Een aantal soorten bivalven was ten onzent alleen van drijvend materiaal bekend totdat LUCAS (1951) vondsten van autochthone exemplaren, vooral van onze zeedijken, bekend maakte. Het gaat om *Heteranomia squamula, Kellia suborbicularis, Lasaea rubra, Sphenia binghami* en *Hiatella gallicana*. Waarschijnlijk hebben wij hier te doen met tijdelijke bewoners van onze kust, exemplaren aangevoerd op drijvende voorwerpen of hun onmiddellijke nakomelingschap. Dat zulke tijdelijke bewoners inderdaad bestaan bewijst het geval van *Littorina neritoides petraea*.

STOCK (1950) en SWENNEN (1955) hebben nauwkeurig beschreven hoe kolonies van deze soort, die in 1949 op de zeedijk bij Den Helder, te Callantsoog en te IJmuiden ontdekt waren, in 1951 achteruit begonnen te gaan en in 1953 vrijwel geheel waren verdwenen. Het laatste exemplaar werd op 21 maart 1954 te IJmuiden gezien. Daarna is de soort, ondanks geregelde waarnemingen op voor haar geschikte plaatsen, in ons land niet weer gevonden. In dit geval lijkt het waarschijnlijker dat de kolonies zijn ontstaan uit aangevoerde eieren en larven dan uit volwassen exemplaren aangespoeld op drijvende voorwerpen.

De meeste op drijvende voorwerpen gevonden soorten maken deel uit van de fauna van het Kanaal en zullen waarschijnlijk door de stroom door het Nauw van Calais zijn aangevoerd. Enkele, zoals *Astarte sulcata* en *A. montagui*, komen daar vrijwel zeker niet vandaan. Het is mogelijk dat zij langs de Britse oostkust naar het zuiden zijn gedreven tot zij in de stroom uit het Nauw van Calais naar het noorden geraakten. Enkele soorten aangetroffen in drijvend materiaal op het strand van de Waddeneilanden zijn misschien, onder daarvoor gunstige uitzonderlijke omstandigheden, direct uit het noorden aangebracht.

Theoretisch lijkt het mogelijk dat de Westindische *Bankia fimbriatula* en *Teredo reynei*, die ieder eenmaal in drijfhout op ons strand werden aangetroffen, door de Golfstroom van de overzijde van de Atlantische Oceaan zijn aangebracht. Ik aarzel deze verklaring te accepteren, omdat men dan eerder het bij tijd en wijle aanspoelen van *Janthina* spec. en *Spirula spirula*, die vaak op deze oceaan drijvend worden gevonden, zou verwachten. Geen van beide is hier echter ooit gesignaleerd, ondanks het speuren van vele verzamelaars, die reeds jaren lang op al wat aan de Nederlandse kust aanspoelt letten.

Ecology of brackish water Mollusca in the Netherlands

by

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INTRODUCTION

Compared with fresh water the most characteristic feature of brackish water is the greater amount of sodium chloride, NaCl, in the latter. This increase in salinity is due to the contamination and mixture with sea water. There are other differences, but the chloride content is the most distinctive one, and the one which can be relatively easily ascertained by chemical analysis. Hence the chloride concentration is commonly used in all hydrological and hydrobiological investigations. Not all brackish waters contain the same amount of NaCl, on the contrary, there is a complete gradation between basins with almost pure sea water (Cl content of the North Sea about 17 gr per l = 17.000 mgr per l) and waters which are fresh (Cl content of fresh water 0.1 gr per l = 100 mgr per l). The area of brackish water in the Netherlands is indicated on the accompanying map (fig. 1). Within this area, however, there are considerable differences in the degree of salinity. The nearer a brackish water district is to the sea, the higher its amount of chloride will be; the nearer it is to fresh water, the lower the salinity.

Seasonal fluctuations in rainfall, or in discharge of river water during the melting season of snow and ice, may cause considerable reduction of the salinity in the brackish water area. It is lowered in winter, but rises in summer through evaporation and penetration of sea water.

A tentative classification for brackish waters was proposed by REDEKE (1922, 1932, 1937).[1]

[1]) Redeke (1932) took the 100 mgr limit as the boundary between fresh and brackish water, because different types of fresh water: from precipitation, from the dunes and from the Rivers Rhine and Vecht all have a Cl concentration lower than 100 mgr per l. It was at the same time the standard limit for the approval of a water for drinking purposes.

It must be admitted, however, that, with the exception of precipitation, at the present day the above-mentioned supply sources contain water with a much higher Cl content, as e.g. the Rhine brings in water of about twice that concentration owing to pollution by waste products from industries in Germany. Consequently the limit for drinking water has been considerably raised. Therefore some limnologists have recommended raising the maximum for fresh water to as much as 300 mgr Cl per l. In the present paper I have maintained the 100 mgr boundary.

Table 1

Cl ion			All salts combined
0.1 gr/l =	100 mgr/l	fresh water	0.185 ‰
0.1— 1.0 „ =	100— 1.000 „	oligohaline	0.185— 1.85 ‰
1.0—10.0 „ =	1.000—10.000 „	mesohaline	1.85 —18.5 ‰
10.0—17.0 „ =	10.000—17.000 „	polyhaline	18.5 —30.0 ‰
17.0 „ =	17.000 „	sea water	> 30.0 ‰

This classification is still a good working principle. It is based on certain conspicuous differences between the organisms (floral and faunal composition, reactions of single species, of a biocoenosis etc.) in each category. Hence it may be taken as a biologically significant classification.

SOME GENERAL CHARACTERISTICS OF BRACKISH WATERS

A common characteristic of all the brackish waters in the world is the striking reduction of the number of species, as compared with the adjoining sea- or freshwater environments. The greater part of this reduced number is of marine origin; a much smaller number is of freshwater origin.

It is especially the mesohaline and polyhaline zones which are avoided by freshwater molluscs. In the oligohaline zone (up to 1000 mgr Cl per l) several freshwater species can occur without obvious harm.

For the Zuiderzee basin, an extensive brackish inland sea in the Netherlands, which used to have a remarkable brackish fauna prior to the year 1932, when it was dammed off from the North Sea, the figures for the reduction of the number of molluscs follow here:

Table 2

North Sea near Dutch coast	Zuiderzee (mesohaline and oligohaline) marine origin	Zuiderzee (mesohaline and oligohaline) freshw. origin	Fresh Water in the Netherlands
about 170 species	11 species 1)	4 species 2)	about 70 species

1) the species are: *Mytilus edulis*, *Cardium edule*, *Macoma balthica*, *Mya arenaria*, *Congeria cochleata*, *Corambe batava*, *Tergipes despectus*, *Embletonia pallida*, *Hydrobia ulvae*, *Littorina littorea*, *L. saxatilis tenebrosa*.

2) the species are: *Dreissena polymorpha*, *Hydrobia stagnalis*, *H. jenkinsi*, *Lymnaea ovata*.

Neither the reason for this strong reduction in number of species, nor for the preponderance of marine species over freshwater species is yet fully understood. It seems that adaptation for sea molluscs is easier than for freshwater molluscs. None of these species can inhabit all three environments.

The numbers of individuals of brackish water species which inhabit this transition zone are generally enormous, as there is not so much interspecific competition as in the sea or in fresh water.

The process of adaptation to a salinity different from that of their original habitat is for molluscs chiefly a function of excretion and respiration. Some species can easily adapt themselves, and have a wide range of tolerance (euryhaline species: those mentioned in table 2 for the Zuiderzee basin). Others, on the contrary, have great difficulty in adapting themselves to a different salinity and their range of tolerance is narrow (stenohaline species: most marine and most freshwater species). As a rule the stenohaline species, even if they undergo a moderate temporary change in Cl content without obvious damage, do not propagate and develop in the brackish environment. The euryhaline species, on the other hand, can complete their entire life cycle in brackish water.

It is easily understood that in brackish water, where the Cl content is so variable, only euryhaline species can live. They have less difficulty in adapting the osmotic concentration of their body fluids and tissues to the different salt concentrations of the water in which they live than do the stenohaline species.

In order to ascertain whether an animal is euryhaline or stenohaline one can approach the problem from two sides, (1) try to find in the field the different salinities at which a species can subsist in nature (statistic ecology), or (2) make experiments, in the field and in the laboratory, on the salt tolerance of a given species by exposing it to different degrees of salinity, provided that the other factors are kept stationary (experimental ecology). It must be borne in mind that the extreme values which an animal may occasionally support in experiments are not always those which it prefers in nature. Both methods are necessary; the statistical method is incomplete without experimental control, and the experimental method always requires confirmation by the facts derived from exact observations in nature.

Of the principal types of feeding among the molluscs, the plankton feeders, the detritus feeders, the browsing snails and the predators, all four are represented in the marine environment. In fresh water predators do not occur. The brackish water mainly follows the marine pattern. Predators are some of the Nudibranchs (*Embletonia pallida*, *Tergipes despectus*), browsing species are *Alderia modesta* and *Limapontia depressa*, the *Littorina* species, the Planorbids, the Lymnaeids. Plankton feeders are all Lamellibranchs; detritus feeders are all the *Hydrobia* species.

Migration to a milieu of variable salinity does not only affect the daily functions of feeding, respiration, circulation and excretion, and the seasonal processes of propagation and development, but also form, size and structure. The effect is different in the various species.

Differences in f o r m are observed in e.g. *Cardium edule* (prolonged posterior part of the shell, reduction of number of ribs), *Mya arenaria* (rounder shell).

Differences in s i z e are generally manifest as a reduction, never as an enlargement: *Mytilus edulis*, *Cardium edule*, *Macoma balthica*, *Mya arenaria.* Freshwater molluscs entering a salter region can also undergo a reduction in size, e.g. *Lymnaea ovata.* The same tendency of dwarfing in brackish water is followed in other animal groups, e.g. fishes.

The reduction in size such as is encountered in *Mytilus edulis*, *Cardium edule*, *Mya arenaria* and *Macoma balthica* can be caused by the slowing down of ciliary movement in brackish water. Recent experiments by SCHLIEPER (1955) and SCHLIEPER & KOWALSKI (1957) have demonstrated that in *Mytilus edulis* the ciliary movement in brackish water is reduced to one half to one third of the activity in sea water. For the animals that would mean that — although living in an environment rich in food — they cannot fully profit from this abundance.

Differences in s t r u c t u r e are apparent in the thinner shell (paucity of lime and of pigment) resulting in more fragile shells with duller colour: *Mytilus edulis*, *Cardium edule*, *Macoma balthica*, *Mya arenaria*, *Lymnaea ovata.* The deficiency of lime, however, has not caused a notable increase in Nudibranchs! It is not improbable that these differences in structure are also a function of the slower ciliary activity and, consequently, of metabolism, as mentioned above.

Is is a well-known fact that brackish water species have a tendency to reduce their power of reproduction (fewer eggs). This is both relevant among the limnogenic and the thalassogenic species. We have no information on the question which factors are responsible for this reduction.

A certain compensation may be found in (1) the longer period of reproduction so that after all an equal number of young is produced, and (2) in the lower number of species in the brackish water environment so that the degree of competition for food is reduced (REMANE & SCHLIEPER, 1958, p. 50-51).

Not only in the salinity, but also in the nature of the bottom and in the vegetation brackish water habitats possess special features. Compared with the marine environment the well-known brown algae *Fucus*, *Ascophyllum*, etc., are absent or rare, occurring only as dwarfed shoots on stones and poles. Green algae, on the contrary, such as *Vaucheria*, *Enteromorpha*, *Cladophora*, *Chaetomorpha*, and various

Diatoms, are often present in great numbers, more abundant than in the sea. On *Enteromorpha* and *Cladophora* we find *Hydrobia ulvae*, young *Littorina littorea* and young *Mytilus edulis.* The felty cushions on sand or mud, produced by *Vaucheria*, are the favourite habitat of *Alderia modesta* and *Limapontia depressa* (DEN HARTOG & SWENNEN, 1952; DEN HARTOG, 1958).

In addition to these algae the brackish water region has received a supply of Phanerogamous plants of freshwater ancestry such as *Zostera*, *Ruppia*, *Zannichellia*, *Potamogeton*, *Phragmites*, *Scirpus*, *Spartina.* These plants are rooted in the sand and mud bottom; they do not require a solid substrate for attachment. Among these plants *Hydrobia stagnalis*, *H. jenkinsi*, *Lymnaea ovata*, and various freshwater molluscs, Gastropods as well as Bivalves, are common, the Hydrobiae and the Bivalves mostly on the bottom, the others on the plants.

Where Hydroids occur the small Nudibranchs *Tergipes despectus* and *Embletonia pallida* feeding on them are abundant. On the incrustating reef-building colonies of *Membranipora crustulenta* which are locally developed in brackish water lakes in the island of Texel, in small pools behind the Hondsbosse dike, in the Kaasjeswater near Zierikzee, in the Terluchtse Wiel near Goes, in the Grote Gat near Oostburg, etc., *Hydrobia stagnalis*, *H. jenkinsi*, and small *Littorina saxatilis tenebrosa* occur.

The sandy mud and the soft mud flats are the type of ground in which *Cardium edule*, *Mya arenaria*, and *Macoma balthica* live, often in great numbers. The density of a one year old cockle population in the Dutch Wadden Sea was calculated by KRISTENSEN (1957, p. 21) to amount to circa one thousand per square metre. KREGER (1940; p. 182) even found more than 2000 per square metre. HAVINGA (1922) obtained in the open Zuiderzee up to 3000 *Mya arenaria* and 550 *Cardium edule* per square metre in the Buiten IJ near Amsterdam. *Macoma balthica* was always much less abundant, amounting to 85 per square metre.

On top of the sandy tidal flats, often along creeks, colonies of *Mytilus edulis* settle locally (KUENEN, 1942; MAAS GEESTERANUS, 1942; VERWEY, 1952). Where groynes or other constructions for protection against surf and currents are erected these structures are soon-overgrown by thick mattresses of *Mytilus edulis.*

TYPOLOGY OF THE BRACKISH WATER HABITATS

A. Rivers and Estuaries (running water)
B. Lakes, Ponds, Pools, Marshes, Canals and Ditches (stagnant water)

All the brackish water in the Netherlands is eutrophic (pH 7 or more); there is no oligotrophic brackish water.

Whereas in most other countries the districts containing brackish water are disjunct [1]), it is a peculiar feature of the Netherlands, with its long coast line, its low-lying country and its widely branched system of lakes, canals, ditches, etc. that all the bodies of water of the brackish area communicate with one another, either as an open communication or through sluices and locks.

A. *Rivers and Estuaries*

Running brackish water is only found in the estuaries with free access to the North Sea in the provinces of Zeeland and Zuid-Holland, and in the extreme NE in the province of Groningen where the River Ems debauches into the North Sea. In all of them the bottom relief has a sharper profile than in stagnant waters.

In these estuaries fresh water flows to the North Sea, at low tide somewhat faster than at high tide. Sea water enters at high tide. It depends on the declivity of the river, on the depth and the configuration of the river bed and on the local tide difference as to where sea water and the effluent of the river will meet. The saltwater influence is directly felt in the more seaward part of the rivers, and indirectly in the more upstream fresh part which is temporarily dammed and held up by high tide. Even at a distance of many miles from the sea there is an inward undercurrent of sea water entering the estuary below the fresh upper layers of water flowing seaward. Hence the bottom salinities are consistently higher than the surface values.

The tide wave is felt as far upstream as Vianen in the River Lek, in the Hollands Diep and in the bifurcations of the Biesbos in the River Merwede and upstream of Antwerp in the River Scheldt. At Lilloo, in Belgium, a few miles downstream from Antwerp, the tidal difference still amounts to a maximum of close on 4-5 m (LELOUP & KONIETZKO, 1956, p. 19). At Bath, on Zuid-Beveland, the normal tide difference is 3.70 to 4.50 m, at spring tide 5 m, at Hansweert 3.40 to 4.30 m, at spring tide 4.80 m, at Terneuzen 3.25 to 4 m, at

[1]) In spite of the discontinuous distribution of brackish water areas the molluscs of the brackish regions in NW Europe are almost similar in all regions.

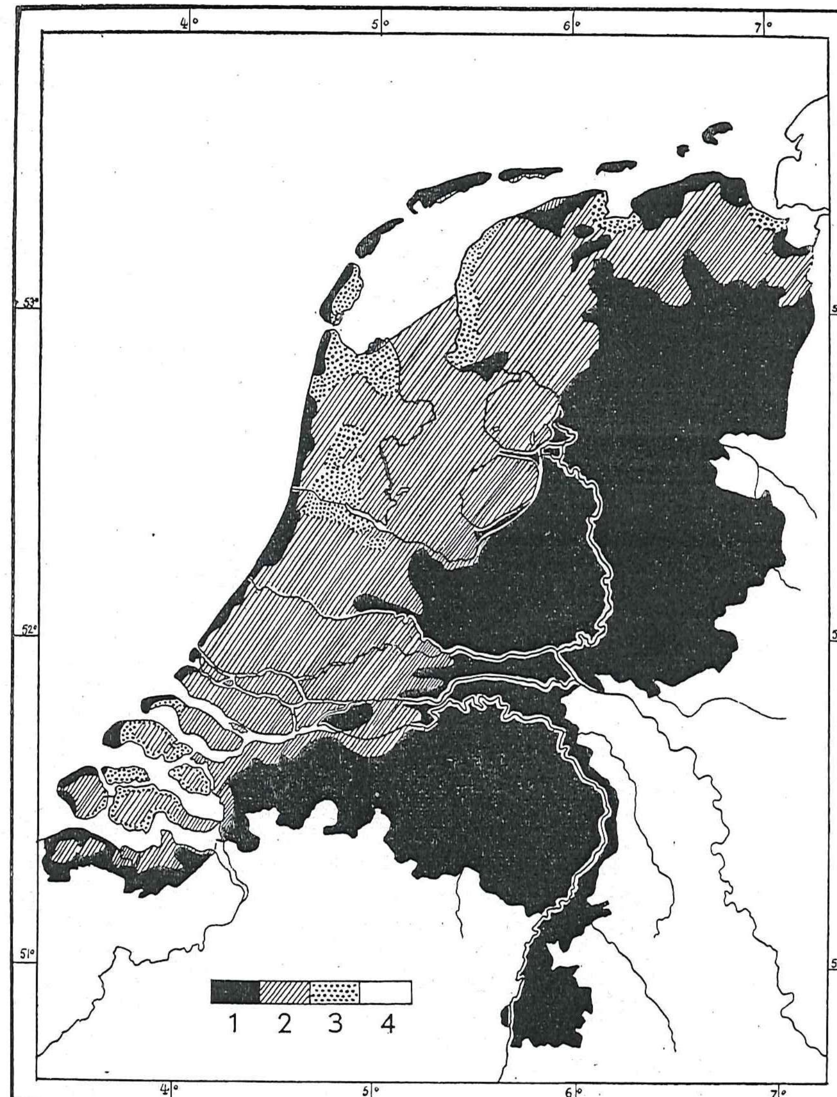

Fig. 1. Regions of (1) fresh water, (2) chiefly oligohaline brackish water, (3) chiefly mesohaline brackish water, (4) polyhaline brackish water and sea water in the Netherlands. After Redeke, 1932, somewhat modified. (Gebieden van (1) zoetwater, (2) voornamelijk oligohalien brakwater, (3) voornamelijk mesohalien brakwater, (4) polyhalien brakwater en zeewater in Nederland).

spring tide 4.60 m and at Vlissingen 2.90 to 3.70 m, at spring tide 4.30 m [1]). The Brielse Maas which was dammed off from the North Sea near Oostvoorne in July 1950 is no longer an estuary, but an oligohaline inland lake.

From the foregoing it is evident that — although there is in the estuaries always a surplus of water displacement towards the sea — the velocity of the current is irregular and comparatively small. Its nature is more a to and fro swinging than a continuous one-way current. In summer, with little river discharge, the sea water enters the estuary farther inland than in winter when there is greater discharge of fresh water.

It is equally clear that there is a continuous fluctuation in the degree of salinity, without a sharp delimination of poly-, meso- or oligohaline areas. This variation is not only in horizontal direction, but there is also a vertical stratification in the water: fresh water or brackish water of little density on top, sea water or polyhaline brackish water at the bottom.

The environment of the more or less sedentary species changes at short intervals from a favourite one to conditions at which they can hardly subsist. Certain organisms are adversely affected and die down, others avoid the ill effect of temporary dilution by closing up or burrowing into the bottom, and finally there is a category which is not so susceptible to low salinity and which maintains what seems to us a precarious existence. Only a great many recurring periodical observations over a longer period can definitely make out the ecological preferences of each species.

In the Westerschelde marine organisms are still found as far as Kruiningen ferry station. Here *Littorina saxatilis rudis*, *Littorina littorea*, *Littorina obtusata littoralis* live among *Fucus* and *Ascophyllum* on the harbour mole, and *Cardium edule* in the sandy mud between groynes (average salinity in summer 20.000-25.000 mgr NaCl per l, in winter 8.000-13.000 mgr NaCl per l). Higher up in the Westerschelde mesohaline to oligohaline conditions reach several miles upstream of the Dutch-Belgian frontier where *Alderia modesta*, *Limapontia depressa* fa. *pellucida*, *Mytilus edulis*, *Macoma balthica*, and *Mya arenaria* almost reach as far as Lilloo at salinities varying between 500 and 850 mgr Cl per l at high tide. Even *Fucus* comes as high as Liefkenshoek opposite Antwerp (LELOUP & KONIETZKO, 1956, p. 31, 75).

[1]) These figures are derived from a survey report on the Westerschelde kindly put at my disposal by the Rijkswaterstaat, Directie Zeeland, Afdeling Studiedienst, Vlissingen.

In the Dutch section of the Westerschelde near Bath young *Cardium edule*, *Macoma balthica*, *Mya arenaria*, and *Scrobicularia plana* live in the mud, *Alderia modesta* on *Vaucheria* cushions on top of the mud on the "schorren" (mud flats) and countless *Hydrobia ulvae* on and in the mud (average salinity near Bath in summer 16.000-21.000 mgr NaCl per l, in winter 4.000-17.000 mgr NaCl per l). The two small Sacoglossans, *Alderia* and *Limapontia*, accompany the estuary throughout its whole length, provided that there are *Vaucheria* cushions on the mud flats in which they can hide and obtain their nourishment.

Downstream from Hansweert marine influence gradually increases. These lower reaches of the estuary display a much more varied fauna than the upstream sections. On the bottom of the deep channel off Terneuzen (depth about 45 m at low tide) *Buccinum undatum*, *Crepidula fornicata*, good-sized *Mytilus edulis*, young *Petricola pholadiformis*, *Venerupis pullastra*, *Zirfaea crispata*, *Saxicava rugosa*, and various other North Sea animals occur. In the littoral zone the three *Littorina* species and *Lepidochiton cinereus* are common (average salinity near Terneuzen in summer 26.000-30.000 mgr NaCl per l, in winter 20.000-25.000 mgr NaCl per l). Further westwards the polyhaline zone imperceptibly merges into true marine conditions (average salinity near Vlissingen in summer 29.000-32.000 mgr NaCl per l, in winter 24.000-30.000 mgr NaCl per l).

Compared with the Westerschelde, the Oosterschelde is quite a different environment. The latter basin does not receive such an enormous volume of fresh water. Hence it has (1) a higher and more constant salinity which is, moreover, almost (2) uniform in the whole area. There is some influence of the tides, but (3) a surf effect is absent. As the Oosterschelde does not receive such quantities of river silt and sewage from the hinterland (4) the silt content of the water is much lower, and (5) the bottom is more sandy instead of muddy. Finally (6) the water temperature is higher and less fluctuating (MULDER, 1956).

From these details it is clear that the Oosterschelde, although penetrating far inland, is predominantly high-polyhaline to marine (average Cl concentration 27.75‰).

Of the biotic communities of the Grevelingen and the Haringvliet we have no detailed information. Our knowledge is equally poor of the Nieuwe Waterweg. The Brielse Maas was dammed off from the North Sea in 1950 and is now changing from mesohaline to oligohaline (LEENTVAAR, 1955). It will be dealt with in the section on stagnant brackish waters.

Further to the north the tidal inlets between the Wadden islands are not true estuaries, as they do not discharge any considerable quantities of fresh water, but form part of the autonomous system of water movements in the Wadden Sea. This entire region contains on the average such high salinities that it can be termed high-grade polyhaline, if not marine. It will be left out of consideration in our further discussion.

The last corner where a true estuary is found lies at the Dutch-German frontier where the River Ems, after forming a wide brackish bay, the Dollard, flows out into the Wadden Sea, later on into the North Sea. The tidal influence is felt many miles upstream from Emden. The tide difference amounts to 2.5-3 m. The depth of the channel in the Dollard is 6-7 m, in the Wadden Sea about 18 m. The surface salinity at high tide diminishes from 10.000-15.000 mgr Cl per l (polyhaline) near the sandbank Paap to 7.000-10.000 mgr Cl per l (mesohaline) in the Dollard Bay and $<$ 1.000 mgr Cl per l (oligohaline) in the lower stretch of the River Ems. In the channel of the estuary the salinity is higher than on the mud flats along the banks. From the point of view of salinity conditions the actual size of the estuary is probably not so important as the relation of freshwater flow to the size of the estuary. This relation is difficult to determine and available data are limited.

In the channel of the Ems estuary no mud is deposited; its bottom is never polluted by hydrogen sulphide. On the mud flats, on the contrary, putrifying black mud is found below a superficial well-aerated, healthy layer of mud. In this superficial mud layer of the Dollard *Cardium edule*, *Mya arenaria*, *Macoma balthica*, *Hydrobia ulvae*, and *H. stagnalis* are plentiful. *Cardium edule*, *Scrobicularia plana*, and *Mytilus edulis* occur in smaller numbers. All of them are euryhaline species (KUENEN & VAN VOORTHUYSEN, 1959).

Until 1932 the Zuiderzee, this wide estuary of the River IJssel and a few smaller streams, used to be a brackish water area ranging from pure fresh water (in the vicinity of the river mouths) to polyhaline (in the Wadden Sea). On account of the relatively small inflow of fresh water, the oligohaline zone in the Zuiderzee was of limited extent, restricted to a narrow coastal strip along the east and south coasts. The mesohaline zone occupied a much greater area, filling almost the entire southern basin till about the bottleneck between Enkhuizen and Stavoren. The polyhaline zone, finally, reached beyond this boundary, gradually merging into the conditions of the Wadden Sea and the North Sea.

Since the building of the enclosing dam, Afsluitdijk (final opening shut in May 1932) no North Sea water could penetrate any longer into the Zuiderzee. Since that date the poly- and mesohaline waters were gradually transformed into an almost uniform oligohaline, practically fresh, condition. Instead of an estuary with tide effect and currents, the Zuiderzee is now an inland lake; its name has been changed to IJsselmeer. The new condition will be discussed at some length in the following section, on the stagnant brackish water.

During the existence of the open Zuiderzee a few species of freshwater molluscs from the rivers IJssel and Zwarte Water, such as *Bithynia tentaculata*, *Valvata piscinalis*, *Theodoxus fluviatilis*, *Sphaerium corneum*, *Dreissena polymorpha*, were transported now and then into the narrow oligohaline zone along the south and east coasts; most of these temporary immigrants died soon.

The polyhaline zone in the extreme north and north-west was inhabited by several marine species: *Lacuna divaricata*, *Littorina obtusata littoralis*, *Rissoa membranacea*, *Buccinum undatum*, *Retusa obtusa*, *Lamellidoris bilamellata*, *Alderia modesta*, *Tergipes despectus*, *Aeolidia papillosa*, *Ostrea edulis*, *Venerupis pullastra*, *Petricola pholadiformis*, *Spisula subtruncata*, and *Scrobicularia plana*. It contained also well developed *Mya arenaria*, *Mytilus edulis*, *Cardium edule*, *Macoma balthica*, and innumerable *Hydrobia ulvae*. Bottom vegetation was scanty; the Bivalves burrowed in sand and sandy mud, the Gastropods lived on shelly sand and among local Eel-grass meadows.

The greater part of the Zuiderzee between these two zones, the polyhaline and the oligohaline, was mesohaline. Here *Mya arenaria*, *Cardium edule*, *Mytilus edulis*, and *Macoma balthica* lived as dwarfed specimens in great abundance in the soft, nearly liquid mud. On, or rather in, the top layer of the mud *Hydrobia ulvae* and *H. stagnalis* abounded. In places where Hydroids grew *Tergipes despectus* was found. There were no endemic Zuiderzee molluscs. Bottom vegetation was scarce or absent.

It is not quite clear why *Mya arenaria*, *Macoma balthica*, *Cardium edule*, and *Mytilus edulis* could only reach such small sizes in the mesohaline Zuiderzee. There was plenty of food, in the plankton as well as in the superficial mud layers. Aeration was sufficient and oxygen content high. Chemical constituents other than chloride content did not differ virtually from those in the Wadden Sea and the North Sea. Whether the salinity was the sole agent responsible for the dwarfing of these animals, and how it affected them, is not fully understood. So much is certain that shortly after the closing of the Afsluitdijk, when the process of freshening continued, the Bivalves gave up altogether.

B. *Lakes, Ponds, Pools, Marshes, Canals and Ditches*

Although in common usage all these waters are termed stagnant, there is hardly ever an entirely motionless water. There is always a certain amount of circulation or current, though wind force, navigation, pumping out surplus water, etc.

A great many of our lakes, ponds, canals, etc. lie below sea level. They are kept at a certain fixed mark by voiding the excess of water to draining courses which carry it towards the sea. Where the water levels are different the inland navigation has to pas through locks.

The chloride content of the stagnant brackish water is variable. During the wet season precipitation can dilute the salinity considerably, during the summer evaporation causes an increase of salinity. Hence certain waters are oligohaline in winter, mesohaline in summer.

On the whole the brackish waters lying close to the sea are generally more saline than those more remote from the sea. This rule is, however, not always valid, as e.g. the Alkmaarder Meer with its 300-600 mgr Cl per l is less saline than the Botshol (570-1325 mgr per l) or the Abcouder Meer (66-1070 mgr Cl per l).

In stagnant brackish waters, no matter whether they are oligo-, meso- or polyhaline, there is usually a stratification of salter water at the bottom and water of less density at the top. This condition is more or less stationary; it does not change with the diurnal rhythm of convection currents, nor with the seasonal rhythm of inversion of water layers, as the heavier salt water never mixes with the lighter fresh water. Consequently there is formed a bottom sheet with hardly any circulation, almost devoid of oxygen, but rich in hydrogen sulphide. In the top layers, more exposed to the atmosphere, the oxygen content is higher. For the plants and animals this means that there is a surface layer with a well developed organic life and an almost abiotic bottom layer where only anaerobic organisms can exist.

These antagonistic conditions are often found in brackish water canals where there is little circulation in the deeper parts, e.g. the Noordzee canal, the canal across Zuid-Beveland, the canal across Walcheren, etc.

On the other hand it is interesting to record that in the Westerschelde, although of considerable depth (locally even to 45 m or more) there is never such a putrifying mud at the bottom, as the gullies are regularly swept out by the currents of the estuary.

Not even in the ancient Zuiderzee or in the present IJsselmeer did there ever occur a layering of the water, because this basin is so shallow that, owing to wind and ship traffic the bottom water is constantly stirred up and kept in motion. There is practically no

vertical salinity gradient and the water is so well aerated that the whole column of water is saturated with oxygen.

Only very few stagnant brackish waters have been surveyed monographically. In some of them the salinity has been measured, but flora and fauna have not been investigated. In others the vegetation or the snail fauna was studied, without, however, paying attention to the physical and chemical qualities of the environment, salinity, pH, temperature, depth. Of the following lakes we only know the Cl content: Ackerdijk lakes (in 1943: 198 mgr Cl per l), Reeuwijk lakes (in 1943: 200 mgr Cl per l), Brasemer Meer (in 1939: 125 mgr Cl per l), Westeinder lake (in 1938: 140 mgr Cl per l), Molmpoel near Aalsmeer (in 1943: 130 mgr Cl per l) (VAN ZINDEREN BAKKER, 1947). An investigation of the mollusc fauna is recommended to future workers.

Although for practical purposes we divide the lakes, ponds, canals, etc. into oligohaline, mesohaline and polyhaline waters, such a classification is not quite satisfactory as the salinity can vary according to the seasons, or on account of other factors: contamination with water of different salinity, with salter subsoil water, etc.

Oligohaline waters are chiefly found in certain districts of the provinces of Groningen, Friesland, Overijssel, Zuid-Holland and parts of Zeeland, mesohaline waters in parts of Groningen, Friesland, Noord-Holland and Zeeland (see map).

Among the oligohaline water the Kagerplassen (Zuid-Holland) were investigated by OTTO (1927). It is a complex of several small lakes and bays, connected by short canals and ditches. The total surface is nearly 350 ha, the maximum depth 4 m, but in most places not more than 2.5 m. The salinity is variable and reaches from practically fresh to just a little over 300 mgr Cl per l. The bottom samples contained black, putrifying mud, with a strong H_2S smell. In the open water vegetation is scanty; only in the littoral region a thick reed belt, mixed with *Juncus*, reed-mace, *Acorus*, *Scirpus*, *Sparganium* and various other plants lend protection to the Gastropods. The Bivalves are represented here too, but also in the more open water. The following molluscs were found: *Ancylus fluviatilis*, *Acroloxus lacustris*, *Lymnaea auricularia*, *L. ovata*, *Planorbis vortex*, *P. contortus*, *P. albus*, *P. crista*, *Lithoglyphus naticoides*, *Bithynia tentaculata*, *B. leachi*, *Viviparus viviparus*, *Valvata piscinalis*, *Theodoxus fluviatilis*, *Dreissena polymorpha*, *Anodonta piscinalis*, *Unio tumidus*, *U. pictorum*, *Sphaerium corneum*, *Pisidium nitidum*, *P. subtruncatum*. They are all typically freshwater species. It is interesting to record that OTTO found only empty shells of *Hydrobia jenkinsi*. At the time of his investigations the species seemed to be extinct in the Kagerplassen.

A somewhat similar environment is the Abcouder Meer. With its 18 ha surface extent it is much smaller than the preceding locality; its depth is on the average 1.5 m, in the deepest places 2.5 m. The Cl content varies from 66 mgr Cl to 1070 mgr Cl per l. This rather high salinity of the Abcouder Meer is due to contamination with the water of a high grade brackish canal in the neighbourhood and to the mesohaline water seeping from a polder, De Ronde Venen, just south of the lake.

During most of the year the Abcouder Meer is oligohaline. Vegetation is scarce, the bottom consists of soft peaty mud. The shores are steep throughout most of the circumference; only in one place is there a foreland of reed and grass, mixed with *Iris* and *Acorus*. Floating waterplants, such as *Potamogeton*, *Nuphar* and *Nymphaea* do not reach far into the open water, but keep close to the littoral belt. Mollusca are rather abundant: *Viviparus viviparus*, *V. contectus*, *Bithynia tentaculata*, *B. leachi*, *Valvata piscinalis*, *V. cristata*, *Lymnaea stagnalis*, *L. ovata*, *L. palustris*, *Myxas glutinosa*, *Planorbis corneus*, *P. vortex*, *P. contortus*, *P. carinatus*, *P. albus*, *P. complanatus*, *Physa fontinalis*, *Anodonta cygnea cygnea*, *A. cygnea zellensis*, *Unio pictorum*, *Sphaerium corneum*, *S. lacustre*, *S. rivicola*, *Pisidium henslowanum*, *P. nitidum*, *P. subtruncatum*, *P. cinereum*, *Dreissena polymorpha*.

These species are all characteristic of fresh or oligohaline water. In spite of the fact that occasionally contamination with mesohaline water takes place, no typical mesohaline molluscs have been found in the lake. This may be explained by the circumstance that the mesohaline water is partly upwelling ground water, devoid of organisms (HEYMANN, REDEKE & WIBAUT-ISEBREE MOENS, 1931).

Somewhat to the south-west of the Abcouder Meer another oligohaline lake is worth mentioning, the Botshol. It is comparatively large, about 105 ha of open water, but very shallow, the depth not exceeding 2.5 m.

With a Cl content between 1050 and 1230 mgr Cl per l in 1943 (VAN ZINDEREN BAKKER, 1947, p. 21) or 570 to 1325 mgr Cl per l in 1949 (WESTHOFF, c.s. 1949, p. 29) it belongs to the oligohaline to low mesohaline type. The relatively high salinity is due to the entering of mesohaline water from canals in the vicinity. The pH is 7 to 7.4, in corners with luxuriant *Sphagnum* growth somewhat lower. The vegetation is abundant, a survey of the flora was given by WESTHOFF c.s. (1949). From a malacological standpoint it is also an interesting habitat, with *Bithynia tentaculata*, *Lymnaea ovata*, *L. truncatula*, *Planorbis albus*, *P. crista*, *P. complanatus*, *Physa fontinalis*, *Dreissena polymorpha*, *Anodonta piscinalis*, *Pisidium obtusale*.

All the species are of limnogenic origin; the mesohaline water does not bring any mesohaline species into the lake.

A survey of the Brielse Maas by LEENTVAAR (1955) led to the following results. A few months after the damming off of the estuary in July 1950 the Cl content sank abruptly from nearly 5000 mgr per l to less than 1000 mgr per l; it normally lies between 200 and 400 mgr. The tidal influence was suspended and strong currents were impeded. Settling of freshwater plants was not directly successful because the water is rather deep (locally at least 10 m), so that only a shallow coastal region of 100 m width is available for plant growth. Molluscs were found in a few littoral stations along the north and south embankments near the dam: *Lymnaea ovata*, *Planorbis planorbis*, *Hydrobia jenkinsi*, *Dreissena polymorpha*.

The most elaborate study of an oligohaline environment in the Netherlands deals with the IJsselmeer (DE BEAUFORT c.s., 1954). After the enclosing dam, the Afsluitdijk, had been completed in 1932 the tide influence stopped and brackish water from the Wadden Sea could no longer enter. Only when ships pass through the locks at the eastern and western extremities of the Afsluitdijk small quantities of polyhaline Wadden Sea water can penetrate. This water keeps to the immediate neighbourhood of the Afsluitdijk; further south it is soon diluted to mesohaline and oligohaline.

There is a slow current from SE to NW through the lake, due to inflow of river water in the SE corner of the IJsselmeer. The bottom is composed of the same fine ooze and the water is equally thick and muddy as during the years of the open Zuiderzee. This bottom composition is not propitious for the development of vegetation. Only in the littoral zone plant life is possible. The open water is still devoid of vegetation.

The salinity sank gradually from, on an average, 6000 mgr Cl per l in 1932 to 1000 mgr in the beginning of 1935 and is now, in 1958, about 160 mgr per l.

Soon after the building of the enclosing dam the fate of the molluscs of the open Zuiderzee was sealed. Even before the ultimate closing of the dam various marine species were already extinct. Adaptation of marine and polyhaline molluscs to an environment of less salinity has not taken place. Perhaps the fall of the salinity has been too abrupt to allow such an adaptation. In the summer of 1934 a few two year old *Mytilus edulis*, *Cardium edule*, *Macoma balthica* and *Mya arenaria* were still alive, but they were in bad condition and did not survive till the end of that year. Hence within two years after the closure of the Afsluitdijk all the molluscs of the marine period had perished.

In the beginning immigration of freshwater molluscs was slow. Not until four years after the closing of the Afsluitdijk could some progress be noticed. From two to four years after this event there was a period in which molluscs were entirely absent from the IJsselmeer.

Migration into the new territory took place chiefly from the two affluents in the SE part of the IJsselmeer, the Rivers IJssel and Zwarte Water. No elements were recruited from the islands Wieringen, Marken, Urk or Schokland.

The dispersal fanned out from the SE corner where the Rivers IJssel and Zwarte Water discharge great quantities of fresh water into the IJsselmeer. Year after year one could observe how new and wider circles became populated, first with a tendency to the northwest, following the direction of the current of the rivers, later on also in a south-western direction. Species with pelagic larvae, such as *Dreissena polymorpha*, or with larvae parasitic on fishes, such as the Naiads, were privileged above other Bivalves and Gastropods in their velocity of dispersal.

Nowadays the southern basin of the IJsselmeer is inhabited by practically all our freshwater molluscs. In the open water of the central part which is still soft and muddy, only Lamellibranchs and *Hydrobia jenkinsi* can subsist. In the littoral zone where vegetation is abundant, the Gastropods are dominant.

The values for the salinities at which molluscs in the previous Zuiderzee and in the actual IJsselmeer were observed show an interesting contrast between the species from thalassogenous and those from limnogenous origin (VAN BENTHEM JUTTING, 1954, p. 239 and p. 250). The first category can tolerate a wide variation between sea water and 800 mgr Cl per l, whereas the second group has a much narrower range, varying between fresh water and circa 300 mgr Cl per l (only in two cases somewhat more, viz. *Lymnaea ovata* and *Dreissena polymorpha*).

In connection with the general investigations of the changes in biotic communities following the closing of the Zuiderzee and reclamation of parts of the IJsselmeer for agricultural purposes, two special surveys were made in the coastal region, in order to ascertain whence the new freshwater flora and fauna took their origin.

For that purpose DRESSCHER (1944, 1954) studied the flora and fauna of the extensive reed, sedge and bulrush fields (Scirpetum maritimi) at both sides of the mouth of the River IJssel. Molluscs were present in amazing numbers: *Theodoxus fluviatilis*, *Bithynia tentaculata*, *B. leachi*, *Valvata piscinalis*, *V. cristata*, *Hydrobia jenkinsi*, *Viviparus viviparus*, *V. contectus*, *Lithoglyphus naticoides*, *Acroloxus lacustris*, *Lymnaea auricularia*, *L. ovata*, *L. palustris*, *L. stagnalis*, *L. truncatula*, *Myxas glutinosa*, *Physa fontinalis*, *Planorbis albus*, *P. carinatus*, *P. complanatus*, *P. contortus*, *P. corneus*, *P. crista*, *P. planorbis*, *P. vortex*, *Segmentina nitida*, *Dreissena polymorpha*, *Anodonta piscinalis*, *Unio pictorum*, *Sphaerium corneum*, *S. lacustre*, *S. rivicola*, *S. solidum*, *Pisidium amnicum*, *P. cinereum*, *P. henslowanum*, *P. milium*, *P. moitessierianum*, *P. nitidum*, *P. subtruncatum*, *P. supinum*.

This is certainly the store-house from where the new immigrants invaded the IJsselmeer once the salinity had become low enough to allow their settlement.

Another survey was made by DE VOS (1941, 1954) of the lakes and pools lying inland along the IJsselmeer just behind the dikes. Several of them are remnants of ancient breaks in the dikes, now repaired. For many years after the transformation of the Zuiderzee into IJsselmeer several of these pools, especially those along the Noord-Holland coast, still contained water with a much higher salinity than the IJsselmeer proper. In this way they formed refuges for the mesohaline organisms at the time when the IJsselmeer itself was already approaching a low oligohaline stage. Yet in the end the Cl concentration was also reduced in these border habitats, the mesohaline animals disappeared and were replaced by freshwater species.

Although the foregoing account does not tell much about the synecology of the species: their quantitative abundance, the relations to biotic and abiotic factors, nor about their autecology: life span, feeding and breeding habits, respiration, excretion, etc., yet our knowledge of the distribution, dispersal, salt tolerance and association has increased considerably.

A complicated system of brackish lakes, pools, canals and ditches is found in the province of Noord-Holland, north of the Noordzee canal, the dune region excepted. Before the closure of the Zuiderzee the waters of this area, which for the greater part lies below sea level, had a relatively high salinity (mesohaline), but since 1932 the Cl content has sunk considerably although the Noordzee canal is still an important supply of high grade brackish water. This does not alter the fact that a number of individual basins, with little contact with neighbouring waters, still possess a salinity of over 1000 mgr Cl per l, locally even to 1600 mgr, depending on contamination with high grade brackish canal water or upwelling subsoil water. The result is an intricate pattern of high and low chloride content, as each polder has its own water regime (VAN NIEUWENHOVEN, 1942; VEEN, 1942; VAN ZINDEREN BAKKER, 1947; REYNE, 1948; VORSTMAN, 1951). These investigations were mostly carried out for other purposes; information on molluscs is scarce or absent. REYNE (1948) tried to measure the yearly deposit of organic sediment in various pools, varying in Cl content from 1000 to 3000 mgr Cl per l. VORSTMAN

(1951) studied the life cycle of *Neomysis vulgaris* in the Barnegat where the concentration varied from 1100 to 1700 mgr Cl per l. VEEN (1942) while investigating the question whether part of the Wijde Wormer (Cl content 130-330 mgr per l) could be recommended for angling, also paid some attention to the snail fauna: *Lymnaea stagnalis*, *L. palustris*, *L. ovata*, *L. auricularia*, *Planorbis planorbis*, *Physa fontinalis*. It is interesting to record that species of the genera *Bithynia*, *Valvata*, *Sphaerium*, *Pisidium* and *Dreissena* were entirely absent.

A more elaborate account of the correlation of water qualities and organisms in polders in Noord-Holland was published by VAN NIEUWENHOVEN (1942). In this report he dealt with some 200 collecting stations, giving a table in which Cl content, vegetation and 18 species of Gastropods of each station were compared. The species found at the highest concentration were *Lymnaea palustris*, *L. ovata*, *Physa fontinalis* and *Planorbis planorbis* (4650 mgr Cl per l). After these followed in decreasing salinity tolerance *Lymnaea stagnalis* (3650 mgr), *Bithynia tentaculata* (2950 mgr), *Hydrobia jenkinsi* (2725 mgr), etc. In the mesohaline and high grade oligohaline collecting sites a number of 4 to 5 species per locality was usual. Lower down, to about 300 mgr Cl per l, 7 to 9 species was the average number on any one station.

Recent investigations for the year 1957 by the Provincial "Waterstaat" of Noord-Holland have demonstrated that since 1941 the values for salinity in the various observations posts as published by VAN NIEUWENHOVEN (1942) have considerably diminished, chiefly as the result of the percolation of this part of the province with the nowadays less saline water of the IJsselmeer.

In most of the over one thousand collecting stations, especially those in the middle and northern parts of the district, the concentration in 1957 was about one half of what it used be some 16 years earlier, e.g. [1])

	1941	1957
Schermer Polder (3 stations)	1180	720
	1725	500
	750	320
Near Berkhout	176	102
Near Abbekerk	670	380
Bergermeer Polder	1010	383

[1]) These figures are derived from a report kindly put at my disposal by the Provincial „Waterstaat" of Noord-Holland, entitled „Noordholland-Onderzoek, 1957. Onderzoek naar het zoutgehalte der boezem- en polderwateren".

Only in the regions just north and south of the Noordzee canal mesohaline conditions still exist, because by inland navigation the highly saline water of that canal is every now and again brought into the waterways and polders of Noord-Holland which correspond with it.

Observations in the Noordzee canal have proved that this very deep waterway from Amsterdam to the North Sea (average depth 12-14 m) is mesohaline throughout its course. Regular sampling stations from IJmuiden in the west to Schellingwoude in the east gave the following figures for January 1959: surface IJmuiden 3200 to 4600 mgr per l, Schellingwoude 1750 to 1780 mgr. At 10 m depth IJmuiden 10.500 to 12.250 mgr, Amsterdam 4600 to 5600 mgr. In other seasons these values can be somewhat different, but the general pattern of salt distribution does not alter very much. [1])

This high Cl concentration is caused by the entering of North Sea water when ships pass through the locks at IJmuiden. The saline water can be traced as far as the Inner IJ near Amsterdam. It is even found farther eastward, beyond the Oranje locks in a funnel-shaped part of the IJsselmeer, the Outer IJ, where values between 200 and 1000 mgr Cl per l, roughly 2 to 7 times as high as the IJsselmeer proper, are found. It penetrates into the Outer IJ from the Noordzee canal when ships pass through the Oranje locks at Schellingwoude.

As we saw above there is a remarkable difference between the salinity of the surface water and that of the bottom water in the Noordzee canal. The transition zone lies between 6 and 7 m depth. Below this layer organic life is sparse, the vegetation because light, so indispensable for assimilation, cannot penetrate so deep, the animal population because in the depth the oxygen content is insufficient for respiration.

The uppermost layers of the Noordzee canal contain the usual mesohaline animal population. Of molluscs there were found: *Hydrobia ulvae*, *H. jenkinsi*, *Alderia modesta*, *Limapontia depressa*, *Embletonia pallida*, *Congeria cochleata*, *Mya arenaria*, *Macoma balthica*. The bottom, however, from about 7 m downward, is very little populated. Here the oxygen concentration is low, and the hydrogen sulphide content high, both factors adversely affecting animal life. Only in places where a current has removed the putrifying mud, animals are more plentiful, as e.g. in the channel flowing lengthwise through the locks at IJmuiden, where at 18 m depth a rich mussel bank (*Mytilus edulis*) with various other animals was found (STOCK & MULDER, 1953).

[1]) For the permission to publish these figures I am very much indebted to the Studiedienst van de Rijkswaterstaat Directie Noordholland, Arrondissement „Het Noordzeekanaal".

About 40 years ago the little lake "De Waal" near Rockanje was investigated for its history, geology, botany and zoology by BLAAUW (1917). The origin of the lake dates back to the Middle Ages when it was dammed off from a tidal current, containing meso- to polyhaline water. After its isolation the Cl concentration sank to values of 1700 mgr Cl per l in 1915, or 3500 mgr in 1916, i.e. low mesohaline conditions.

The depth of the lake is 1 to 1.5 m, the vegetation is poor in species, but rich in individuals of *Ceratophyllum demersum*, *Myriophyllum spicatum*, *Potamogeton pectinatus*, and *Enteromorpha*. Among the animals the most peculiar feature of the lake was the development of "coral-reefs" formed by *Membranipora crustulenta*. So plentiful even was this Polyzoon that the local people had piled up the calcareous colonies to a heap of about 1.5 m height and 3 m diameter in the middle of the lake.

Of the molluscs we have only very little information, a few empty shells of *Lymnaea stagnalis*, *L. auricularia*, *L. ovata*, and *Planorbis crista* being the only species recorded. We are not certain whether they had actually lived in the lake, or whether they were washed in from ditches in the neighbourhood. Odd valves of *Scrobicularia plana* sticking into the bottom mud are a reminescence from the period when the lake was still a tidal channel.

The lake is now a nature reserve and has been re-investigated by HOFKER (1940) shortly before the war. He arrived at new results, slightly different from those of BLAAUW, on the origin of the lake. On the vegetation and the faunal composition, however, no new data are available.

The last area where some ecological work on mesohaline waters was carried out lies in the province of Friesland where OTTO & WIELINGA (1933) surveyed the canals in the district between Franeker and Harlingen. Although variable, the Cl concentration at that date was rather high, 990 to 14.600 mgr per l, denoting mesohaline conditions. Molluscs were not numerous: *Hydrobia ulvae*, *H. stagnalis*, *H. jenkinsi*, *Mytilus edulis*, *Dreissena polymorpha*, *Congeria cochleata*, *Mya arenaria*. New investigations, however, are desirable to ascertain if the present day conditions are still in accordance with these facts.

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