

## The *Aplexa hypnorum* coenosis in Zuid-Beveland

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The ecological demands of *Aplexa hypnorum* (L., 1758) seem to differ considerably from those of most other water snails. This species lives almost always on light to moderately clayey bottoms in small ditches which completely dry out during the summer. The number of species which are able to survive such circumstances is relatively small. It is not surprising, therefore, that the habitat in which *A. hypnorum* lives is characterized by a poor, but very outstanding assemblage of species. The common occurrence of the species in the former island of Zuid-Beveland (DEN HARTOG, 1963) enabled me to start a quantitative investigation on its biocoenosis, and to compare my results with those of other investigators.

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### METHODS:

The method of the surface-census for the investigation of mollusc communities was recommended by MÖRZER-BRUYNS (1947) in his thesis. In accordance with this, all molluscs from small square sample plots are collected, separated into living and dead ones, counted, and particularities, if any, are noted down. For the study of water molluscs this method is not very adequate. It is possible, however, to obtain mud and sand samples from the bottom by means of a grab. In stagnant fresh water the Ekman-grab especially is very useful. The grab samples have to be sieved and subsequently the obtained molluscs and other animals can be counted, measured and preserved. The surface-census as well as the grab-method are useless when we want to survey the animals living between the waterplants. Therefore, I applied another quantitative sampling method, which is

already in use by English limnologists. In an homogeneous biotope it is possible to obtain quantitative data by collecting the animals during a determined time-unit. MANN (1955) used this method for his quantitative studies on leeches, and REYNOLDSON (1958) applied it for sampling triclads. Although these investigators recommended the time-unit of an hour, the luxuriance of the water-snail fauna in Zuid-Beveland is sufficient to allow the investigator 30 minutes for collecting.

There are several objections which can be put forward against such a time-census. In the first place the method is not very exact. The numbers collected within half an hour have no absolute value as a result of the fact that the person of the collector becomes a factor. His tempo is not always the same. In an open vegetation he will no doubt work more accurately than, for example, in a ditch where he is hindered by high reed or the sharp stalks of sedges. Weather conditions also play a part. The effect of wind on the water surface is very inconvenient for collecting in ponds and larger water areas. Cloudy weather greatly influences the transparency of the water. Optimal results can be obtained only when the weather is fair. Moreover, the data obtained by different collectors may be insufficiently comparable as a consequence of differences in eye-sight, working tempo, handiness and accuracy. The results which were obtained during the investigation of the life cycle of *Aplexa hypnorum* (DEN HARTOG & DE WOLF, 1962) with the help of the time-census method are, however, sufficiently consistent for confidence in its applicability for coenological studies.

The surveys given here have been kept as homogeneous as possible. The molluscs were collected by Mr. L. DE WOLF while the other creeping invertebrates were collected at the same time by Mr. A. J. SANDEE. In table 1 the data are given only for those groups for which a reliable picture is obtained. The species which live in the mud and can not be collected by the time-census method, as e.g. tubificids and micro-organisms (Ostracoda, Cladocera, Copepoda, rotifers and small turbellarians), are omitted. Water insects also were not studied. The description of the *Aplexa* coenosis, is thus far from complete. For a real quantitative inventory of a biocoenosis, the habitat has to be sampled using several methods and a team of specialists must be available for the identification of the material. This is, however, a Utopian scheme. For practical reasons coenological studies have to be limited to one or a few taxonomic groups with which the investigator is familiar.

## FAUNISTIC COMPOSITION:

The *Aplexa* coenosis was surveyed in 12 localities in the period from May 29th to June 5th, 1962. The results are given in Table 1 on p. 52/53. The nomenclature of HEUKELS & VAN OOSTSTROOM, Flora van Nederland, edition 14, 1956, is followed for botanical names.

In the 12 localities a total of 3422 living molluscs was counted. The bulk consists of 3 species only, namely

*Aplexa hypnorum* with 1125 specimens or 32.9%,  
*Lymnaea ovata* with 1641 specimens or 48.0%, and  
*Lymnaea palustris* with 606 specimens or 17.7%.

Only 50 specimens or 1.4% of the total number belong to other species. The average number of species in a sample is 3.67.

The coenosis is well-characterized by *Aplexa hypnorum*, which is not only faithful to the biotope of the temporarily dry ditches, but is also one of the dominant snails in it. The two species of *Lymnaea*, *L. ovata* and *L. palustris*, which also dominate in this biotope, are ubiquitous and occur in all eutrophic fresh and oligohaline, standing and slowly running waters. They are useless for the characterization of the community. *Planorbis leucostoma*, although not common in Zuid-Beveland, seems to be a faithful species of the *Aplexa* community as it has been found there only together with *A. hypnorum*.

As the temporarily dry ditches and the permanently water-containing ditches are mostly in open communication with each other, an exchange of species may take place. This may explain the occasional occurrence in the *Aplexa* coenosis of some species which are not resistant to a more or less protracted drought, e.g. *Planorbis planorbis*, *Physa fontinalis*, *Lymnaea stagnalis*, and *Sphaerium corneum*. On the other hand, a few specimens of *Aplexa hypnorum* may sometimes be found in the *Lymnaea ovata*-*Planorbis vortex* coenosis.

Among the other animal groups the small flatworms, belonging to the Neorhabdozoela, *Dalyellia viridis* and *Phaenocora unipunctata* may be regarded as faithful species of the *Aplexa* coenosis. These small flatworms were found sometimes without *A. hypnorum*, but always in similar habitats.

Further companion species belong to the more ubiquitous aquatic animals. *Asellus aquaticus*, *Dugesia lugubris* and *Chlorohydra viridissima* are the more frequent species and the occurrence of *Glossiphonia complanata*, *Polycelis tenuis* and *Dendrocoelum lacteum* is sporadic.

TABLE 1.

The *Aplexa hypnorum* coenosis in Zuid-Beveland

|  | 1   | 2   | 3   | 4   | 5   | 6   | 7   | 8  | 9  | 10  | 11  | 12  | T    |
|--|-----|-----|-----|-----|-----|-----|-----|----|----|-----|-----|-----|------|
| <i>Aplexa hypnorum</i> (L.)            | 169 | 273 | 146 | 13  | 80  | 14  | 37  | 25 | 66 | 123 | 117 | 62  | 1125 |
| <i>Planorbis leucostoma</i> Mill.      | —   | —   | —   | —   | —   | —   | 5   | —  | 13 | —   | —   | —   | 18   |
| <i>Lymnaea ovata</i> (Drap.)           | 38  | 646 | 395 | 47  | 8   | 80  | 113 | 56 | 16 | 102 | 96  | 44  | 1641 |
| <i>Lymnaea palustris</i> (Müll.)       | —   | —   | 5   | 187 | 80  | 101 | 191 | 16 | 3  | 2   | 2   | 19  | 606  |
| <i>Planorbis planorbis</i> (L.)        | 1   | —   | 7   | —   | —   | —   | —   | 2  | —  | —   | —   | —   | 10   |
| <i>Lymnaea stagnalis</i> (L.)          | 4   | —   | —   | —   | —   | —   | —   | —  | —  | —   | —   | —   | 4    |
| <i>Physa fontinalis</i> (L.)           | —   | —   | —   | 1   | —   | —   | —   | —  | —  | —   | —   | —   | 1    |
| <i>Sphaerium corneum</i> (L.)          | —   | —   | 1   | —   | 11  | —   | —   | —  | —  | —   | 5   | —   | 17   |
| Total number of specimens              | 212 | 919 | 547 | 255 | 179 | 195 | 346 | 99 | 98 | 227 | 220 | 125 | 3422 |
| Turbellaria:                           |     |     |     |     |     |     |     |    |    |     |     |     |      |
| <i>Dugesia lugubris</i> (Schmidt)      | 1   | —   | 1   | —   | —   | —   | 6   | —  | 4  | —   | —   | —   | —    |
| <i>Polycelis tenuis</i> Ijima          | —   | —   | —   | —   | —   | —   | —   | 8  | —  | —   | —   | —   | —    |
| <i>Dendrocoelum lacteum</i> (O.F.M.)   | —   | —   | —   | —   | —   | —   | —   | —  | 13 | —   | —   | —   | —    |
| <i>Phaenocora unipunctata</i> (Oerst.) | —   | 24  | 36  | —   | —   | —   | —   | 1  | —  | 38  | —   | —   | —    |
| <i>Dalyellia viridis</i> (G. Shaw)     | —   | —   | 12  | —   | 79  | 23  | —   | —  | 17 | —   | —   | —   | ±75  |
| Hirudinea:                             |     |     |     |     |     |     |     |    |    |     |     |     |      |
| <i>Glossiphonia complanata</i> (L.)    | —   | —   | —   | 12  | —   | 6   | —   | —  | —  | —   | —   | —   | —    |
| <i>Haemopsis sanguisuga</i> L.         | 2   | —   | —   | 26  | —   | —   | —   | 1  | —  | —   | —   | —   | —    |
| Crustacea:                             |     |     |     |     |     |     |     |    |    |     |     |     |      |
| <i>Asellus aquaticus</i> (L.)          | 16  | 1   | —   | —   | 1   | 8   | —   | 1  | —  | 5   | 14  | —   | —    |
| <i>Gammarus duebeni</i> Lillj.         | —   | 7   | —   | —   | —   | —   | —   | —  | —  | —   | —   | —   | —    |
| Hydrozoa:                              |     |     |     |     |     |     |     |    |    |     |     |     |      |
| <i>Chlorobryda viridissima</i> (Pall.) | +   | —   | —   | +   | +   | +   | +   | +  | —  | —   | +   | +   | —    |
| <i>Pelmatochydra oligactis</i> (Pall.) | —   | +   | —   | —   | —   | —   | —   | +  | —  | —   | —   | —   | —    |
| Fishes:                                |     |     |     |     |     |     |     |    |    |     |     |     |      |
| <i>Pungitius pungitius</i> (L.)        | +   | —   | —   | +   | +   | +   | +   | +  | —  | —   | +   | —   | —    |

## LEGENDA

1. Goes, ditch near the Television tower. Sparse vegetation with *Pbragmites communis*, *Agrostis stolonifera* and *Glyceria fluitans*; 29-V-1962.
2. Wolphaartsdijk, ditch along the Nieuwe Veerweg near the junction with the Bolleweg. Closed vegetation of *Pbragmites communis*; 29-V-1962.
3. Nieuwdorp, ditch along the Noord-Kraayertse Weg. Scattered vegetation of *Scirpus maritimus*, *Alopecurus geniculatus*, *Equisetum palustre* and *Lysimachia nummularia*; 30-V-1962.
4. Ditch along the main road Heinkenszand - 's Heerenbroek. Closed vegetation of *Agrostis stolonifera* and *Glyceria fluitans*, with interspersed *Pbragmites communis*, *Juncus articulatus*, *Equisetum fluviatile*, *Galium palustre*, *Mentha aquatica*, *Lysimachia nummularia* and *Callitriche obtusangula*; 30-V-1962.
5. Ovezande, ditch in the south-western part of the Louisepolder. Vegetation of *Polygonum amphibium*, *Agrostis stolonifera*, *Mentha aquatica*, *Lysimachia nummularia* and *Scirpus lacustris* ssp. *glaucus*; 30-V-1962.
6. Hoedekenskerke, ditch in the Oosterzwapelpolder, opposite the Nieuwe Hoondertpolder. Open vegetation of *Alisma plantago-aquatica*, *Equisetum palustre*, *Mentha aquatica*, *Lemna minor* and *L. gibba*; 4-VI-1962.
7. Kapelle, ditch along the Hillewerfweg near the junction with the Plasweg. Closed vegetation of *Pbragmites communis* interspersed with some plants of *Ranunculus sceleratus*, *R. baudotii* and *Callitriche obtusangula*; 29-V-1962.
8. Biezeling, ditch between „Veldzicht” and „Smokkelhoek”. Vegetation of *Pbragmites communis* (dominant), *Phalaris arundinacea*, *Agrostis stolonifera* and *Callitriche obtusangula*; 4-VI-1962.
9. Kapelle, den Bok, ditch. Vegetation of *Pbragmites communis* and *Typha latifolia*; 4-VI-1962.
10. Yerseke, ditch in the Molenpolder. Vegetation of *Pbragmites communis*; 1-VI-1962 (Den Hartog & De Wolf, 1962).
11. Krabbendijke, ditch along the railway in the Nieuw Krabbendijkse polder. Scattered plant growth of *Pbragmites communis*, *Mentha aquatica*, *Veronica catenata*, *Rumex crispus*, *Nasturtium* cf. *microphyllum*, *Lysimachia nummularia*, *Callitriche obtusangula*, *Ranunculus baudotii* and a closed layer of the moss *Acrocladium cuspidatum*; 5-VI-1962.
12. Ditch along the Frederikadijk east of Krabbendijke. Open vegetation of *Pbragmites communis*, *Nasturtium* cf. *microphyllum* and *Ranunculus baudotii*; 5-VI-1962.

*Haemopsis sanguisuga* tolerates desiccation very well, but this species is more common along larger bodies of water. No doubt, this very voracious leech preys on the snails in the *Aplexa* coenosis. The stickleback *Pungitius pungitius* is a common inhabitant of the *Aplexa* ditches, but it leaves them before the beginning of the summer drought.

It is remarkable that the brackish-water fauna is so scantily represented in the *Aplexa* habitats. *Gammarus duebeni* has been found only occasionally, while among the micro-organisms collected and identified by me, only *Macrostomum hamatum* Luther may be regarded as a brackish-water species.

#### RELATIONSHIP BETWEEN THE APLEXA COENOSIS AND THE VEGETATION:

Although no phytocoenological surveys were made, it is still clear from my notes on the accompanying vegetation, that the *Aplexa*-coenosis is not bound to any special plant community.

In 5 of the 12 localities vegetation was scanty, in another 5 *Phragmites communis* was the dominant species. In the remaining two localities *Agrostis stolonifera* and *Polygonum amphibium* were respectively the main species. The vegetations from these localities were too sparse to be identified with certain plant associations, but the accompanying plants belong to 3 groups:

1. Species of the *Agropyro-Rumicion*, the alliance which is characteristic for stress zones between contrasting regimes of environment, in this case for the transition zone between wet and dry (VAN LEEUWEN, 1958). Some of these plants are able to withstand protracted inundations (*Agrostis stolonifera*, *Polygonum amphibium*, *Menba aquatica*), while others can colonize these periodically dry places by creeping shoots (*Lysimachia nummularia*). The vegetations of the surveys 3, 4, 5, 8 and 11 may be considered to be examples of this alliance.
2. Species of the *Glycerieto-Sparganion*, the alliance of the edges of ditches, in which the water flows very gently (*Glyceria fluitans*, *Alisma plantago-aquatica*, *Nasturtium* cf. *microphyllum*).
3. Species of the *Callitricho-Batrachion*, the alliance of amphibious water plants, which is characteristic for shallow and temporarily dry ponds and ditches (*Ranunculus baudotii*, *Callitriche obtusangula*).

*Aplexa hypnorum* does not occur in luxuriant waterplant communities nor in well-developed communities of the *Agropyro-Rumicion*. In fact the species inhabits those ditches whose bottoms are just the lower limit of the *Agropyro-Rumicion* and just the upper limit of the *Callitricho-Batrachion*. The habitat of the *Aplexa* coenosis is on the average just too wet for the *Agropyro-Rumicion* and results in a fragmentary development of this alliance, as only its most eurytopy representatives intrude into the ditches. On the other hand, the bottom is mostly dry for too long a time to enable successful establishment of the *Callitricho-Batrachion*. Moreover, the development of the vegetations is greatly influenced by the yearly cleaning of the ditches.

#### SOME RECORDS OF THE APLEXA COENOSIS IN OTHER REGIONS:

The aquatic mollusc fauna of Zuid-Beveland is poor, and the coexistence of *Aplexa hypnorum* and *Planorbis leucostoma* could be a local phenomenon. From observations made in other areas and from records in literature it appears, however, that both species have been found often together. The results of the investigations made in Zuid-Beveland may be considered to be representative for the southwestern part of the Netherlands.

In the island of Goeree-Overflakkee *A. hypnorum*, *P. leucostoma* and the flatworm *Phaenocora unipunctata* have been found together in a temporarily dry ditch near Dirksland. HENRARD (1946) recorded *A. hypnorum* and *P. leucostoma* as concurring in Voorne, and according to him this combination may be found in several places in the Netherlands. In the island of Schouwen I found only *P. leucostoma* in temporarily dry ditches, and could not find *A. hypnorum*, although this species was recorded by KUIPER (1944). In a moist dune valley on this island BUTOT (n.p.) recently discovered a few dead specimens of *A. hypnorum* together with *P. leucostoma*, some of which were alive.

On the Pleistocene soils in the eastern and southern parts of the country the combination of *A. hypnorum* and *P. leucostoma* is also widely distributed, but there *Lymnaea glabra* (Müll.) seems to join the community, and also some *Pisidium* species may occur. KUIPER (1949) found *A. hypnorum* and *L. glabra* together in a drainage-furrow near Duizel (province of Noord-Brabant). In the surroundings of the Mantinger Bos in the province of Drente *A. hypnorum*, *P. leucostoma*, *L. glabra* and a few other species were recorded as occurring together (KUIPER, 1952). Another example of the coexistence of *A. hypnorum* and *L. glabra* was given also by KUIPER (1955)

from De Klomp (province of Gelderland). It is, however, questionable whether *L. glabra* is a true member of the *Aplexa* coenosis. The life cycles of *A. hypnorum* and *L. glabra* are in some respects very similar, but the patterns of distribution in the Netherlands are very different. Moreover, in the regions where both species occur, they are found more often apart than together.

The coexistence of *A. hypnorum* and *P. leucostoma* has been observed also in other European countries. LAIS (1926) mentioned some instances from the north-eastern part of France, NELSON (1880) and BOYCOTT (1936) recorded the combination from Great Britain and HAESSLEIN (1956, 1960) found both species often together in Württemberg (South Germany). Although the coexistence of these species is a common feature, the ecological tolerance of *P. leucostoma* is considerably wider than that of *A. hypnorum*, and it occurs as well in habitats where the latter never has been found. It is not uncommon, for example, in small eulittoral creeklets in the fresh-water tidal area of the rivers Rhine and Meuse (Biesbosch). So *P. leucostoma* is only locally faithful to the *Aplexa* coenosis. However, regionally it has to be regarded as a characteristic species of temporary and unstable aquatic habitats. HAESSLEIN (1956) described from the Nördlinger Ries in Württemberg a *Valvata pulchella* association, which he considered to be characteristic for river valleys and lowland marshes. He regarded *Valvata pulchella* Studer (= *V. macrostoma* Steenbuch) *Aplexa hypnorum* and *Segmentina nitida* (Müll.) as faithful species of this community, and according to his table *Planorbis leucostoma* is extremely abundant in it. Although this *Valvata pulchella*-association is certainly not identical with the *Aplexa* coenosis, described from the south-western part of the Netherlands, both communities are closely related in ecological respect. The main difference in faunistic composition, is the high abundance of *Valvata pulchella*, which in the Netherlands is rare and limited to a few localities in the proximity of the rivers Rhine and Waal. Other differences are the abundance of some Sphaeriidae and the constant occurrence of *Bithynia tentaculata* (L.) and *Planorbis contortus* (L.). These features indicate that the dry period must be rather short.

In the region of the Pegnitz HAESSLEIN (1960) found *Aplexa hypnorum* and *Planorbis leucostoma* also as members of the *Radix peregra* association, which he considered to be characteristic for mountainous marshes. This association does not seem to be very homogeneous. Several surveys of it published by HAESSLEIN (1960) show only slight differences with the surveys made by me of the *Aplexa* coenosis in Zuid-Beveland.

## THE APLEXA COENOSIS DURING THE SUMMER DROUGHT:

The surveys of the *Aplexa* habitats in Zuid-Beveland were made just before the beginning of the summer drought. When the dry period starts, *Lymnaea ovata*, *L. palustris* and *A. hypnorum* assemble in the lowest places of the ditches, and hide under all kinds of objects, pressing the aperture of the shell close to the substrate. Many of them die.

I kept some *A. hypnorum* in a small water-filled tank, which was allowed to dry out in the sun. After 3 weeks drought 50% of the specimens were yet alive, especially the smaller ones. This observation agrees very well with the result of field investigations carried out in the Molenpolder at Yerseke (DEN HARTOG & DE WOLF, 1962). In 1960 a number of small animals survived a drought period of ca. 2 months, but not one large specimen was so successful. In 1961 and 1962, when the drought lasted for respectively 3 and 4 months not a single specimen survived. I never observed that the animals dug themselves in the bottom of the ditch, as has been recorded by VAN BENTHEM JUTTING (1933, p. 190), FRÖMMING (1956, p. 152), ADAM (1960, p. 163) and BUTOT (1962, p. 120). CLESSIN (1872) thought that perhaps the animals hid in the mud, as he could not find them when the ditches were dry. I have seen, however, several specimens which had slightly sunk into the soft mud surface, but not one *Aplexa* was found by sifting mud samples. I think, therefore, that the species overcomes the drought period in the form of its eggs.

Among *L. ovata* also many specimens become victims of the drought. In Yerseke a month after the beginning of the dry period I collected a large number of *L. ovata*. It appeared that of these only 10% was still alive, and they were mostly the smaller individuals. However, this species is able to survive a drought period of 4 months, since it was present during the whole drought period from the middle of June to the end of October 1962. The young specimens were seen actively creeping and climbing against the plants, even when they were exposed to sunshine.

Young *L. palustris* also can survive a drought of 4 months, but the losses in individuals seem even larger than in *L. ovata*.

*P. leucostoma* is rare in Zuid-Beveland. I have no observations on the method of aestivation in this species. It seems to close its aperture with a mucose membrane (FRÖMMING, 1956).

During the drought the hydrobiotope changes into a land biotope, enabling land animals to colonize the dry bottoms of the ditches. Near Yerseke I noted the following slugs and snails in the dry *Aplexa*

biotope: *Limax maximus* L., *Deroceras reticulatum* (Müll.), *D. laeve* (Müll.), *Succinea* cf. *elegans* Risso, *Cochlicopa lubrica* (Müll.), *Cepaea nemoralis* (L.) and *Arianta arbustorum* (L.).

#### A COMMUNITY OF OUTCASTS?

In his work on the ecology of the British fresh-water molluscs BOYCOTT (1936) paid much attention to the ecological group of the species which are always or nearly always found in habitats which seem very unfavourable to aquatic animals. He thought that these species had been driven by pressure of competition from the "good" localities into "ecological slums", i.e. small bodies of water which dry up in summer, or which are for other reasons not very suitable to aquatic molluscs. He gave as examples *Lymnaea glabra* and *Planorbis leucostoma* (sub nomine *P. spirorbis*). In free nature *L. glabra* has been found only in temporarily dry, soft-water localities. In an aquarium it grows and reproduces in hard water as well. According to BOYCOTT *P. leucostoma* has "a distinct addiction to drying ponds, marshes and other bad places", while it is absent from permanent aquatic habitats. However, in larger places where competition between the species is not so severe as is the case in small ponds, *P. leucostoma* may be found also, e.g. along the banks of lakes. BOYCOTT, supposing that *Aplexa hypnorum* (sub nomine *Physa hypnorum*) could tolerate bad conditions although it preferred better circumstances, believed that this species in fact did not belong to the above group. Here, according to me, he made an error of thought. The species which are driven into the slums by competitive seclusion do not necessarily prefer such places as a habitat. In many cases the reverse will be the case. These species can maintain themselves only by their capacity to live under unfavourable circumstances, where they are not subjected to competition, or are able to compete with success. The "bad places" must be seen as refugia for these species. Although these species have under natural circumstances certainly their optimum in such stations, it is questionable whether they prefer them.

The competition hypothesis of BOYCOTT (1936) is not proved. He did not mention even which species exercise the "competitive pressure". It is known from experience with several taxonomical groups that competition has to be seen as an equilibrium between two ecologically equivalent species. The competing species are thus mostly congeners, or species with very similar adaptations. They do not have necessarily to be hostile to each other but availability of food, rate of reproduction and tolerance to unfavourable circumstances are

the factors that mostly decide which species will finally survive in a certain biotope. Thus competition between two species is not a struggle, which is pursued with changing success, but in contrast it proceeds according to fixed laws and the result in every place is usually a foregone conclusion. When *L. glabra* and *P. leucostoma* are considered in the light of the above generalizations it appears that they must be in competition respectively with other *Lymnaea* species and with other small *Planorbis* species. Further it is improbable that *A. hypnorum* competes with *Lymnaea* species, as it usually coexists with them. However, species of the genus *Physa* may exercise competitive pressure. In this connection it is interesting that BOYCOTT (1936) did not give any record of the coexistence of *A. hypnorum* and *Physa fontinalis*, although he recorded *A. hypnorum* from several "good places" with species combinations which may be referred to to the *Lymnaea ovata* — *Planorbis vortex* coenosis and the *Lymnaea stagnalis* — *Planorbis corneus* coenosis (HONER, 1963). In Zuid-Beveland I once found two specimens of *A. hypnorum* in a permanently water-containing ditch near Ovezande, together with numerous *Planorbis vortex*, *P. planorbis*, *Lymnaea ovata* and *L. palustris*, thus in the *Lymnaea ovata* — *Planorbis vortex* coenosis. These specimens of *A. hypnorum* were from a quantitative point of view not important, and came no doubt from an adjacent *Aplexa* coenosis.

The remark of BOYCOTT (1936) that the stress of competition in spacious habitats should be less than in small habitats also has to be proved. The occasional occurrence of *P. leucostoma* and *A. hypnorum* along the banks of lakes can not be regarded as proof, since a lake is not a homogeneous habitat, but consists of several sub-habitats. I myself have found *A. hypnorum* only once along the banks of a large body of water, viz. along the Groote Gat near Oostburg in Zeeuwsch-Vlaanderen. This brackish-water broad shows an annual salinity fluctuation from 0.5 to 7.8‰ Cl' and to consider it as a single habitat is a serious mistake. In the broad itself *A. hypnorum* is absent, but the narrow strip between the wide reed-fringe and the dike, which in summer is completely dry, is a suitable habitat for the species. During the time that the strip is submerged, salinity is usually low enough to make the occurrence of *A. hypnorum* possible.

The *Aplexa* coenosis consists of a number of ubiquitous species, tolerant to unfavourable circumstances and resistant to a protracted drought period. According to the argumentation of BOYCOTT the faithful species of the coenosis have to be regarded as outcasts, as they are driven in this extreme habitat owing to their inferiority in the competition with other species. However, I wonder whether

competition is the only factor determining the occurrence of *A. hypnorum* in temporarily dry ditches. In Zuid-Beveland several shallow, permanently wet fresh-water ditches occur and these are only populated by *Lymnaea ovata*; although *A. hypnorum* would be free from competitive stress in these ditches, I did not succeed in finding even one specimen.

There are some reasons to suppose that *A. hypnorum* shows some preference for the temporarily dry habitats. In the first place the species lives just at the lower limit of the *Agropyro-Rumicion*, and just at the upper limit of *Callitricho-Batrachion*, thus it has a very narrow vertical range. Its absence from the *Callitricho-Batrachion* can not be explained by the competition factor, as in these vegetations only *L. ovata* and *L. palustris* occur.

Furthermore, NEKRASSOW (1929) found that the lamellation of the spawns and egg-membranes of *A. hypnorum* is much more complicated than in the spawns of *Physa fontinalis*. He regarded this feature as an adaptation to the environment, as it would increase the resistance of the eggs against desiccation.

A study of the life cycle of *A. hypnorum* at Yerseke (DEN HARTOG & DE WOLF, 1962) showed that species is very well adapted to the annual cycle of the habitat, as each summer the original generation falls victim to the extremes of the environment, but the species survives in the new generation of eggs.

Therefore, it seems to me, that *A. hypnorum* may not be regarded as an outcast, which is driven in unfavourable stations by competition. On the contrary, it prefers the "ecological slums". The *Aplexa* coenosis is not an assemblage of species which have been driven together as the result of competitive seclusion, but has to be seen as a community which is well-adapted to unfavourable environmental circumstances.

## REFERENCES

- ADAM, W., 1960. Mollusques I. Mollusques terrestres et dulcicoles. Faune de Belgique, p. 162-163.
- BENTHEM JUTTING, T., VAN, 1933. Mollusca (1) A. Gastropoda prosobranchia et pulmonata. Fauna van Nederland vol. 7, p. 189-191.
- BOYCOTT, A. E., 1936. The habitats of fresh-water mollusca in Britain. J. Anim. Ecol. vol. 5, p. 116-186.
- BUTOT, L. J. M., 1962. Malacologisch onderzoek op Goeree. Jaarb. Wetensch. Gen. Goeree-Overflakkee 1961, p. 142-172.
- CLESSIN, S., 1872. Die Lebensweise der *Physa hypnorum*. Korresp. Blatt Zool.-mineral. Ver. Regensburg vol. 26, p. 170-171.
- FRÖMMING, E., 1956. Biologie der mitteleuropäischen Süßwasserschnecken. Berlin, p. 1-313.
- HARTOG, C. DEN, 1963. The distribution of the snail *Aplexa hypnorum* in Zuid-Beveland in relation to soil and salinity. Basteria vol. 27, p. 8-17.
- HARTOG, C. DEN, & L. DE WOLF, 1962. The life cycle of the water snail *Aplexa hypnorum*. Basteria vol. 26, p. 61-72.
- HAESSLEIN, L., 1956. Mollusken und Molluskengesellschaften der Gewässer der Nördlinger Ries. Jb. Ver. Vaterl. Naturk. Württemberg, vol. 111, p. 174-199.
- 1960. Weichtierfauna der Landschaften an der Pegnitz. Abh. Naturhist. Ges. Nürnberg, vol. 29 nr. 2, p. 1-148.
- HENRARD, J. B., 1946. Bijdrage tot de kennis der molluskenfauna van Oostvoorne. Basteria vol. 10, p. 25-32.
- HONER, M. R., 1963. Freshwater larval Trematodes in the Netherlands: a synecological study of their occurrence. Thesis, Utrecht, p. 1-116.
- KUIPER, J. G. J., 1944. Bijdrage tot de kennis van de niet-mariene mollusken van de Provincie Zeeland. Basteria vol. 9, p. 1-29.
- 1949. Enkele vondsten van zeldzame slakken in Limburg en Noord-Brabant. Corresp. bl. Ned. Mal. Ver. no. 31, p. 216-219. (mimeographed).
- 1952. De excursie naar het Mantinger bos (20 mei 1951). Corresp. bl. Ned. Mal. Ver. no. 43, p. 376-377. (mimeographed).
- 1955. *Lymnaea glabra* (Müller). Corresp. bl. Ned. Mal. Ver. no. 59, p. 561. (mimeographed).

- LAIS, R., 1926. Zur Molluskenfauna des Gebietes zwischen Maas und Mosel. Arch. Molluskenk. vol. 58, p. 25-36.
- LEEUEWEN, C. G. VAN, 1958. Enige opmerkingen over het Agropyrumicium crispum Nordh. '40 in Nederland. Corresp. bl. Flor. Vegetatie Onderz. Nederland no. 11, p. 117-123 (mimeographed).
- MANN, K. H., 1955. The ecology of the British fresh-water leeches. J. Anim. Ecol. vol. 24, p. 98-119.
- MÖRZER BRUYNS, M. F., 1947. Over levensgemeenschappen. Thesis, Utrecht, p. 1-195.
- NEKRASSOW, A. D., 1929. Vergleichende Morphologie der Laiche von Süßwassergastropoden. Z. Morph. Ökol. Tiere vol. 3, p. 1-35.
- NELSON, W., 1880. On the association of *Limnaea glabra*, *Physa hypnorum* and *Planorbis spirorbis*. Journ. of Conch. vol. 3, p. 115-116.
- REYNOLDSON, T. B., 1958. The quantitative ecology of lake-dwelling Tricladids in northern Britain. Oikos vol. 9, p. 94-138.

## SAMENVATTING

De *Aplexa* coenose, welke karakteristiek is voor in de zomer droogvallende slootjes op min of meer kleihoudende bodems, werd beschreven aan de hand van 12 opnamen, gemaakt op Zuid-Beveland volgens de tijdcensus-methode. De coenose wordt hoofdzakelijk samengesteld door drie soorten waterslakken, de kensoort *Aplexa hypnorum* (L.) en de beide ubiquisten *Lymnaea ovata* (Drap.) en *L. palustris* (Müll.). Een tweede lokaal bruikbare kensoort *Planorbis leucostoma* Mill. is slechts zeer spaarzaam vertegenwoordigd op Zuid-Beveland. Twee andere kensoorten konden worden aangewezen onder de vertegenwoordigers van andere diergroepen, n.l. de beide platwormen *Phaenocora unipunctata* (Oerst.) en *Dalyellia viridis* (G. Shaw). De coenose is wijd verspreid in Nederland, alsmede in West- en Midden-Europa en de Britse eilanden.

Er werd geen binding waargenomen van de *Aplexa*-coenose aan enige plantengemeenschap. De coenose komt slechts daar tot ontwikkeling, waar de slootbodem juist met de benedengrens van het *Agropyro-Rumicion* samenvalt, maar ook te lang droogvalt, om een behoorlijke ontwikkeling van een tot het *Callitricho-Batrachion* behorende waterplantengemeenschap mogelijk te maken.

In het licht van de concurrentie-hypothese van BOYCOTT (1936) zou de *Aplexa* coenose opgevat moeten worden als een gezelschap van weinig kieskeurige ubiquisten, die resistent zijn tegen een voor waterslakken uiterst ongunstige milieufactor als uitdroging. De kensoorten zouden slechts tot deze ongunstige biotoop beperkt zijn, omdat ze zich elders ten gevolge van concurrentie met andere soorten niet kunnen handhaven. Het is echter zeer waarschijnlijk, dat *A. hypnorum* een zekere preferentie heeft voor langdurig droogvallende slootjes, want ze ontbreekt in het *Callitricho-Batrachion*, waar de milieuomstandigheden minder extreem zijn en waar ze evenmin concurrentie met andere soorten behoeft te vrezen. De levenscyclus van deze soort is zeer goed aangepast aan de bijzondere milieuomstandigheden en de eipakketjes vertonen speciale lamellaire structuren, die als adaptaties aan een langdurige droogteperiode kunnen worden opgevat.