Ecology of freshwater Mollusca in the Netherlands

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Although the Netherlands is a country rich in water, genuine fresh water is not as widespread as one might expect, because many water basins in the coastal region are more or less penetrated by sea water so that a mixture of salt and fresh, i.e. brackish water, is formed.

The areas where truly fresh water is found are (1) the dune district and (2) those regions on the accompanying map (fig. 1) which are marked in black, including the district of the big rivers above the limit of tide influence and the diluvial, sandy part of the country. The boundary between the two regions divides the country into two almost equal parts, a northwestern and a southeastern area. This boundary lies at about 5 m above sea level where sea water cannot penetrate. In these regions no brackish water is found. Some "tongues" of fresh water, especially as surface water of rivers, occasionally penetrate into the brackish water area, but these "tongues" are unstable and of a passing nature; they do not materially influence the general pattern.

The salinity of all the freshwater basins, although not being uniform, never exceeds 100 mgr per l (0.1‰ Cl) and is generally much lower. The other chemical constituents are very variable in the different freshwater districts. They will be discussed when dealing with each type of fresh water separately.

I. TYPOLOGY OF THE FRESHWATER BIOTOPES

The following is a classification of the various categories of freshwater basins in the Netherlands (after REDEKE, 1948):

A. Rivers, Brooks and Springs
   1. Eutrophic
   2. Oligotrophic
B. Lakes, Ponds, Pools and Marshes
   1. Eutrophic
   2. Oligotrophic
C. Canals and Ditches

A. *Rivers, Brooks and Springs*

The freshwater region in the Netherlands comprises the drainage systems of the two big rivers (1) Rhine (till about Vianen) with its branches IJssel and Waal, and (2) Meuse [1]) and of numerous smaller rivers and brooks. The headwaters of the Rhine and the Meuse and of some of the smaller rivers do not lie in Dutch territory, but either in Belgium, France, Germany or even in Switzerland. IJssel and Waal are side effluents of the River Rhine. All of them are natural waters (although many are no longer in a natural state) and are in constant motion, in a gradient from source to mouth. They can be termed running water. Their average temperature varies between 0° C in winter and 20° C in summer.

Most of the rivers and brooks are eutrophic, rich in electrolytes, chiefly calcium and nitrates. The oxygen concentration is high, and generally the silt and mud content also. The pH varies between 7 and 8. Where the current is not too strong, vegetation is mostly abundant. Most of the Dutch rivers are lowland rivers (only a few brooks in South Limburg have a mountainous character, SMISSAERT, 1959) and the beds of all have been intensively modelled by man in order to obtain stable sides, preventing erosion and scouring as much as possible. Consequently there is little variation in general character, although local variations do occur. In the riverbed, fully exposed to the current, only few molluscs can live: *Unio crassus batavus*, *U. pictorum*, and *Sphaerium solidum* being the only species which, by partly burrowing in the soil, can stand such extreme velocities.

The quiet parts of meanders, the eddies where the current slows down along groynes, the cut-off sections or "ox-bows" which are still more or less in open communication with the stream, present more favourable habitats for plant and animal life. The rooted vegetation in these protected corners consists of reed (*Phragmites communis*), reed-mace (*Typha*), *Sparganium*, *Glyceria*, *Sagittaria*, *Potamogeton*, *Callitriche*, *Fontinalis* and several more. The more the plants spread, the more the current is impeded, and the habitat can finally assume a pondlike character. Stones and submerged stalks are overgrown by green algae, *Cladophora*, Diatoms and the like. The bottom consists of silt or mud (LEENTVAAR, 1957a).

Molluscs living in such communities are: *Bithynia tentaculata*, *Valvata cristata*, *V. macrostoma*, *Viviparus viviparus*, *Lymnaea ovata*, *L. stagnalis*, *Planorbis carinatus*, *P. vortex*, *P. vorticulus*. The stones

[1]) The River Scheldt, as far as its course is on Dutch territory, is no longer a freshwater river, but a brackish estuary.

are an appropriate substrate for *Ancylus fluviatilis* and *Theodoxus fluviatilis*. On and in the mud *Lithoglyphus naticoides*, *Unio tumidus*, *U. crassus batavus*, *Anodonta piscinalis*, *Pseudanodonta complanata*, *Sphaerium rivicola*, *S. solidum*, *Pisidium amnicum*, *P. henslowanum*, *P. supinum*, *P. moitessierianum*, and *P. tenuilineatum* occur.

The population of obsolete rivers and backwaters along the riverbed which have almost acquired the character of ponds or canals will be discussed in the paragraphs on Lakes and Ponds, and Canals. In some of them fluviatile elements can still be traced as e.g. *Lithoglyphus naticoides* in the rivers Vecht and Eem. This same species together with *Sphaerium solidum* and *S. rivicola* inhabits a few Frisian lakes which communicate with the rivers Tjonger and Boorne (VAN BENTHEM JUTTING, 1947).

A classification of the Dutch rivers based on their population of molluscs, as is customary in regard to fishes, is not possible. The rivers Rhine, IJssel and Waal belong to the bream zone. Only the River Meuse in its upper part, till about the weir at Grave, belongs to the *Barbus* zone. Below this weir the bream zone of the Meuse begins. For the mollusca this borderline has no significance.

Among the small rivers and brooks on the diluvial sands some are very poor in calcium and other nutrient salts. They are unproductive or oligotrophic. This poverty is partly caused by the geological nature of their catchment area, containing only small amounts of such substances in the soil, and partly by the supply of acid water from moors and peaty soils which they receive. Their pH varies between 5 and 7. In their upper course they may be oligotrophic, in their lower course eutrophic, e.g. some of the small rivers and brooks in Noord-Brabant which carry water from the fens and from the peat bogs in the Peel district, and similar effluents of peat bogs in Drente. In the densely populated country of the Netherlands the oligotrophic rivers become more and more eutrophied through all the sewage from human civilization, through fertilizers used in agriculture and through the waste products of industry.

The rate of flow can vary considerably according to the water supply by direct rainfall and by the amount of discharge from the drainage area.

Vegetation is usually not very abundant: *Ranunculus fluitans*, *Potamogeton fluitans*, *Ceratophyllum*, *Myriophyllum spicatum*, some *Elodea* etc. Among the small eutrophic rivers several ones contain ferruginous deposits, others are rich in humic substances.

For molluscs the oligotrophic rivers and brooks with their acid water are not at all attractive. Apart from some stray *Lymnaea ovata* and *Ancylus fluviatilis* few other molluscs occur. *Pisidium cinereum* and, occasionally, *P. milium*, *P. hibernicum*, *P. subtruncatum*, and *Sphaerium corneum* are found (KUIPER, 1942); their shells are mostly very thin through deficiency of calcium carbonate.

In those parts of the oligotrophic rivers which are transformed into eutrophic streams the vegetation and the molluscs assume the character of those in eutrophic rivers as described before.

Eutrophic small rivers, such as are found in Drente (Hunze), Overijssel (Dinkel, Regge), Gelderland (Berkel, Oude IJssel, various streamlets near Winterswijk), Noord-Brabant (Dommel, Aa, Mark, Vliet) and Limburg (Niers, Roer, Swalm) can contain together with a fairly rich vegetation a satisfactory population of molluscs. The greater the rivers are, the more species they contain and the large Bivalves *Unio* and *Anodonta* live only in the largest rivulets (Dinkel, Oude IJssel, Grote Beek). This coincidence may partly be attributed to their obligatory parasitic larval stage on the gills or fins of fishes, for which a fish population in the same biotope is a necessity. It is a remarkable fact that *Ancylus fluviatilis* and *Theodoxus fluviatilis* seem to avoid the brooks and small rivers in the province of Drente. A satisfactory explanation for this absence has not yet been given. It may have something to do with the brown colour of the water, or the slow flow, or the absence of stones for attachment in these streamlets, although other species of molluscs do not suffer by it.

Springs are not common in the Netherlands and most of them do not contain any molluscs at all. In the southern part of the province of Limburg in, presumably, subterranean wells the small Hydrobiid snail *Avenionia bourguignati* was discovered in 1942 by VENMANS (1943 a and b). The only other freshwater snail associated with it was *Valvata cristata* (VAN REGTEREN ALTENA, 1946).

B. *Lakes, Ponds, Pools and Marshes*

In the second place the freshwater region of the Netherlands comprises a number of lakes, ponds, pools, fens, marshes, swamps etc. Some of them are natural waters and some have been dug by man. Most of them are of small size and little depth, with gently shelving shores. Only the "wielen" or "washes" (remnants of ancient breaches in the dikes, now repaired) can attain a depth of maximal 15 m. The Dutch lakes can in no way be compared to the extensive, deep lakes in Scandinavia, Scotland, Germany, Switzerland etc. (VAN HEUSDEN, 1945; LEENTVAAR, 1956 and 1958).

To a certain extent the shallow Dutch lakes are easier to investigate than the large bodies of water in foreign countries. For the large lakes greater instruments and boats, more effort and personnel are

required. On the other hand there is much greater diversity in the hydrographical and biological conditions in the small, shallow lakes and ponds. Even small variations in temperature, light, water movement, chemical composition etc. can cause considerable effect, far more than in great lakes. It is, therefore, absolutely necessary to examine the shallow lakes more frequently, at least during a one year's course, but, preferably, during several years in succession. In this way the study of small lakes is very time consuming and requires much perseverance of the scientist before a reasonable result can be obtained.

To the general public the lakes are just stagnant waters, but where these lakes are fed by an affluent and voided by an effluent some slight water movement is present. An additional form of circulation in lakes is brought about by the wind which agitates the superficial water layers, even to wave force, with a surf zone along the embankment on the leeward side. In this way mixing of water layers is effectuated; lakes and ponds with absolutely standing water are very rare. Such a condition is mostly found in marshes and swamps only.

The surface temperature of the shallow lakes follows the temperature of the air more quickly than that in rivers, and in summer it can rise to 25° or 30° C. The lower sheets of water never attain this high figure; here values of 15°-20° C are usual in summer. If there is little mixing in the water a stratification: higher, warmer water of small density at the surface and lower, cooler water of greater density at the bottom, can be observed (summer stagnation). In the cold season the surface water sinks and brings the lower layers in upward movement and circulation.

As the depth of the lakes is generally small and the surface which is in contact with the atmosphere is extensive, oxygen content is usually high. Carbon dioxide assimilation by plants contributes to this condition.

Only in the "wielen" (washes) there is a distinct thermocline (Sprungschicht) in summer. It is a level, at variable depth, where the temperature abruptly decreases. The thermocline is the boundary between the superficial water layers (epilimnion) which follow the daily rhythm of heating at day time and cooling at night, and a zone below this boundary where the sun heat cannot penetrate and the water has an almost even temperature of 8°-10° C (hypolimnion).

Just as the running water the lakes and ponds can be divided into oligotrophic or eutrophic, according to the amount of calcium, hydrocarbonate and nitrate which they contain. Oligotrophic lakes are found in all the provinces of the freshwater area, in the northern

part of the country on the diluvial drift of the arctic ice cap, in the southern part on the diluvial deposits of fluviatile origin accumulated by the rivers Rhine and Meuse. Both types of deposits are poor in electrolytes and mineral salts. The boundary between the two areas is an ice-pushed hill range, stretching in NW-SE direction in the provinces of Noord-Holland, Utrecht and Gelderland.

Where, as in many places in Drente and Noord-Brabant, the deeper soil layers contain a sheet of loam, numerous water basins of various size and various depth could originate. In places with a more loose, sandy subsoil through which the water percolates more easily, such lakes and ponds are far less numerous (freshwater areas of the provinces of Gelderland, Utrecht and Noord-Holland). Their water level shows considerable variations, as it depends chiefly on the amount of precipitation.

Some of the lakes and ponds are depressions in, or at the periphery of, peat bogs, collecting the drainage water of these peaty soils and, consequently, carrying acid water (pH 4-6) often of a brown colour on account of the humic substances which they contain.

Most of the lakes and pools in the heath country, on the contrary, are clear, with just a little turbidity on windy days. The "vennen" in Noord-Brabant are probably formed by wind erosion and later on modelled by water erosion of the diluvial sandy soil (pH 4.5-6). The surface temperature in summer can amount to 26° C, in winter the shallower lakes freeze till the bottom.

The smaller types and the marshes and swamps may dry up completely in summer. In the oligotrophic lakes there is never a thermocline.

Vegetation in the oligotrophic lakes is generally not abundant. In the shallow parts where the bottom is sandy such plants as *Littorella uniflora*, *Juncus bulbosus fluitans*, *Sparganium angustifolium*, *Narthecium ossifragum*, *Scirpus caespitosus* grow along the banks (Littorellion of plant sociology), *Eleocharis palustris*, *Comarum palustre*, *Carex fusca* and other Carices, *Sphagnum obesum* and *S. cuspidatum*, *Eriophorum* div. sp. in the deeper parts (Caricion fuscae of plant sociology), and *Batrachium hololeucum*, *Lobelia dortmanna*, *Utricularia minor*, *Isoetes lacustris* and *I. echinospora*, *Nitella flexilis* in the more open water (Isoetetum of plant sociology).

The animal life of the oligotrophic lakes (REDEKE & DE VOS, 1932) consists of species which can only live in these unproductive environments ("steno-ionic" animals), or of species which can equally well inhabit oligotrophic and eutrophic waters ("eury-ionic" animals). The absence of eutrophic animals in a certain lake is a positive indication that the water is oligotrophic.

Molluscs are generally absent, there are no oligotrophic molluscs. Occasionally a dwarfed *Lymnaea ovata* or *Pisidium cinereum* are found. They are thin-shelled, depauperate specimens, presumably washed into the oligotrophic milieu from a eutrophic environment.

Typical oligotrophic lakes are e.g. the Gerritsflesch near Kootwijk (DRESSCHER, e.a., 1952), various lakes in Drente and some of the "vennen" in Noord-Brabant.

As in the case of the oligotrophic rivers these oligotrophic lakes, ponds and marshes are also getting more and more eutrophied.

The eutrophic lakes and ponds carry a considerable concentration of calcium and other nutrient salts. Their pH is high (7-8) and their vegetation in the littoral zone is abundant and varied: *Phragmites*, *Equisetum*, *Iris*, *Butomus umbellatus*, *Typha angustifolia*, *Sagittaria*, *Sium latifolium*, *Menyanthes trifoliata*, *Sparganium erectum*, *Acorus calamus*, *Schoenoplectus lacustris*, and many others (Scirpeto-Phragmitetum of plant sociology), and in the deeper water *Nymphaea alba*, *Nuphar luteum*, various species of *Potamogeton*, *P. compressus*, *P. crispus*, *P. densus*, *Myriophyllum verticillatum*, *Ceratophyllum demersum*, *Hydrocharis morsus-ranae*, *Stratiotes aloides*, *Chara*, *Elodea*, etc. These communities belong to the Potamion euro-sibiricum of plant sociologists. Locally there can be some variation in the composition of the flora, certain plants dominating in one area, others in a more distant place.

In the bigger lakes (depth 3-4 m) there is usually a distinct limitline between the shore vegetation and the central open water with its submerged flora. In the smaller lakes, however, the transition between the two areas is more gradual.

The eutrophic lakes are an almost ideal habitat for freshwater mollusca, especially in the littoral zone. This region is inhabited by almost all our freshwater molluscs with the exception of those species which are typical for running water. Among the Bivalves *Anodonta cygnea cygnea* and *A. c. zellensis*, *A. piscinalis*, *Unio pictorum*, *U. tumidus*, *Dreissena polymorpha*, *Sphaerium corneum*, *S. lacustre*, *Pisidium cinereum*, *P. obtusale*, *P. subtruncatum*, *P. nitidum*, *P. hibernicum*, *P. milium*, *P. pseudosphaerium* are the most common elements, among the Gastropods *Viviparus contectus*, *Bithynia tentaculata*, *B. leachi*, *Valvata piscinalis*, *V. cristata*, *Aplexa hypnorum*, *Physa fontinalis*, *Lymnaea stagnalis*, *L. ovata*, *L. auricularia*, *L. palustris*, *Myxas glutinosa*, *Planorbis corneus*, *P. planorbis*, *P. carinatus*, *P. vortex*, *P. leucostoma*, *P. contortus*, *P. complanatus*, *Segmentina nitida*, and *Acroloxus lacustris* are the most frequent ones.

Although mostly common in flowing water *Theodoxus fluviatilis* and *Ancylus fluviatilis* can also live in the littoral zone of some of

the large meres in Friesland, in the lakes round Giethoorn and round Nieuwkoop and in the Vecht region north of Utrecht. In these lakes they are bound to the leeward side where the wind force is greatest, causing the water to be thoroughly mixed and aerated.

In the zone of submerged vegetation *Pisidium subtruncatum*, *P. milium*, *P. nitidum*, *Sphaerium corneum*, several small Planorbids, two *Valvata*'s and both species of *Bithynia* are generally found (KUIPER, 1947).

Sphaerium lacustre is not at all rare in the Netherlands; it occurs both in the freshwater area and in regions where the salinity slightly exceeds 100 mgr per 1. Yet it does not inhabit any one place where one looks for it, but its distribution is somewhat "patchy". It lives often in great quantities in poor habitats: drying pools, marshes in the wood with loamy or sandy bottom, small pools for watering cattle, temporary pools in building sites, etc.

In concluding I quote here from ELLIS (1941, p. 239) "While it is in general true that molluscs do not exhibit any specific associations with any particular plant communities, nevertheless it is quite possible to speak of characteristic fenmolluscs, reed-swamp molluscs etc. Each plant formation, such as reed-swamp, swamp-carr etc., has its distinctive molluscan community, although many species overlap and are common to different habitats".

In the "wielen", where a distinct zonation of surface and bottom water exists and no thorough circulation takes place, the bottom water is generally poor in oxygen through the decomposition of organic matter descending from the top layers. Flora and fauna in this hypolimnion are poor or absent, the vegetation because no light can penetrate to these depths (lower than 5 m) and the fauna because the deficiency of oxygen prevents animal life in anaerobic circumstances. Even in the epilimnion of the "wielen" vegetation is not abundant. The shores slope down rather steeply (steeper than in lakes or ponds) and through the isolated situation of the "wielen" little or no dispersal of seeds can take place (LEENTVAAR, 1956, 1958).

In the littoral zone *Lymnaea stagnalis*, *L. auricularia*, and *L. ovata* live just under the water surface. In the lower shore layers (but always above the thermocline) *Unio* and *Anodonta* are burrowing into the sides of the bank.

In winter the littoral molluscs of the lakes and ponds migrate to the bottom of the water and hide themselves among the fallen vegetation in the mud. Their metabolism in this season is extremely low: feeding, breathing, excretion and other functions drop to very small values. During these months the bottom layer is the region with the highest water temperatures, circa 4° C.

C. *Canals and Ditches*

The third type of freshwater basins in the Netherlands are the canals and ditches, in which our country is particularly rich. All of them are artificially made water courses, the larger canals for inland navigation and storage of water, the smaller ones, including the ditches, for irrigation and draining. Here again the general public opinion is that canals and ditches are bodies of still water. Yet there is always some displacement and circulation of the water masses by ships passing through, or by pumping away the surplus of water during winter and after heavy rains. The canals have the advantage of an almost constant water-level, with a slow flow and without floods.

In their physical properties: temperature, chemical composition, eutrophy, they are very similar to the shallow eutrophic lakes of the previous paragraph. Where the banks are not too steep the vegetation in the canals, and even more so in the ditches, can be very rich, but it is often impeded by the needs of navigation which prefers a clean bottom and bare shores. The ditches between the meadows and the agricultural plots are periodically cleaned in order to warrant a satisfactory drainage of the land. Although this implies a rigorous destruction of many organisms the beneficial consequence is that the ditches do not get obstructed by too luxuriant a vegetation.

The molluscan fauna of the canals and ditches is so similar to that of the lakes and ponds that it is not necessary to repeat their names here.

In small ditches on the diluvium, often nearly dry in summer, with a bottom deposit of alder and poplar leaves *Lymnaea glabra* is locally abundant. Apart from *Aplexa hypnorum* there are rarely other species living in such extreme circumstances. It is an indicator species for fresh water on diluvial soil.

Another amphibious freshwater gastropod is *Lymnaea truncatula*, the liver-fluke snail. It generally does not live fully submerged, but prefers the sides of the shallow "greppels", i.e. drainage trenches on the meadows. These "greppels" as a rule do not contain water and are overgrown with grass. Yet their surface is more moist and marshy than the ordinary pasture land. Only after heavy rains in winter and spring, and sometimes in autumn the "greppels" can temporarily contain some water, and this is precisely the season when *Lymnaea truncatula* can be transported by the surface water from one trench to another. In the water containing ditches between the meadows *Lymnaea truncatula* is rare or absent.

In canals which receive water directly from river systems fluviatile molluscs have now and then been found, e.g. *Lithoglyphus naticoides* in the Zuid-Willemsvaart. The dispersal of *Dreissena polymorpha* has been greatly facilitated by the digging of canals and the increase of ship traffic. The pelagic larvae of this Bivalve attach themselves to the ship's hull and are thus carried far and wide all over the country.

Mention must be made of an introduced Bladder snail, *Physa acuta*, in the Netherlands. Since the first record of this South European species in our country in 1912 (VAN HEURN, 1912) time and again colonies have been reported from various districts, but the Acute bladder snail seems never to have acquired a firm foothold and the populations become extinct after some time (e.g. severe winters). It makes the impression that *Physa acuta* has not naturalized in our waters, but that each time a new invasion makes a start.

Whereas most oligotrophic animals cannot tolerate the slightest increase in chlorine content of the water, many species of the eutrophic environment in the freshwater area are not at all so susceptible and can equally thrive in water containing a small degree of salinity (oligohaline water).

For many years, but especially since the beginning of the 20th century, pollution of fresh water in the Netherlands has assumed ever increasing dimensions and has become disastrous in certain districts. This pollution is partly due to the sewage effluents from towns and villages and partly to the waste products of industries in our country (paper-mills in Gelderland and Limburg, straw-board mills and potato-flour factories in Drente and Groningen, sugar factories in Noord-Brabant, laundry-works in Gelderland) and in Germany and Belgium. The effects are of different quality. In not too serious cases of pollution the flora and fauna are destroyed only locally and temporarily, but in case of discharges on a larger scale the destruction is much more radical. Yet one is astonished to see how organisms can adapt themselves to unfavourable environments containing poisonous waste products of industries such as acids, ammonia, chlorine, salts of metals, tar, etc. At the points of discharge of such toxic substances the local fauna and flora are killed, but at some distance from the focus of pollution where the concentration is reduced and the organic matter is broken down by bacteria (biological purification of the water) vegetation and animal life restore themselves step by step.

II. RELATIONSHIPS BETWEEN FRESHWATER MOLLUSCA AND OTHER ORGANISMS

Most of the relevant environmental influences, the chemical, the physical and the edaphic factors, such as oxygen content, lime, pH, temperature, light, water movement, depth, bottom, have already been discussed in the chapter on the nature of the biotopes. A few remarks on the relations of the mollusca to the vegetation and to other animals, together forming the biotic factors, may follow here.

The relations with the vegetation are mainly concerned with (1) food, (2) oxygen, and (3) protection and substrate. There are no species of freshwater molluscs which have distinct relations to definite species of plants, as e.g. certain insects have. If we regularly find a particular mollusc population in a certain plant association, this does not mean that the molluscs are in a state of dependency on that special vegetation, but that both components, plants and molluscs, grow in a place which on other grounds is favourable for both categories.

The relations of freshwater molluscs with other animals can theoretically be (1) a state of indifference, (2) of mutual advantage, (3) of enemy-prey relation or (4) of parasitism. In our country instances of *mutualism* are unknown. So long as molluscs and other animals live simultaneously in the same piece of water without any harm for the participants, the case can be called *indifferent*. Only too soon the balance can pass to the *predator-prey* relation when e.g. snails and Bivalves are hunted by waterfowl, amphibians, larvae of water beetles, leeches, etc. The molluscs are never the hunters, but always the prey. On the whole they form an easy prey as they do not posess means to defend themselves actively. They can only keep out intruders by retiring into their shell (Pulmonates), retiring and shutting their operculum (Prosobranchs) or closing the shell-valves (Lamellibranchs).

Only the avoidance reaction of *Physa fontinalis* towards intruding leeches recently studied by FRIESWIJK (1957) can be called an active defence reaction.

Parasitism can be manifest in two different ways. The mollusc can either be (1) the passive victim of parasitism by another animal, or (2) the mollusc is the active parasitising agent.

In the first case the action of the intruder can be relatively harmless, acting only as a "room-mate" (e.g. epibiontic algae, worms, Hydroids, Polyzoa, insect larvae, Protozoa etc.) which settle on the exterior of the shells of molluscs, or the watermites, living on the gills of Bivalves, without causing harm. Another instance of harmless

commensalism is the protection which Naiads (*Unio* and *Anodonta*) provide for the larvae of the Bitterling (*Rhodeus amarus*). Towards the moment of spawning (middle of April to middle of June) the female Bitterling immerses her 2.5 cm long ovipositor into the exhalant siphon of the mussel and presses her eggs one after another into the Bivalve. After this the male fish pours its sperm into the inhalant siphon of the mussel, and within the latter's body fertilisation of the fish eggs takes place. The eggs are then ranged neatly between the gill filaments of the mussel, undergo their metamorphosis to larval fishes, and finally reach the stage at which they can leave the mussel and start their free life as young fishes. The Bitterling larvae do not live at the expense of the Naiads, but are fed by their own vitelline mass. The whole process takes about four weeks, and it would be interesting to know how great in our country the ratio of infested mussels can be, and whether there is any preference of the Bitterlings for the large and roomy *Anodonta* over the smaller and narrower *Unio*.

More serious, even sometimes fatal to the molluscs, are a number of other animals. The more one studies freshwater molluscs, the more it appears that their life is constantly menaced by numerous parasites, especially worms. These intruders pass part of their life cycle in the molluscs, attacking and digesting the tissues of their host. If this inconvenience does not last too long, the molluscs can recover after the parasite has left. But if the destruction is of longer duration the mollusc is entirely ruined. Most of the cases in which freshwater molluscs are intermediate hosts in the developmental cycle of a trematode worm pass unnoticed to human observation. Only a few instances have affected the human sphere of interest, viz. schistosomiasis in tropical countries, dermatitis and distomatosis in our latitude (SALOMÉ, 1954; WIBAUT, 1944). Dermatitis is a rather harmless affection with papulae of the human skin, caused by the cercariae of a trematode worm. The second vector in this life cycle is a freshwater snail, *Lymnaea* or *Planorbis*. Infection takes place chiefly in summer when the cercariae swarm out in the season during which people are bathing.

Distomatosis (or fasciolariosis) is a disease of sheep and cattle caused by the cercariae of the trematode worm *Fasciola hepatica* which also has an alternation of generations. In the sheep (and cattle) lives the sexual generation, in the snail, *Lymnaea truncatula*, the asexual generation of the worm. The mature flukes live in the sheep's liver, producing great quantities of eggs which are deposited with the host animal's faeces on the grass of the meadows. In the moist environment ciliated larvae, called miracidia, hatching from

the eggs, swarm round for a short time, and penetrate into the pulmonary cavity and the mid-gut gland of the *Lymnaea*. Here they hibernate, developing first into rediae and then into cercariae. In the following summer the cercariae are liberated by the snail, swarm round for a short time and settle down on a blade of grass or other plant where they encyst and pass a short resting period. When browsing in the meadows the sheep are infested with cysts which pass through the stomach to the intestine. Through the gall duct they reach the liver of the host animal and develop into a broad, flat worm of about 30 mm length. These flukes live on the liver tissues of the sheep, and in severe cases ruin the entire liver, causing the host to sink fast and, finally, to die. Economically the damage by the liver fluke amounts in the Netherlands to several millions of guilders per annum. It is a remarkable fact that in our country and in most other European countries the liver fluke of sheep is so specifically tied to *Lymnaea truncatula*, whereas in other continents where this snail does not occur, other species of *Lymnaea* are equally acceptable as intermediate hosts.

The second pattern of parasitism in which the mollusc is the dominating organism includes the Naiads which have an obligatory parasitic phase on fishes. The larvae of these Bivalves are small, doublevalved creatures which, after having been liberated from the mother, live through a planctonic stage. During this time they await an opportunity to hook in on the gills or the fins of a passing fish. Once settled they stimulate the tissues of the victim to react to the presence of the intruders by forming a sheet of cells over the mussel larva. In this way the larva is encysted and protected during the time of its metamorphosis. In this period it is fed by the blood cells of the fish. After a few weeks when the larva has completed its metamorphosis the cyst bursts open, and the young Naiad falls to the bottom of the water where it now can start its free existence. As the fishes are active swimmers the Naiad larvae are carried over great distance and the "spat" on the whole falls in places far away from where they were born. When the fishes are strongly infested with Naiad larvae their vitality may be seriously impeded. In our country I never heard of any complaints of the fishermen in this respect.

A somewhat mysterious case of toxic influence of molluscs on Entomostraca (and a few other freshwater organisms) has recently been described in Austria by KÜHNELT & DÖLLING (1952). They observed that certain species of crustaceans never occurred in the same pools or in the same sections of large lakes as certain freshwater snails. Transferred to the laboratory the same phenomenon

was manifest: when brought together in one aquarium the crustaceans died, but the snails survived. *Planorbis corneus*, *Viviparus viviparus*, *Lymnaea ovata* and, to a lesser extent, other species of *Lymnaea* were responsible for the remarkable conduct of the crustaceans. How this intoxication worked has not yet been fully ascertained; presumably it was through metabolic products. It reminds one of a similar toxic effect of *Lymnaea peregra* on certain freshwater fishes in Germany, as described by WUNDSCH many years earlier. The authors made some preliminary experiments, without, however, definite results. The problem is recommended to future students and might serve as a clue to the understanding of the intolerance of certain organisms in the same biotope.

III. SPECIAL INVESTIGATIONS IN THE NETHERLANDS

Monographs on freshwater rivers, canals or lakes in the Netherlands are extremely scarce. Of the running water continuous observations during a year's cycle were never made. The Meuse investigations of 1918 (ROMIJN c.s., 1918) were not more than a preliminary reconnaissance. Among the stagnant waters there are a few more or less complete surveys of oligotrophic waters (REDEKE & DE VOS, 1932; MIDDELHOEK, no date; DRESSCHER, e.a., 1952). From a malacological point of view they are almost sterile.

A more favourable environment for molluscs are the eutrophic lakes, but even of these habitats descriptions are few or fragmentary. About the first monographic treatment was the doctor thesis of HAVINGA (1919) dealing with the flora and fauna of the Zuidlaarder Meer. This is a rather extensive lake (725 ha) of an average depth of about 1 m, in a few spots 1.50 to 1.75 m. The bottom consists of sand, partly covered with a layer of peat. The water is entirely fresh. It is supplied by the small River Hunze which enters the lake in the SE corner and leaves the Zuidlaarder Meer as Drentse Diep in the NW tip. Hence there is a regular slow current traversing the lake. The water of the lake and of the Hunze, as well as the drainage water of the surrounding land is eutrophic. The gently sloping shores carry a broad girdle of vegetation, locally even to 100 m wide. It is the ordinary Scirpeto-Phragmitetum and the Potamion eurosibiricum community. In the open water the submerged vegetation consists of *Potamogeton densus, P. perfoliatus*, and *Chara*.

HAVINGA gave a list of 14 species of molluscs observed during his studies. This rather low number can certainly be augmented by more intensive collecting. The Gastropods chiefly inhabit the littoral zone, the Bivalves the open water.

Another Dutch freshwater lake, famous as a sanctuary for birds, is the Naardermeer. It is a lake of somewhat over 700 ha extension, with an average depth of 1 to 1.30 m. The bottom consists of sand, locally covered by layers of peat. The water was oligohaline (till 480 mgr Cl per l) in the years before the closing and reclaiming of the Zuiderzee. Since, however, this brackish inland sea was dammed off from the North Sea so that it is gradually freshening up, while at the same time the water level was lowered, no brackish ground water can penetrate and well up in the Naardermeer any longer; the oligohaline condition has made room for the fresh state, the salinity not exceeding 100 mgr per 1.

In the southern section of the lake where water from the hilly Gooi district seeps continuously towards the Naardermeer, the Cl content is always lower than in the northern section.

On the whole the Naardermeer is eutrophic, its pH lies, according to VAN ZINDEREN BAKKER (1942), between 7 and 8.6. Only in a few sheltered peat holes with abundant *Sphagnum* growth the pH is lower, about 4.3 to 5.5.

From the banks to the deeper parts the lake has gently shelving shores. There is a broad marginal zone of vegetation, stretching from the Scirpeto-Phragmitetum on the landward side, through the zone of *Nymphaea alba*, *Nuphar luteum*, *Potamogeton* species, *Stratiotes aloides*, etc., to the open water where among the submerged vegetation *Potamogeton* species, *Vaucheria dichotoma*, *Nitellopsis obtusa* and *Chara* species cover wide areas.

A short time after its official assignment as a nature reserve in 1906 VAN DER SLEEN (1917) published a list of the mollusca of the Naardermeer. During the years 1923 and 1924 the lake was regularly visited for biological investigations by students of the Amsterdam University. The extensive malacological collections were studied by VAN REGTEREN ALTENA (1936), VAN BENTHEM JUTTING & KUIPER (1942) and KUIPER (1947).

The mollusc population is typical for stagnant (or almost stagnant) water, animals of running water are absent. Hence we find *Unio pictorum* and *U. tumidus*, but not *U. crassus batavus*. Of *Sphaerium* the species *corneum* and *lacustre* are present, but *S. rivicola* and *S. solidum* are absent. The Pisidia are represented by 11 species, but the fluviatile *P. moitessierianum* and *P. tenuilineatum* and the "ponderosum" modifications of others are absent.

Similar features denoting the lake character of the Naardermeer are relevant among the 23 species of freshwater Gastropods, while the inhabitants of running water, such as *Viviparus viviparus*, *Valvata macrostoma*, *Lithoglyphus naticoides*, and *Ancylus fluviatilis* are absent.

KUIPER (1947) who carried out ecological investigations in the Naardermeer, especially the subdivision Spookgat, during the last world war came to the conclusion that the mollusc fauna of the lake is relatively poor in species, as some species which are common in neighbouring lakes, are either totally absent or only represented in small quantities in the Naardermeer. On the other hand a few species which are rare in the rest of our country, are quite abundant in the Naardermeer (e.g. *Planorbis riparius*) [1].

Another striking feature is the small degree of variability in the shells of the freshwater molluscs in the Naardermeer; their outward appearance is rather uniform. Whether this is a consequence of their genetic constituents or of the ecological conditions in the lake remains an open question.

North of the town of Utrecht and south of the Naardermeer a series of lowland lakes, together called the Vechtplassen, stretches in almost N-S direction parallel to the River Vecht, although at some distance eastward of it. Some of these lakes are natural waters, but many were excavated by man in previous centuries to procure peat for fuel. Most of the lakes are shallow, with an average depth of 1.5 m, but in recent years in some of them sand is sucked up for building purposes and for construction of roads, even to depths of 25 m.

Although most of the lakes are in more or less open communication with each other there are local differences in the chemical composition of the water and in the vegetation. On the whole the lakes contain fresh water, only in the Botshol the Cl content is somewhat higher, up to 1000 mgr per 1. (WESTHOFF c.s., 1949). In the flora and fauna these differences are hardly perceptible. The pH of the Vechtplassen is 6-8.

The lake complex near the village of Kortenhoef was studied by a team of biologists who published a detailed monograph in 1955 (MEYER & DE WIT, a.o., 1955). Among the vegetation the usual zonation from land to open water can be distinguished, and particular attention was paid to the various plant successions.

Unfortunately there are no details on the mollusc fauna of this area. The just mentioned Kortenhoef book mentions only *Lymnaea*, *Planorbis*, and *Bithynia tentaculata*. One can be sure that the list of species which actually live in the Kortenhoef area is many

[1] Since 1947 *Planorbis riparius* has been reported from several more localities in the Netherlands, e.g. the lakes near Giethoorn, various lakes and ditches in the Vecht district near Maartensdijk, Houten, Maarssen, Loenen, Vreeland, Kortenhoef, Loosdrecht, Vinkeveen, Bovenkerk, Bussum, and the lakes round Nieuwkoop. Hence the species is not so rare as was originally supposed.

times longer. It is unlikely that certain fluviatile elements which still occur in the River Vecht have penetrated into the lakes east of this river, because there has hardly ever been an open communication between the Vecht and the lakes. Among the rooted vegetation and among the plankton organisms no traces of such infiltration have been found.

In addition to the lakes just mentioned, the Naardermeer and the Kortenhoef lake complex, there are a great number of lakes more in the Vechtplassen district. Some of these were discussed by VAN ZINDEREN BAKKER (1947). His book deals in the first place with the botanical aspects and the ecology of the plant associations. Some details are given on the origin and the history of the lakes and on the chemical qualities of the water, but there is no account on the mollusc population.

In a short paper on the gastropods of the valley of the River IJssel and, later on, in his doctor thesis on biosociology MÖRZER BRUYNS (1943, 1947) compared the biosociology of plants and molluscs in various habitats (freshwater and land) in the valley of the IJssel near Gorssel, and in a few valleys of small brooks flowing into the IJssel. He gave some very instructive transects (tables 1, 2, 9 and 10 of the 1947 publication) starting from the riverbed, crossing the foreland, up to the higher grasslands and finally to the hedgerows and woods at some distance from the river. These transects clearly demonstrate the differentiation in the various biotopes. Freshwater molluscs were only found in pools near the River IJssel. The deeper pools contain water permanently, even in the dry season when the level is low. The shallower pools dessicate completely in summer.

The pools where water is always available have a soft clayey bottom. The vegetation consists of representatives of the Potamion euro-sibiricum, with plenty of *Nuphar luteum* and *Nymphoides peltata*. *Valvata piscinalis* is extremely common. To a lesser degree *Acroloxus lacustris*, *Planorbis vortex*, and *Bithynia tentaculata* are present, whereas *Bithynia leachi*, *Physa fontinalis*, *Lymnaea auricularia*, *Anodonta cygnea*, *Viviparus contectus*, *Planorbis albus*, *Lymnaea stagnalis*, *Sphaerium* cf *solidum*, *Valvata cristata*, *Planorbis carinatus*, and *Unio pictorum* constitute a diminishing scale of frequency.

In the higher zones along the river freshwater molluscs are often concentrated alive as drift during floods, but they do not settle there permanently. This area is only inhabited by land snails.

Of the lakes and pools in the NW corner of Overijssel a preliminary botanical survey was published by VAN DIJK & WESTHOFF (1955). Here again no information on the malacofauna of this interesting region was given.

A section of this district, the Kierse Wijde, was visited by a party of Amsterdam students of biology. Not only the vegetation was considered, but a few short faunistical lists were also included (MEYER, 1950). The number of molluscs amounted to twelve: *Planorbis albus*, *P. carinatus*, *P. complanatus*, *P. vorticulus*, *Bithynia tentaculata*, *Lymnaea ovata*, *L. palustris*, *L. stagnalis*, *Physa fontinalis*, *Acroloxus lacustris*, *Pisidium nitidum*, and *P. subtruncatum*.

In the dune district some research was carried out in the Zwanenwater (REDEKE, 1903), in a few small ponds in the vicinity of Den Helder (DEN HARTOG, 1950), in the lake called De Muy in the island of Texel (VAN BENTHEM JUTTING, 1956) and in the Dodemanskiste and a few more pools in the island of Terschelling (LEENTVAAR, 1957b).

In the Zwanenwater only plankton investigations were made. The report mentioned a few rooted plants which suggest the classification of the littoral vegetation in the Scirpeto-Phragmitetum and of the open water vegetation in the Potamion euro-sibiricum. The salinity (only one sample) amounted to 124 mgr Cl per 1, which is somewhat higher than normal dune water. Evidently this amount did not affect the vegetation. There are no data on the mollusca of the Zwanenwater.

A few miles S of Den Helder there are lying in the dunes a series of small pools which were investigated by DEN HARTOG (1950). It is an assemblage of different origin and age, and of different ecological conditions. Some of these pools are natural, some were dug in 1914 and some were formed by bomb explosions during the second world war.

To start with the last category, the bomb craters, DEN HARTOG described them as poor in vegetation and poor in snails, only *Lymnaea ovata* and *Planorbis vortex* occurring. The pH varied between 5.8 and 6.5. The second group, the pools dug in 1914, have a much richer vegetation. As they are not in communication with each other the pH and the vegetation are different in the various pools. Some amounted to a pH of 6.9 to 7.3 and others to 6.6 to 7. The mollusc population was also different in these pools. One contained only *Lymnaea stagnalis*, another *L. stagnalis*, *Planorbis complanatus*, *P. crista*, and *Pisidium nitidum*, the third *Lymnaea stagnalis* and *Planorbis crista* and a fourth *Lymnaea ovata*, *L. palustris*, and *Bithynia tentaculata*. This diversity is more a matter of different origin and history of the pools, and difficulties of dispersal for the molluscs than the result of different ecological circumstances. The last group of ponds are of more remote origin. Some of them are definitely oligotrophic with a pH of 5.2 to 5.5, containing a sparse vegetation

and almost no mollusca. Only a few thin, depauperate specimens of *Lymnaea ovata* were found. In those pools in which the pH amounts from 6.4 to 6.7 the vegetation and the mollusca were more abundant. The following species were found: *Lymnaea stagnalis*, *L. palustris*, *L. ovata*, *Planorbis corneus*, *P. planorbis*, *P. carinatus*, *P. crista*, *Bithynia tentaculata*, *B. leachi*, *Sphaerium corneum*, and *Pisidium nitidum*.

In the island of Texel some observations were made in a dune lake "De Muy", a shallow pool of some considerable extension, with an abundant vegetation. No results of salinity samples or pH samples are available, but the mollusc population indicates a freshwater environment with a high degree of eutrophy. The following mollusca have been observed: *Physa fontinalis*, *Lymnaea palustris*, *L. ovata*, *L. truncatula*, *Planorbis complanatus*, *P. crista*, *P. albus*, *Pisidium nitidum*, *P. obtusale*.

In July 1947 DE VOS (1949) took various samples of freshwater organisms in twelve localities in the island of Vlieland. Only five of these sites contained a few molluscs, viz. *Lymnaea ovata*, *Planorbis crista*, *Pisidium milium*, *P. nitidum*, *P. obtusatum*, and *P. subtruncatum*. Although no details of the quality of the water were given, we can safely take it that the water was completely fresh in these habitats.

The island of Terschelling contains a few dune pools of rather divergent nature. Most of them are oligotrophic, with a low pH and a special, not very abundant vegetation. Only the Dodemanskiste and Griltje Plakje are inhabited by a few mollusca. In the Dodemanskiste *Lymnaea ovata*, *Planorbis vortex*, *Pisidium nitidum*, *P. milium*, *P. obtusale* and in Griltje Plakje *Valvata cristata*, *Physa fontinalis*, *Lymnaea ovata*, *Planorbis planorbis*, *P. leucostoma*, *P. vortex*, *P. crista*, *P. albus*, *Segmentina nitida*, *Pisidium obtusale*, and *Sphaerium corneum* (VAN BENTHEM JUTTING, 1956; LEENTVAAR, 1957b). Two other pools investigated by LEENTVAAR were eutrophic with a pH of round 7 and an abundant vegetation of *Phragmites*, various species of *Potamogeton* and *Chara*. Yet their mollusc population was poor which may be attributed either to the small age of one of them (Van Hunenplak, dug in 1951, no mollusca) or to the remote situation (Badhuisplak, with *Planorbis albus*, *Lymnaea ovata*, and *Pisidium* sp.).

A few freshwater pools in the dunes near Oostvoorne were visited by HENRARD in 1934. In his publication (HENRARD, 1946) the author gave no data on the salinity and the pH of these pools, and only very few on their vegetation. In the shallowest pools which dry in summer few living molluscs were found. Two larger lakes, the "Kwakjeswater" and "Breede Water" contained 17 and 4 species respectively. In the Kwakjeswater: *Valvata piscinalis*, *Bithynia tentaculata*, *Lymnaea stagnalis*, *L. palustris*, *L. ovata*, *L. truncatula*, *Planorbis vortex*, *P. complanatus*, *P. albus*, *P. contortus*, *Segmentina nitida*, *Physa fontinalis*, *Sphaerium corneum*, *S. lacustre*, *Pisidium milium*, *P. nitidum*, *P. subtruncatum*, and in the Breede Water: *Lymnaea stagnalis*, *L. ovata*, *L. palustris*, and *Planorbis vortex*.

The fauna of a small reed pool in the dunes near the "Groene Strand" in the island of Voorne, investigated in 1957, yielded only four species of water snails: *Lymnaea truncatula*, *L. palustris*, and two unidentified species of *Planorbis* (MÖRZER BRUYNS & WESTHOFF, 1957).

With the foregoing account of the ecology of some Dutch freshwater lakes the number of lakes is not at all exhausted. There are many more lakes still awaiting investigation. It is shameful to state that ecological surveys, especially from a malacological viewpoint, are rare or absent. This kind of field work may be recommended to the members of the Netherlands Malacological Society in the coming 25 years.

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