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The life cycle of the water snail Aplexa hypnorum

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Aplexa hypnorum (L., 1758) is a water snail which usually is considered rather uncommon. Therefore it was a pleasant surprise to discover a large population of this species in a ditch in the Molenpolder at Yerseke within a distance of 50 m from our laboratory. As *Aplexa hypnorum* is known to occur in shallow ditches which dry out in summer and which may be frozen from top to bottom in winter, it was thought that it would be interesting to investigate the life cycle of this snail in comparison with the life cycle of *Physa fontinalis* (L.), a snail living in more permanent waters and recently studied by DE WIT (1955). For this purpose every month samples of *Aplexa hypnorum* were collected. The investigation was started in March 1960 and is being continued. Here the results of our investigations up to August 1962 will be dealt with.

HABITAT

The ditch in which *Aplexa hypnorum* occurs is situated in the Molenpolder and borders on one side the slope of the road Yerseke-Kruiningen and on the other an orchard. The bottom consists of rather calcareous, moderately humose and very sandy sea clay (soil-type 7, according to the soil map of the Netherlands). The water has a salinity varying from 0.25‰ to 1.85‰ Cl' and is more or less polluted by rubbish dumping. As the depth is small, temperature fluctuations are considerable both in the course of the day as well as in the course of the year. In winter time the ditch is soon completely frozen when frost starts. In contrast in the early summer temperatures may rise in the daytime above 18° C. In summer the ditch dries out completely.

The vegetation of the ditch consists of a closed growth of *Phragmites communis* Trin., which is mown every year. As a consequence of this mowing the water is exposed to the sunlight in the time before the reed starts sprouting again, which happens in the second half of April. In that period the water is covered mainly by floating brownish, foamy tufts of diatoms and bluegreen algae, but the duckweed *Lemna minor* L. occurs as well.

Besides the snail *Aplexa hypnorum,* which is the dominant organism, the snail *Lymnaea ovata* (Drap.) is also rather numerous. Only a few *Lymnaea palustris* (O. F. Müller) are present. Other invertebrates accompanying *Aplexa* are the Rhabdocoelian flatworm *Phaenocora unipunctata* (Oersted), the isopod *Asellus aquaticus* (L.) and oligochaete worms.

METHODS

Each month as many *Aplexa* as possible were collected in 30 minutes. The animals were counted, the maximum height of their shells was measured and then they were returned to the ditch. From this point the maximal shell height will be referred to as the size of the animal. The use of a determined time-unit for collecting makes the samples comparable to each other. The absolute numbers give a good idea of the abundance of the species.

The data obtained from the monthly measurements are given in Table 1 and are graphically expressed in Fig. 1 and 2. From these data the mean shell height of each sample has been calculated, but when it was evident from the data and the graphs that two size-groups representing different generations were present the mean sizes of both groups were determined separately. The same was done for the maximum and minimum sizes in every sample. These derived data are given in Table 2. In Fig. 3 the mean sizes of the shells are graphically expressed. In the same figure the mean monthly temperatures as well as the mean temperatures for every ten days period, as calculated from hourly observations at Flushing, are given. These data are derived from the „Maandelijks Overzicht der Weersgesteldheid in Nederland", published by the Royal Netherlands' Meteorological Institute (K.N.M.I.).

OBSERVATIONS ON THE LIFE CYCLE

For practical reasons we will discuss the investigations in three periods. The first period is from March 28th, 1960, up to July 26th, 1960, that is from the beginning of the investigation to the end of

TABLE 1 : SIZE FREQUENCY IN APLEXA HYPNORUM

Date	Size in mm. 1	1½	2	2½	3	3½	4	4½	5	5½	6	6½	7	7½	8	8½	9	9½	10	10½	11	11½	12	12½	13	Number x
28- 3-'60	-	1	6	9	4	7	4	6	2	2	1	-	1	1	3	1	-	-	-	-	-	-	-	-	1	49
26- 4-'60	-	-	-	-	3	4	3	12	11	13	24	20	19	11	11	8	5	2	1	-	-	2	1	2	-	152
31- 5-'60	-	-	-	-	1	3	1	3	6	17	19	23	17	12	9	3	5	2	1	1	1	-	-	-	-	124
24- 6-'60	-	-	-	-	-	-	-	1	11	19	10	3	1	-	-	-	-	-	-	-	-	-	-	-	-	45
26- 7-'60	-	-	-	-	-	-	1	4	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
25- 8-'60	-	31	17	3	3	1	3	2	3	4	13	9	9	10	5	1	-	-	-	-	-	-	-	-	-	114
1-10-'60	3	28	51	74	25	7	6	4	-	2	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	203
31-10-'60	-	2	8	37	46	49	28	14	11	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	200
28-11-'60	-	1	3	25	26	38	35	25	10	9	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	173
27-12-'60	-	-	1	3	8	12	16	16	10	9	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	76
31- 1-'61	-	-	1	3	15	25	23	14	6	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	91
25- 2-'61	-	2	9	27	57	86	87	66	53	30	11	7	1	-	-	+	+	-	-	-	-	-	-	-	-	437
30- 3-'61	-	-	-	1	2	7	20	21	35	64	60	50	63	63	26	16	8	4	2	-	-	-	-	-	-	442
28- 4-'61	-	-	-	-	-	1	-	1	2	7	9	8	9	19	20	30	48	45	46	41	34	24	5	-	-	349
29- 5-'61	-	-	-	-	-	-	-	-	2	4	1	10	16	16	21	26	34	37	42	38	28	14	5	-	-	294
22- 6-'61	-	-	-	-	-	-	-	-	-	1	4	7	12	14	12	25	28	19	20	15	9	2	2	1	-	171
24- 7-'61	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
30- 8-'61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
28- 9-'61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30-10-'61	183	91	33	13	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	324
4-12-'61	5	74	73	22	10	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	188
10- 1-'62	-	10	21	24	7	5	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	71
5- 2-'62	-	6	11	30	22	8	4	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	85
22- 2-'62	-	8	26	51	35	24	12	8	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	166
20- 3-'62	-	-	13	26	31	45	24	12	3	6	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	164
26- 4-'62	-	-	-	2	3	9	12	22	28	36	23	16	10	6	2	-	-	-	-	-	-	-	-	-	-	169
23- 5-'62	-	-	-	-	-	-	-	-	-	-	1	1	1	6	7	20	21	42	14	10	6	1	-	-	-	130
25- 6-'62	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	2	6	8	8	5	1	1	-	-	35
25- 7-'62	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

x) Every sample was collected in 30 minutes.

the first period of drought. The second period is from August 25th, 1960, to June 22nd, 1961, that is from the time there was again

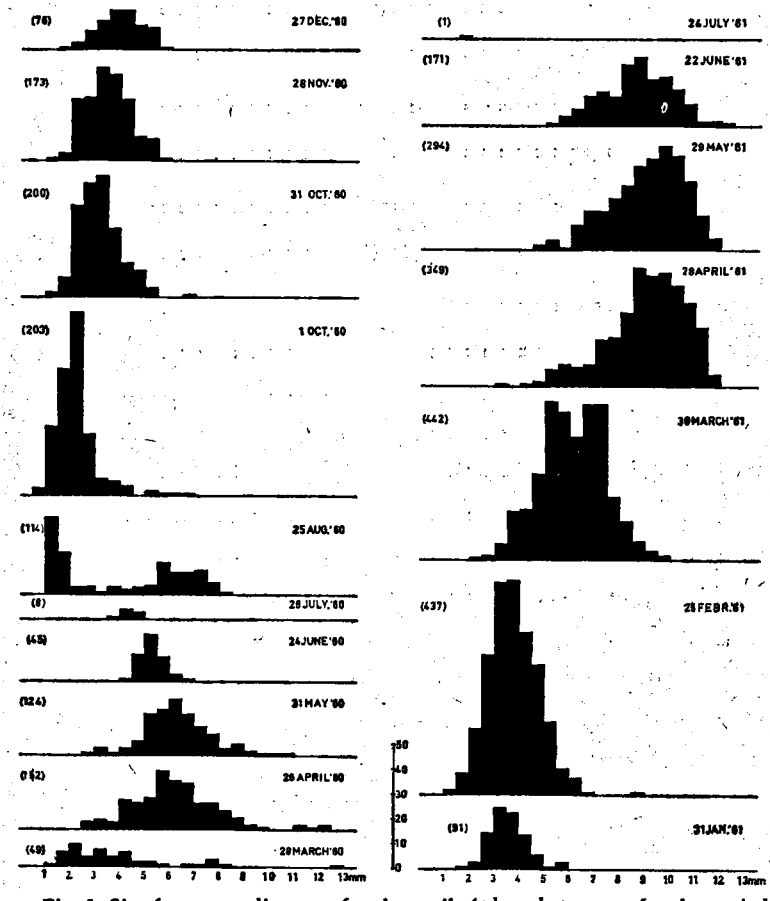

Fig. 1. Size frequency diagrams for the snail *Aplexa hypnorum* for the period March 28th, 1960 - July 24th, 1961. The number of individuals is given on the vertical axis and the size on the horizontal axis. The total number collected in 30 minutes is given between brackets.

water in the ditch up till the beginning of the drought of the following summer. The third period from October 30th, 1961, to June 25th, 1962, is also determined by the end of one and the beginning of the next drought period.

a. Period I (March 28th, 1960 - July 26th, 1960):

The investigation was started on March 28th. In the first sample already some remarkable facts were observed. In the first place the occurrence of a specimen of 13 mm was surprising as the other animals measured between 1.5 and 8.5 mm. No doubt this larger

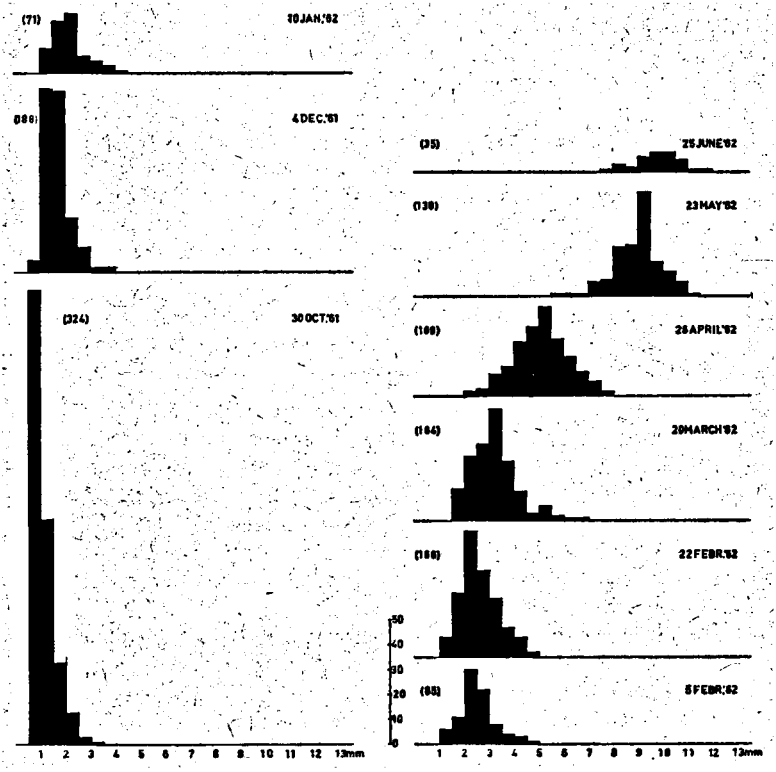

Fig. 2. Size frequency diagrams for the snail *Aplexa hypnorum* for the period October 30th, 1961 - June 25th, 1962. The number of individuals is given on the vertical axis and the size on the horizontal axis. The total number collected in 30 minutes is given between brackets.

animal represented an older generation. On April 25th also a few specimens between 11.5 and 12.5 mm were found, but after that time this old generation disappeared.

Secondly we found in the first sample that the graphical expression of the size-group 1.5-8.5 mm showed a slight second maximum.

This may be ascribed to inexperience in collecting *Aplexa*. In later samples such a second maximum did not occur, so we may consider that this whole size-group represents one generation.

With the rising of temperature in April a rapid growth started. The mean size, which was 3.95 mm at the end of March, increased to 6.36 mm at the end of April. A rise of the minimum and the maximum sizes was noted also. By the end of May the quantity of water had decreased considerably, and this may have hampered further growth, although the rise of temperature continued. The mean size increased in May only slightly and the maximum size rose to 11 mm.

During June and July the ditch was completely dry. At the end of June 45 living snails were found under stones and pieces of wood, but 180 empty shells were also found. At the end of July the number of living snails was reduced to 8. They were found in the moistest places of the ditch bottom. It was remarkable that the mean size of the shells decreased also.

b. Period II (August 25th, 1960 - June 22nd, 1961):

At the end of August there was again water in the ditch, and the snails which were collected clearly belonged to two generations, which showed a slight overlap in size. A considerable number of snails must, therefore, have survived the drought period. The surviving generation was, however, not very successful in the following months, as on October 1st 5 specimens were found and on October 31st only one. One snail that survived the winter was collected on February 25th.

The new generation, on the contrary, did very well. The mean size, which was 1.87 mm at the end of August, increased to 3.69 mm on November 28th. From that time to the end of February the average size was almost stationary, as the increase amounted to less than 0.5 mm.

From October a decrease of the numbers of *Aplexa* was noted. This was at first ascribed to mortality. However, at the end of February the number suddenly increased more than four times, without the slightest indication that new eggs had hatched. Mortality may indeed have played a part in the decrease, as in December the ditch was cleaned and the reed was mown, while in January the ditch was frozen for some time. The increase can only be explained by accepting the existence of many young specimens buried in the bottom and which came out of the mud at the beginning of spring.

In March and April when the rise in temperature started, growth

proceeded very rapidly. On April 28th the mean size was already 9.26 mm. In this time the minimum as well as the maximum sizes showed an increase. In May growth continued, but both the mean and the maximum size remained unchanged; only the minimum size rose from 3.5 to 5 mm. However, the number of *Aplexa* decreased obviously owing to mortality of the larger animals. On June 22nd, a short while before the beginning of the drought period even the mean size decreased as a consequence of mortality.

TABLE 2: MEAN, MINIMUM AND MAXIMUM SIZES OF SOME GENERATIONS OF APLEXA HYPNORUM.

	Generation A				Generation B				Generation C				Generation D			
	Number	Mean size	Minimum size	Maximum size	Number	Mean size	Minimum size	Maximum size	Number	Mean size	Minimum size	Maximum size	Number	Mean size	Minimum size	Maximum size
28- 3-'60	1	13			48	3.95	1½	8½								
26- 4-'60	5	12	11½	12½	147	6.36	3	10								
31- 5-'60					124	6.61	3	11								
24- 6-'60					45	5.57	4½	7								
26- 7-'60					8	4.63	4	5								
25- 8-'60					58	6.50	4	8½	56	1.87	1½	4				
1-10-'60					5	5.08	5½	7	198	2.40	1	4½				
31-10-'60					1	7			199	3.38	1½	5½				
28-11-'60									173	3.69	1½	6				
27-12-'60									76	4.17	2	6				
31- 1-'61									91	3.85	2	6				
25- 2-'61					1	9			436	4.02	1½	7				
30- 3-'61									442	6.34	2½	10				
28- 4-'61									349	9.26	3½	12				
29- 5-'61									294	9.28	5	12				
22- 6-'61									171	8.89	5½	12½				
24- 7-'61													1	2		
30- 8-'61																
28- 9-'61																
30-10-'61													324	1.33	1	3½
4-12-'61													188	1.93	1	4
10- 1-'62													71	2.42	1½	4½
5- 2-'62													85	2.76	1½	5
22- 2-'62													166	2.86	1½	5
20- 3-'62													164	3.44	2	7
26- 4-'62													169	5.33	2½	8
23- 5-'62													130	9.24	6	11½
25- 6-'62													35	10.03	8	12

c. Period III (July 24th, 1961 - June 25th, 1962):

On July 24th the ditch was completely dry and many empty shells of *Aplexa* were found lying around on the bottom. Only one living specimen, 2 mm in height, could be found. In August and September not a single living individual was observed. Terrestrial animals migrated from the banks into the dry bottom of the ditch, among others the land planarian *Rhynchodemus terrestris* (O. F. Müller) and the slug *Deroceras reticulatum* (O. F. Müller). In September the reed was mown and the ditch was cleaned.

At the end of October there was again water in the ditch. Numerous young specimens were found and these represented the new generation. Not a single specimen of the old generation survived the drought period of three months.

As the drought period ended in the middle of autumn, growth started late and proceeded slowly. As a result the hibernating animals were smaller than in the preceding year. In the beginning of December the mean size was only 1.93 mm, but by the end of February it had increased to 2.86 mm, although the conditions for growth were unfavourable during this winter. From December 23rd to January 3rd the ditch was frozen. On January 10th it was free of ice again, but at the end of January and the beginning of February the ditch was covered by ice. However, it was possible to take a sample on February 5th. After this time the ditch again became ice-covered and on February 22nd, when a sample was taken again, pieces of ice were drifting on the water. After that day the ditch was frozen yet for at least two weeks. Nevertheless, in this year also the number of *Aplexa* had increased considerably by the end of February.

As March was also a cold month, growth was slow and by March 20th the mean size had increased only to 3.44 mm. With the rise of temperature in April rapid growth started and was continued in May. On May 23rd the mean size amounted to 9.24 mm, and minimum as well as maximum sizes had greatly increased. At the same time the first spawns of *Aplexa* were found. On June 25th the ditch was dry again and yet 35 living specimens were found besides 172 empty shells.

DISCUSSION

From our data it is evident that the growth of a new generation starts when there is water again in the ditch after a period of drought. When the young snails hatch from the eggs is, however, not known. As the spawn, which is not easy to find, is deposited by the parent snails not long before the period of drought starts, and as young specimens never have been observed before this time, we think that the eggs withstand desiccation by remaining in the mud and do not hatch before there is water in the ditch again. However, we do not want to exclude the possibility that the young snails hatch already during the period of drought, and stay in the mud being protected there from too intense a desiccation. The find on July 24th, 1961, of a specimen 2 mm in height not long after the beginning of the drought may be an indication that the supposition is right. The fact that specimens of the size-group 1.5-2 mm are present during

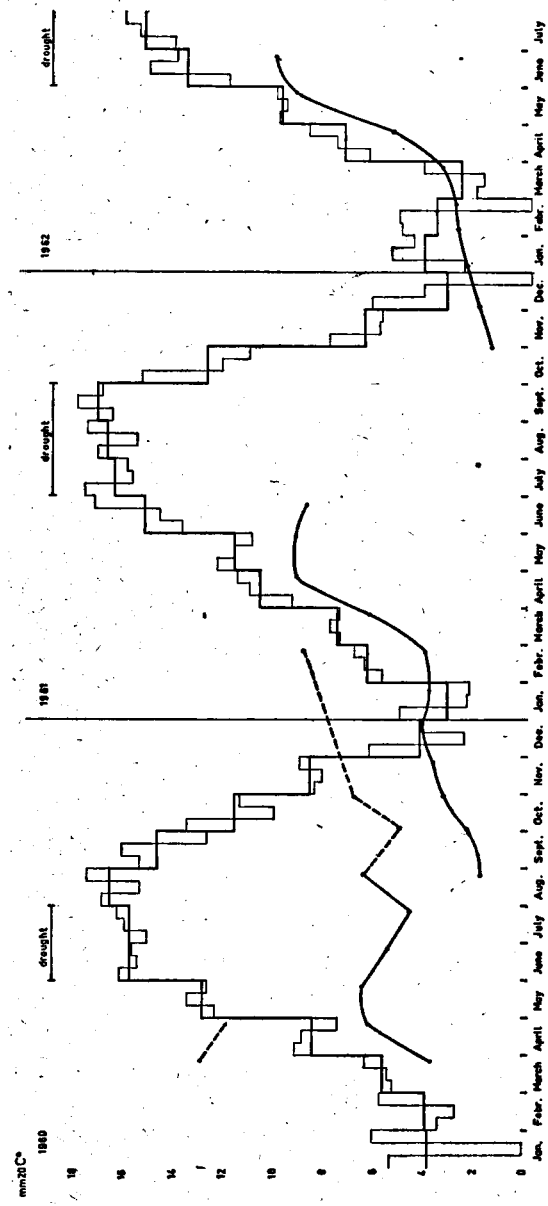

Fig. 3. The influence of temperature on the growth of *Aplexa hypnorum*. The mean sizes of *Aplexa hypnorum* are given from March 28th, 1960 to June 25th, 1962. In cases where the number is too small for determining a reliable average a broken curve has been drawn.
The mean monthly temperatures, (thick line) and the mean temperatures for every 10 days period (thin line), are given from January 1960 up to July 1962.

the whole autumn and winter, indicates, on the other hand, that hatching may occur at least during the whole autumn.

The growth becomes slower towards the end of the autumn owing to falling temperature. The size of the hibernating animals is dependent on the time when growth starts. In 1960 it began already in August and in 1961 not before October. At the end of November 1960 the mean size of the animals was 3.69 mm, but at the beginning of December 1961, only 1.93 mm.

Although mortality plays a part in the decrease of numbers, as was noted in the autumn of 1960 and 1961, it is highly probable that many specimens remain in the bottom of the ditch to the end of February. At that time they emerge from the mud and this seems to be independent of the temperature. In February 1961 the mean temperature was 6.4° C, in February 1962, in contrast only 3.6° C, but in the last week of that month the temperature fell to —0.2° C.

The winter does not harm the animals as they can tolerate frost, but the size remains nearly stationary during that season.

In spring growth starts again when temperature rises above 7° C. In 1960 growth had not started by the end of March, as the mean temperature was only 5.8° C. In February 1961 growth did not start at a mean temperature of 6.4° C, yet in March when the mean temperature was 7.6° C growth was already considerable. In March 1962, when cold weather prevailed and the mean temperature was only 2.6° C no growth was observed, but in April when the mean temperature was 7.5° C growth obviously had started.

The growth in spring continues for about two months. Then the mean size approaches its maximum. In 1961 the maximum was already reached at the end of April, more than two months before the drought started. In 1962 the mean size of the snails reached its maximum at the end of May, about four weeks before the start of the period of drought. In 1960, however, growth had stopped already after only a month at the end of April, long before the normal mean size of a mature population was reached, and long before the drought period began. It is probable, that the small quantity of water in the ditch was the limiting factor for the growth. Nevertheless, the maximum size reached by some specimens was 11 mm.

The drought starts in June or in July and lasts for two or three months. In 1960 a considerable number of immature *Aplexa* survived a drought of two months. After that not a single mature specimen was found alive. It appears from our observations that the smallest specimens have the best chance for surviving the unfavourable period. At the end of May before the period of drought started the mean size of the snails was 6.61 mm and the maximum size 11 mm.

By the end of June, when the ditch had become dry these figures decreased respectively to 5.57 and 7 mm, and in July even to 4.63 and 5 mm. The decrease of the numbers during the drought was due partly to mortality and partly to the fact that as the snails hide themselves in the mud they are then difficult to find. The fact that the younger stages of *Aplexa hypnorum* are the most resistent to unfavourable circumstances is in strong contrast to what is found in many other aquatic snails. In *Pseudamnicola confusa* (Frauenfeld), *Assiminea grayana* Fleming, *Littorina neritoides petraea* (Mont.) and *Leucophytia bidentata* (Mont.) the youngest stages are the most sensitive to unfavourable conditions.

When the drought begins the animals creep to the lowest situated and moistest spots or hide under stones, wood and other objects, and stay there with the aperture of the shell closely pressed against the bottom. Small specimens which held this position for three weeks, and which were put in water, crept about actively within a quarter of an hour. The larger specimens, however, had died already for the greater part. The time that the snails can maintain themselves is for the main part dependent on the quantity of precipitation, and the division of the latter in the course of the drought. Other factors as shelter and shade are also of importance.

Normally the life span of *Aplexa hypnorum* coincides with the time between the end of the summer drought in the one year and the beginning of the drought in the next year. For the generation 1960-61 this time was 10 months, and for the generation 1961-62 only 8 months. Sometimes several small snails survive a drought, as happened in 1960, and these may become older than a year.

When we compare the life cycle of *Aplexa hypnorum* with that of *Physa fontinalis* the difference is evident. According to DE WIT (1955) the latter species produces two generations in a year, a hibernating generation which starts to grow at the end of June and continues its existence up to the end of May in the following year, and a spring generation which starts in the beginning of May and lasts to the middle of August of the same year. *Aplexa hypnorum* produces only one generation in a year and this is comparable to the hibernating generation of *Physa*. The absence of a spring generation in *Aplexa* may be considered an adaptation to environmental conditions.

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SAMENVATTING

De levenscyclus van *Aplexa hypnorum* (L.) werd bestudeerd in een sloot in de Molenpolder bij Yerseke van maart 1960 tot augustus 1962. Iedere maand werden gedurende 30 minuten zoveel mogelijk slakjes verzameld, welke in het laboratorium werden geteld en gemeten, om daarna naar de sloot te worden teruggebracht. De resultaten van de metingen zijn weergegeven in Tabel 1 en Fig. 1 en 2. In Tabel 2 worden de gemiddelde grootte, alsmede de minimale en maximale afmetingen vermeld, gerangschikt per generatie.

Na de zomerse droogteperiode verschijnen in de sloot vele jonge slakjes, welke gestadig groeien tot het eind van november. Tussen november en het eind van februari staat de groei vrijwel stil, doch zodra de temperatuur is gestegen boven 7° C groeien de slakjes binnen 2 maanden uit tot geslachtsrijpe dieren met een gemiddelde grootte van 9-10 mm. Wanneer de sloot in de zomer uitdroogt sterven de dieren. Deze cyclus, welke als de normale beschouwd kan worden, werd doorlopen door de generaties 1960-61 en 1961-62. De generatie 1959-60, welke slechts gedeeltelijk werd bestudeerd, vertoont enige afwijkingen. De groei van deze generatie hield al lang voor het begin der droogteperiode op bij een gemiddelde grootte van 6,61 mm. Verder overleefde een aantal kleine exemplaren de droogteperiode, maar deze dieren stierven vrijwel alle in het begin van de herfst. De jonge dieren schijnen het minst gevoelig voor ongunstige milieu-omstandigheden te zijn.

Opvallend was dat zowel in 1960 als in 1961 gedurende de herfst het aantal dieren afnam doch in de daarop volgende maand februari een buitengewoon sterke toename te zien gaf. Het is zeer waarschijnlijk, dat deze dieren gedurende het gehele najaar al in de modder geleefd hebben, daar geen enkele aanwijzing werd gevonden, dat het hier om pas uitgekomen dieren gaat.

De levensduur van *Aplexa hypnorum* bedraagt 8-10 maanden, maar dieren die een droogteperiode overleven kunnen wellicht ouder dan een jaar worden.