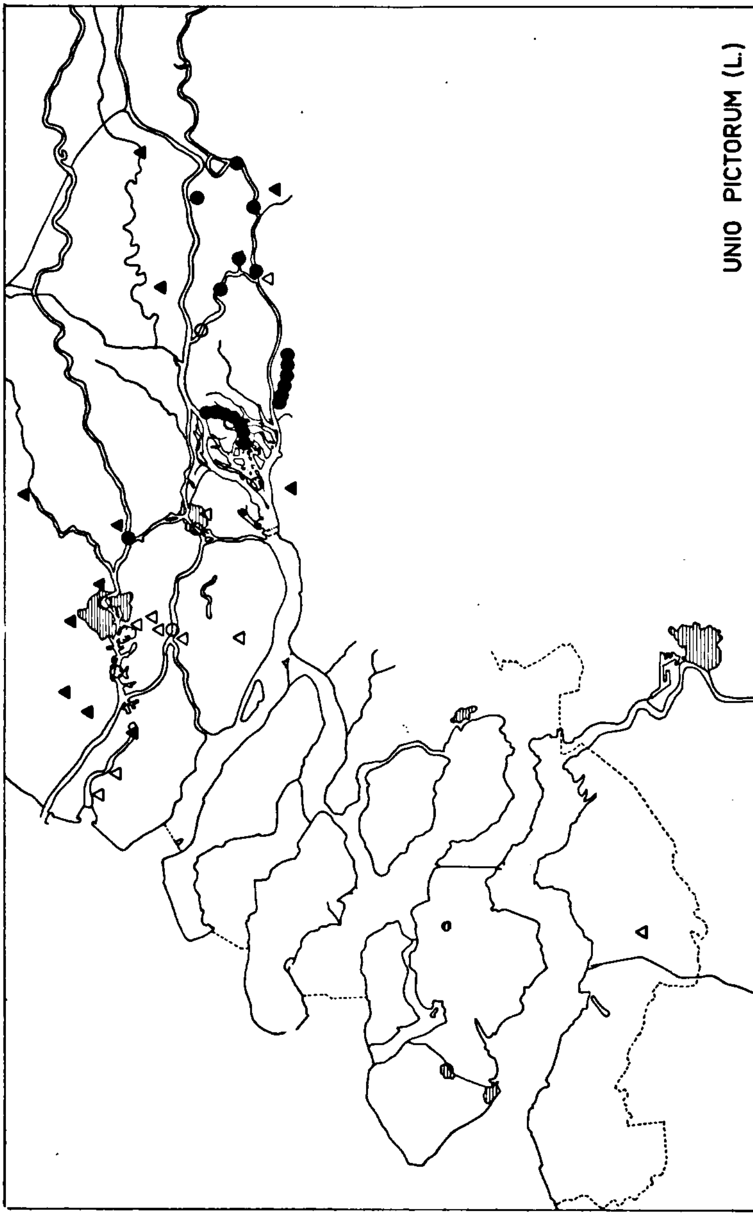

Fig. 9. Distribution of *Unio pictorum*. Symbols as in fig. 7.

	Steurgat									Ruigt		
No. sample:	446	447	448	449	450	451	452	453	454	455	456	457
Anodonta anatina	6(45)	–(1)	2(7)	–(2)	–(–)	–(–)	–(3)	1(–)	–(27)	–(6)	–(1)	–(4)
Pseudanodonta complanata	–(3)	–(–)	–(2)	–(1)	–(–)	–(1)	–(–)	–(1)	–(4)	–(5)	–(–)	–(–)
Unio pictorum	22(93)	3(16)	13(22)	4(16)	–(1)	3(9)	8(5)	–(7)	1(45)	–(19)	–(5)	–(5)
Unio tumidus	43(502)	5(26)	26(135)	3(56)	1(2)	3(40)	4(36)	–(27)	2(226)	–(54)	–(34)	1(39)
Unio crassus batavus	–(9)	–(–)	3(5)	–(–)	–(–)	–(2)	–(1)	–(–)	–(7)	–(2)	–(–)	–(3)
Total:	71	8	44	7	1	6	12	1	3	–	–	1

→ increasing current-velocity

Table 1. Occurrence of unionids in the blind-ending creek Steurgat-Ruigt in the Brabantse Biesbosch. From left to right the maximum current-velocities increase from nearly zero to about 0.9 m/sec., although it is not known what exact relation exists between distance and current-velocity. Each sample was obtained by five minutes dredging with the oyster-dredgde described above. During each of these periods roughly the same distances were covered. Numbers in brackets denote dead, but still intact double valves, the other numbers live specimens.

	East	–	Oude Maasje		–		West		–	Bergse Maas
No. sample:	458	459	460	461	462	463	464	465	466	467
Anodonta anatina	9	2	2	3	1	1	4	2	1	–
Pseudanodonta complanata	1	–	–	–	–	–	–	–	–	–
Unio pictorum	21	12	4	14	7	14	1	2	4	–
Unio tumidus	27	7	4	7	4	2	2	1	4	–
Unio crassus batavus	–	–	–	–	–	–	–	–	–	–

→ increasing current-velocity

Table 2. Occurrence of unionids in the blind-ending creek Oude Maasje near Geertruidenberg. Nos. 458-466 are samples taken in the very slow running Oude Maasje, 467 a sample taken just outside this creek in the Bergse Maas. Same sampling-method employed as in table 1.

muddy sediments; also some specimens were found on medium sand, but these may have been transported to this environment by the current. Regarding its resistance to pollution, *U. pictorum* seems to occupy an intermediate position between *U. crassus batavus* and *U. tumidus.* JAECKEL (l.c.) mentions 1.67‰ Cl′ as the maximum salinity tolerated by this species. We have, however, no observations from localities with a salinity above 0.3‰ Cl′. Owing to difficulties in accessibility *U. pictorum* is probably only found inside the dikes in the area where the fresh water of the Rhine and the Meuse exerts its influence and in Zeeuws-Vlaanderen, where the influence of fresh water from the higher Belgian territory is felt. The record from Zeeuws-Vlaanderen is the first of a live in situ specimen from the province of Zeeland. The species is completely absent on the islands. This species will certainly penetrate into the future Delta lakes.

Anodonta anatina (L., 1758)

Van Benthem Jutting, 1943, p. 137-140; Adam, 1960, p. 334-335; Ellis, 1962, p. 22-26.

Distribution: *A. anatina* is a Palaearctic species, but its exact distribution is not fully known, as it is often confused with *A. cygnea.* It is a common species in the Netherlands. Its distribution in the area investigated is given in fig. 10.

Localities: Province of Zuid-Holland: Poeldijk (RMNH), Boonervliet, Maasland (W), Vlaardingse Vlietlanden, Maasland (NHMR), Zweth between Delft and Rotterdam (NHMR), Overschie, Rotterdam (RMNH), Bergse plas, Rotterdam (RMNH), Nieuwe Maas near Rotterdam (RMNH), Capelle aan de IJssel (RMNH), Nieuwerkerk aan de IJssel (RMNH), Hollandse IJssel near Moordrecht (†, ZMA), Reeuwijkse plassen, Gouda (RMNH), Heindijksloot, Oostvoorne (†, Henrard, 1946), Brielse Meer near Steenen Baak, near Brielle, near Zwartewaal and near Nieuwersluis (W), Brielle (W), castle near Rhoon (†, ZMA), Oude Maas near Poortugaal (†, ZMA), Oude Maas near Rhoon (†, ZMA), harbour of Rhoon (†, ZMA), Oude Maas near Heinenoord (†, ZMA), Oude Maas near Dordrecht (†, RMNH), Binnenbedijkte Maas, Maasdam (†, ZMA), harbour of Strijen (W), Schuwachtse polder, Lekkerkerk (RMNH), Giessen near Giessen-Ouderkerk (RMNH), Leerdam (RMNH). Province of Gelderland: Wageningen (†, RMNH), Tiel (†, card index Ned. Malacol. Ver.), Kil van Hurwenen, Hurwenen (W), Afgedamde Maas near Nederhemert (W) and Aalst (W). Province of Noord-Brabant: Roodevaart near Zevenbergen (†, W), De Dood, Brabantse Biesbosch (W), Pauluszand, Brabantse Biesbosch (W), Steurgat near Werkendam, Brabantse Biesbosch (W), Afgedamde Maas near Rijswijk (†, ZMA), Afgedamde Maas near Giessen (†, ZMA), Heusdens Kanaal

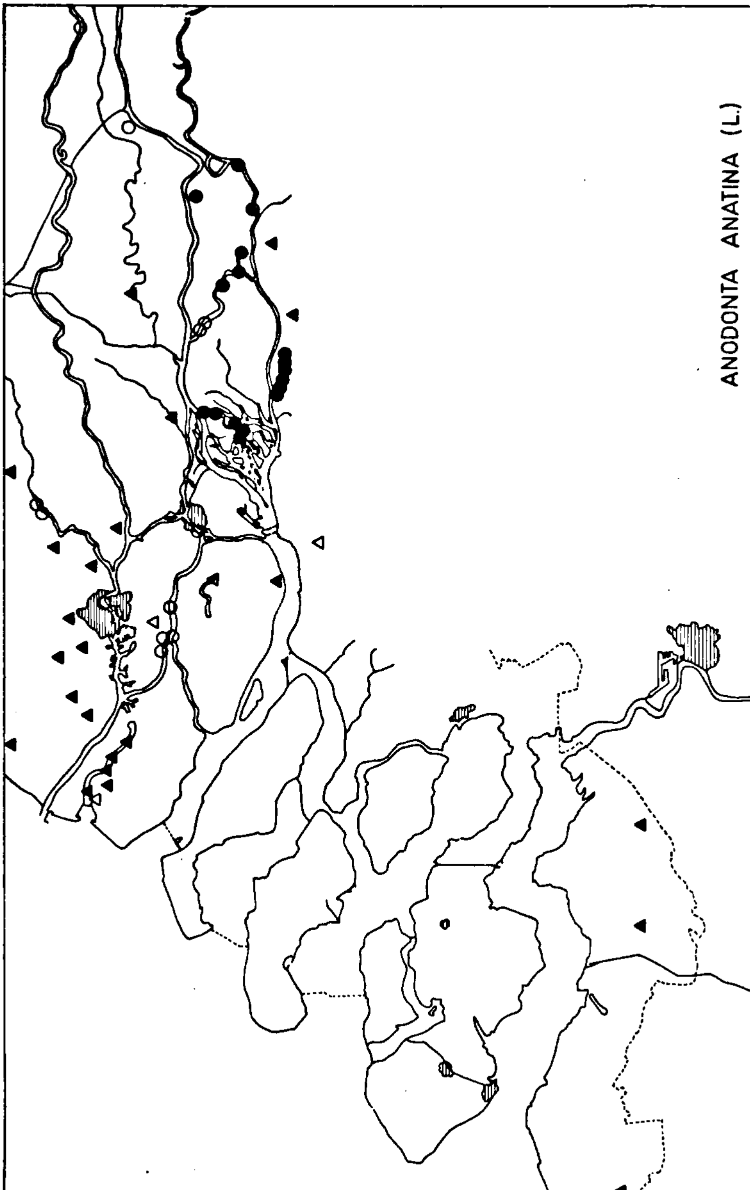

Fig. 10. Distribution of *Anodonta anatina*. Symbols as in fig. 7.

(W), Oude Maasje from Keizersveer to Kapelse veer (W), Maas near Hedel (RMNH), Maas near Empel (ZMA), Lange straat between Capelle and Waalwijk (W), Nieuwe Wiel, Haarsteeg (ZMA). Province of Zeeland: Kanaal Brugge-Sluis, Sluis (W), Axelse Kreek, Axel (W), Clingepolder near Clinge (W).

Ecology: *A. anatina* has been found by us in river habitats as well as in stagnant inland waters. A decided preference for flowing water, as indicated by ELLIS (1962), has not been observed in the Delta area. It is indeed found more in running waters than *A. cygnea,* but on the other hand, if compared to the three species of *Unio,* it is decidedly a species of stagnant waters.

From tables 1 and 2 it appears that in riverine habitats *A. anatina* is most abundant in localities with the lowest current velocities. In the Biesbosch area it is especially numerous in the inundated polder De Dood where very low current-velocities occur. In accordance with this preference for low current-velocities and stagnant waters it occurs as much in inland waters as *Unio pictorum.* In running waters the shells were observed to be usually much thicker than in stagnant waters.

Although ELLIS (l.c.) records a preference for a sandy rather than a muddy bottom, we have very few records from sandy bottoms. We found the species mostly in muddy sediments with abundant plant remains. JAECKEL (l.c.) indicates a salinity tolerance of 1.67‰ Cl′. The highest value at which we found this species was about 0.9‰ Cl′ (Brielse Meer—personal communication by Mr. R. PEELEN).

According to THIEL (1929) and VAN BENTHEM JUTTING (1943) the glochidia of *Anodonta* are expelled in February-June. In that period the Haringvliet and other estuaries sometimes contain fresh water (PEELEN, l.c.), but nevertheless these sea-arms seem to have prevented freshwater fishes crossing from one island to another. Therefore we find *A. anatina* only in the freshwater area of the Rhine and Meuse basins and in Zeeuws-Vlaanderen where freshwater (and freshwater fishes) may come down from the higher situated Belgian area. The records from Zeeuws-Vlaanderen are the first of living specimens from the province of Zeeland. We suppose that *A. anatina* will become a common inhabitant of the future Delta lakes.

Anodonta cygnea (L., 1758)

Van Benthem Jutting, 1943, p. 131-137; Adam, 1960, p. 331-334; Ellis, 1962, p. 18-22.

Distribution: *A. cygnea* seems to have a Palaearctic range, although its exact distribution is imperfectly known due to confusion with other species. It is a common species in the Netherlands. Owing to the gradual merging of *A. cygnea cygnea* (L.) into *A. cygnea zellen-*

sis (Gmel.) we did not always distinguish between those subspecies. Typical *A. cygnea* seems to be rare in the Delta area. The distribution of the species is given in fig. 11.

Localities: Province of Zuid-Holland: Boonervliet, Maasland (W), Vlaardingse Vlietlanden, Maasland (NHMR), Overschie, Rotterdam (†, RMNH), Hillegersberg, Rotterdam (*A. cygnea cygnea*; †, RMNH), Prins Alexanderpolder, Rotterdam (RMNH), Capelle aan de IJssel (RMNH), Nieuwerkerk aan de IJssel (RMNH), Schuwachtse polder, Lekkerkerk (RMNH), Berkenwoude (RMNH), Heindijksloot, Oostvoorne (†, Henrard, 1946; RMNH), Brielle (RMNH), Rockanje (*A. cygnea cygnea*; †, Henrard, 1946; RMNH), near churchyard (†, ZMA) and near castle (W, ZMA, RMNH) of Rhoon, Oud-Beyerlandse kreek, Oud-Beyerland (†, W), Oude Diep, Numansdorp (†, ZMA), Dordrecht (†, ZMA), Giessen near Giessen-Oudekerk (RMNH), Galatheepolder, Ooltgensplaat (†, W, RMNH). Province of Noord-Brabant: Lange Reeweg, Hooge Zwaluwe (W), Alm near Veen (RMNH), Lange straat between Capelle and Waalwijk (W), Doeveren near Heusden (†, W) Oude Maasje near Heusden (RMNH). Province of Zeeland: 'Mon Plaisir', Noordgouwe (†, W; this species?), 'Duinvliet', Oostkapelle (†, Kuiper, 1944; ZMA), 'Berkenbosch', Oostkapelle (†, Kuiper 1944; ZMA), 'Der Boede', Koudekerke (†, Kuiper, 1944; *A. cygnea cygnea*), Clingepolder near Clinge (W).

Ecology: We do not have any observations of *A. cygnea* in a river habitat and all old records that we could check, were from inland waters. Nevertheless on September 7, 1949, a live specimen was washed ashore on the beach of the Hook of Holland, possibly carried to sea from somewhere in the Rhine. We assume however that in the Delta area, *A. cygnea* is essentially a species of stagnant waters. As it is still absent in the Brielse Meer, created in 1950, where *A. anatina* nowadays is abundant, we conclude that it is moreover a species of the smaller, stagnant waters. Probably related to its preference for these small-sized habitats is the common occurrence of hermaphroditism, possibly an adaptive mechanism to such habitats. TOMLINSON (1966) explains the advantages of such a mechanism. In all localities where we obtained *A. cygnea,* it was found living on muddy bottoms rich in organic matter.

JAECKEL (l.c.) mentions a salinity tolerance of about 1.0‰ Cl'. However, we did not find specimens at salinities higher than 0.3‰ Cl'. Nevertheless *A. cygnea* is the only species known to have been present on the islands of the Delta area, although nowadays it has disappeared there owing to the large inundations in 1944/45 and 1953 (figs. 2 and 3). It may have been introduced there with the fairly frequent imports of freshwater fishes for angling, but if unionids

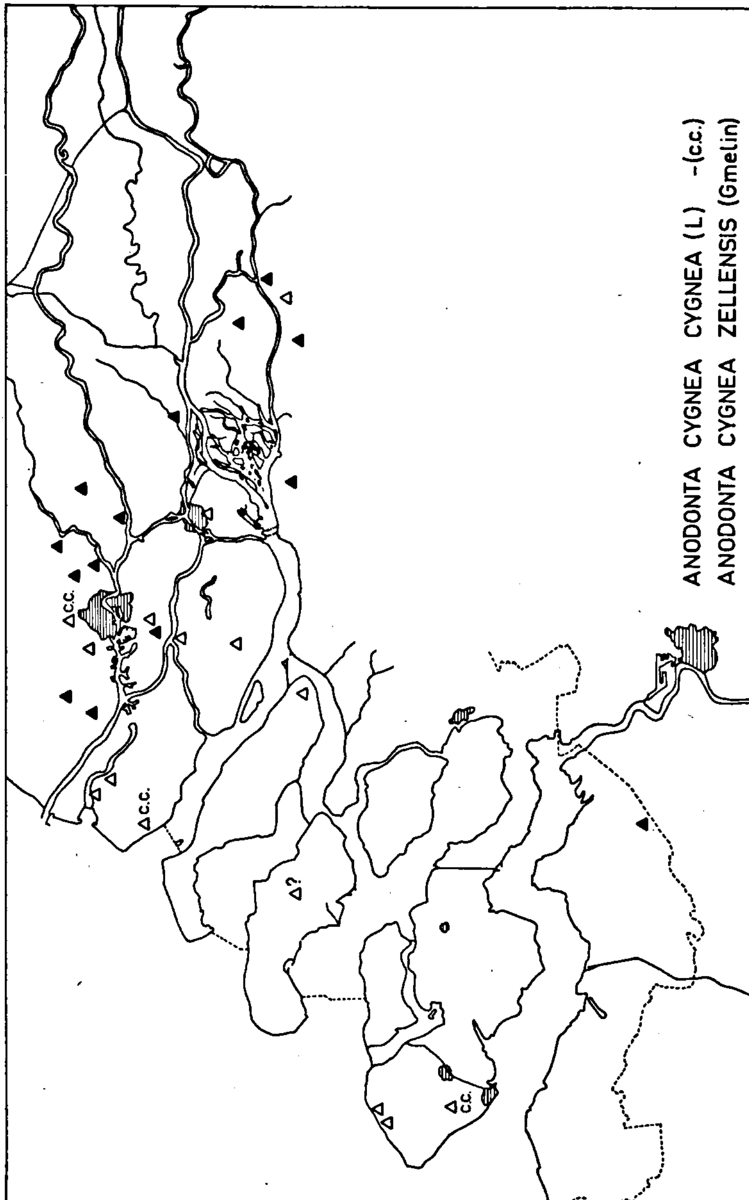

Fig. 11. Distribution of *Anodonta cygnea*. Symbols as in fig. 7.

did arrive in this way, it happened only very rarely. Moreover one may ask why only this species should have been introduced in this way, as all other species have always been absent on the islands of the Delta area. The distribution of *A. cygnea* in this way may have been facilitated by its hermaphroditism. Nevertheless we believe it to be possible that it has been introduced for its own sake on account of its large size. This supposition is supported by the fact that four of the five localities of *A. cygnea* on the islands were ponds of old estates. The locality Berkenbosch for example was an artificial pond without any surface connection with other waters. Aerial dispersal of this species by birds (REES, 1965) seems highly improbable because of its size.

The occurrence of *A. cygnea* in the freshwater area of the Rhine and the Meuse and in Zeeuws-Vlaanderen may have originated in a more natural manner. We were not able to find a difference in ecology between the subspecies *A. cygnea cygnea* and *A. cygnea zellensis*. We do not expect that this species will become very important in the future Delta lakes, although it may extend its range on the islands as a result of improved accessibility.

Pseudanodonta complanata (Rossmaessler, 1835)

Van Benthem Jutting, 1943, p. 141-142; Adam, 1960, p. 336-337 (s.n. *Pseudanodonta elongata* Holandre, 1836); Ellis, 1962, p. 26-27 (s.n. *Anodonta complanata* Rossmaessler, 1835).

Distribution: *P. complanata* occurs in north-western and central Europe. The populations of Great-Britain, northern France, Belgium, the Netherlands and western Germany (as far east as the Weser) are considered by some authors to represent a separate subspecies: *P. complanata elongata* (Holandre, 1836). The species is rare in the Netherlands. Its distribution in the area investigated is shown in fig. 7, p. 26.

Localities: Province of Zuid-Holland: Nieuwe Maas near Vijfsluizen (†, NHMR), Nieuwe Maas near Rotterdam (†, RMNH), Oude Maas near Rhoon (†, ZMA, RMNH). Province of Gelderland: Afgedamde Maas near Nederhemert (RMNH). Province of Noord-Brabant: Gat van de Kleine Hil, Brabantse Biesbosch (†, W), Steurgat, Brabantse Biesbosch (†, W), Oude Maasje near Kapelse Veer (W), Maas near Empel (ZMA). Moreover the species is recorded from the canal from Bruges to Sluis on Belgian territory (ADAM l.c.)

Ecology: Owing to the small number of observations it is difficult to discuss the ecology of *P. complanata*. All observations were made in river habitats, but mostly (if not always) in places with only low current-velocities. This is also recorded by VAN BENTHEM JUTTING (1959). Low current-velocities are accompanied by muddy bottoms and indeed our scanty records are all from muddy bottoms. As *P. complanata* nowadays only lives in the Meuse and its branches, we suppose that it is susceptible to pollution. As the species did not penetrate into the polders in the freshwater area of the Rhine and the Meuse, it cannot be expected to occur on the islands of the Delta area, where indeed it is absent. It is not likely that this species will penetrate into the future Delta lakes.

DISCUSSION

The ecological ranges of the Dutch species of freshwater mussels show an extensive overlap, due to the large ecological amplitude of most of these species. Nevertheless one may construct a diagram based on the current-velocity (fig. 12), into which all Dutch species may be assembled. Possibly an exception has to be made for *Pseudanodonta complanata,* owing to lack of data. The diagram by MENTZEN (1926) is not primarily based on the current-velocity, but on the type of river. Even in fast running rivers almost stagnant pits may occur, where species intolerant to high current velocities may live. The creeks investigated by us, however, were nearly everywhere of the same depth and width, thus causing a regular increase in the current-velocity. Moreover, the diagram of MENTZEN differs from ours by the fact that he does not distinguish *A. cygnea.* In our diagram water-movements (current) decrease from left to right; this is accompanied by a decrease in the median grain-size of the sediments.

The ecological distribution of the Dutch freshwater mussels may be caused in two ways. It is of course possible that it is caused by the environmental requirements of the mussels themselves, as is the case in so many other species. However, for unionids there is still another possibility, namely that their ecological range is partly governed by the ecological range of the species of fish which the molluscs need for their larval development. COKER et al. (1921) pointed out that many American species of unionids were able to complete their larval development only in a limited number of species of freshwater fish, mostly one to three species. DAVENPORT & WARMUTH (1965) confirmed these findings. As far as I know this phenomenon has not yet been investigated for European freshwater mussels, but from the distribution of e.g. *Unio crassus batavus* one is inclined to expect it to occur here also.

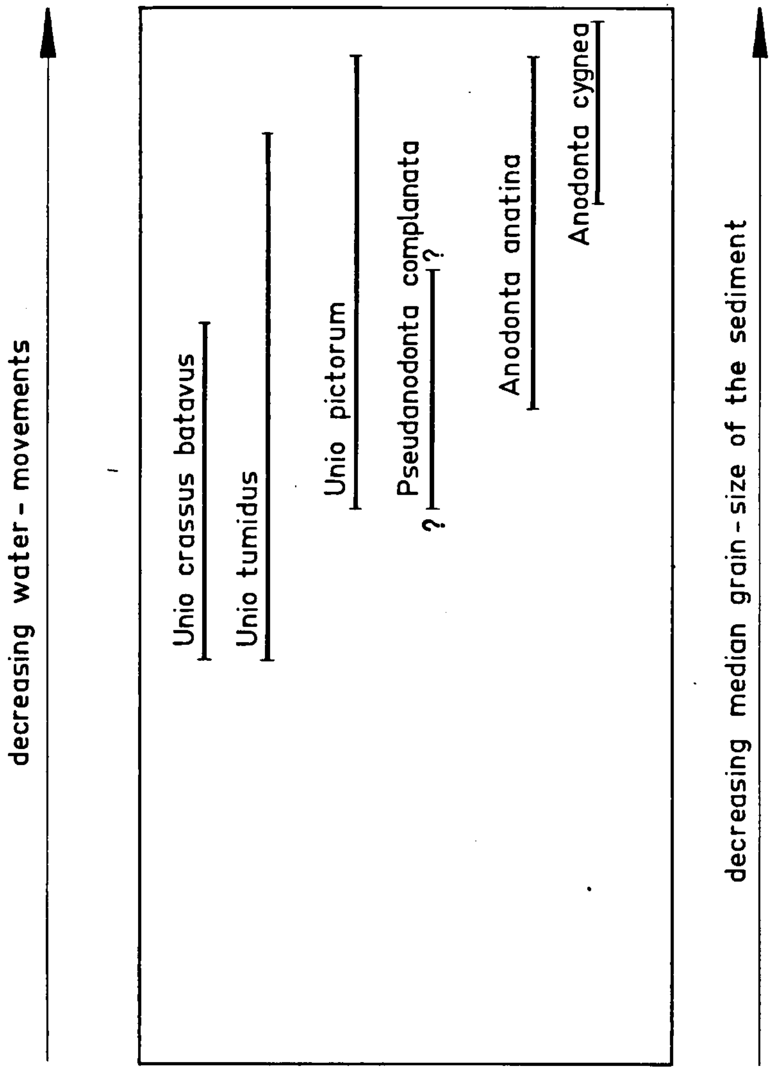

Fig. 12. Ecological diagram of the Dutch unionids.

SUMMARY

The distribution and ecology of the freshwater mussels of the family Unionidae was studied in the estuarine area of the rivers Rhine, Meuse and Scheldt. Only in the 10th century A.D. this area became inhabitable for unionids. Their distribution at present has been greatly influenced by the many inundations by salt and brackish water, most recently in 1953. Therefore the ecological conclusions must be based mainly on data from the freshwater area of the rivers.

It is remarkable that in this area no type of species has evolved in the family Unionidae, that is adapted to the intertidal zone of the freshwater tidal area. The lower reaches of the river Rhine and its branches are too much polluted to support unionids, except for *Unio tumidus,* some specimens of which were found at a few particularly suitable places.

A description is given of the distribution and ecology of *Unio crassus batavus, U. tumidus, U. pictorum, Anodonta anatina, A. cygnea* and *Pseudanodonta complanata.* These species seem to have different ecological ranges (fig. 12). It is suggested that these ecological differences may be partly caused by host-relationships of the larvae to particular species of freshwater fishes.

SAMENVATTING

De verbreiding en het voorkomen van zoetwatermossels van de familie Unionidae werd door ons bestudeerd in het estuariumgebied van de rivieren Rijn, Maas en Schelde. Dit gebied, ook bekend als het Deltagebied, werd pas in de 10de eeuw na Chr. bewoonbaar voor unioniden. De huidige verbreiding is sterk beïnvloed door de veelvuldige inundaties met zout of brak water, de laatste maal in 1953. Daarom moesten de oecologische conclusies voornamelijk getrokken worden uit het zoetwatergebied van de grote rivieren.

In dit gebied is het een opmerkelijk feit dat in de familie Unionidae geen type soort is ontstaan, dat is aangepast aan de getijzone van het zoetwatergetijdengebied. De Rijn en zijn zijtakken bleken te zeer verontreinigd om unioniden te kunnen herbergen, uitgezonderd enkele exemplaren van *Unio tumidus* op enkele relatief gunstige plaatsen.

De verbreiding en oecologie van *Unio crassus batavus, U. tumidus, U. pictorum, Anodonta anatina, A. cygnea* en *Pseudanodonta complanata* worden beschreven. Deze soorten schijnen een verschillende oecologische amplitude te hebben, hetgeen schematisch is weergegeven in fig. 12. De mogelijkheid bestaat dat deze oecologische verschillen gedeeltelijk worden veroorzaakt door de relatie van de larven tot hun gastheer, namelijk bepaalde soorten zoetwatervissen.

REFERENCES

ADAM, W., 1960. Mollusques. Tome I: Mollusques terrestres et dulcicoles. Faune de Belgique, Bruxelles, 402 pp.

ANONYMOUS, 1956-1966. Bericht der Experten-Kommission über die physikalisch-chemische Untersuchung des Rheinwassers. (1953-1954). Ber. Physik.-Chem. Unters. Rheinwass., vol. 2 (1954-1956), 3 (1956-1958), 4 (1959-1960). Ctd. as Tafeln der physikalisch-chemischen Untersuchungen des Rheins, sowie der Mosel/Koblenz 1961, 1962 and Zahlentafeln der physikalisch-chemischen Untersuchungen des Rheins sowie der Mosel/Koblenz. 1963, 1964, 1965. Intern. Komm. zum Schutze des Rheins gegen Verunreinigung.

ANONYMOUS, 1961. Verslag over de stormvloed van 1953. 's-Gravenhage, 714 pp.

BENTHEM JUTTING, T. VAN, 1943. Mollusca (I) C. Lamellibranchia. Fauna van Nederland, vol. 12, Leiden, 477 pp.

BENTHEM JUTTING, W. S. S. VAN, 1947. Lijst van gemeenten als vindplaatsen van Nederlandsche mollusken. Basteria, vol. 11, pp. 54-87.

BENTHEM JUTTING, W. S. S. VAN, 1959. Ecology of freshwater Mollusca in the Netherlands. Basteria, vol. 23, suppl., pp. 106-131.

BRUIN, M. P. DE & M. H. WILDEROM, 1961. Tussen Afsluitdammen en Deltadijken I. Noord-Beveland. Middelburg, 304 pp.

BUTOT, L. J. M., n.d. (1960a). Malacologisch onderzoek op Schouwen. In: Verslag van het biologen-werkkamp op Schouwen 18-25 juli 1960, hoofdstuk 7, 20 pp. Mimeographed report R.I.V.O.N.

BUTOT, L. J. M., 1960b. De molluskenfauna van Zuidoost Walcheren, speciaal met betrekking tot het natuurreservaat Rammekenshoek. Basteria, vol. 24, pp. 30-39.

BUTOT, L. J. M., 1962. Malacologisch onderzoek op Goeree. Jaarb. Wetensch. Gen. Goeree-Overflakkee, 1961, pp. 142-171.

COKER, R. E., A. F. SCHIRA, H. W. CLARK & A. D. HOWARD, 1921. Natural history and propagation of freshwater mussels. Bull. Bur. Fish., vol. 37, pp. 77-181.

DAVENPORT, D. & M. WARMUTH, 1965. Notes on the relationship between the freshwatermussel Anodonta implicata Say and the alewife Pomolobus pseudoharengus (Wilson). Limnol. Oceanogr., vol. 10, suppl., pp. 74-78.

ELLIS, A. E., 1962. British freshwater bivalve molluscs. With keys and notes for the identification of the species. Synopses Brit. Fauna Linn. Soc. London, vol. 13, pp. 1-92.

HARTOG, C. DEN, 1961. Die faunistische Gliederung im südwestniederländischen Deltagebiet. Int. Revue Ges. Hydrobiol., vol. 45, pp. 481-485.

HARTOG, C. DEN, 1963. The amphipods of the deltaic region of the rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area. I. Introduction and hydrography. Neth. J. Sea Res., vol. 2, pp. 29-39.

HARTOG, C. DEN, 1965. Laciniaria biplicata, een vroege bewoner van Zuid-Beveland? Basteria, vol. 29, pp. 15-17.

HENRARD, J. B., 1946. Bijdrage tot de kennis der molluskenfauna van Oostvoorne. Basteria, vol. 10, pp. 25-32.

HEUSDEN, G. P. H. VAN, 1945. Waarnemingen in eenige 'wielen' in de Betuwe. Tijdschr. Kon. Ned. Aardrijksk. Gen., vol. 62, pp. 118-124.

HIGLER, L. W. G., 1964. Enige gegevens over de fauna van duinplassen op Voorne. Biol. Jaarb. Dodonaea, vol. 32, pp. 345-351.

HORVATH, A., 1966. About the mollusks of Tisza before the river control. Tiscia, vol. 2, pp. 99-102.

JAECKEL, S. G. A., 1962. Ergänzungen und Berichtigungen zum rezenten und quartären Vorkommen der mitteleuropäischen Mollusken. In: Die Tierwelt Mitteleuropas. 2. Band. Lief. 1. Ergänzung, pp. 25-253.

JANSSEN, A. W., 1958. Problemen rond het Brielse Meer. Amoeba, vol. 34, pp. 96-98.

JANSSEN, A. W. & E. F. DE VOGEL, 1965. Zoetwatermollusken van Nederland. Den Haag, 160 pp.

JONG, J. D. DE, 1960. The morphological evolution of the Dutch coast. Geol. & Mijnb., vol. 39, pp. 638-643.

KONDRAT'EV, G. P., 1963. The effect of temperature on filtration by freshwater mussels (In Russian). Nauchn. Dokl. Vysschei Shkoly Biol. Nauka, vol. 3, pp. 17-20 (Biol. Abstr., vol. 46, p. 14338).

KOUWE, J. J. & B. VRIJHOF, 1958. De landbouwwaterhuishouding in de provincie Noord-Brabant. Comm. Onderz. Landbouwwaterhuish. Ned.-T.N.O. Rapport no. 12, 5 maps, 239 pp.

KRUIZINGA, P., 1936. Schelpen van zoetwatermossels aan het Zuidhollandse strand. De Lev. Nat., vol. 40, pp. 199-205.

KUIPER, J. G. J., 1944. Bijdrage tot de kennis der niet-mariene mollusken van de provincie Zeeland. Basteria, vol. 9, pp. 1-29.

LEENTVAAR, P., 1955. De ontwikkeling van de flora en fauna van de Brielse Maas na de afsluiting. De Lev. Nat., vol. 58, pp. 232-239.

LEENTVAAR, P., 1958. Observations on the plankton of some inland waters, especially 'wielen' in the Netherlands. Beaufortia, vol. 6 (73), pp. 171-197.

LEVEN, J. A. VAN 'T, B. VAN DER WEERD & J. J. LINDENBERGH, 1958. De landbouwwaterhuishouding in de provincie Zeeland. Comm. Onderz. Landbouwwaterhuish. Ned.-T.N.O. Rapport no. 10, 5 maps, 188 pp.

MENTZEN, R., 1926. Bemerkungen zur Biologie und Ökologie der mitteleuropäischen Unioniden. Arch. Hydrob., vol. 17, pp. 381-394.

PARMA, S., 1966. Hydrobiologisch onderzoek in de Biesbosch. Mimeographed report R.I.V.O.N., 87 pp.

PEELEN, R., 1967. Isohalines in the Delta area of the rivers Rhine, Meuse and Scheldt. Neth. J. Sea Res., vol. 3, pp. 575-597.

REDEKE, H. C., 1941. Pisces (Cyclostomi-Euichthyes). Fauna van Nederland, vol. 10, Leiden, 331 pp.

REES, W. J., 1965. The aerial dispersal of Mollusca. Proc. Malac. Soc. London, vol. 36, pp. 269-282.

SLUIS, P. VAN DER, G. G. L. STEUR & I. OVAA, 1965. De bodem van Zeeland. Toelichting bij blad 7, Bodemkaart van Nederland, schaal 1 : 200.000. Wageningen, 87 pp.

STEUSLOFF, U., 1926. Muscheln der Nette bei der Leuther Mühle. Natur am Niederrhein, vol. 2, pp. 1-6 (not seen; cited from VAN BENTHEM JUTTING, 1943).

STOL, Ph. Th., & B. VRIJHOF, 1958. De landbouwwaterhuishouding in de provincie Zuid-Holland. Comm. Onderz. Landbouwwaterhuish. Ned.-T.N.O. Rapport no. 9, 5 maps, 319 pp.

TEXEIRA DE MATTOS, L. F., 1925. Het eiland De Tien Gemeten. De waterkeeringen, waterschappen en polders van Zuid-Holland, vol. 8, pp. 891-917.

TEXEIRA DE MATTOS, L. F., 1941. Het eiland Goedereede en Overflakkee. De waterkeeringen, waterschappen en polders van Zuid-Holland, vol. 10, pp. 1-1054.

THIEL, M. E., 1929. Zur Biologie unserer Süsswasser-Muscheln. Zeitschr. Morphol. Ökol. Tiere, vol. 13, pp. 65-116.

TOMLINSON, J., 1966. The advantages of hermaphroditism and parthenogenesis. J. Theor. Biol., vol. 11, pp. 54-58.

TRIMPE BURGER, J. A., 1960. Geologie en archeologie in het Deltagebied. Geol. & Mijnb., vol. 39, pp. 686-691.

VAAS, K. F., 1961. Das Arbeitsfeld des Hydrobiologischen Institutes, Abteilung Delta-Untersuchungen, in den Niederlanden. Int. Revue Ges. Hydrobiol., vol. 46, pp. 292-295.

VISSER, W. C., 1958. De landbouwwaterhuishouding van Nederland. Comm. Onderz. Landbouwwaterhuishouding Ned.-T.N.O. Rapport no. 1, 159 pp.

VOO, E. E. VAN DER, 1965. Bruine ratten op mosselvangst. De Lev. Nat., vol. 68, pp. 311-312.

WESTERHOFF, J. J., 1947. Overzicht van uitvoering en verloop van de zout- en brakwaterinundaties tijdens de Duitse bezetting als militaire maatregel uitgevoerd. De inundaties van 1944 en 1945 in Nederland. Deel I. Goes, mimeographed.

WIBAUT-ISEBREE MOENS, N. L., 1956. Rivierenonderzoek 1954-1955. Mimeographed report.

WILDEROM, M. H., 1964. Tussen Afsluitdammen en Deltadijken. II. Noord-Zeeland. Middelburg, 415 pp.

WOLFF, W. J., 1966. Meerkoeten en strandgapers. De Lev. Nat., vol. 69, pp. 217-220.

ZONNEVELD, I. S., 1960. De Brabantse Biesbosch. Een studie van bodem en vegetatie van een zoetwatergetijden delta. Versl. Landbouwk. Onderz., vol. 65-20, 210 + 396 pp.