



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

by

Vlaams Instituut voor de Zee W.J. WOLFF
Flanders Marine Institute



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INTRODUCTION

This paper is the second of a series on the distribution and ecology of Mollusca in the estuarine region of the rivers Rhine, Meuse and Scheldt. For a description of the area we refer to the paper on the family Unionidae (Wolff, 1968), the first of the series. Since publication of this paper the Delta works have so far caused no essential changes in the hydrography of the area. We have employed the sampling methods mentioned in the previous paper and also incorporated the literature data in the same way. The persons mentioned in the first paper have once again in various ways assisted the writer, for which once more he would like to express his gratitude.

FAMILY DREISSENIDAE

Dreissena polymorpha (Pallas, 1771)

Van Benthem Jutting, 1943: 204-210; Adam, 1960: 361-362; Ellis, 1962: 66.

Distribution: *Dreissena polymorpha* ranges from Russia to western Europe; it is a common species in the Netherlands. Its distribution in the area investigated is shown in fig. 1.

Localities¹: Province of Zuid-Holland: Reeuwijkse Plassen (RMNH); Gouwe near Gouda (RMNH); Kralingse Plas, Rotterdam (RMNH); Nieuwe Maas, Rotterdam (†, RMNH); Brielse Meer, nearly

¹ RMNH = Rijksmuseum van Natuurlijke Historie, Leiden; ZMA = Zoologisch Museum, Amsterdam; NHMR = Natuurhistorisch Museum, Rotterdam; W = own observations; † = formerly observed, now absent.

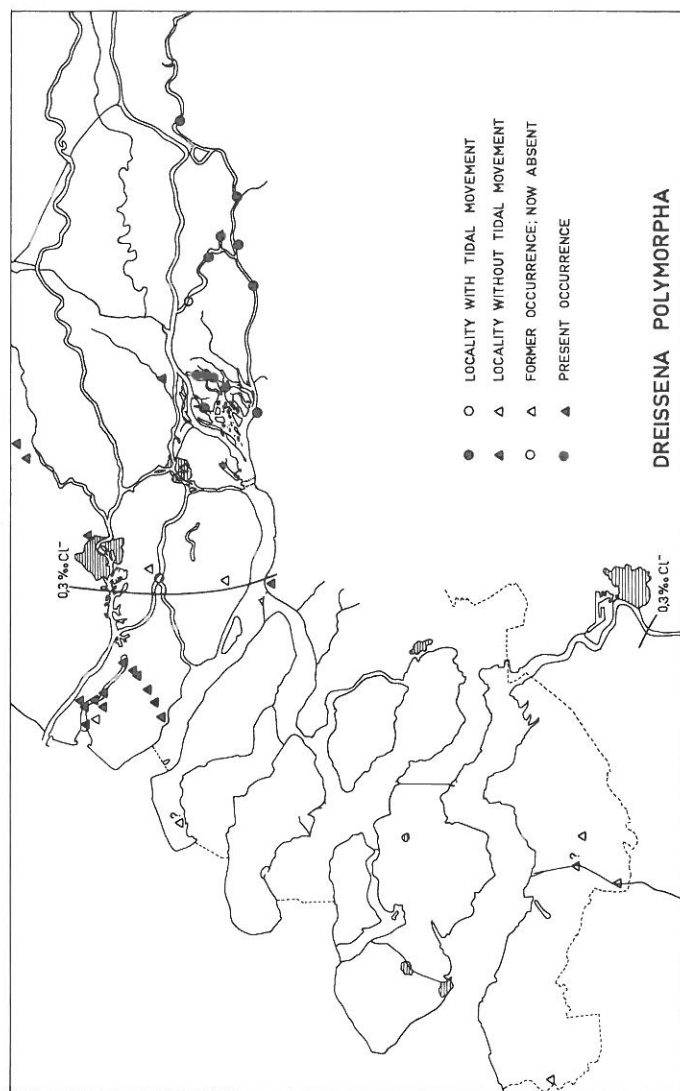


Fig. 1. Distribution of *Dreissena polymorpha* in the Delta area. Isohalines after Peelen (1967), representing situation during mean river discharge before 1964.

everywhere in the lake (Leentvaar, 1955; Janssen, 1958; W); Heindijksloot, Oostvoorne (†, Henrard, 1946); town-moats of Brielle (W); Kanaal door Voorne from Hellevoetsluis to Nieuwersluis (RMNH; Janssen & Janssen-Kruit, 1967; W); Rhoon (†, RMNH); Oude Diep near Numansdorp (†, ZMA); Dordrecht (†, RMNH); Giessen near 'Giessen-Oudekerk' (RMNH); Ouddorp, Goeree (†, possibly only washed ashore on the beach; Van Benthem Jutting, 1943). Province of Gelderland: Maas near Aalst (W). Province of Noord-Brabant: Town-moats of Willemstad (W); harbour of Moerdijk (W); Boomgat, Steurgat and Ganzenest in the Brabantse Biesbosch (W); Maas near Rijswijk (†, ZMA); Amer near Drimmelen (W); Bergse Maas near Drongelen (W); Maas near Nederhemert (RMNH), Heusden (W), Hedel (W) and Lith (RMNH, W). Province of Zeeland: Kanaal van Brugge naar Sluis, on Dutch territory (†, W); Axelse Sassing (†, W); Kanaal van Gent naar Terneuzen near Sas van Gent († W). Probably "een sluisput in het Kanaal van Terneuzen naar Sas van Gent" (Van Benthem Jutting, 1943; cited by Kuiper, 1944) means the village Sluiskil along this canal, because material from this locality is preserved in the Zoölogisch Museum, Amsterdam.

Ecology: Since the beginning of the 19th century *D. polymorpha* occurs in the Netherlands (Van Benthem Jutting, 1943), thus it has had ample time to disperse to all available and accessible biotopes. Its distribution in the Delta area therefore will be a demonstration of its ecological and distributional possibilities.

Although *D. polymorpha* tolerates fairly high salinities, it has nevertheless failed to spread to the islands of the Delta area. Jaeckel (1962) mentions about 2.6‰ Cl' as the maximum salinity tolerated by *D. polymorpha*, but he seems to have overlooked the data by Van Benthem Jutting (loc.cit.) of 6.43‰ and 6.76‰ Cl'. The salinity tolerance of the species needs a few more comments. If we consider *Congeria cochleata* a brackish-water species, then *D. polymorpha* occupies the second place in salinity tolerance among all Dutch freshwater mussels. In the Brielse Meer, with a mean salinity of about 0.3‰ Cl', it has endured a maximum of about 1‰ Cl'. In the town-moats of Willemstad it regularly experiences salinities of up to about 2‰ Cl', whereas Jansen & Jansen-Kruit (1967) record 1.514‰ Cl' as the maximum that *D. polymorpha* has had to endure. Their observations of a decrease in numbers with an increase in salinity are confirmed by our own data from the same localities. We arranged their data in a different way in fig. 2. From

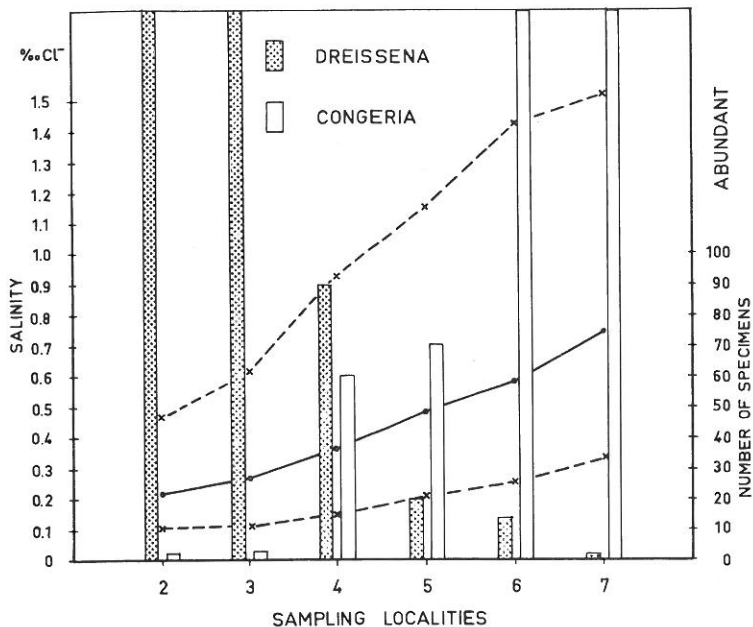


Fig. 2. Distribution of *Dreissena polymorpha* and *Congeria cochleata* in the Kanaal door Voorne (Canal through Voorne). The sampling localities are arranged to show an increasing mean salinity from left to right. The solid line indicates mean salinity, the broken lines the upper and lower limits of salinity.

these data we conclude that the maximum salinity *D. polymorpha* can thrive in is about 0.5‰ Cl⁻, but that, temporarily, they may survive much higher values, e.g., those recorded by Jaeckel (loc.cit.) and Van Benthem Jutting (loc.cit.). It is noteworthy that nearly all observations of *Dreissena* living under conditions of increased salinity were made in inland waters with only slight daily fluctuations in salinity. We did not find specimens in the estuaries above a mean salinity of about 0.3‰ Cl⁻. Therefore we conclude that *Dreissena* is unable to live under estuarine conditions.

The absence of the species on the islands of the Delta area may be explained as follows. Firstly, the ponds and ditches with fresh or slightly brackish water are usually rather small and may dry out during the summer. Moreover, these are only connected with the estuaries by means of an intricate drainage system with a direction of waterflow towards the estuaries, and are thus not easily pene-

trated by the planctonic larvae of *Dreissena*. The lower courses of these drainage systems moreover often contain water with a high salinity, especially in late summer. As the larvae of *D. polymorpha* are released in June-September (Thiel, 1929), it is obvious that these meet the highest salinities during their planctonic phase, most probably with a detrimental effect. Moreover, the estuaries themselves also reach the highest salinities in the summer.

Dispersal in the northern part of the Delta area evidently originated from populations in the rivers Rhine and Meuse, whereas the population recorded in Zeeuwsch-Vlaanderen probably originated from Belgian ancestors.

During the last few years *D. polymorpha* has disappeared from a large part of its range in the Delta area; this is partly caused by the inundations of this area with salt and brackish water in 1944/45 and in 1953 (Wolff, 1968), but probably more in particular by the increasing pollution of the Rhine and some smaller waters. Nowadays we do not know of the existence of any station of this species in the Rhine itself, although several localities in the fairly clean Meuse and its tributaries are known to us. Its extension in recent years in the Brielse Meer is contrary to this decrease of its range. This lake was cut off from the North Sea in 1950 and already in the first winter its salinity fell to about 1‰ Cl⁻. According to Leentvaar (1955) the species was found for the first time in 1952 and possibly already in 1951 occurred in the lake. Janssen (1958) states that it was very abundant in 1954. Thus *D. polymorpha* has colonized the Brielse Meer in the same rapid way as it did the IJsselmeer (= the former Zuiderzee, see Van Benthem Jutting, 1965). We have also observed that in the Brielse Meer unionids colonized new biotopes much more slowly; the first unionids were found here only in 1965 (*Anodonta anatina*, Wolff, unpublished data). *D. polymorpha* nowadays has a flourishing population in this lake.

We have found *D. polymorpha* on several substrates: stone, bricks, wood, and particularly often on the posterior ends of unionids, which many times become completely deformed. *D. polymorpha* seems to prefer the calmest parts of the rivers and also stagnant lakes and canals. We have never found specimens fully exposed to the current (up to 1 m/sec), although suitable substrate (stones and wood) was amply available. In the freshwater tidal area we have never observed the species above mean low water level.

We expect that *D. polymorpha* will rapidly colonize the future Delta lakes.

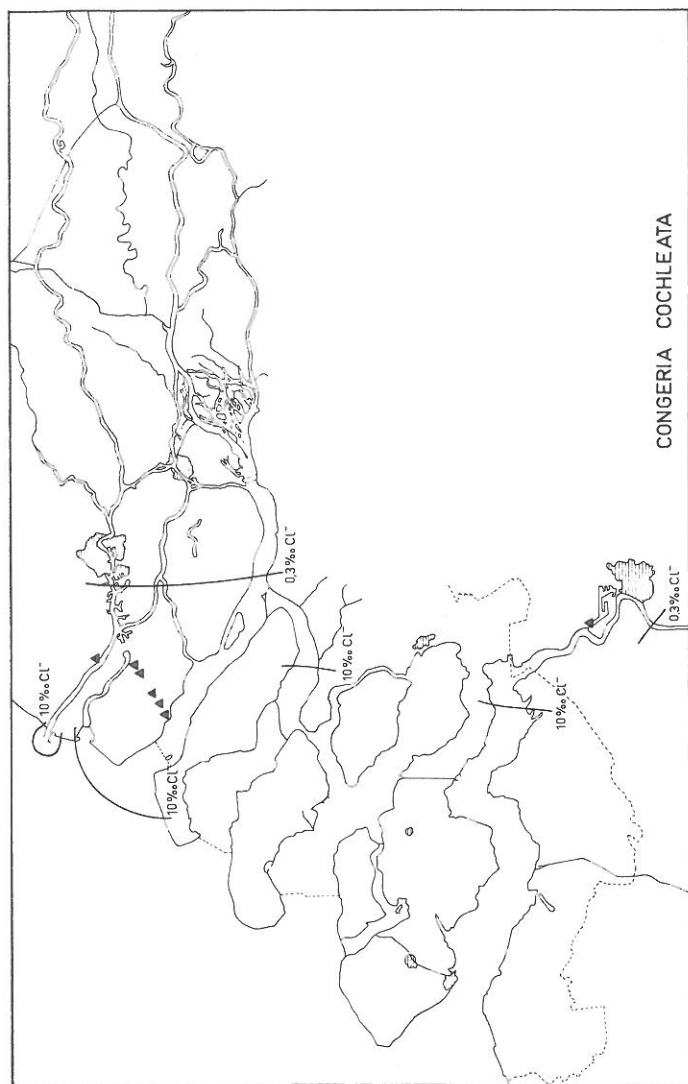


Fig. 3. Distribution of *Congeria cochleata* in the Delta area. Isohalines and symbols as in fig. 1.

Congeria cochleata (Kickx, 1835)

Van Benthem Jutting, 1943: 210–214; Adam, 1960: 362–363 (s.n. *Dreissena cochleata*).

Distribution: *Congeria cochleata* occurs locally in western Europe (France, Germany, Belgium, Netherlands) and is absent in Great-Britain. In the Netherlands it is recorded from the provinces of Friesland, Noord-Holland, Zuid-Holland (Van Benthem Jutting, 1943), and Groningen (Schuitema, 1967), but generally it is rather rare. Its distribution in the Delta area is shown in fig. 3.

Localities: Province of Zuid-Holland: Maassluis (†, RMNH); Hel-levoetsluis and Kanaal door Voorne up to Nieuwersluis (RMNH, W; Janssen & Janssen-Kruit, 1967). Belgium: Antwerp (Adam, 1960; Janssen & De Vogel, 1965).

Ecology: *C. cochleata* is a species typical of brackish waters. Nevertheless, it is rare in the Delta area with its large variety of brackish waters. However, Den Hartog (1964) has made a distinctive difference between the brackish water of estuaries with large daily and annual fluctuations in salinity and the stagnant brackish waters with only slight daily fluctuations, but sometimes large annual fluctuations. *C. cochleata* only seems to occur in waters of the second type. According to Van Benthem Jutting (1943) its salinity tolerance is between 1.91 and 5.10‰ Cl', as was also recorded by Jaeckel (1962) for the "Nord-Ostsee Kanal", Janssen & Janssen-Kruit (1967) record specimens from localities with salinities varying between 0.1 and 1.5‰ Cl', but they state that optimal conditions occurred at a mean value of 0.75‰ Cl' (no stations with a higher mean salinity having been sampled by them), with maxima and minima of respectively 1.5‰ Cl' and 0.3‰ Cl'. From fig. 2 it appears that the minimum value of the annual mean salinity tolerated by *C. cochleata* is about 0.3‰ Cl', although it is possible that the species may not be able to propagate at such low salinities. An upper limit for its occurrence is more difficult to indicate. There are many incidental observations of *C. cochleata* living at high salinities of up to 14.6‰ Cl' (Otto & Wielinga, 1933), but certainly the limit of its normal occurrence, i.e. of localities where it does propagate, is much lower. *C. cochleata* seems moreover restricted to

waters with only slowly occurring variations in salinity.

Its scarce occurrence in the Delta area may have several causes. In the first place its introduction into an area depends probably on shipping-traffic. All records are indeed from larger and smaller ports: Antwerp, Hellevoetsluis and Maassluis. From these ports the species may have spread into surrounding brackish canals and waterways with slight variations in salinity. However, such waterways do not exist between the docks of Antwerp and the Delta area. The only waterway from Hellevoetsluis inland is the brackish "Kanaal door Voorne" (Canal through Voorne), but since Voorne was formerly an island, *C. cochleata* probably did not succeed in crossing the surrounding estuaries with their large daily fluctuations in salinity. After the closure of one of these estuaries, resulting in the Brielse Meer, the water probably became fresh too rapidly to temporarily become a habitat for *Conger*. The waters surrounding the port of Maassluis are fresh or nearly so, so that here *C. cochleata* does not have any possibilities for an extension of its range.

The other brackish waters in the Delta area do not harbour the species, probably due to difficult accessibility or because the salinity is too high (Kanaal door Walcheren: up to 16.5‰ Cl⁻; Kanaal door Zuid-Beveland: up to 14.5‰ Cl⁻).

We have no data about the depth range of this species, nor do we have extensive data on the nature of the substrate to which it is attached. We have found *C. cochleata* on stones and on wood. If the brackish period during the conversion to purely fresh water of the future Delta lakes will last long enough, it is indeed possible that *C. cochleata* may temporarily inhabit these lakes. Lack of accessibility, however, will probably remain an important limiting factor.

DISCUSSION

In an estuarine environment in the Netherlands there are only a few species of filter-feeding lamellibranchs attached to a firm substrate. In the euhaline and polyhaline reaches of the Dutch estuaries only *Ostrea edulis* and *Mytilus edulis* live or used to live in large numbers. *Ostrea edulis* normally does not tolerate salinities much lower than about 15‰ Cl⁻, whereas the lower limit for the regular occurrence of *Mytilus edulis* is about 8-10‰ Cl⁻. Before the introduction of the alien species *Dreissena polymorpha* and *Conger cochleata*, filter-feeding lamellibranchs attached to a firm substrate were not found below salinities of about 10‰ Cl⁻ in the estuaries

and rivers of Western Europe. The introduction of *Dreissena polymorpha* filled part of this gap. The upper limit for *D. polymorpha* in an estuary seems to be about 0.3‰ Cl'. Below this limit this species seems able to live almost everywhere. No doubt *D. polymorpha* has occupied here an existing vacant niche. One would expect that the gap between 0.3 and 8-10‰ Cl' would be occupied by *Congeria cochleata*. This species does indeed live in brackish waters with salinities between such values, but only in stagnant inland waters and not in estuaries. Thus, in those parts of the Dutch estuaries where the mean salinity is between about 1 and 10‰ Cl' filter-feeding lamellibranchs attached to a firm substrate are absent. There are several factors which may be responsible for this phenomenon. In the first place, one may think of the large daily fluctuations in salinity, although other organisms are well able to tolerate such fluctuations. Another factor, however, seems to be much more important. This part of the estuary is usually characterized by strong sedimentation of mud (Postma & Kalle, 1955). It is easily conceivable that even a thin layer of mud on top of a firm substrate is disadvantageous to the settling of the larvae of e.g., *Congeria cochleata*.

SUMMARY

In this paper the distribution and ecology of two lamellibranchs, *Dreissena polymorpha* and *Congeria cochleata*, in the estuarine area of the rivers Rhine, Meuse and Scheldt in relation to the hydrography of that area, are discussed. Attention is drawn to the fact that in this Dutch estuary area formerly filter-feeding lamellibranchs attached to firm substrates did not occur below mean salinities of about 8-10‰ Cl'. The introduction of *Dreissena polymorpha* filled the gap below about 0.3‰ Cl', but between about 1 and 10‰ Cl' still no such species occur. Sedimentation of mud is thought to be mainly responsible for this phenomenon.

SAMENVATTING

In dit artikel wordt de verspreiding en oecologie van twee soorten bivalven, *Dreissena polymorpha* en *Congeria cochleata*, in het Delta-gebied in verband met de hydrografie van dit gebied behandeld. De aandacht wordt speciaal gevestigd op het feit dat op harde substraten

vastzittende, zich door filtermethoden voedende, tweekleppigen oorspronkelijk ontbraken beneden gemiddelde zoutgehalten van ongeveer 8-10‰ Cl'. De soort *Dreissena polymorpha* heeft deze open oecologische plaats bij zoutgehalten onder ongeveer 0.3‰ Cl' gevuld, maar tot dusverre ontbreken dergelijke soorten nog bij zoutgehalten tussen ongeveer 1 en 10‰ Cl'. Waarschijnlijk is afzetting van slib op het harde substraat als oorzaak hiervoor aan te wijzen.

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Boekbespreking

NORA F. MCMILLAN, 1968. *British Shells*. Wayside and Woodland Series, Frederick Warne & Co. Ltd., Londen/New York. 196 pp., 4 fig., 80 pl. Prijs 50 shillings.

Tot "British Shells" verscheen was er in Groot-Brittannië geen modern samenvattend boek over de plaatselijke zee-, land- en zoetwatermollusken; wel bestonden er voortreffelijke werken over de mariene tweekleppigen (Tebble), de landnaaktslakken (Quick) e.a. Nora McMillan heeft nu getracht in kort bestek alle Britse mollusken samen te vatten. Is zij daarin op bevredigende wijze geslaagd?

Het boek bestaat uit enige inleidende hoofdstukken, een beschrijving van de soorten (ruim honderd bladzijden), suggesties betreffende literatuur en een lijst van de Britse mollusken (ruim 35 pagina's), welke laatste gesplitst is in een lijst van zeemollusken en een van land- en zoetwatermollusken, het geheel gevolgd door een naamregister. De tachtig platen bestaan uit kleurenfoto's (26 platen), geschilderde kleurenplaten (zes platen) en lijntekeningen (48 platen). Totaal zijn 355 soorten afgebeeld.

