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The Mollusca of the estuarine region of the rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area. III. The genus Pisidium

by

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INTRODUCTION

This paper is the third in a series on the distribution and ecology of the Mollusca occurring in the Delta area in the southwestern part of the Netherlands. An introduction to this study was given in the first paper, together with a description of the area investigated and its hydrography (Wolff, 1968). The sampling methods were also described in that paper, but the oyster-dredge proved to be ineffective for sampling *Pisidium*. A new method consisted of the sieving (1 mm sieve) of soil samples obtained from the surface of the intertidal mudflats in the freshwater tidal area of the Biesbosch. This method proved to be of great value during the present investigation.

When our sampling was completed, the Delta works had not yet affected the hydrography of the area, as described in our first paper (Wolff, loc.cit.).

SYSTEMATIC PART

Pisidium amnicum (Müller, 1774) (fig. 1)

Van Benthem Jutting, 1943:153-156; Adam, 1960:339-340; Ellis, 1962:38-39.

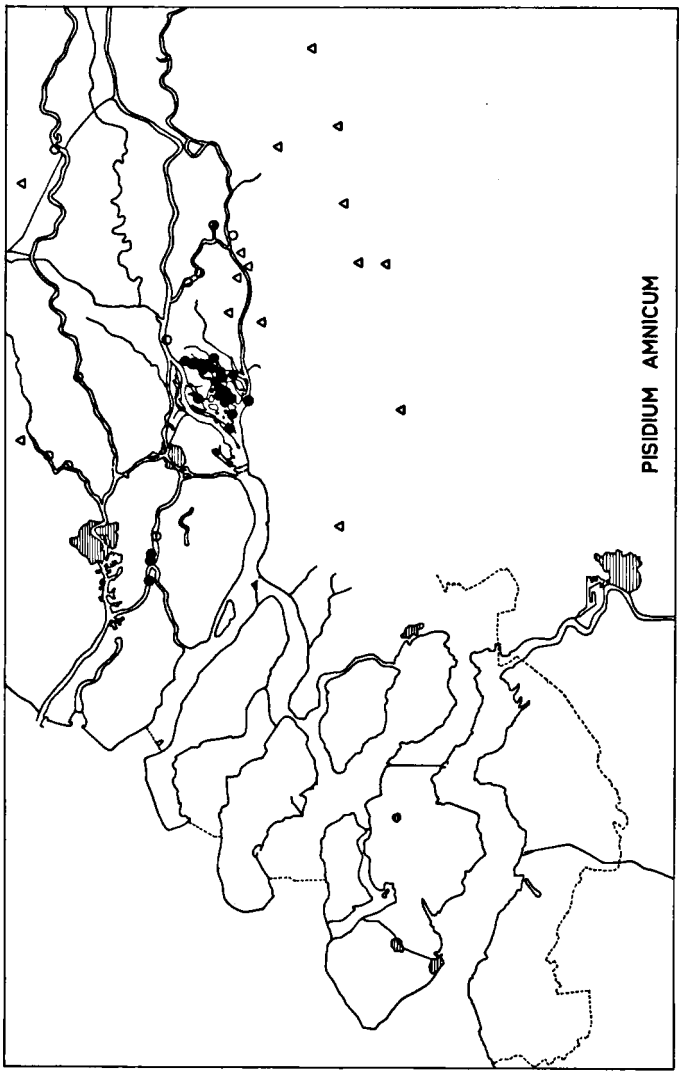

Fig. 1. Distribution of *Pisidium amnicum*. Dots denote records from outside the dikes, i.e., in tidal or running water; triangles denote records from inside the dikes, i.e., mostly in stagnant water.

Distribution: Palaearctic, also in NE. America. In Europe common north of the Pyrenees and the Alps, very rare south of these mountain ranges. Seldom found at altitudes over 500 m (Kuiper, 1966). A fairly common species in the Netherlands, but never recorded from the province of Zeeland.

Localities[1]: Province of Zuid-Holland: Gouwe near Gouda (ZMA); Hollandse IJssel near Moordrecht (NMV) and near Snellerak (ZMA); Lek near Ammerstol (Kuiper, 1942); Oude Maas near Poortugaal (W) and near Heinenoord (ZMA); Kooigat near Rhoon (W). Province of Utrecht: Wijk bij Duurstede (Van Benthem Jutting, 1947); Cothen (Kuiper, 1942). Province of Gelderland: Afgedamde Maas near Neder-Hemert (ZMA); Tiel (Van Benthem Jutting, 1947). Province of Noord-Brabant: Oude Riet near Oud- en Nieuw-Gastel (Kuiper, 1942); Amer near Drimmelen; Brabantse Biesbosch, Gat van de Binnennieuwesteek, Noordergat van de Vissen, Gat van de 130, Buitenkooigat, Gat van de Slek, Ruigt, Jeppegat, Nauw van Paulus, Boomgat, Keizersdijk, Noord-Bevert, Steurgat, Corneliapolder and Noordplaat (W); Nieuwendijk near Almkerk; Babyloniënbroek (K); Genderen (ZMA); Boven-Merwede near Sleeuwijk (K); Afgedamde Maas near Op-Andel (Kuiper, 1942), and near Rijswijk (Van Benthem Jutting, 1947); Waspik; Heesbeen near Heusden (Kuiper, 1942); Zuid-Willemsvaart near 's-Hertogenbosch (K); Herpt (Van Benthem Jutting, 1947); Doeveren (Kuiper, 1942); Ginniken en Bavel (Van Benthem Jutting, 1947); Tilburg (Kuiper, 1942); Goirle; Oisterwijk; Boxtel; Vegchel (Van Benthem Jutting, 1947).

Ecology: Most authors agree that *P. amnicum* is a species characteristic of rather slow rivers, canals, and lakes. It also occurs in ditches, connected with waters of these categories (Kuiper, 1942, 1965), as our present investigation has confirmed. As already indicated by Kuiper (1944), the species is not expected to occur on the islands of the Delta area, because fluviatile biotopes are absent.

The predominantly brackish nature of the waters of these islands also inhibits its occurrence there. Jaeckel (1962) records a maximum tolerance of 0.3‰ Cl' as observed in several areas, but mentions a value of 1.2-1.8‰ Cl' which was said to be endured in the Frisches Haff. According to Koli (1961), the species does not occur in

1 Abbreviations: NMV = card index Mollusken-Comité, Nederlandse Malacologische Vereniging; NHMR = Natuurhistorisch Museum, Rotterdam; RMNH = Rijksmuseum van Natuurlijke Historie, Leiden; ZMA = Zoölogisch Museum, Amsterdam; K = J.G.J. Kuiper collection; W = Delta-Instituut voor Hydrobiologisch Onderzoek (W.J. Wolff).

brackish water. In the Delta area it is always found in waters with a mean salinity of 0.3‰ Cl′ or less. According to Peelen (1967), the locality in the Oude Maas has a mean salinity of about 0.3‰ Cl′, but nearly all other localities, especially those in the Biesbosch, have mean salinities of about 0.1‰ Cl′. It may be concluded that *P. amnicum* does not tolerate high salinities.

The same holds good for its tolerance of pollution. Since we failed to discover a single specimen either in the heavily polluted Rhine or most of its branches, where in the past it was found several times, the animal seems to have disappeared from these waters. Nevertheless, it still occurs in the Oude Maas, which is possibly somewhat less polluted than the other branches of the Rhine, and also in the

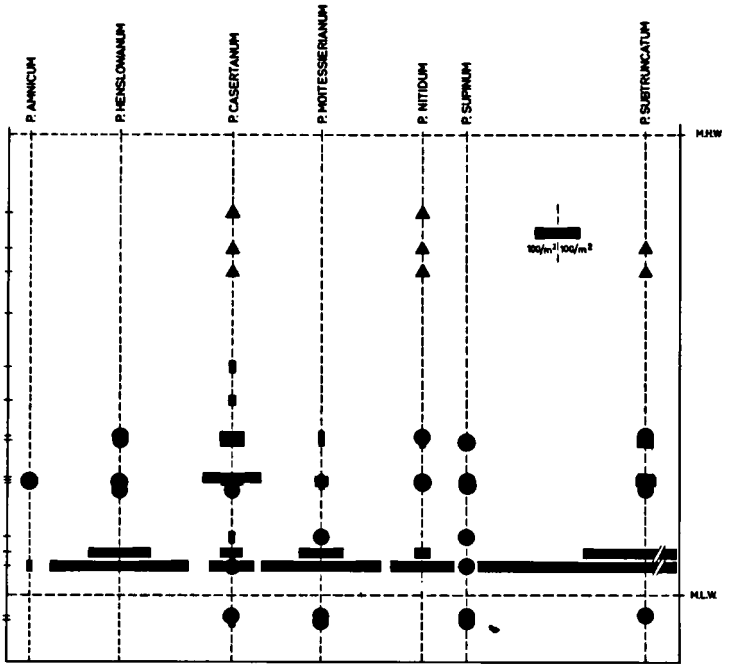

Fig. 2. Vertical distribution of various species of *Pisidium* in the Biesbosch. MHW = mean high water level, MLW = mean low water level. Triangles denote records published by Heyligers (1965), dots those of single individuals found during our investigations. The width of the bars denotes the density of each species at various levels during our investigations. The level of the samples is indicated on the axis at the left side.

parts of the Brabantse Biesbosch influenced by the Rhine as well as the Meuse. Although a slight degree of pollution apparently may be tolerated, it is not possible to give exact figures on the degree of pollution that can be supported.

P. amnicum lives in stagnant water (lakes, ditches, canals) although usually where there is some movement of the water due to the wind or passing ships, as well as in running water (rivers). In the freshwater tidal area of the Biesbosch, which may be considered a modified fluviatile habitat, it endures maximum current velocities of about 0.8 m/sec. during normal tides. During storms, this value certainly lies higher.

Its tolerance of a fairly wide range of current velocities is related to its occurrence in a fairly wide range of types of sediment. In ditches and canals the species may be found on muddy bottoms, but in the Biesbosch area it also occurs on fine and medium grade sands (Inman, 1952) up to a median grain size of 340 μ. Most samples containing *P. amnicum* had a median grain-size varying between 150 and 300 μ.

The species has been found down to a depth of 6 m, deeper places having rarely been sampled. In the litoral zone of the freshwater tidal area it occurs only in low densities (up to 11 specimens sq.m.) up to about 50 cm above the mean low waterline, the total tidal difference being about 200 cm (fig. 2). In the litoral zone the species occurs only on the muddiest places.

Pisidium moitessierianum Paladilhe, 1866 (fig. 3)

Van Benthem Jutting, 1943:181-183; Adam, 1960:352-353; Ellis, 1962:61-63.

Distribution: Europe, perhaps Palaearctic. A lowland species, living mainly north of the Alps, but with a very scattered distribution. Very rare in the Mediterranean countries (Kuiper, 1966). It is rather rare in the Netherlands, where it lives mainly in the large rivers.

Localities: Province of Zuid-Holland: Hollandse IJssel near Moordrecht (ZMA); Brielse Meer near Zwartewaal (W); Beneden-Merwede near Giessendam (Van Bruggen, 1957); Ammerstol? (Kuiper, 1942, p. 31). Province of Gelderland: Afgedamde Maas near Neder-Hemert (K). Province of Noord-Brabant: Brabantse Biesbosch, Boerenplaat (Heyligers, 1961), Gat van de Binnennieuwesteek, Noordergat van de Vissen, Kooigat, Buitenkooigat, and Steurgat, Oude Maasje near Waspik (W).

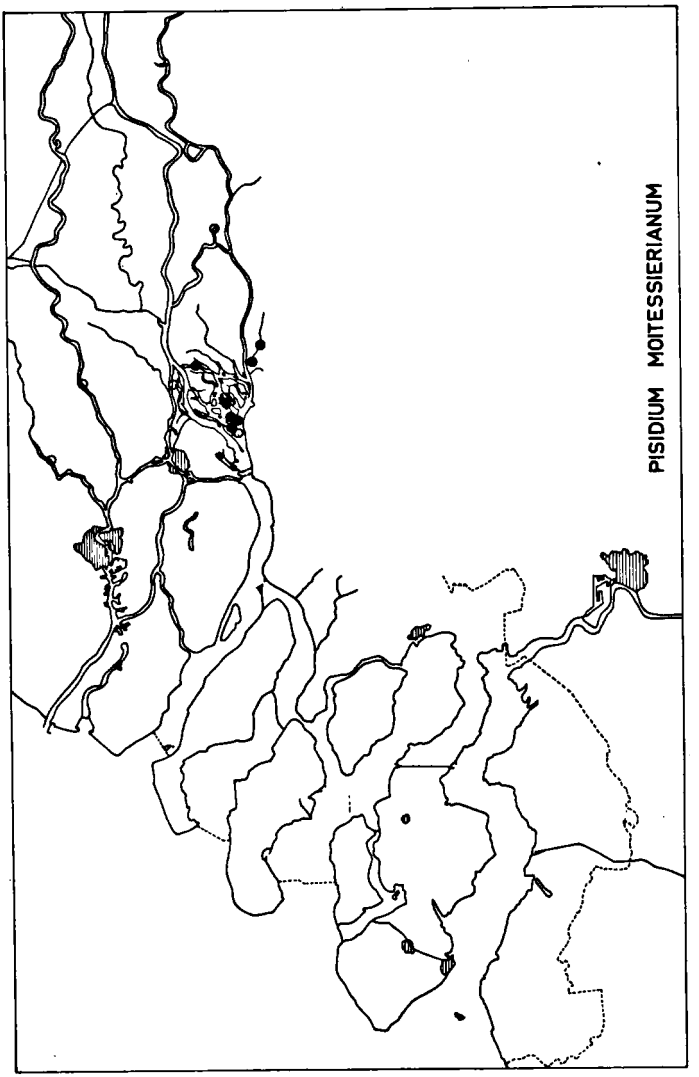

Fig. 3. Distribution of *Pisidium moitessierianum*. Symbols as in fig. 1.

Ecology: *P. moitessierianum* inhabits the mud of slow rivers and large lakes (Kuiper, 1942; Van Benthem Jutting, 1943, 1959; Adam, 1960). For this reason the species is absent on the islands of the Delta area, where no such habitats occur and the inland waters are predominantly brackish.

Van Benthem Jutting (1954) mentioned 0.2‰ Cl′ as the upper limit of its salinity tolerance. From this and from our data we assume that its upper limit is certainly not over 0.3‰ Cl′ These values are reached in the Biesbosch in the Noordergat van de Vissen, where salinities of 0.3‰ Cl′ occur sporadically, and in the Brielse Meer (Lake Brielle), where the species was found to occur at a locality with a salinity ranging between 0.1 and 0.9‰ Cl′ during the year before the observation (personal communication of Mr. R. Peelen). Its tolerance to salinity, however, seems to be less than that of *P. amnicum* and most other pisidiids in the Netherlands.

P. moitessierianum seems to have vanished altogether from the Rhine and its branches, no doubt owing to pollution. Nevertheless, we were able to demonstrate its occurrence in the part of the Biesbosch influenced by the Rhine, so it seems to be able to withstand a slight amount of pollution.

We found *P. moitessierianum* in an area without any current (Brielse Meer) only once, but most of the observations were made in creeks and gullies of the freshwater tidal area with a maximum current velocity of 0.8 m/sec. during normal tides and even higher values during storm tides. We were not able to determine exactly the lower limit of the current velocity required, but it may amount to about 0.1 m/sec. We are inclined to assume that the species has a preference for the quieter parts of rivers.

The fairly wide range of current velocities is reflected in the composition of the substrate. We found this species on very fine sand, but also on fine and medium-grade sands (Inman, loc.cit.). The median grain-size of the sediment of the samples containing *P. moitessierianum* ranges from 70μ to 270μ.

In the freshwater tidal area of the Biesbosch *P. moitessierianum* occurs intertidally in muddy sediments up to a level of 70 cm above mean low water level, the total tidal range being about 200 cm. In sandy sediments the level reached is only 25 cm above mean low water; thus, the larger amount of water held by the finer types of sediment evidently extends the vertical distribution into the intertidal area. Near low water level the species occurs in a density of about 265 specimens/sq.m. Nevertheless, neither *P. moitessierianum* nor *P. amnicum* is very well suited for life in the intertidal zone.

Pisidium tenuilineatum Stelfox, 1918

Van Benthem Jutting, 1943:183-185; Adam, 1960:354-355; Ellis, 1962:63-64.

P. tenuilineatum is recorded only from two localities in the Delta area (Rotterdam and Neder-Hemert). Because we were unable to trace any other specimens during the present investigation, we prefer not to say anything further about this species. It is not impossible that, owing to water pollution, it has disappeared completely from the region covered by our investigations.

Pisidium supinum Schmidt, 1850 (fig. 4)

Van Benthem Jutting, 1943:159-161; Adam, 1960:350-351; Ellis, 1962:52-54.

Distribution: *P. supinum* is known from Europe, the eastern part of N. America, and Lake Baikal in Siberia. The species is absent from countries south of the Alps and the Pyrenees. It is a typical lowland species, not found at altitudes of over 300 m (Kuiper, 1966). In the Netherlands it is rather rare and probably absent over large areas.

Localities: Province of Zuid-Holland: Hollandse IJssel near Moordrecht (ZMA); Brielse Meer near Zwartewaal and near Nieuwersluis (W); Oude Maas near Rhoon (ZMA; NHMR); Lek near Ammerstol (K). Province of Utrecht: Cothen (Kuiper, 1942). Province of Gelderland: Afgedamde Maas near Nederhemert (K). Province of Noord-Brabant: Steenbergen; Ginneken en Bavel (Van Benthem Jutting, 1947); Brabantse Biesbosch, Boerenplaat (Heyligers, 1961), Gat van de Binnennieuwesteek, Kooigat, Buitenkooigat, Ganzenest, Jeppegat, Nauw van Paulus, Noord-Bevert, Oude Maasje near Waspik and near Keizersveer (W); Tilburg (Kuiper, 1942); Oisterwijk (Van Benthem Jutting, 1947).

Ecology: *P. supinum* characteristically is a species of slow rivers and it is absent from lakes and canals (Kuiper, 1942, 1965). Ellis (1962), however, records this species from canals in England, and during our investigations we found it in the Brielse Meer (Lake Brielle). But it must be admitted that from an ecological point of view the distinction between slow rivers and "stagnant" canals is an arbitrary one. Its requirements may be best characterized by "a preference for a certain, but small, amount of water movement." This situation does not occur on the islands of the Delta area and, indeed, *P. supinum* is absent here.

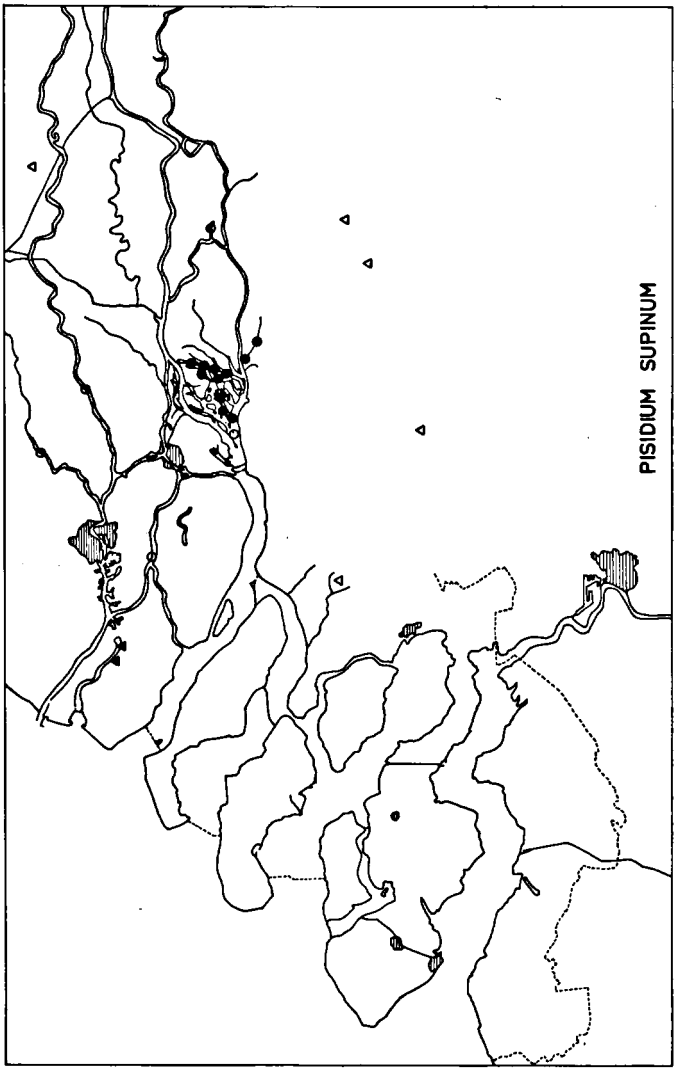

Fig. 4. Distribution of *Pisidium supinum*. Symbols as in fig. 1.

According to Van Benthem Jutting (1954) the species was found at a maximum salinity of 0.2‰ Cl'. From this and our observations it may be deduced that the maximum salinity tolerated by this species is not over 0.3‰ Cl'. This value may temporarily be reached in the Gat van de Binnennieuwesteek in the Brabantse Biesbosch, whereas the salinity in the Brielse Meer in the year before we collected our samples varied between 0.1 and 0.9‰ Cl'.

P. supinum seems to be very sensitive to pollution. We were unable to collect specimens in the polluted Rhine and its branches, but it proved to be fairly common in the comparatively clean Meuse and its branches.

As mentioned above, *P. supinum* almost always occurs in running water. In the Biesbosch area it was frequently encountered on the bottom of creeks with maximum current velocities of 0.8 m/sec. during normal tides and still higher values during storm tides. Higher velocities probably occur on the bottom of the main rivers, but here the accompanying transport of sand probably inhibits all forms of macrobenthonic life.

The fairly high current velocities of the localities where *P. supinum* was collected can also be deduced from the nature of the substrate. We found the species on fine- and medium-grade sands (Inman, loc.cit.) with a median grain-size ranging from 150μ to 270μ. In the intertidal area *P. supinum*, unlike the other species of *Pisidium* occurring there, is as numerous (or better, as rare) on sandy sediments as on more muddy sediments (fig. 2).

P. supinum only occurs in small numbers in the intertidal area, not exceeding 13 specimens/sq.m. It was found intertidally up to 70 cm above mean low water level, on sandy as well as on more muddy sediments. The total tidal range in this area amounts to about 200 cm. The maximum depth at which we found this species was about 6 m; deeper places have been rarely sampled.

Pisidium henslowanum (Sheppard, 1823) (fig. 5)

Van Benthem Jutting, 1943:156-159; Adam, 1960:351-352; Ellis, 1962:54-55.

Distribution: Palaearctic; *P. henslowanum* inhabits almost all of Europe as well as the eastern part of N. America, where it probably has been introduced by man (Kuiper, 1966). In the Netherlands the species is fairly common.

Localities: Province of Zuid-Holland: Gouwe near Gouda

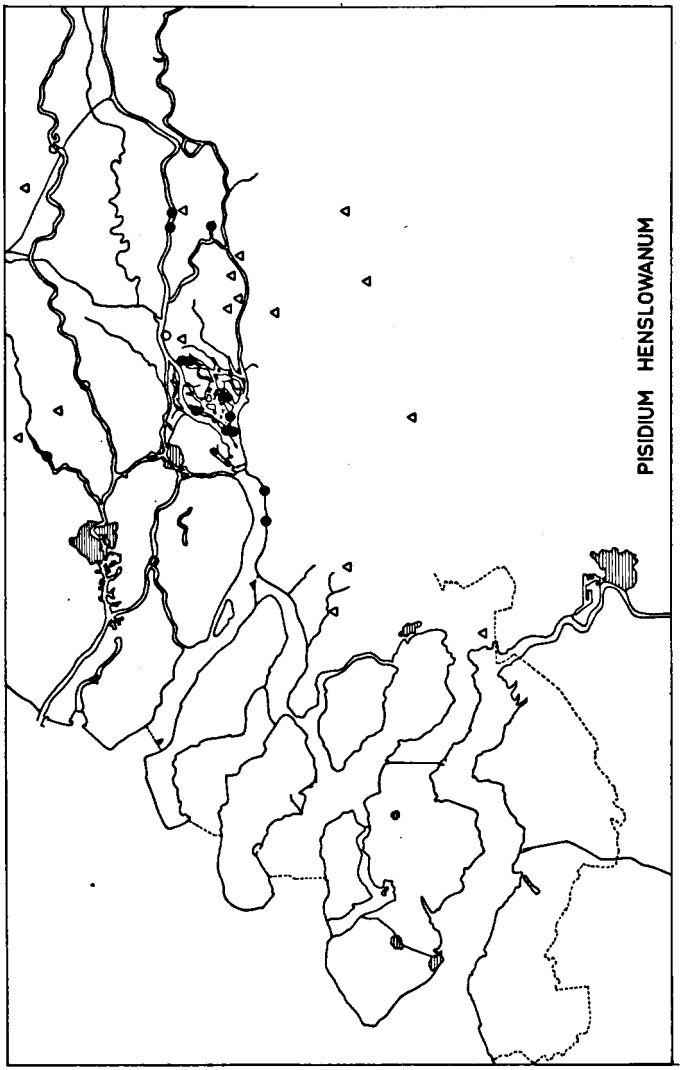

Fig. 5. Distribution of *Pisidium henslowanum*. Symbols as in fig. 1.

(RMNH); Hollandse IJssel near Moordrecht (ZMA); Stolwijk (K); Lek near Ammerstol (Kuiper, 1942); Brielse Meer near Brielle (W); Rhoon (NHMR). Province of Gelderland: Waal near Zaltbommel and near Nieuwaal (W); Zaltbommel; Afgedamde Maas near Nederhemert (K). Province of Noord-Brabant: Noordpolder, Ossendrecht (Kuiper, 1942); Doornedijkje, Steenbergen (K); Oud- en Nieuw-Gastel (Kuiper, 1942); Ginniken en Bavel (Van Benthem Jutting, 1947); Hollands Diep near Roodevaart and near Klundert; Brabantse Biesbosch, Gat van de Binnennieuwesteek, Spieringsluis, Noordergat van de Vissen, Gat van de Slek (W); Boerenplaat (Heyligers, 1961) and Steurgat (W); Boven-Merwede near Sleeuwijk; Werkendam (K); Genderen (ZMA); Drongelen; Meeuwen near Eeten (K); Waspik; Heesbeen near Heusden (Kuiper, 1942); Oisterwijk (Van Benthem Jutting, 1947); Tilburg (Kuiper, 1942).

Ecology: *P. henslowanum* occurs in a fairly wide range of habitat, although it seems to prefer a moderate amount of water movement. In the Netherlands this situation may occur in large rivers, in several small rivers, in canals and lakes, and sometimes also in the larger ditches (Kuiper, 1942, 1965). Since such habitats are absent on the islands of the Delta area *P. henslowanum* is absent in this region.

According to Koli (1961) the species does not occur in brackish water, whereas Van Benthem Jutting (1954) records 0.24‰ Cl' as its upper limit. According to Jaeckel (1962) its maximum salinity tolerance is about 0.9‰ Cl'. In the Delta area the highest known salinity tolerated by the species is found in the Brielse Meer, with a salinity varying between 0.1 and 0.9‰ Cl' in the year before we collected our samples, and also along the Hollands Diep, where the salinity may rise temporarily to well above 0.3‰ Cl'. Its resistance to pollution is rather considerable. We found the species in two grab-samples from the polluted Waal (= Rhine) near Zaltbommel and therefore consider it as belonging to the most pollution-tolerant species of the pisidiids of the Netherlands.

The species was only found in rather muddy sediments. The median grain-size of samples in which we collected it ranged from 110μ tot 170μ, or according to Inman (loc.cit.): fine and very fine sands with a high content of detritus. The nature of the sediment reveals that the current velocity where *P. henslowanum* lives is not very high. It seems to prefer the quiet parts of the rivers. Current velocity probably does not greatly exceed about 0.1 m/sec.

In the intertidal zone of the freshwater tidal area of the Biesbosch (fig. 2) the species is numerous (more than 300

specimens/sq.m.) just above mean low water-level in sediments containing a high proportion of water. Single specimens may be found up to about 70 cm above mean low water, the tidal range being about 200 cm. The greatest depth at which we encountered the species was about 4.5 m.

Pisidium casertanum (Poli, 1791) (fig. 6)

syn. *Pisidium cinereum* Alder.

Van Benthem Jutting, 1943:172-176 (s.n. *P. cinereum*); Adam, 1960:340-341; Ellis, 1962:40-42.

Distribution: Cosmopolitic. In the northern hemisphere the most frequent and most variable species of the genus; in the southern hemisphere more scattered in its distribution. Common in New Zealand and SE. Australia. Often the only species on small oceanic islands (Kuiper, 1966). Up to 3600 m altitude (S. America). Common in the Netherlands, occurring in several types of water.

Localities: Province of Zuid-Holland: Hollandse IJssel near Moordrecht (ZMA); Brielse Meer near Brielle, Zwartewaal and Nieuwersluis (W); Rockanje (Henrard, 1946); Oude Maas near Goidschalxoord and Heerjansdam; Hollands Diep near Strijensas and near Willemsdorp; Zuid-Maartensgat, Zuidhollandse Biesbosch; Oosthaven, Nieuwe Merwede (W). Province of Gelderland: Afgedamde Maas near Nederhemert (K). Province of Noord-Brabant: Woensdrecht (Kuiper, 1942); Moerstraeten, Wouw (K); Halsteren; Zoom between Bergen op Zoom and Pindorp (W); Noordpolder, Ossendrecht (Kuiper, 1942); Oudenbosch; Rozendaal; Rucphen; Etten en Leur; Ginniken en Bavel; Chaam (Van Benthem Jutting, 1947); Hollands Diep near Tonnekreek, Noordschans, Klundert and near Roodevaart; Amer near Lage Zwaluwe; Brabantse Biesbosch, Gat van de Binnennieuwestreek; Kooigat, Buitenkooigat, Halfweg (W), Sluishoek, Langeweer, Kromme Hoek (Heyligers, 1961), Noordplaat and Steurgat (W); Boven-Merwede near Sleeuwijk; Heusden (K); Herpt (Van Benthem Jutting, 1947); Dongen (K); Tilburg (Kuiper, 1942); Oisterwijk (Van Benthem Jutting, 1947). Province of Zeeland: Renesse (K); Eede near Aardenburg; Spui near Terneuzen (W).

Ecology: According to our observations and previous records from our region *P. casertanum* occurs mainly in large and small rivers and lakes, and only seldom penetrates into larger and smaller ditches. This is not in complete agreement with the descriptions of

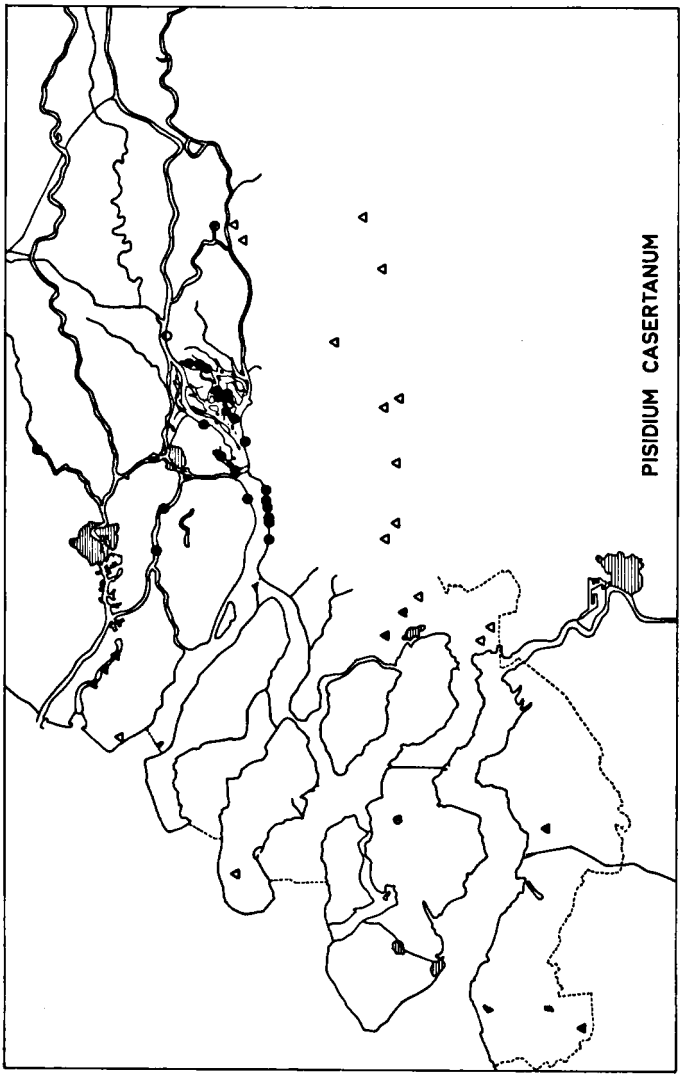

Fig. 6. Distribution of *Pisidium casertanum*. Symbols as in fig. 1.

the authors mentioned above. Our observations agree better with those of Kuiper (1942), who found the species mainly in the upper part of small rivers on Pleistocene soils in the province of Noord-Brabant, in ditches communicating with these rivers, and in scattered localities in the dune area along the North Sea coast. We now add to these localities those in the Brielse Meer (Lake Brielle, created as recently as 1950) and several in the freshwater tidal area of the large rivers, a habitat at that time not sampled by Kuiper.

According to Koli (1961, 1964) and Van Benthem Jutting (1954) the species does not occur in salinities of over 0.3‰ Cl′. According to Jaeckel (loc.cit.), however, the maximum salinity tolerated by *P. casertanum* is about 1.7‰ Cl′. Indeed, together with *P. subtruncatum*, *P. casertanum* penetrates the brackish part of the estuaries further than any other species. It is still found in the Hollands Diep near Tonnekreek and near Noordschans, north of Klundert, where the annual mean salinity is about 0.3‰ Cl′, but where much higher values (up to 3 - 5‰ Cl′) may occur temporarily. The species is also abundant in the Brielse Meer, with a salinity varying between 0.1‰ and 0.9‰ Cl′. *P. casertanum* is certainly one of the most tolerant species with respect to salinity.

P. casertanum is also fairly tolerant with respect to pollution. It is by no means rare along the Oude Maas, Hollands Diep, and Nieuwe Merwede, all branches of the polluted Rhine. On the other hand we did not find the species in samples taken upstream.

P. casertanum was encountered in localities with almost stagnant water as well as in others with a fairly strong current of up to about 0.8 m/sec. during normal tides and even higher during storm tides.

In accordance with these conditions, the nature of the substrate also varies considerably. We found the species in sediments with a median grain-size ranging from 120 μ to 270 μ, according to Inman very fine to medium-grade sands. In willow coppices of the freshwater tidal area it was even found in very soft types of mud (Heyligers, 1955, 1961, 1965).

Its vertical distribution in the litoral zone of the freshwater tidal area, where the total tidal range is about 200 cm is considerable. We found it on sandy as well as on muddy sediments up to about 100 cm above mean low water level. Heyligers (loc.cit.) records this species from 36 to 62 cm below mean high water level in soft mud containing a high proportion of water. The species is probably to be found throughout the intertidal zone.

Lastly, it should be mentioned that nearly all specimens collected by us in the Brielse Meer and in the freshwater tidal area, as well as

those recorded by Heyligers (loc.cit.), appear to belong to the forma *ponderosa* Stelfox.

Pisidium personatum Malm, 1855 (fig. 7)

Van Benthem Jutting, 1943, p. 177-179; Adam, 1960, p. 345-346; Ellis, 1962, p. 44-46.

Distribution: *P. personatum* occurs in Europe, except for northern Scandinavia, and also in N. Africa (Kuiper, 1966). It is a common species in the dune area and in the Pleistocene part of the Netherlands; in the Holocene "polder" area it is, however, rather rare.

Localities: Province of Gelderland: Nederhemert (Van Benthem Jutting, 1947). Province of Noord-Brabant: Moerstraeten, Wouw (K); Zundert; Chaam (Van Benthem Jutting, 1947); Sluisweg, Dongen (ZMA); Brabantse Biesbosch, Buitenkooigat (W); Sluishoek, Lange Weer and Kromme Hoek (Heyligers, 1961); Lage Zwaluwe; Hollands Diep near Moerdijk; Boven-Merwede near Sleeuwijk (W); Afgedamde Maas near Rijswijk (ZMA); Haaren (Van Benthem Jutting, 1947). Province of Zeeland: Renesse; Hoogduin, Oostkapelle (Kuiper, 1944).

Ecology: *P. personatum* is characteristically a species of small stagnant waters, ditches which dry up in summer, and brooklets (Kuiper, 1942; Ellis, loc.cit.). The distribution in the area investigated by us is completely in accordance with these data. *P. personatum* is found in some ditches on Pleistocene soils in the province of Noord-Brabant, in a few localities in the dune area, and in the region of the rivers and the freshwater tidal area. In the latter area, however, it was only found once, viz., in a sample originating from the bottom of a gully. Most observations are from draining ditches and the like in the extensive willow coppices of this area. In these willow coppices Heyligers (loc.cit.) sampled three localities well below mean high water level, and found *P. personatum* to be present in all of them. We only sampled this habitat sporadically, but the species is probably common in this type of habitat all over the freshwater tidal area. Nevertheless, this habitat does not seem very favourable, because specimens are usually somewhat stunted in these localities (Heyligers, loc.cit.).

Since there are no data in the literature, it is difficult to discuss its tolerance to salinity and pollution, but it is probably only slight.

Because we did not find *P. personatum* in localities with running

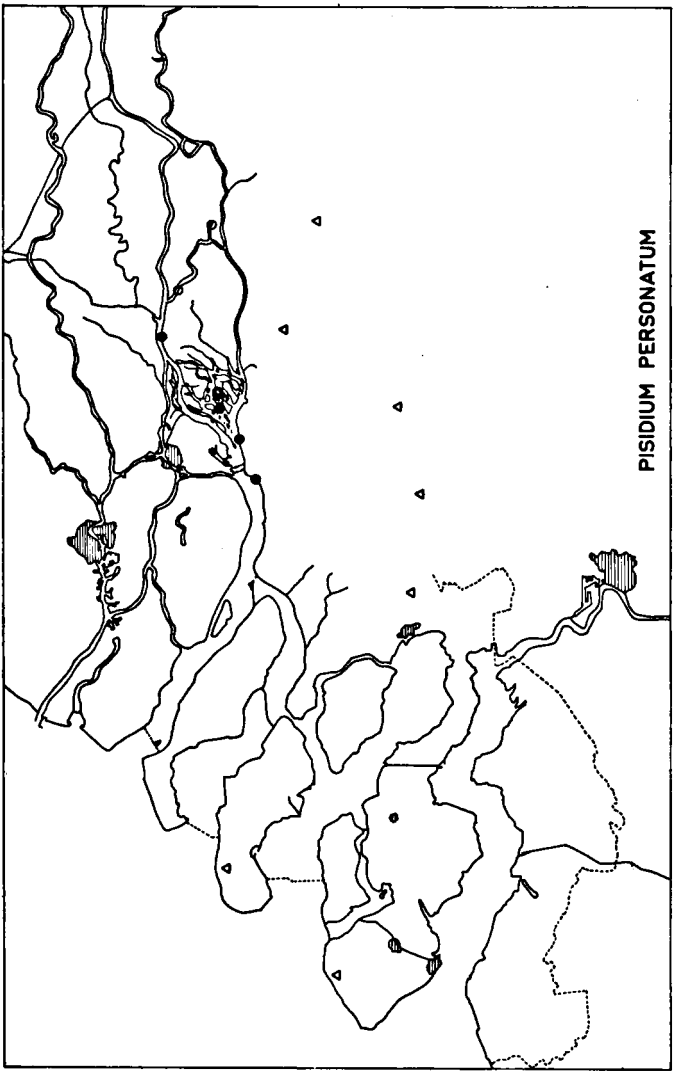

Fig. 7. Distribution of *Pisidium personatum*. Symbols as in fig. 1.

water, it is impossible to say anything about its reactions to various kinds of current velocity. The sediment of the localities where it was found generally consisted of soft or very soft muds, often containing a fair amount of detritus.

Its vertical distribution in the Biesbosch area is rather unusual. Heyligers (loc.cit.) found it between 36 and 62 cm below mean high water level, the total tidal range being about 200 cm. We did not find it at all in the intertidal area. Therefore, we suppose that it being restricted to the upper part of the tidal zone is explained by the absence of comparatively strong currents here. In this region the tide comes in very gently and receeds even more slowly.

Pisidium obtusale (Lamarck, 1818) (fig. 8)

Van Benthem Jutting, 1943:170-181; Adam, 1960:344-345; Ellis, 1962:46-48.

Distribution: Palaeartic, perhaps even Holarctic; common in Europe north of the Alps and the Pyrenees, rare south of these mountains (Kuiper, 1966). It is a common species in the Netherlands, although it occurs somewhat less frequently in the polder areas.

Localities: Province of Zuid-Holland: Branddijk, Rockanje (Henrard, 1946); Goudswaard (W). Province of Utrecht: Veenendaal (Van Benthem Jutting, 1947). Province of Noord-Brabant: Veerweg, Steenbergen (K); Oudenbosch (Kuiper, 1942); Wouw (K); Breda (Van Benthem Jutting, 1947); Brabantse Biesbosch, Sluishoek, Lange Weer (Heyligers, 1961) and Ruwenhennip (W); town-moats of Heusden (K); Orthen and Esch (Kuiper, 1942) near 's Hertogenbosch; Haaren; Liempde; St. Oedenrode (Van Benthem Jutting, 1947). Province of Zeeland: Oosterdoodkist, Schouwen (Butot, 1961); Oostkapelle (K); Louisepolder, Ovezande (W); Witte Weel, Biezelinge (ZMA); Nieuw-Krabbendijksepolder, Krabbendijke (W); Weel Blazekoppolder, Ovezande (personal communication of W.J. Kuiper); Schoondijke (Kuiper, 1944); Mauritspolder, IJzendijke; Zandstraat near Philippine (W).

Ecology: *P. obtusale* has an ecological distribution rather different from the other Dutch species of the genus. As a rule it is found, often in great densities, in habitats usually considered unfavourable to molluscs. In our investigation it proved to be the most common (or better: least rare) species on the islands of the Delta area.

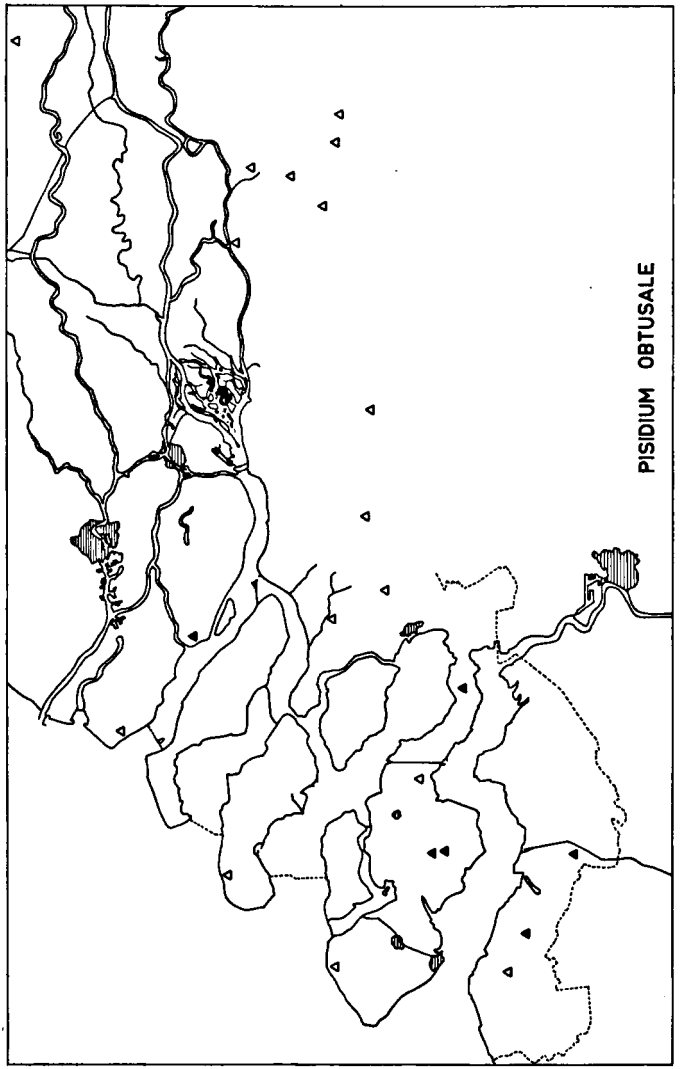

Fig. 8. Distribution of *Pisidium obtusale*. Symbols as in fig. 1.

Therefore, this species of all pisidiids of the Netherlands probably has the greatest chance to be subject to passive transport. This is probably due to its exclusive occurrence in very shallow waters.

Judging from the distribution of our records, aerial dispersal by means of birds and insects seems the most probable mechanism, because most localities on the islands have always been surrounded by salt or brackish waters. Fernando (1954) and Rees (1965) give several examples of aerial dispersal; some arguments in favour of its occurrence in the genus *Pisidium* have been put forward by the senior author (Kuiper, 1963, 1964, 1966a).

Our data on this species do not permit drawing any conclusions about the tolerance for salinity and pollution, but Koli (1964) records it from a salinity of 0.6-1.5‰ Cl^{-}.

All localities where *P. obtusale* was observed are characterized by the absence of, or only very slight, water movements. Consequently, the substrate almost always consists of soft mud, mostly with a fair amount of organic debris or even of living plants.

In the freshwater tidal area of the Biesbosch *P. obtusale* was only found in some localities in the willow coppices between 36 and 62 cm below mean high water level, the total tidal range being about 200 cm. These places are characterized by a muddy bottom and only feeble currents.

Pisidium nitidum Jenyns, 1832 (fig. 9)

Van Benthem Jutting, 1943:164-166; Adam, 1960:342-343; Ellis, 1960:59-60.

Distribution: Holarctic, occurring even north of the Arctic Circle. In Europe most frequent north of the Alps; scattered south of these mountains (Kuiper, 1966). The species is common in the Netherlands.

Localities: Province of Zuid-Holland: Gouwe near Gouda; Hollandse IJssel near Moordrecht (ZMA) and near Ouderkerk aan de IJssel; Brielse Meer near Brielle, near Zwartewaal and near Nieuwersluis (W); Quackjeswater, Rockanje (Henrard, 1946); Rhoon (W); Sliedrecht (K); Lek near Ammerstol (Kuiper, 1942); Hollands Diep near Strijensas (W) and near Willemsdorp (K); Oosthaven, Nieuwe Merwede; Zuid-Maartensgat, Zuidhollandse Biesbosch (W). Province of Gelderland: Kil van Hurwenen (W). Province of Utrecht: Rhenen (Van Benthem Jutting, 1947); Lopikerkapel; Cothen (Kuiper, 1942). Province of Noord-Brabant: Zuidpolder, Ossendrecht; Woensdrecht;

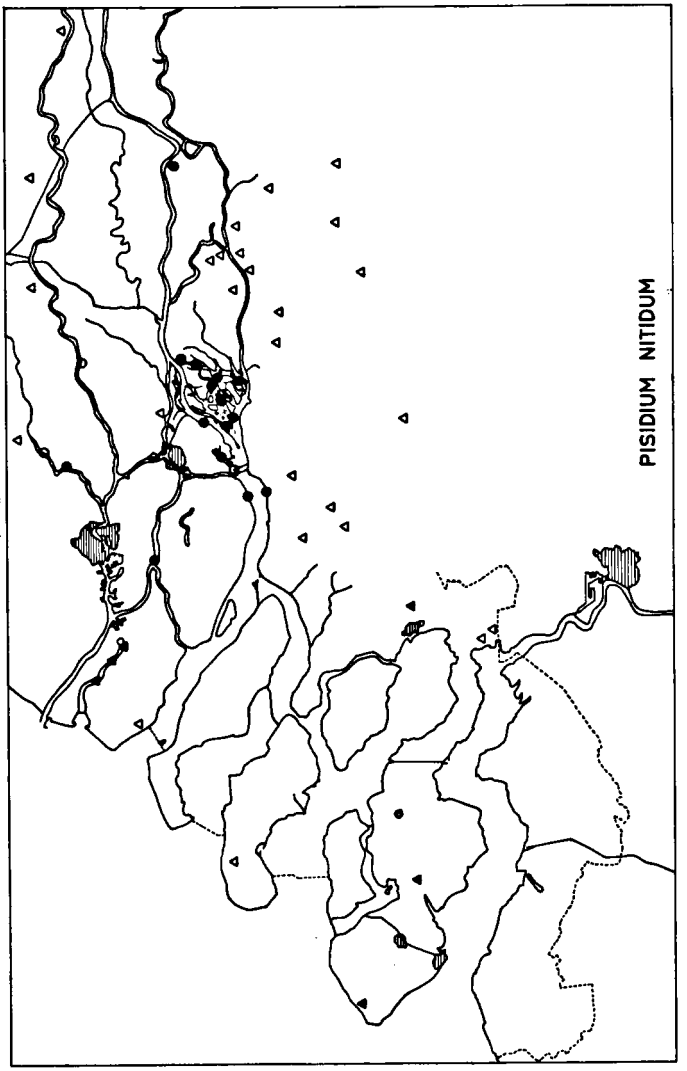

Fig. 9. Distribution of *Pisidium nitidum*. Symbols as in fig. 1.

Oud- en Nieuw-Gastel; Standdaarbuiten; Fijnaart; Roville, Zevenbergen (Kuiper, 1942); Hollands Diep near Roode Vaart; Brabantse Biesbosch, Noorder Jonge Deen, Gat van de Binnennieuwesteek, Buitenkooigat, Halfweg, Sluishoek (W, Heyligers, 1961), Kromme Hoek (Heyligers, 1961), De Dood, Ganzenest, Ruwenhennip, Sloot van St. Jan, Steurgat and Gat van 't Hoofd, Werkendam (W); Babyloniënbroek (K); Veen; Aalburg; Afgedamde Maas near Op-Andel; Waspik (Kuiper, 1942); 's-Gravenmoer (Van Benthem Jutting, 1947); Doeveren (Kuiper, 1942); Ginniken en Bavel (Van Benthem Jutting, 1947); Orthen near 's Hertogenbosch (Kuiper, 1942); Tilburg; Oisterwijk; Boxtel (Van Benthem Jutting, 1947). Province of Zeeland: Renesse (Kuiper, 1944); Golflinks, Domburg (W); Noordkaagertseweg, Nieuwdorp (W).

Ecology: *P. nitidum* is a species with a fairly wide ecological range, occurring in small, stagnant waters as well as in large rivers. This can also be concluded from our observations. It was found in ditches, small rivers, small pools in the dune area, the Brielse Meer (Lake Brielle), the osier beds of the freshwater tidal area, the intertidal mudflats of the freshwater tidal area and in grab-samples from the bottom of the gullies and of the main river. It is also one of the species that have been able to spread to the islands of the Delta area. This large ecological range is well in agreement with the conclusions of Kuiper (1942).

Jaeckel (loc.cit.) records a maximum salinity tolerance of 1.9‰ Cl′, whereas Koli (1961) gives a maximum value of 1.2 – 1.5‰ Cl′. Nowhere in the Delta area these values are reached. In the Hollands Diep the species lives at a mean salinity of below 0.3‰ Cl′, but temporarily it may have to endure much higher values there. In the Brielse Meer during the two years before the present observations the salinity fluctuated between 0.1 and 0.9‰ Cl′.

P. nitidum is able to tolerate fairly strong pollution, since it was found in several localities along the Nieuwe Merwede, the Hollands Diep, and the Oude Maas, all branches of the polluted Rhine.

P. nitidum can stand fairly high current velocities, because it was found in some grab-samples from the Buitenkooigat in the Biesbosch area, where maximum values of 0.8 m/sec may be measured during each tidal cycle. It is possible, however, that the few specimens found here were washed down from the small drainage ditches in the surrounding willow coppices. The species has also been found in small stagnant pools.

In accordance with the great variety in conditions of water-move-

ments, the nature of the substrate in the localities where *P. nitidum* occurs also varies greatly. In the samples of the Buitenkooigat, mentioned above, the sediment can be characterized as medium grade sand with a median grain-size of about 270 μ (Inman, loc.cit.), but there are also localities where the substrate consists of very soft mud.

We found *P. nitidum* down to a depth of 3 m. In the intertidal zone of the freshwater tidal area, *P. nitidum* occurs in a density of almost 150 specimens/sq.m just above mean low water level. Up to 70 cm above this level we sampled it in small numbers (up to 12 specimens/sq.m) in the mudflats, but Heyligers (loc.cit.) found it to be abundant in the upper part of the intertidal zone, 36 to 62 cm below mean high water level, the total tidal range being about 200 cm. These specimens, however, appear to live under unfavourable conditions, because they were somewhat stunted.

The forma *crassa* Stelfox was observed in the Zuid-Maartensgat and in the Brielse Meer near Nieuwersluis.

Pisidium milium Held, 1836 (fig. 10)

Van Benthem Jutting, 1943:161-163; Adam, 1960:341-342; Ellis, 1962:48-50.

Distribution: Holarctic. Occurring throughout Europe but especially north of the Alps and the Pyrenees. Also collected in Africa (Kuiper, 1966). It is a common species in the Netherlands.

Localities: Province of Zuid-Holland: Stolwijk (K); Oude Maas near Goidschalxoord (W); Dubbeldam (K); Veldsloot, Sliedrecht (coll. Butot); Rockanje, Quackjeswater (Henrard, 1946). Province of Utrecht: Cothen, Lopikerkapel (Kuiper, 1942). Province of Noord-Brabant: Zuidpolder, Ossendrecht; Woensdrecht; Oudenbosch; Oud- en Nieuw-Gastel; Standdaarbuiten; Kade, Fijnaart; Zevenbergen (Kuiper, 1942); Brabantse Biesbosch, Kromme Hoek (Heyligers, 1961), Sloot van St. Jan and Sluishoek (W); Werkendam; Nieuwendijk near Almkerk; Drongelen; Woudrichem (K); Veen; Aalburg; Afgedamde Maas near Op-Andel; Waspik (Kuiper, 1942); Heusden (K); Herpt (Van Benthem Jutting, 1947); Orthen, 's Hertogenbosch (Kuiper, 1942); 't Wild, Alem (ZMA); Oosterhout, Ginniken en Bavel; Chaam; Boxtel; St. Michielsgestel; St. Oedenrode (Van Benthem Jutting, 1947); Esch near 's Hertogenbosch (Kuiper, 1942). Province of Zeeland: Golflinks, Domburg (W); Oranjezon, Vrouwenpolder (ZMA); Voormalig Fort St. Livinus, Koewacht; Heikant (W).

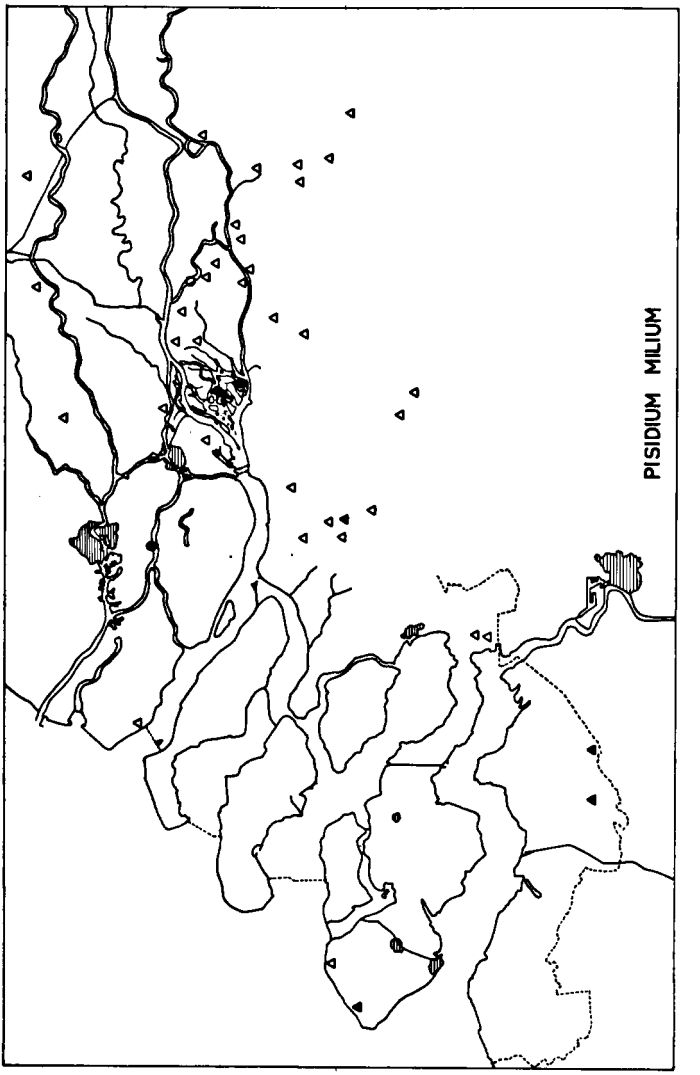

Fig. 10. Distribution of *Pisidium milium*. Symbols as in fig. 1.

Ecology: *P. milium* has a wide ecological range in the Netherlands, closely resembling that of *P. nitidum*. Although it is one of the most ubiquitous and common species in the Netherlands (Kuiper, 1942), it distinctly avoids the running water of the large rivers since we did not find it in any of our grab-samples from those rivers or from the freshwater tidal area of the Biesbosch. The only localities outside the dikes are a few sites in the willow coppices of the freshwater tidal area.

According to Koli (1961), the species does not occur in brackish water; Jaeckel (loc.cit.) records a maximum salinity tolerance of 0.3‰ Cl'.. In the Delta area this value is certainly not reached anywhere.

P. milium does not seem to be very resistant to pollution, but the available data are too small to be conclusive.

Among the many localities mentioned by Kuiper (1942) there are only a few with running water. We ourselves only found the species in localities with little or no current. The only ones with moving water are those in the willow-coppices of the Biesbosch, where *P. milium* occurs sparsely in soft mud just under mean high water level. Apparently, the species does not feel at home here. In almost all other localities, the species occurs on soft types of mud, which are often rich in organic debris.

Pisidium hibernicum Westerlund, 1894 (fig. 11)

Van Benthem Jutting, 1943:168-170; Adam, 1960:353-354; Ellis, 1962:57-59; Kuiper, 1966b:42-46.

Distribution: Palaearctic. In Europe common north of the Alps and even very common in Scandinavia, also north of the Arctic Circle (Kuiper, 1966); a fairly common species in the Netherlands.

Localities: Province of Zuid-Holland: Stolwijk (K). Province of Utrecht: Cothen (Kuiper, 1942). Province of Gelderland: Nederhemert (Van Benthem Jutting, 1947). Province of Noord-Brabant: Zuidpolder, Ossendrecht; Standdaarbuiten; Oud- en Nieuw Gastel (Kuiper, 1942); Doornedijkje, Steenbergen (K); Oudenbosch (Kuiper, 1942); Oosterhout (Van Benthem Jutting, 1947); De Dood, Brabantse Biesbosch (W); Nieuwendijk near Almkerk (K); Veen; Aalburg; Afgedamde Maas near Op-Andel; Doeveren (Kuiper, 1942); Herpt (Van Benthem Jutting, 1947); Elshout, Drunen (K); Orthen, 's Hertogenbosch; Waspik (Kuiper, 1942); Ginniken en Bavel; Chaam; Oisterwijk, St. Oedenrode (Van Benthem Jutting, 1947); Esch near 's Hertogenbosch (Kuiper, 1942).

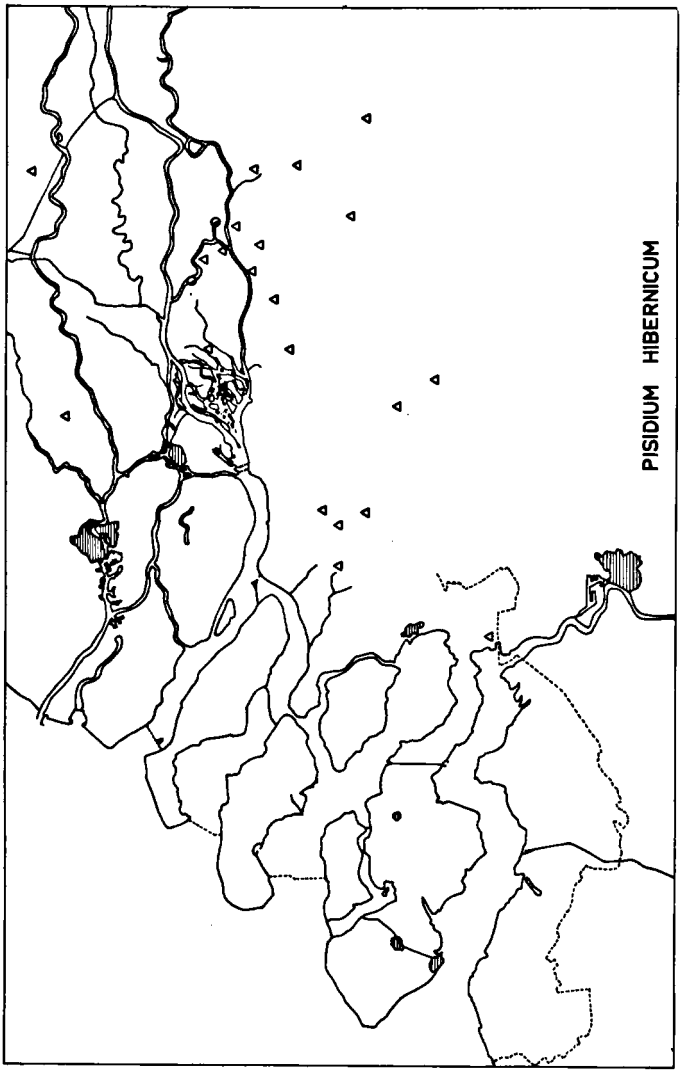

Fig. 11. Distribution of *Pisidium hibernicum*. Symbols as in fig. 1.

Ecology: During our sampling operations we were only able to find *P. hibernicum* once. It was not found at all in the large rivers and in the freshwater tidal area, except for one locality within a "polder", i.e., ecologically outside the area. Our conclusions must therefore be based on Kuiper's (1942) data and our own largely negative results.

We are unable to discuss the salinity or pollution tolerance of the species and there are no relevant data in the literature.

From the foregoing it is evident that *P. hibernicum* avoids the large rivers. Because of its presence in brooks in the Pleistocene parts of the Netherlands, this avoidance cannot be attributed to water movements. It is conceivable that the species avoids waters with a large amount of suspended matter or rich in electrolytes.

P. hibernicum was found on muddy substrates, but the number of observations is insufficient to permit a description of its actual preferences.

Pisidium subtruncatum Malm, 1855 (fig. 12)

Van Benthem Jutting, 1943:170-172; Adam, 1960:348-349; Ellis, 1962:51-52.

Distribution: *P. subtruncatum* has a Holarctic distribution. It is one of the commonest species in Europe, especially north of the Alps and the Pyrenees. Also present in N. Africa (Kuiper, 1966). In the Netherlands it is the commonest species of *Pisidium*.

Localities: Province of Zuid-Holland: Gouwe near Gouda; Hollandse IJssel near Moordrecht (ZMA) and near Ouderkerk aan de IJssel (W); Lek near Ammerstol (Kuiper, 1942); Brielse Meer near Brielle, near Zwartewaal and near Nieuwersluis; Kerkhoekweg, Brielle (W); Quackjeswater, Rockanje (Henrard, 1946); Oude Maas near Goidschalxoord; Zuid-Maartensgat, Zuidhollandse Biesbosch; Ouddorp (W). Province of Utrecht: Lopikerkapel; Cothen (Kuiper, 1942). Province of Gelderland: Culemborg (Kuiper, 1942); Waal near Zaltbommel (W). Province of Noord-Brabant: Zuidpolder, Ossendrecht; Willemstad; Zevenbergen (Kuiper, 1942); Hollands Diep near Tonnekreek, near Noordschans, Klundert and near Roodevaart; Brabantse Biesbosch, Noordergat van de Vissen, Gat van de Binnennieuwesteek, Kooigat, Buitenkooigat, Gat van de Slek (W), Lange Weer, Kromme Hoek (Heyligers, 1961), Sluishoek, Halfweg, Ganzenest, De Dood, Sloot van St. Jan, Steurgat and Gat van 't Hoofd, Werkendam (W); Op-Andel; Veen; Aalburg; Waspik; Afge-

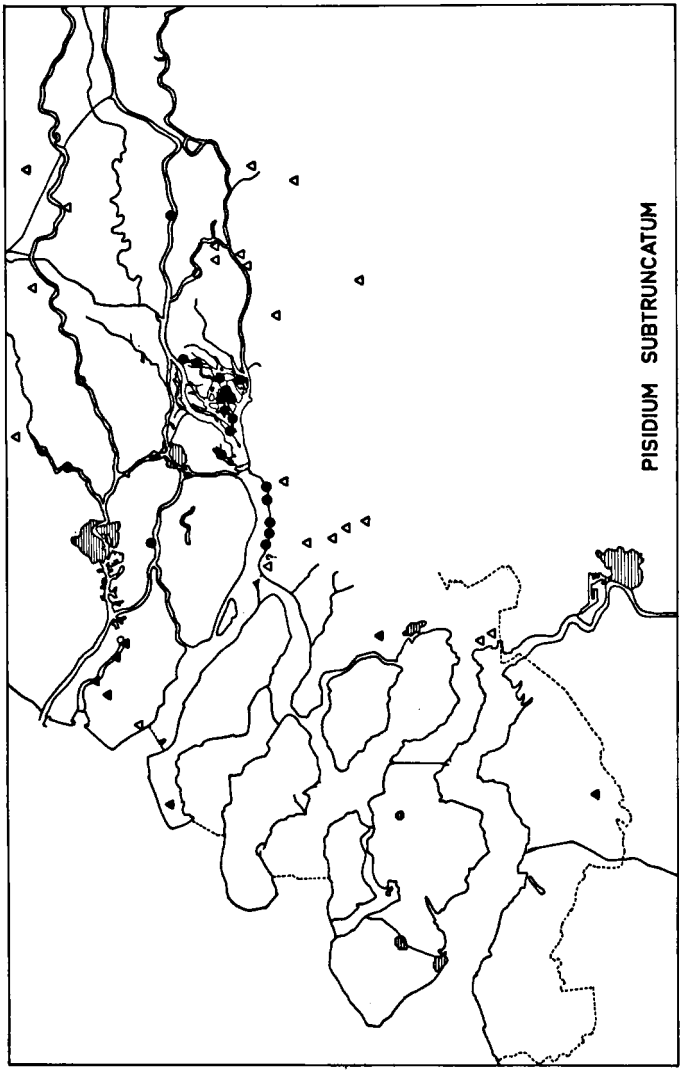

Fig. 12. Distribution of *Pisidium subtruncatum*. Symbols as in fig. 1.

damde Maas near Op-Andel; Doeveren; Heesbeen, near Heusden; Esch and Orthen near 's Hertogenbosch; Tilburg (Kuiper, 1942). Province of Zeeland: Voormalig Fort St. Livinus near Koewacht (W).

Ecology: *P. subtruncatum* is the species with the largest number of recorded localities in the Netherlands. This, however, is not reflected in our results. Although we found it in moderate abundance in the large rivers and the freshwater tidal area, it proved to be rather rare in the inland waters sampled. It should be mentioned that we were only able to record one locality in the province of Zeeland.

P. subtruncatum is fairly resistant to high salinities. Jaeckel (loc.cit.) records 1.9‰ Cl′. as the maximum salinity endured by this species, whereas Koli (1961) records a maximum value of 1.2 - 1.5‰ Cl′. We found the species in fairly large numbers in the Brielse Meer where in the two years before our sampling the salinity had varied between 0.1 and 0.9‰ Cl′. Along the Hollands Diep it normally lives at a salinity of below 0.3‰ Cl′, but temporarily this value may increase to 3-5‰ Cl′. Together with *P. casertanum*, *P. subtruncatum* penetrates furthest into the brackish parts of the estuaries.

P. subtruncatum is also rather resistant to pollution, as shown by its occurrence along the Hollands Diep, the Oude Maas and the Waal, all containing water from the polluted Rhine.

P. subtruncatum lives under various conditions of water movement: it is found in stagnant ditches, but also in the tidal gullies of the Biesbosch, where current velocities of up to 0.8 m/sec occur during part of the tidal cycle.

Accordingly, the species inhabits a wide variety of substrates: muddy substrates with much organic debris; but also sandy ones with a median grain-size of up to 270 μ.

In the freshwater tidal area it is abundant in the mudflats of the intertidal zone. Near mean low water level a density of 777 specimens/sq.m. was reached, and we found it in reasonable numbers up to 70 cm above this level. Heyligers (loc.cit.) collected the species at 52 and 62 cm below mean high water level, the distance between mean high and mean low water level being about 200 cm. At 36 cm below mean high water level Heyligers failed to obtain the species. Below low water level we found it down to 4 m depth.

The forma *incrassata* Ellis was found to occur in some localities in the freshwater tidal area of the Biesbosch, and in the Brielse Meer near Nieuwersluis.

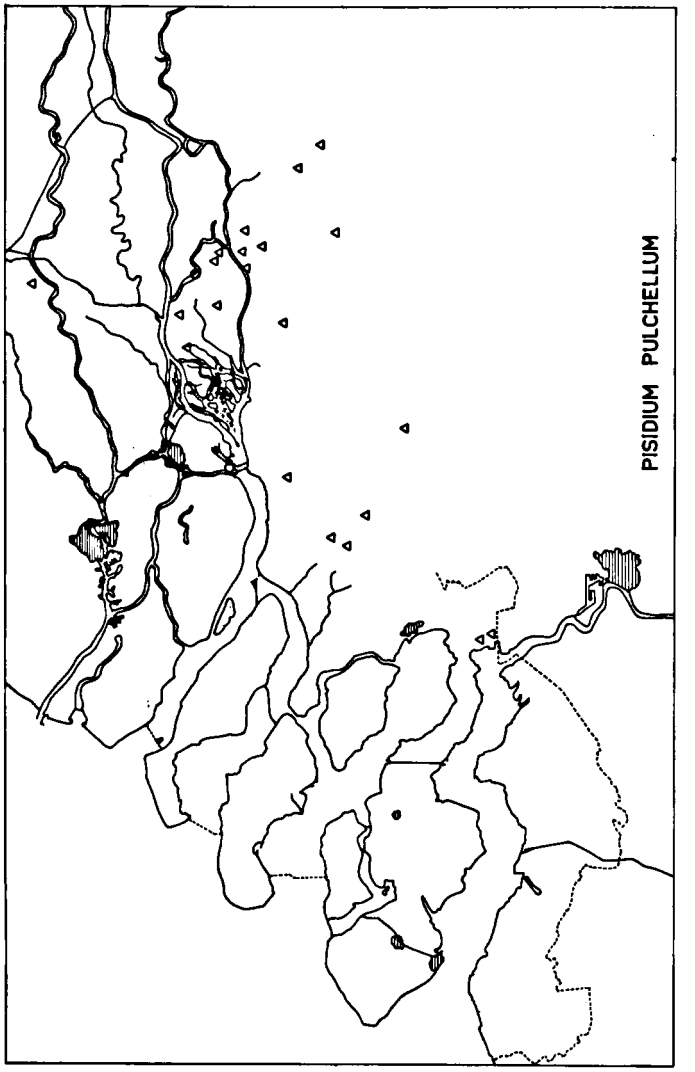

Fig. 13. Distribution of *Pisidium pulchellum*. Symbols as in fig. 1.

Pisidium pulchellum Jenyns, 1832 (fig. 13)
Van Benthem Jutting, 1943:166-168; Adam, 1960:347-348; Ellis, 1960:60-61.

Distribution: Restricted to parts of Europe. The species has been found in the lowland plains of northern Germany, Poland, the former Baltic States, and the adjoining areas of low altitude. Also in the British Isles and in southern Scandinavia (Kuiper, 1966). The species is not uncommon in the Netherlands.

Localities: Province of Zuid-Holland: Willemsdorp, Dubbeldam (K). Province of Utrecht: Lopikerkapel (Kuiper, 1942). Province of Noord-Brabant: Zuidpolder, Ossendrecht; Oudenbosch; Oud- en Nieuw Gastel; Standdaarbuiten; Zevenbergen (Kuiper, 1942); Brabantse Biesbosch, Ganzenest (W); Nieuwendijk, Almkerk; Woudrichem (K); Veen (Kuiper, 1942), Babyloniënbroek (K); Aalburg; Afgedamde Maas near Op-Andel; Waspik; Doeveren (Kuiper, 1942); Herpt near Heusden, Ginniken en Bavel (Van Benthem Jutting, 1947); Elshout; Drunen (ZMA); Oisterwijk; Boxtel (Van Benthem Jutting, 1947); Esch near 's Hertogenbosch (Kuiper, 1942).

Ecology: During our investigations we found only one specimen of *P. pulchellum*, so it is evidently a rare species in the Delta area. However, there is a fair number of records from the surrounding areas (see particularly Kuiper, 1942). These observations seem to suggest that the species is an inhabitant of muddy ditches and pools without or with little water-movement. The records from outside the dikes in the freshwater tidal area are also from more of less isolated, stagnant pools.

Owing to the small number of observations on *P. pulchellum* we are unable to say more about the ecology of the species in the Delta area.

Pisidium pseudosphaerium Schlesch, 1947[2] (fig. 14)
Kuiper, 1947:35-46 (s.n. *P. favrei*); Ellis, 1962:50-51.

Distribution: *P. pseudosphaerium* is known from N. Ireland, Great Britain, France, Switzerland, Austria, the Netherlands, Germany, N. Italy, Czechoslovakia, Poland, NW. Russia, Hungary, Finland, Sweden, and Denmark, always at low altitudes (Kuiper, 1966,

2 See Bowden & Heppell, 1968:258.

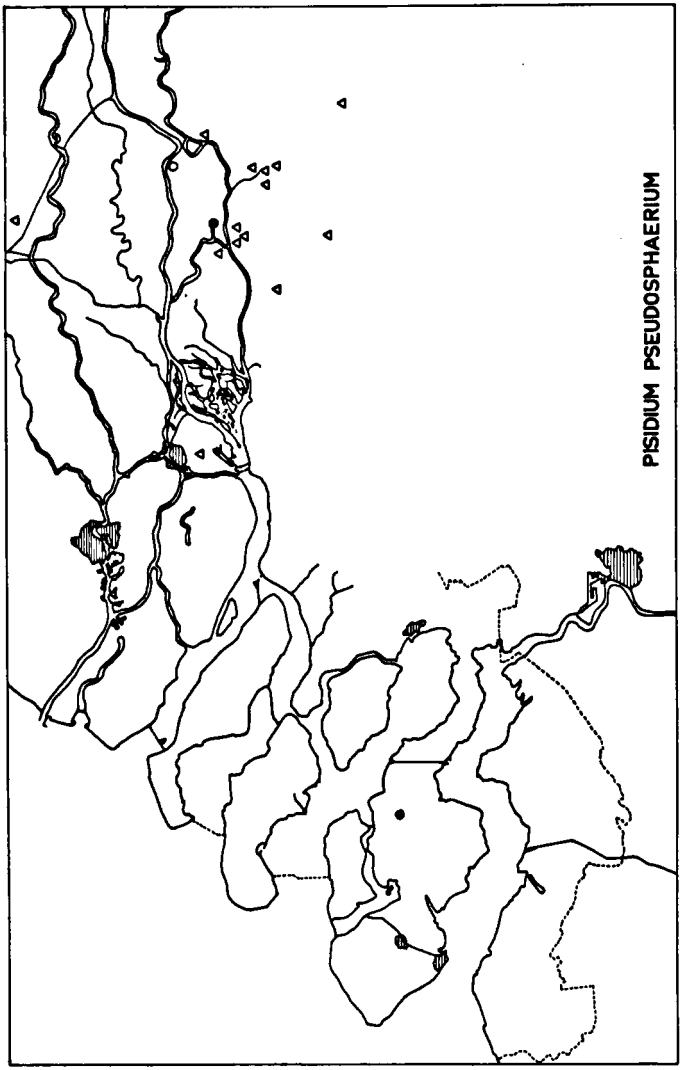

Fig. 14. Distribution of *Pisidium pseudosphaerium*. Symbols as in fig. 1.

1966c). In the Netherlands it is rather rare, although it may sometimes be collected in large numbers.

Localities: Province of Zuid-Holland: Dubbeldam (Kuiper, 1947). Province of Utrecht: Houten (Kuiper, 1947). Province of Gelderland: Kil van Hurwenen, Zaltbommel (Kuiper, 1947); Afgedamde Maas, Nederhemert (K). Province of Noord-Brabant: Aalburg; Heusden, town-moats; Oudheusden; Herpt near Heusden; Waalwijk; 't Wild near Alem; Oisterwijk; St. Oedenrode; Engelen, 's Hertogenbosch; De Pettelaar near 's Hertogenbosch; Orthen near 's Hertogenbosch (Kuiper, 1947).

Ecology: During our investigations we did not find a single specimen of *P. pseudosphaerium* in the Delta area. Kuiper (1947), however, recorded a fair number of observations from the surrounding areas and also some from the Delta area proper. Its habitat is described by Kuiper (1965) as "eutrophic broads, marshes, ditches in peaty areas, with a preference for sandy bottoms". Koli (1964) mentions the species from shallow bays in Finland with a very stable salinity and generally a rich vegetation of aquatic plants. Since such habitats are absent in the greater part of the Delta area, it is evident that *P. pseudosphaerium* does not feel at home there. Because of the lack of data we are unable to draw further ecological conclusions on the occurrence of this species in the Delta area.

DISCUSSION

There are appreciable ecological differences between the various species of *Pisidium* occurring in the Delta area. Therefore, it is to be expected that not all will colonize the future Delta lakes and that those which will do so, will not do so simultaneously.

All Delta lakes will be filled with fresh water through an inlet near Willemstad in the extreme northeastern corner of the area. Because the amount of fresh water coming in will always be rather small, passive aerial dispersal of pisidiids seems most important. This type of dispersal has already been demonstrated by Fernando (1954), who found pisidiids on water bugs, and by Rees (1965), who mentions several cases of passive aerial dispersal for other species of molluscs. Kuiper (1966a) has shown that *P. casertanum* probably has arrived on small oceanic islands by means of passive dispersal by migrating birds. Therefore, and also due to the topography of the

Delta area, the Delta lakes will presumably be first colonized by pisidiids brought in by birds and water insects. In another paper (Kuiper, 1964) the possibility is mentioned that fishes may transport some species of *Pisidium*. In the Delta area this could be important for species such as *P. amnicum* and *P. moitessierianum*. Lastly, transport by currents, although probably not very important (expected current velocities less than 5 cm/sec), should not be ruled out completely.

For the next part of the study we assumed that aerial dispersal will be the most important mechanism, and we therefore attempted to determine which species will colonize the future Delta lakes in this way and also which species will be the first to do so. For this, we have investigated the ten factors listed below. We tried to find out whether the reactions of the various species to the various points would favour introduction into the Delta lakes and if so, to what degree. In most cases we have adopted the scale "small-moderate-large", to grade the reactions of a species to a certain factor. "Small" denotes reactions making a certain species unsuitable for introduction into the Delta lakes; "large" means reactions strongly favouring its introduction. The following points were considered.

1. Salinity. The species with a broad tolerance for increased salinities will be able to colonize the freshening Delta lakes first. Tolerance is expressed as: low-moderate-high-very high.

2. Pollution. The species with a high tolerance for pollution will be better suited for colonization, because the polluted Rhine water will probably be used for the process of freshening the Delta lakes. Tolerance is expressed as: low-moderate-high.

3. Range of the size of the waters inhabited. Species occurring in waters of all sizes will have a better chance to find a suitable area of water after aerial transport. Probably they would also have a better chance to become the subject of such transport. The range is expressed as: small – large.

4. Effects of the size of the waters inhabited. The species inhabiting comparatively small waters must generally be more tolerant of rapid changes and extremes of such factors as temperature and concentrations of electrolytes than inhabitants of larger bodies of water. The more tolerant species probably have better chances. The influence of these factors is expressed as supposed tolerance and thus the reverse of the size of the waters inhabited (small – large).

5. Tolerance for absence of water-movements. It seems reasonable to assume that the amount of water-movement is related to the amount of food and dissolved oxygen available for pisidiids. The

discharge of excretion products may also be important. Probably the species that are least dependent on water-movements have the best chance of immigrating into the future Delta lakes. The grading expresses the tolerance for absence of water-movements, which is the reverse of the amount of water-movement: low-moderate-high.

6. The range of substrates occupied. Species inhabiting many different types of substrate seem to have a better chance of finding an appropriate type of substrate when introduced into a lake than species with a preference for only one type. The range of substrate inhabited is often, but not always, also an expression of the range of water-movements tolerated. Expressed as: small-large.

7. Vertical distribution in the freshwater tidal area. A large vertical distribution indicates a high tolerance for dessication, rapid changes of temperature, and shortening of the period of feeding. It is probably also connected with the ability to inhabit a wide range of substrates. A high tolerance for these factors implies a better chance of being introduced into a new environment. The range of the vertical distribution is expressed as: not occurring intertidally-small-large.

8. Occurrence in shallow non-tidal water. The depth of occurrence in non-tidal water influences the chance of being subject to aerial dispersal and is also an expression of the tolerance of the species for changes in the environment, especially changes in temperature. Shallow occurrence facilitates aerial dispersal and means a higher ecological tolerance. Therefore, this factor is expressed as: low (= only occurring in deep water) – high (= occurring in shallow water, in some cases also in deep water).

9. The abundance of a species also influences its chance of being the subject of passive dispersal. The abundance or density per square metre of the species is therefore expressed as: low-high.

10. Results of passive aerial distribution. The occurrence of various species on the islands of the Delta area may be used as a measure of the chance of a species to become the subject of passive aerial dispersal. The number of known localities on these islands is expressed as: none-small-large.

In Table 1 the results of this classification are expressed as follows: small, low: + ; moderate: ++; large, high: +++; very large, very high: ++++; other categories: – or ? as the case may be. The species with the highest number of symbols have, in our opinion, the best chance of rapidly colonizing the future Delta lakes. These species are *P. casertanum*, *P. henslowanum*, *P. nitidum*, and

Factor	1 ++++	2 +++	3 ++	4 ++	5 +++	6 ++	7 ++	8 ++	9 ++	10 ++	24
Species	**Salinity**	**Pollution**	**Range of sizes**	**Effect of sizes**	**Water movement**	**Range of substrate**	**Freshwater tidal area**	**Bathymetric distribution**	**Abundance**	**Occurrence in Delta area**	**Total**
amnicum	++	++	+	+	++	++	+	+	+	-	13
moitessierianum	++	+	+	+	+	++	++	+	++	-	13
supinum	++	+	+	+	+	+	++	++	++	-	12
henslowanum	+++	+++	++	++	++	+	++	++	++	-	19
casertanum	++++	+++	++	++	++	++	++	++	++	+	22
personatum	++	++	++	++	++	+	+	++	+	+	16
obtusale	++	?	+	++	+++	+	-	++	++	++	15+
nitidum	+++	+++	++	++	+++	++	++	++	++	+	22
milium	+	+	+	++	+++	+	+	++	++	+	15
hibernicum	?	+	+	++	++	+	-	++	+	-	10+
subtruncatum	++++	+++	++	++	++	++	++	++	++	+	22
pulchellum	?	?	+	++	++	+	-	++	+	-	9+
pseudosphaerium	+	?	+	++	+	+	-	++	++	-	10+

Table 1: Probability of colonization of the future Delta lakes by species of Pisidium, predicted on the basis of the effect of ten different ecological factors. The degree of reaction to these influences is expressed by the number of symbols, i.e., the more positive the reaction the higher the number of symbols. For further explanation see text.

P. subtruncatum. It is interesting to see that three of these four species belong to the species with a Holarctic distribution and an abundant occurrence all over Europe (Kuiper, 1963). The fourth species of this group, *P. milium,* seems to have a smaller ecological range.

A second group that will probably also be introduced fairly soon into the Delta lakes and their surroundings, is formed by *P. personatum, P. obtusale,* and *P. milium,* all with an intermediate number of symbols. The remaining species do not seem to be important in this respect.

Lastly, we should like to compare our forecasts with the results of Van Benthem Jutting (1954), who studied the introduction of *Pisidium* into the IJsselmeer (Lake IJssel), which has been dammed off from the North Sea in 1932. The first pisidiids were found in 1937, near the mouth of the River IJssel. As might be expected, both *P. nitidum* and *P. subtruncatum* belong to our first category of species, i.e., those expected to be introduced soon into the Delta lakes. By 1943, four species had spread all over the lake: *P. casertanum, P. henslowanum, P. nitidum,* and *P. subtruncatum*; three other species, *P. amnicum, P. moitessierianum,* and *P. supinum* were only found (1943 or earlier) in the immediate vicinity of the mouth of the River IJssel (except for one specimen of *P. moitessierianum*, found in the centre of the area). Since, due to the topography of the area, river transport of pisidiids is much more unlikely in the Delta area than in the IJsselmeer, these observations give additional support to our predictions.

SUMMARY

The ecology and distribution of 13 species of *Pisidium* in the estuarine area of the rivers Rhine, Meuse and Scheldt have been investigated. These are *P. amnicum, P. moitessierianum, P. supinum, P. henslowanum, P. casertanum, P. personatum, P. obtusale, P. nitidum, P. milium, P. hibernicum, P. subtruncatum, P. pulchellum,* and *P. pseudosphaerium.* From the data obtained it is concluded that four species will colonize the future fresh Delta lakes in an early stage: *P. casertanum, P. henslowanum, P. nitidum,* and *P. subtruncatum.* Later this group will probably be followed by *P. personatum, P. obtusale,* and *P. milium.*

SAMENVATTING

De oecologie en verspreiding van 13 soorten van het geslacht *Pisidium* zijn onderzocht in het gehele Deltagebied van Rijn, Maas en Schelde. De onderzochte soorten zijn *P. amnicum, P. moitessierianum. P. supinum, P. henslo-*

wanum, P. casertanum, P. personatum, P. obtusale, P. nitidum, P. milium, P. hibernicum, P. subtruncatum, P. pulchellum en *P. pseudosphaerium*. De oecologische gegevens van al deze soorten zijn gecombineerd in een tabel, op grond waarvan conclusies zijn getrokken over de snelheid van kolonisatie van de toekomstige Deltameren door de verschillende soorten. Verwacht wordt dat de eerste soorten zullen zijn *P. casertanum, P. henslowanum, P. nitidum* en *P. subtruncatum*. Later zullen waarschijnlijk nog volgen *P. personatum, P. obtusale* en *P. milium*. Deze voorspellingen zijn in overeenstemming met hetgeen werd gevonden tijdens de verzoeting van het IJsselmeer.

REFERENCES

ADAM, W., 1960. Faune de Belgique. Mollusques, Tome I. Mollusques terrestres et dulcicoles: 1-402. Brussel.

BENTHEM JUTTING, T. VAN (= W.S.S. VAN), 1943. Mollusca (I) C. Lamellibranchia. Fauna van Nederland 12:1-477. Leiden.

———, 1947. Lijst van gemeenten als vindplaatsen van Nederlandsche mollusken. Basteria 11:54-87.

———, 1954. Mollusca. In: L.F. de Beaufort (ed.), Veranderingen in de flora en fauna van de Zuiderzee (thans IJsselmeer) na de afsluiting in 1932: 233-252. Amsterdam.

———, 1959. Ecology of freshwater Mollusca in the Netherlands. Basteria 23, suppl.: 106-131.

BOWDEN, J., & D. HEPPELL, 1968. Revised list of British Mollusca 2. Unionacea – Cardicea. J. Conch. 26:237-272.

BRUGGEN, A.C. VAN, 1957. New data on recent Dutch Mollusca, a critical compilation. Basteria 21:46-52, 74-82.

BUTOT, L.J.M., 1961. Malacologisch onderzoek op Schouwen. In: Verslag van biologen-werkkamp op Schouwen 18-25 juli 1960, hoofdstuk 7, 20 pp. Mimeographed report R.I.V.O.N., Bilthoven.

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

FERNANDO, C.H., 1954. The possible dispersal of Pisidium by Corixidae (Hemiptera). J. Conch. 24:17-19.

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

HEYLIGERS, P.C., 1955. Biosociologische studies in de grienden van de Brabantse Biesbosch. Mimeographed report R.I.V.O.N., Bilthoven.

———, 1961. De bodemfauna van de grienden. In: C.J. Verheij

(ed.), De Biesbosch, land van het levende water: 85-117. Zutphen.

———, 1965. The soil fauna in the osier beds of the Brabantse Biesbosch. In: R. Tüxen (ed.), Biosoziologie, Internat. Symp. Internat. Ver. Vegetationsk., Stolzenau/Weser, 1960: 199-210. The Hague.

INMAN, D.L., 1952. Measures for describing the size distribution of sediments. J. Sed. Petr. 22:125-145.

JAECKEL, S.G.A., 1962. Ergänzungen und Berichtigungen zum rezenten und quartären Vorkommen der mitteleuropäischen Mollusken. In: A. Zilch & S.G.A. Jaeckel, Mollusken. Tierw. Mitteleur. 2 (I) Ergänzung: 25-253.

KOLI, L., 1961. Die Molluskenfauna des Brackwassergebietes bei Tvärminne,, Südwestfinnland. Ann. Zool. Soc. Vanamo 22:1-22.

———, 1964. Ueber einige Pisidien (Pelecypoda) im Brackwassergebiet Tvärminne, Südwestfinnland. Ann. Zool. Fenn. 1:80.

KUIPER, J.G.J., 1942. Beiträge zur Ökologie der niederländischen Pisidien. Basteria 7:23-40.

———, 1944. Bijdrage tot de kennis der niet-mariene mollusken van de provincie Zeeland. Basteria 9:1-29.

———, 1947. Bijdrage tot de kennis der zoetwaterweekdieren van het natuurmonument Naardermeer. Basteria 11:2-53.

———, 1963. Hauptzüge der Verbreitung des Genus Pisidium in Europa. Arch. Moll. 92:247-252.

———, 1964. Sur la présence des espèces du genre Pisidium dans les eaux lacustres des Pyrénées–Orientales. Vie et Milieu 15:677-685.

———, 1965. Familie Pisidiidae. In: A.W. Janssen & E.F. de Vogel, Zoetwatermollusken van Nederland: 95-111. Amsterdam.

———, 1966. La distribution des espèces vivantes du genre Pisidium C. Pf. en France. J. Conchyl. 105:181-215.

———, 1966a. Note on the Pisidia (Pisidium C. Pf.) of the Azores, the Canary Islands and Madeira. Bol. Mus. Municip. Funchal 20:34-37.

———, 1966b. The status of Pisidium hibernicum Westerlund. J. Conch. 26:42-46.

———, 1966c. Notes sur le Pisidium rambottianum Adami et sur la présence de Pisidium pseudosphaerium Benthem Jutting & Kuiper en Italie. Atti Soc. Ital. Sci. Nat. & Mus. Civ. Stor. Nat. Milano 105:393-397.

PEELEN, R., 1967. Isohalines in the Delta area of the rivers Rhine,

Meuse and Scheldt. Neth. J. Sea Res. 3:576-596.
REES, W.J., 1965. The aerial dispersal of Mollusca. Proc. Malac. Soc. London 36:269-282.
WOLFF, W.J., 1968. The Mollusca of the estuarine region of the rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area. I. The Unionidae. Basteria 32:13-47.