

B A S T E R I A

TIJDSCHRIFT VAN DE NEDERLANDSE
MALACOLOGISCHE VERENIGING

VOL. 19, NO. 4, PAG. 45—76

24 - XII - 1955

The life cycle and some other biological details of the fresh-water snail *Physa fontinalis* (L.) (continued)

by

W. F. DE WIT

c. Incidental data of other stations.

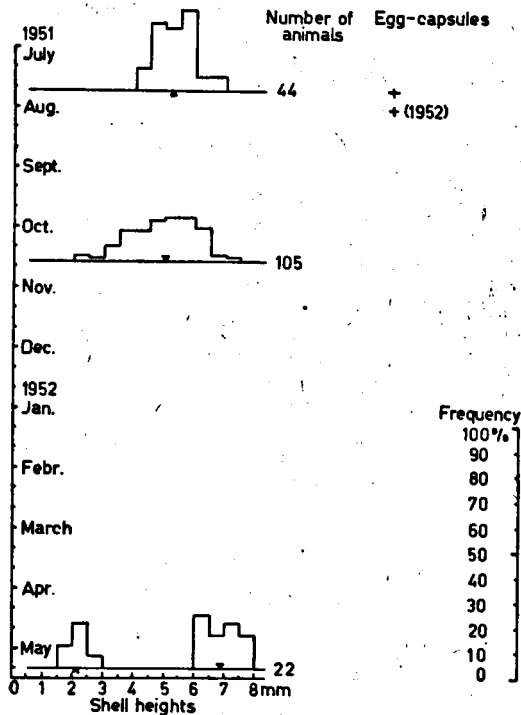
Although in general *Physa* of other locations was collected by searching the plants instead of by sieving, a procedure with which juvenile specimens are easily overlooked, in some cases conclusions as to the life history are possible.

At Bovenkerk (graph 4), 22-6-1951, a number of animals and some capsules were collected. The mean height amounted to 5.3 mm. On October 18th of the same year the average value was smaller, viz. 4.9 mm. According to the observations of Botshol, the growth was at least 0.5 mm per week in the period after the first observation, so it is unlikely that we are dealing with the same generation: the catch of October 18th concerns the wintering generation. On 10-5-1952 the snails had grown to a mean of 6.9 mm, whilst young ones of the new generation — undoubtedly the spring generation, cf. p. 43 — were already present. In the beginning of August 1952 again egg capsules were found.

The specimens of *Physa fontinalis* (L.) from Bovenkerk were smaller than those of Botshol. The data support the hypothesis that at least 2 generations per annum exist.

In the environment of Callantsoog, a village south of Den Helder on the North Sea coast, the wintering generation of 1951 appeared to die only in the course of June. Just east of the village of Callantsoog, in a ditch south of the Abbestederweg, 21 specimens of a size of 5.8—9.5 mm (mean 7.0 mm) were found on June 5th, whereas on the 24th out of 105 specimens the height of the largest shell amounted to 2.9 mm. So the wintering generation disappeared in the spell from 5th till 24th June.

At a station north of Callantsoog, in a ditch behind the dunes, the average heights on 9th and 12th June were 6.9 and 8.4 mm respectively. On the 29th and the 30th of the same month these values were 3.5 and 3.6 mm. Consequently the last adult snails died between 12th and 29th June.

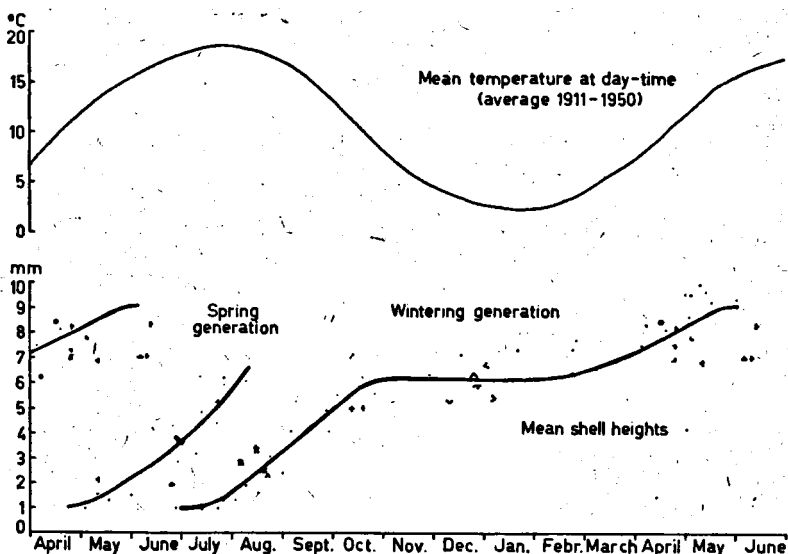


Graph 4. Frequency of the shell heights at Bovenkerk 1951-1952.

The occurrence of adults at Callantsoog on a later date as compared with Botshol may be explained from differences in climate (cf. the *Maandelijkse Overzichten van de Weersgesteldheid*, published by the Royal Netherlands Meteorological Institute). *Viz.* in the months of May and June the temperature at Callantsoog is about 2° C. lower than at Botshol.

For examining *Harnischbia vara* (Gtgh), a midge of which the larva lives under the mantle digitations of *Physa fontinalis* (L.), several other locations were visited on various dates. The mean values of the measurements, together with the previous records from Botshol,

Bovenkerk and Callantsoog, are represented in graph 5. The impression is gained that generally *Physa fontinalis* (L.) produces 2 generations annually.



Graph 5. Survey of the mean shell heights of *Physa fontinalis* (L.) collected during several years from various habitats (20).

d. Discussion of literature-data.

The sizes of shells of *Physa*, reported in various faunistic papers are cited hereafter. LEHMANN (1873): 8—12 mm; CLESSIN (1877): 10.5 mm, the largest ones approach 12 mm; HAZAY (1881): 8 mm; LAMEERE (1895): 12 mm; CHEMIN (1926) and L. GERMAIN (1931): 8—12 mm; ODHNER (1929): 10.7 mm; EHRMANN (1933): 9.5—10.5 mm, normally smaller, rarely up to 14 mm; VAN BENTHEM JUTTING (1933): up to 15 mm; MACAN (1949): about 12 mm and finally MANDAHL—BARTH (1949): 9—11 mm, var. *bulla* 10—13 mm.

This is in good agreement with the maximum heights of snails from Botshol, being 9—10 mm normally, whilst the largest ones measured 12 mm. Presumably all figures relate to the wintering generation.

There are some indications suggesting that in other European countries, too, there are 2 generations. HAZAY (1881) mentioned the occurrence of two breeding-periods of fresh-water pulmonates in

Hungary, (1) mid-April to the end of May and (2) beginning of August to mid-September. In Poland, near Krakow, WIERZEJSKI (1905) found *Physa* laying eggs in April in an early spring, otherwise in May, and this was continued until September. He collected capsules especially in May and the beginning of June, later on fewer, in August hardly any and in September many more. Animals, collected in a mild month of February, produced eggs as early as March in aquaria. This closely concurs with my observations, which concerned two generations. In contrast with this, NEKRASSOW (1929) reported from the river Kljasma near Moscow on *Physa fontinalis*: "Die massenhafte Eiablage erfolgt in der Sommermitte von Juli bis zur ersten Augushälfte". Possibly *Physa* produces only one generation per year in this climate.

4. REPRODUCTION

a. Period of oviposition.

The wintering generation starts laying eggs at the end of March or in the beginning of April. This was ascertained in 1953 and 1954 at Botshol.

Not a single capsule of *Physa* could be found on 5-3-1953, whereas 19 specimens were found on 20-3. In 1954 the search for capsules had a negative result on 27-3, but on 7-4 10 capsules were collected.

Here the temperature plays an important rôle, as is shown by the following observations. At room temperature the wintering generation could be induced to lay eggs as early as November. Animals collected in December become very lively at room temperature, begin to mate and lay eggs before long. In the field apparently copulations start as soon as the temperature is sufficiently high. However, other factors play a part as well, because, though in 1954 evidently oviposition started later than in 1953, the temperatures, the mean as well as the maximum values, were higher. Possibly the rather severe winter of 1954 had some influence.

DEWITT (1954, p. 124) observed copulating pairs of *Physa gyrina* Say in the field only during the month of April. "However, snails collected from November through April copulated when brought into the laboratory." (loc. cit.).

According to PRECHT (1936), the temperature at which *Planorbis corneus* (L.) commences oviposition is fixed at 12° C. For *Ancylus fluviatilis* Müller BONDESEN (1950) established a temperature of 7° C., and for *Physa fontinalis* (L.) I found a minimum temperature of 7—8° C. in 1953. Nevertheless it must be assumed that the temperature is not always the same for each species, but may vary from year to year and in different biotopes. E.g. on 21-3-1953 I found

3 capsules of *Planorbis corneus* (L), but the temperature had not exceeded 7—8° C. (cf. PRECHT).

Perhaps there is some conformity with the phenological observations on wild plants. In this respect recent studies (WILCKE, 1953 a & b) showed that the beginning of flowering of a number of plants was strikingly correlated with the sum of the daily temperatures, called "heat-sum". This magnitude could be calculated starting January 31st and held good in the 21 cases of wild plants inspected, observed during 12 years. It explains why the existing temperatures do not determine the start of flowering, but it stresses the importance of the temperatures during a preceding interval of time. As a matter of fact, the specific "heat-sum" was different for each species.

Unfortunately, it will be impracticable to collect the same amount of data on snails as was possible in the case of the wild plants with the cooperation of many workers in the whole country.

On 30-5-1953 I only succeeded in collecting 1 adult *Physa*. As the first capsules appeared about 21-3 (see above), the breeding-season proves to be approximately 2½ months, viz. from mid-March until the end of May.

The first juveniles were found in the catch of May 2nd. The embryonic development of the first-laid eggs thus requires about 6 weeks and presumably this period is shorter for the later capsules, in connection with the prevailing higher temperatures.

The snails of the spring generation began oviposition about June 27th 1953. Consequently the time necessary for maturation here was about 2 months, in accordance with HOLZFUSS (1914). On August 8th eggs were still found, on the 22nd no more. Here the breeding period amounted to about 6 weeks. This is in good agreement with the 5—7 weeks in 1952, as may be deduced from graph 1.

The embryonic development needs less time in summer — less than 2 weeks — as is shown in graph 2; on 8-8-1953 23 capsules were collected, a number of which, according to micro-examination, was obviously fresh. On the other hand, on 22-8-1953 not a single capsule could be traced, and even only few animals in the height-groups 0.5—1 and 1—1.5 mm, apparently freshly emerged young ones, were present.

In 1952 (graph 1) the situation was different: the duration of the presence of capsules was somewhat longer and even on September 27th 1 capsule was found, which, however, at room temperature soon hatched. It must have been produced by the spring generation, and its development was delayed by the sudden set-in of colder weather (in August the average air-temperature was 18½° C. — normally 18° C. —; in September 12½° C. — normally 15½° C. —).

	1951	1952	1953	1955
Mean temperature in May and April ¹⁾	10.7° C.	13.4° C.	12.9° C.	10.1° C.
Maximum temp. " " ¹⁾	13.7° C.	16.8° C.	15.5° C.	13.3° C.
Last observation of adult specimens	May 26th	May 10th	May 30th	June 4th
Number of specimens collected	108	4	1	17
Adults absent on	—	May 24th	—	—
Mean temperature July 10th - August 20th	—	18.0° C.	18.4° C.	—
Maximum temp. " " "	—	20.8° C.	21.7° C.	—
Last observation of adult specimens	—	Aug. 16th	Aug. 8th	—
Number of specimens collected	—	7	10	—
Adults absent on	—	Aug. 30th	Aug. 22nd	—
Last observation of capsules	—	Sept. 27th	Aug. 8th	—
Number of capsules collected	—	1	23	—
Capsules absent on	—	Oct. 25th	Aug. 22nd	—

¹⁾ Average of the air-temperatures of ten-day periods from the Monthly Reviews of the Weather Conditions, published by the Royal Netherlands Meteorological Institute (Maandelijkse Overzichten van de Weersgesteldheid).

Table 4. Comparison of some temperatures supposed to be important for the duration of life.

A comparison of the observations in the years 1951, 1952 and 1953 gives us an impression of the possible negative correlation between the temperature and the length of the life of the snails (see table 4). In connection with the prevailing temperatures before the death of the spring generation the observations of WREDE (1928, p. 317) on *Physa fontinalis* (L) are interesting: "20—25° C. Einige Tiere sind kontrahiert, andere sind sehr lebhaft; viele sterben, wenn sie einige Tage dieser Temperatur ausgesetzt sind, obwohl Sauerstoffmangel ausgeschlossen ist."

In the month of August in the upper layers of the water, especially between water plants (the milieu where *Physa* preferably lives) often very high temperatures could be measured, even up to 27° C. at 5 p.m. These conditions are very unfavourable for the snails. With due reserve, it might be concluded that relatively high temperatures correspond to a shorter duration of life.

In the field both generations show a definite difference with respect to the start of oviposition: The wintering animals are much larger than those of the spring generation in the beginning of the reproduction period. In the first case the snails have long been sexually mature, but unfavourable factors — mainly the low temperatures — delay propagation. In the other case, copulation etc. start as soon as they are mature, in other words: The beginning of reproduction of the wintering generation is defined by external, that of the spring generation by internal factors.

b. The relation between the size of the animals and the number of eggs per capsule.

The number of eggs in a capsule may vary considerably. The records of authors vary accordingly: PFEIFFER (1821) 12—18; MOQUIN-TANDON (1855) 5—20; LEHMANN (1873) 2—30; HAZAY (1881) 20—30; WIERZEJSKI (1905) 1—20, mean 10; PELSENEER (1920) 2—42; NEKRASSOW (1929) about 10, rarely 16—20; GERMAIN (1931) 5—22; VENMANS (1949) 6—27, mean 15 and finally BONDESEN (1950) up to 20.

From graphs 1 and 2 it is obvious, that the wintering generation at Botshol at the height of its breeding-season produces on an average 16—20 eggs per capsule, against only 6—8 for the spring generation in its breeding period. In 1953, when the observations were made as quantitatively and frequently as possible, the average of the first few capsules early in the spring was 11 eggs. Subsequent capsules contained more and more eggs and the average increased to a maximum of 19. With only two exceptions, all capsules contained 4 or more eggs, and in the course of time the maximum rose to 41

(see above, PELSENEER, 1920). In 1954 the picture was the same: on April 7th the average was 11.5, and on May 1st 16 eggs per capsule, the maxima being 16 and 35 respectively.

Station and date	Height of the shell in mm ¹⁾	Number of eggs per capsule ¹⁾
Bovenkerk 22-7-1951	5.27 ± 0.09	5.0
Botshol 6-4-1952	8.29 ± 0.13	16.1 ± 0.6
30-4-1952	9.52 ± 0.27	17.4 ± 0.9
12-7-1952	4.83 ± 0.12	7.3 ± 0.3
2-8-1952	5.89 ± 0.25	7.0 ± 0.4
16-8-1952	6.29 ± 0.17	8.0 ± 0.5
30-8-1952	† ²⁾	8.1 ± 0.9
21-3-1953	not determined	10.8 ± 0.7
4-4-1953	7.51 ± 0.22	14.4 ± 0.6
18-4-1953	8.06 ± 0.20	16.3 ± 0.5
2-5-1953	8.62 ± 0.20	17.4 ± 0.5
16-5-1953	9.29 ± 0.21	19.1 ± 0.5
30-5-1953	† ²⁾	18.5 ± 1.8
11-7-1953	6.2 ± 0.15	8.0 ± 0.24
25-7-1953	5.9 ± 0.27	7.6 ± 0.5
8-8-1953	6.0 ± 0.14	5.9 ± 0.6
7-4-1954	8.26 ± 0.35	11.5 ± 1.3
1-5-1954	9.34 ± 0.37	16.2 ± 0.4
20-7-1954	4.36 ± 0.14	5.6 ± 0.3
17-8-1954	5.08 ± 0.36	6.0 ± 0.2
4-6-1955	9.66 ± 0.30	16.8 ± 1.6

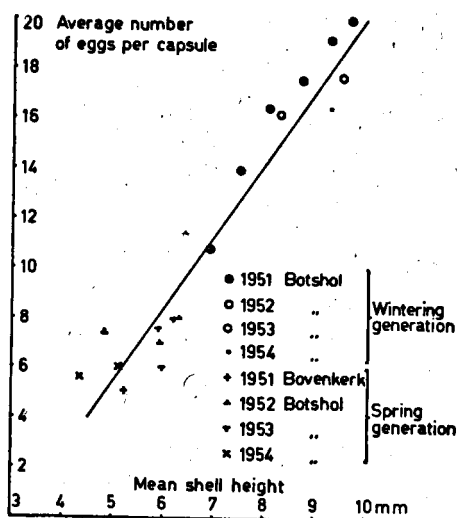
¹⁾ The arithmetic mean $\bar{x} = \frac{\sum x}{n}$ and the mean deviation of the mean $\pm \frac{\sigma}{\sqrt{n}}$; $\sigma = \sqrt{\frac{\sum (x - \bar{x})^2}{n-1}}$ are mentioned. ²⁾ All adult specimens dead.

Table 5. Relation between the mean values of the shell heights and the number of eggs per capsule of *Physa fontinalis* (L.).

For the spring generation the relation is less clear (cf. table 5): in 1952 the average increased, in 1953 it decreased and in 1954 it slightly rose again.

When the number of eggs per capsule is plotted against the heights of the shells (graph 6), a marked positive correlation between these two becomes apparent: large animals produce capsules with

more eggs than smaller ones. This correlation has also been proved statistically significant.¹⁾



Graph 6. Relation between the average number of eggs per capsule and the mean shell heights.

The above-mentioned correlation is indicated by PRECHT (1936) for *Planorbis corneus* (L.), although no sizes are recorded. A small race laid capsules with 1—46 ova (mean of 257 capsules: 15.6), whereas a larger race produced capsules with 16—82 ova (mean of 43 capsules: 53.5). For the same species the figures of OLDHAM (1930) confirm this conclusion: from 2 snails, emerged in 1922, 63 capsules were obtained during some months in 1925, with 28 eggs on an average; in 1926 the mean of 39 capsules was 33 eggs. As a matter of fact, in 1925 the animals were smaller than in 1926.

FELIKSIK (1939, table 5, p. 33) reported that in April the mean number of ova per capsule for *Myxas glutinosa* (Müller) in the field was 29 and in May this increased to 53.

¹⁾ The correlation coefficient $r = \frac{\Sigma (x - \bar{x})(y - \bar{y})}{\sqrt{\Sigma (x - \bar{x})^2 \Sigma (y - \bar{y})^2}} = + 0.978 \pm 0.010$.

Assuming a number of degrees of freedom of 16 the chance of fortuitous correlation in this case is much less than 0.1% (see BROWNLEE, 1949). The equation of the line of regression is $Y = 2.90X - 9.18$; Y = the number of eggs per capsule; X = mean height.

The fact that DEWITT (1954, p. 126) did not establish a close correlation with *Physa gyrina* Say, is perhaps due to the differences between field and aquarium observations which could not be completely separated. This author used snails collected in the field for aquarium experiments; in the beginning the number of eggs per capsule is almost the same as found in nature, but later on this decreases rapidly under the artificial conditions.

Above (p. 53) the existence of a positive correlation of the mean number of eggs per capsule to the mean shell height is demonstrated. However, it must be taken into account, that the capsules, as found in nature, were of various ages. Thus the capsules collected on 2-5-1953 had already partly been deposited about 21-3, when the average shell height amounted to 6.9 mm, whilst on 2-5 this value was 8.6 mm. We therefore will try to find a better relation, taking this fact into consideration. The fortnightly observations in the spring of 1953 are most suitable.

The animals deposit in the course of the time several capsules with a variable number of eggs. So in reality we fixed the average number of eggs per capsule from the 1st till the n th capsule, deposited on the date of observation or a short time before. Nevertheless, an approximation of the real situation is possible. In table 6 the data of the spring breeding season of 1953 are reproduced. This table needs an explanation. On the 21st of March only capsules were collected. The necessary corresponding mean height of the shells fails, but it can be deduced graphically: we find 6.9 mm. The error that we thus make will be small. Moreover, the number of animals is unknown. Apparently the number of snails collected on the other dates fluctuates only between relatively narrow limits, viz. 13—23, mean $18\frac{1}{2}$. We will take this number for March 21st. Here the error will be larger, but the figure is of minor importance, as will be shown hereafter.

In view of the method of collecting applied, it may be taken that on an average the capsules collected derive from the animals collected with them. We calculate how many capsules and eggs are produced per animal (cf. table 6, columns 7 & 8). The first juveniles were collected on May 2nd (column 3); their sizes indicate recent emergence. It is permissible to count them potentially as eggs, and the real number of eggs totally produced was larger. The corrected number is given in brackets.

On May 16th the number of juveniles was much larger, viz. 364. Here, too, a correction is applied. The exact number of capsules must have been higher as well, and this is at least 10.

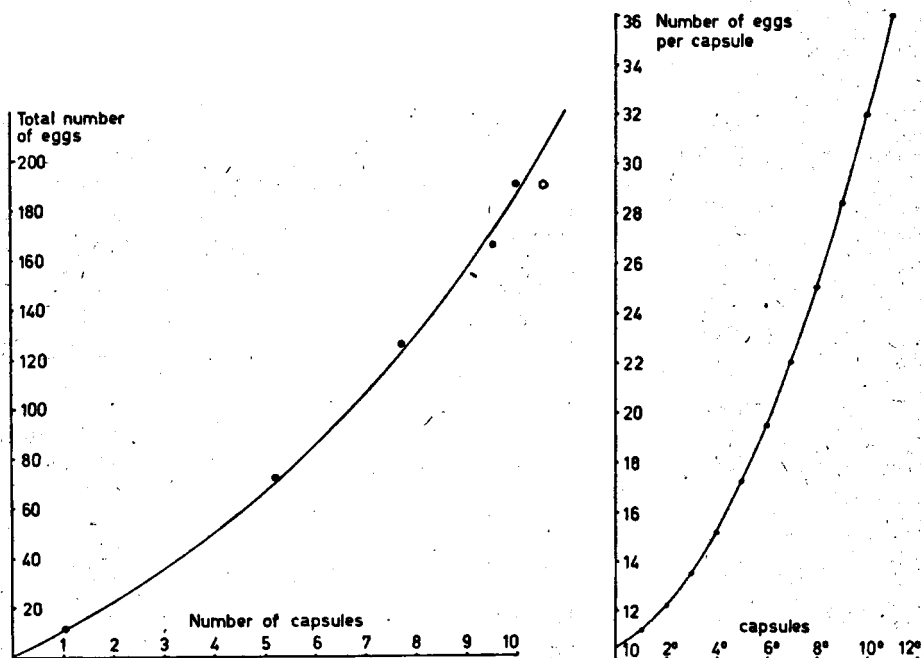
The number of eggs per capsule increases: after 1 capsule the

1953	Mean shell height (mm)	Number of snails ¹⁾	Number of capsules	Number of ova ²⁾	Average number of ova per capsule	Number of capsules per animal ²⁾	Number of ova per animal ²⁾	Calculated number of eggs per capsule as a function of the order in which they are deposited
21/3	6.9 ²⁾	18½ ⁴⁾	19	206	10.84	1.03	11.1	11.2
4/4	7.51	13	68	944	13.90	5.23	72.6	17.6
18/4	8.06	20	154	2519	16.34	7.70	126.0	24.0
2/5	8.62	18	171	2970	17.38	9.50	165.0	30.1
		(13)		(2983)		(9.54)	(165.8)	
16/5	9.29	23	211	4024	19.08	9.18	175.0	30.8
		(364)		(4388)		(10.6)	(190.5)	

1) Number of juveniles mentioned in brackets. 2) Corrected numbers in brackets. 3) By interpolation. 4) Not determined, average of the numbers on the other dates.

Table 6. Data on the egg-capsules collected in the spring of 1953 at Boshol (cf. text).

mean is 10.8, after 5.2 capsules 13.9, after 7.7 16.3, after 9.5 17.4 and finally after > 10 capsules about 19.1. The first-laid eggs (March 21st) are partly included in the figures of May 2nd and all in those of April 4th and 18th and the same argumentation is applicable with regard to the material of other dates. What is observed in an integral, and the exact number of eggs per capsule belonging to the subsequent capsules can be calculated by differentiation.

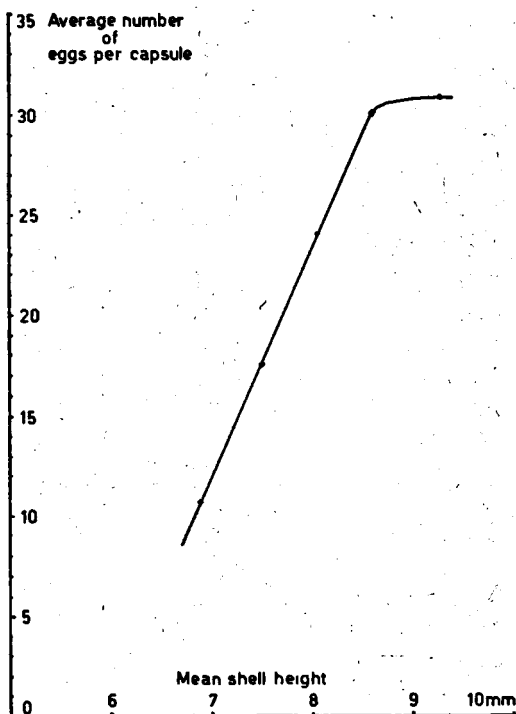


Graph 7. (left) Total number of ova laid after the production of a number of capsules (Botshol, spring 1953).

Graph 8. (right) Number of eggs in the successive capsules as calculated from graph 7 (Botshol, spring 1953).

In graph 7 the number of ova is plotted against the number of capsules. Graph 8 shows the graphically differentiated curve: the number of eggs increases with the order in which the capsules are laid at an increasing rate. The curve of graph 8 may be represented empirically (by means of continued differentiation) by the equation $p_n = 10.5 + 0.5 n + 0.165 n^2$, where p_n = the number of eggs

per capsule as a function of n , the number of capsules per animal. Graph 7 (ova versus capsules) is approximately represented by: $o_n = 10.5 n + 0.25 n^2 + 0.055 n^3$, in which $o_n =$ the total number of ova as a function of n .



Graph 9. Relation between the mean shell heights and the calculated number of eggs per capsule (Botshol, spring 1953).

An approximating correction for the number of juveniles on May 16th is now possible. Per adult animal 15.2 juveniles were found, deriving from the same number of eggs. It is reasonable to assume, that these early-hatched eggs come from the capsules produced first. From graph 7 we can now estimate that these 15.2 ova derive from 1.4 capsules on an average. We collected on the above date 9.2 capsules per animal, but in all at least 10.6 capsules per animal must have been laid.

Returning to the problem of the relation between the number of

eggs per capsule and the size of the animals (i.e. the shell heights), we can deduce from table 6 and graph 8 that the snails with a mean shell height of e.g. 8.06 mm and with a mean number of capsules laid of 7.7, will produce capsules with 24 eggs on an average (18-4-1953). These values are reported in the last column of table 6.

The result is shown in graph 9, where (in this case) a linear relation is found between the calculated number of eggs and the height of the shells with a maximum of about 31 eggs on an average. Moreover we could establish, that the wintering generation may produce 10—11 capsules per animal and that the mean total egg production per animal may amount to about 200.

c. Mortality.

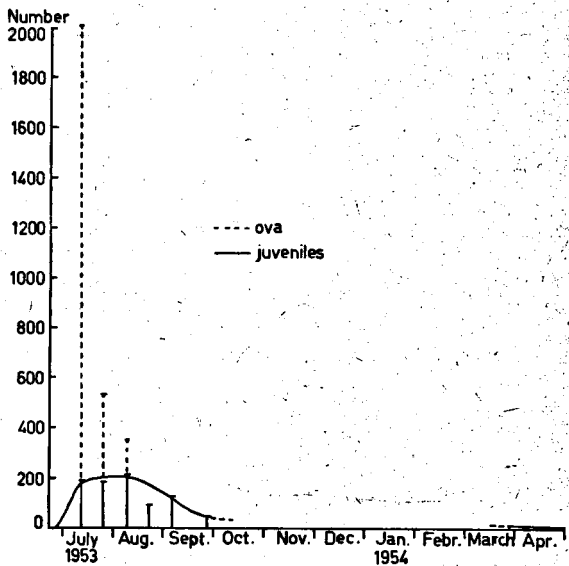
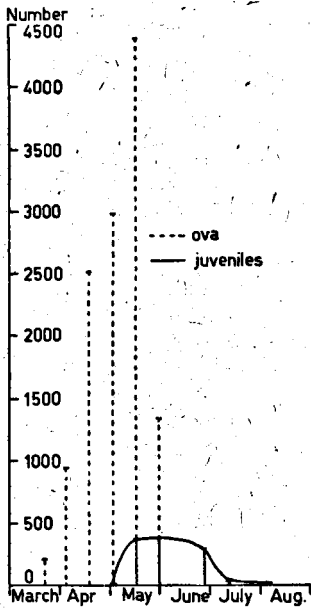
We now will try to find out what happens with the eggs. The full-grown embryos leave the capsules by rasping themselves with their radula through the jelly-like envelopes until they have freed themselves. The first few embryos are soon followed by the others of the same capsule. We therefore seldom will find capsules in this stage with more than one or two eggs that still have to hatch; these last eggs then contain almost full-grown living embryos. The remark of PELSENEER (1925, p. 295) on sterile eggs — without an egg-cell —: "*Limnaea stagnalis* et *Physa fontinalis*, toute dernière coque" is not clear to me, as I never noticed anything like that.

Parasites are not present in the capsules laid by the wintering generation, and in natural circumstances I have never found capsules that were attacked. Therefore it is not likely that a quantity worth mentioning is lost by predatism; practically all eggs develop and hatch. Nevertheless the number of eggs present in a certain amount of plant material is much larger than the number of juveniles found afterwards: the young ones rapidly decrease in number¹⁾. Graphs 10, 11 and 12 give an impression of the course of the quantity of snails per unit of plant material.

The maximum number of remaining juveniles of the spring generation 1953 amounted to about 400, but the total number of young ones and eggs exceeds 4000, consequently about 9/10 of the newly emerged snails died (graph 10).

¹⁾ This agrees well with the observations of BOYCOTT (1936, p. 123, loc. cit.): „One sees a pond, for instance, with vast numbers of capsules of *Limnaea peregra* or *Planorbis complanatus*, and on searching through them one finds that the eggs are developing in a healthy way almost without exceptions. Yet in two or three weeks time it may be quite difficult to find young ones much more numerous than adults will be later on: the weeding out seems to occur very soon after birth and the viviparous species are relatively immune.”

On an average the amount of young ones is constant for some time (mid-May till the end of June), but afterwards it falls off quickly, whilst the first capsules of this generation are found.

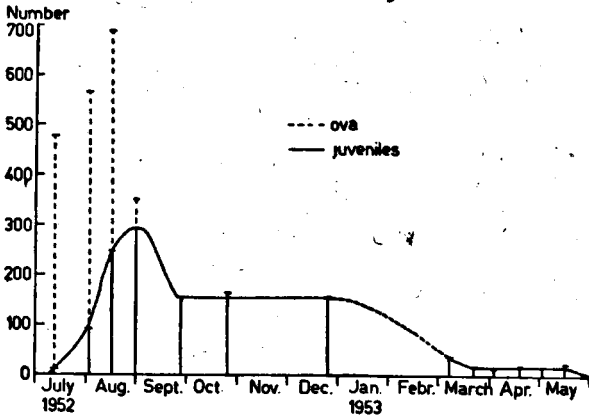


Graph 10. (left) Impression of the mortality among the animals of the spring generation Botshol 1953.

Graph 11. (right) Impression of the mortality among the animals of the wintering generation Botshol 1953.

In this season the temperatures are so high, that the development needs about 2 weeks. WIERZEJSKI (1905, p. 518) reported an embryonic period of about 15 days in June, yet on p. 515 the author remarks, that in July "die vollständige Ausbildung unter normalen Bedingungen gewöhnlich nur 4 Tage in Anspruch nimmt". Presumably this is a misprint. HAZAY (1881, p. 44) mentions 15 days to be necessary for the development. DEWITT (1954) reported an embryonic development in *Physa gyrina* Say at 20—30° C of 7—8 days, at 30° C this time was even decreased by 24—36 hours. It must be admitted that the fortnightly observation in this period is not sufficient to obtain a clear impression. In view of the rapid development it is likely that the capsules present on a certain date, have largely hatched

a fortnight later, so that of those found then most or all are assumed to be different from the former and should be added to them. For the months of July and August 1953 we then calculate about 2300 eggs, whilst a maximum of about 200 juveniles are found (graph 11); in that case too at least 9/10 of the snails succumbed in an early stage. The only parasites — if parasites they are — of the eggs in summer are ciliates (cf. p. 65) but their occurrence is rather rare. Here, too, nearly all eggs hatch.



Graph 12. Impression of the mortality among the animals of the wintering generation Botshol 1952.

In accordance with the spring generation the amount of snails emerged from the eggs remains more or less constant for some time, then decreases sharply (end of September), whilst after the winter months of January and February 1954 about 10 specimens only were left.

For the wintering generation of 1952 (graph 12) the relations are somewhat different. The numbers of eggs observed are somewhat smaller, viz. totally about 1400. We have to bear in mind here that capsules laid and hatched between July 12th and August 2nd — a spell of 3 weeks — have escaped observation; consequently the true number must have been higher. The maximum number of juveniles found is about 300, so at least 80% died. In the autumn their quantity remained nearly constant (circa 150), but after the winter only few are left. This is in good agreement with the 96% mortality found by D. K. MCE. KEVAN (1943) for *Stagnicola catascopium* (Say).

The wintering generation produces about 10 capsules and 200 eggs (see p. 58). With regard to the spring generation we only can make an estimate, because of the rapid changes. In 1952 about 150 specimens of *Physa fontinalis* (L.) were collected on 28th June, just before the first capsules were observed, and in all about 180 capsules were found. Thus the animals of the spring generation brought forth 1 or 2 capsules on an average. In 1953 these figures were: 230 *Physas* and 300 capsules, consequently the mean is 1 or 2 capsules as well. These contain on an average 6—8 ova.

Summarizing we may state that the contribution to the reproduction per animal amounts to about 200 eggs for the wintering generation and to 8—15 for the spring generation.

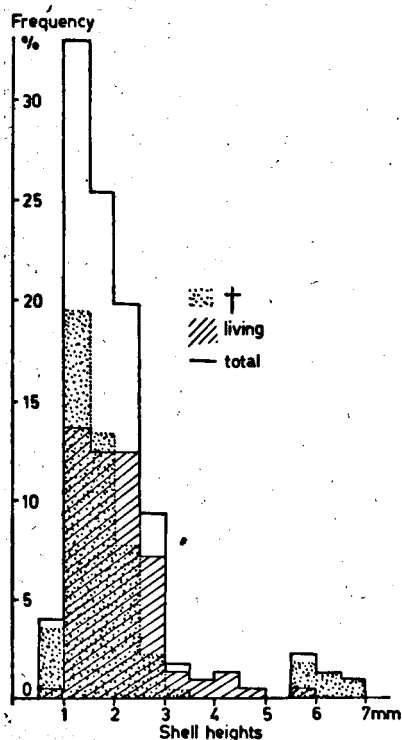
The extremely high mortality of the newly emerged snails is demonstrated by the following. Whether the snails were collected dead or alive has not been taken into account in the treatment of the material, it being assumed that the dead specimens died recently. Generally the empty shells vanish quickly. They sink to the bottom and thus are not collected together with the plant material. During the breeding season of the spring generation the mortality of the juveniles as well as of the adults is high. The vegetation is then luxuriant, and in calm weather the empty shells stick to the vegetation for some time. On August 8th 1953 the number of empty shells was exceptionnally high (about 50%) and because of that reason they were measured separately (graph 13). Obviously the dead specimens are among the smallest — wintering generation — and the largest snails — spring generation —. This supports the distinction of the snails according to the frequency curves we made on p. 40.

d. Particulars of the capsules: substrates, abnormalities and possible parasites.

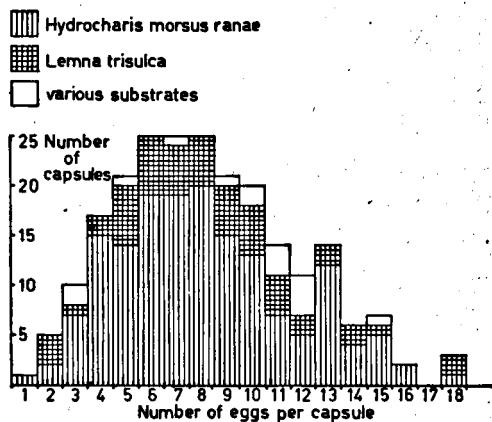
The substrates employed by the snails vary with the season. In spring, the breeding period of the wintering generation, only few plants are left in the ditch. In the beginning the snails lay their eggs on any kind of substrate: *Rhizoclonium hieroglyphicum* (C. A. Agardh) Kützing — an alga —, *Lemna trisulca* L., *Potamogeton pectinatus* L., rests of plants like *Rumex hydrolapathum* Huds., *Iris pseudacorus* L. etc. and on young plants of *Mentha aquatica* L., *Nasturtium officinale* R. Br. etc.. Towards the end of this period when the winterbuds of *Hydrocharis morsus-ranae* L. have developed into good plants, this plant is the preferred substrate for the capsules. In one case a shell of *Lymnaea stagnalis* (L.) had been chosen.

In summer, when the spring generation starts oviposition, *Hydrocharis morsus-ranae* L. is the dominating plant besides the alga *Rhi-*

zoelonium hieroglyphicum (C. A. Agardh) Kützing. By far most of the capsules are then deposited on the frogbit. An example is given



Graph 13. (left) Comparison of the frequency of the shell heights of the living and of the dead snails (collected at Botshol, 8-8-1953).



Graph 14. (right) Distribution of the capsules of *Physa fontinalis* (L) on various substrates (collected at Botshol, 11-7-1953).

in graph 14. Of a total of 227 capsules 160 were found on *Hydrocharis*, of which 91 on the swimming leaves, 37 on the leaf-stalks and 31 on the leaf-sheaths; 51 were on *Lemna trisulca* L. and 16 on various substrates like grasses, *Nasturtium* and algae. There may be some preference for the floating leaves of *Hydrocharis* as a horizontal and level subsoil, though other parts of the plants are employed as well. It is questionable whether the stimulating effect, observed by RAVEN & BRETSCHNEIDER (1942) after the addition of *Hydrocharis* to aquaria lacking waterplants, on the egg-laying of *Lymnaea stag-*

nalis (L.) has a similar effect in the field on *Physa fontinalis* (L.), since a ny stimulus loses its effect when applied permanently. VAN NIEUWENHOVEN & LEVER (1946) remarked that almost exclusively the leaves had the stimulating effect, and scarcely the stalks. The question will be discussed in detail on p. 66 (notes on the behaviour). Graph 14 demonstrates, that the duckweed *Lemna trisulca* L. may serve as a substrate for both large and small capsules; in this case too there was no preference.

Abnormal eggs were generally rare. BONDESEN (1950) distinguishes as abnormal eggs e.g. dwarf and giant eggs, eggs without development, eggs without an egg-cell, and eggs with two or more egg-cells. The high percentage of abnormal cases observed by that author in experiments in aquaria using *Ancylus fluviatilis* Müll. was not noticed with *Physa* in the field. A marked difference between normal, dwarf and giant eggs of *Physa* was only detectable in a few cases, and particularly much larger eggs were very rare. Only the measuring of a large number of eggs enables us to decide whether their size is abnormal. Dwarf eggs were more numerous, though scarcely one in a thousand was found. They often differed morphologically.

Number of egg cells per egg		0	1	2	3	5	6	many	Number of capsules	Total number of eggs
Produced by the wintering generation	number of eggs	23	16,527	72	3	2	1	1	989	16,629
	0/00	1.4	993.9	4.3	0.2	0.1	0.1	0.1		
Produced by the spring generation	number of eggs	—	4,154	7	3	—	—	—	565	4,164
	0/00	—	997.6	1.7	0.7	—	—	—		

Table 7. Frequency of the occurrence of eggs without or with more than one egg-cell in capsules of *Physa fontinalis* (L.) in the field.

Eggs lacking an egg-cell were somewhat more frequent (see table 7), 23 of a total of about 20,000. When the capsules of the spring generation are compared with those produced by the wintering one, it is striking that eggs without an egg-cell do not occur among the former.

The phenomenon of the absence of egg-cells in breeding experiments with *Physa fontinalis* (L.) was first noticed by WIERZEJSKI

(1905). In bad conditions the number of eggs per capsule decreased to 1, in which the cell sometimes lacked, and even capsules without any eggs or egg-cells were found. The same facts have been recorded from *Planorbis corneus* and *Lymnaea stagnalis* by BLOCH (1938, pp. 163 and 164) in the aquarium. DEWITT (1954, p. 127) reported eggs without an egg-cell and capsules without eggs in his aquarium experiments with *Physa gyrina* Say. My experiments confirm their observations, it is a typical degeneration phenomenon. Possibly the presence of eggs without an egg-cell in the capsules in the spring — from the wintering, adult animals — has to be understood in this way, although the number of eggs per capsule was normal in these cases.

Eggs of *Physa fontinalis* (L.) with more than one egg-cell ("twins" etc.) have been found by several authors (WIERZEJSKI, 1905: up to 20; PELSENEER, 1920: 2—32; LÖHNER, 1924: > 20).

Various authors (e.g. CRABB, 1931; BONDESEN, 1950) argued, that among gastropods twins etc. do not originate from one egg-cell, but that two or more egg-cells happen to have gone into one egg. A similar event is conceivable when studying the way in which a capsule is formed in *Lymnaea stagnalis* (L.), described in detail and figured by BRETSCHNEIDER (1946).

In Botshol I found among about 21,000 eggs 79 "twins", 6 "triplets", 2 "quintuplets", 1 "sextuplet" and 1 egg containing many egg-cells (see table 7). Out of about 26,000 eggs of *Physa gyrina* Say DEWITT (1954, p. 127) observed 22 eggs with two or more egg-cells. The tendency of producing "twins" was accompanied by the production of eggs lacking an egg-cell. A certain hereditary predisposition in this respect is demonstrated by WINSOR & WINSOR (1932) but a mendelian relation did not occur. Consequently it is possible that a population of some species produces many more "polyvitelline" eggs than another. LÖHNER (1924) concluded that specimens of *Physa fontinalis* (L.) poisoned by copper ions produced more "polyvitelline" eggs than normally. From the photograph that he adds it is clear that these are especially the last-laid eggs of the capsule, which contain 2 egg-cells, whilst the very last one has more than 20 cells.

From my own experience with aquarium-reared capsules, I can state that it frequently concerned the last eggs in a capsule. Possibly there is a deficiency of materials (albumens) for the formation of normal eggs from the available egg-cells.

In spring I often came across eggs of insects in the capsules of *Physa fontinalis* (L.), mostly one or two, but occasionally up to ten. In nearly all instances these had been deposited in the pallium ge-

latinusum (cf. BONDESEN, 1950) or underneath it, between the eggs. Some of the eggs developed and the third larval stage could be identified as a larva of the water beetle *Haliplus ruficollis* De Geer (see HENDRIKSEN, 1930, and J. R. HICKMAN, 1929). The larva left the capsule, without damaging the developing embryos of *Physa*. The young snails emerged normally and were not attacked; the larvae fed on vegetable matter. The occurrence of the eggs of *Haliplidae* in the capsules of *Lymnaea* and *Physa* is mentioned by NEKRASSOW (1929). Their presence should merely be assumed being incidental.

The water beetles of the genus *Haliplus* normally feed on the content of plant cells and lay their eggs within the cells, especially of thread-algae, but also of various other water plants. The presence of an egg-capsule apparently does not prevent the beetles from depositing their eggs. *Peltodytes*, the most important genus of the *Haliplidae* except *Haliplus*, lays its ova on the plants; these were not met upon the capsules.

In the summer capsules from time to time partially developed or undeveloped eggs, filled with ciliates, were observed. I could not establish whether these acted as parasites of the eggs and consequently killed them, or whether, on the contrary, the eggs died and the ciliates found a welcome nourishment in them. In the spring capsules ciliates were never observed.

Several authors (GIARD, 1908; GLASCOTT, 1893; STEVENS, 1912; NEKRASSOW, 1929) mention the occurrence of a parasitic rotifer, *Proales gigantea* (Glascott) (size about 0.5 mm) in the capsules of *Physa* and *Lymnaea*-species. Laboriously the animals work themselves through the various egg-envelopes to the inside of an egg, kill the embryo and there lay their eggs. In this way every snail egg may contain a small family of *Proales*-specimens. Unfortunately, I did not find them in the capsules inspected.

5. SOME NOTES ON THE BEHAVIOUR

Physa is one of the most rapid snails and moreover responds very quickly to attacks etc. PELSENEER (1935, p. 198) reports a velocity of 6 cm/min. I could confirm this observation: even snails with a shell height of 5 mm may move at the rate of 6—7 cm/min. A comparison with some other fresh-water pulmonates, larger and smaller (e.g. *Planorbis corneus* — max. diameter 35 mm — : 7 cm/min; *Lymnaea stagnalis* — max. height 65 mm — : 8.5 cm/min.; *Ancylus fluviatilis* — max. diameter 9 mm — : 1.3 cm/min., PELSENEER, 1935) stresses the liveliness of our Bladder snail.

The speed of the newly emerged juveniles already attracted the

attention of HAZAY (1881), who remarked: "Das austretende Thierchen ist weisslich, sehr lang, sein spitzes Fussende reicht über die Schale hinaus dasselbe bewegt sich mit ausserordentlicher Schnelligkeit."

In an aquarium it is a fairly normal phenomenon that under certain conditions pulmonates are found outside the water, staying motionless on the walls. Especially Lymnaeidae and Planorbidae show this habit, but I never observed it in *Physa fontinalis*. Perhaps this is connected with the fact that the natural habitat of *Physa* is never a temporary water, which may serve as a good habitat of a number of Lymnaeidae and Planorbidae.

On the contrary DEWITT (1954, p. 130) reported that many young *Physa gyrina* Say crawled out of the water, but established (p. 132) that this *Physa* species may be found in semi-permanent waters.

RAVEN & BRETSCHNEIDER (1942) could induce *Lymnaea stagnalis* to produce egg capsules in a very limited time (say about three hours, dependent on the temperature) by adding frogbit, *Hydrocharis morsus-ranae* to the glasses, which did not contain any waterplant. VENMANS (1949) found under experimental conditions an effect after the introduction of frogbit with respect to *Physa fontinalis*, but did not notice the exact time after which oviposition took place. The surprising effect on *Lymnaea stagnalis*, observed by RAVEN & BRETSCHNEIDER and still in use at the Zoological Laboratory of the University of Utrecht for controlling egg production thus is not established with certainty in the case of *Physa fontinalis*. From my own experience *Physa fontinalis* in glasses without waterplants can be stimulated to oviposit after the addition of e.g. water-thyme, *Elodea canadensis*, but not in a similar short time thereafter. Whether other waterplants were present in the experiments of VENMANS before the introduction of *Hydrocharis* is not described.

DEWITT (1954) did not observe a change in the pattern of oviposition of *Physa gyrina* after the addition of *Elodea*, but in his experiments, too, it is not clear whether or not other waterplants were present before the introduction. In his case "a change of water (20—23° C.) served to stimulate *Physa gyrina* to oviposit within one to two hours." (loc. cit., p. 125).

The experiments of RAVEN & BRETSCHNEIDER (1942) on this object were extended by VAN NIEUWENHOVEN & LEVER (1946). These authors did not establish an effect after the introduction of *Elodea* on the oviposition of *Lymnaea stagnalis*, but in my opinion the water of their aquaria might have contained too much oxygen to be con-

siderably increased by *Elodea*. They concluded, that "in nature the effects of temperature and oxygen content, which both increase with illumination will probably intensify each other mutually".

The majority of the eggs of *Physa fontinalis* are laid in the very early morning, first mentioned by PELSENEER (1926), which I can confirm wholly: out of 27 capsules 23 were deposited at night or early in the morning. Moreover DEWITT (1954) reported: "in the laboratory, *Physa gyrina* oviposited throughout a 24-hour period but showed a definite tendency to lay eggs during the early morning hours."

The oxygen content of the water, which is at a minimal value during the night due to the respiration of plants and animals, is increased by the plants by assimilation, especially by those with floating leaves which receive most of the solar radiation after sunrise. Moreover the temperature of the superficial water layers — the preferred place for oviposition in the field — is increased. Presumably these factors — considering the observations of the above mentioned authors — provide the stimuli for the oviposition under natural conditions.

Many excellent observations on *Physa fontinalis* have been carried out by PELSENEER (e.g. 1935). According to this author a copulation takes two hours. I, too noticed snails mating for several hours. In *Physa gyrina* according to DEWITT (1954), this amounted to one hour.

6. SUMMARY

The life cycle and some other biological details of the fresh-water pulmonate *Physa fontinalis* (L.) were studied in the field during some years. The main locality was at Botshol, a polder about 15 km south of Amsterdam.

There, as well as on some other spots, two generations of *Physa* per annum occurred: a spring generation from early in May till the middle of August and a wintering generation from the close of June until the end of May of the next year. The principal differences between the two generations are compiled in the table on the next page.

The beginning of oviposition by the wintering generation is determined by external factors, mainly the temperature. The time of oviposition by the spring generation depends on internal factors, viz. sexual maturity.

It has been established that there is a significant positive correlation between the number of eggs per capsule and the size of the animals.

	SPRING GENERATION	WINTERING GENERATION
Period of occurrence	End of June till end of May	Early of May till mid-August
Maximum life	11 months	3½ months
Average maximum height of shell	about 9 mm	about 6 mm
Breeding period	End of March till end of May	End of June till mid-August
Number of eggs per capsule	2—42	1—18
Average number of eggs per capsule	16—18	6—8
Average number of capsules per animal	about 10	1 or 2

Table 8. Comparison of spring and wintering generations.

No clear preference for particular substrates was observed. Abnormal eggs were rarely present in the field; eggs lacking an egg-cell were only produced by the wintering generation, and presumably may be looked upon as a sign of decay.

All the adult animals of both generations die after the breeding season. Nearly all eggs hatch, but among the very young snails mortality is high, at least 90%.

In the winter months, when the temperature is 6° C. or lower for 4—5 months, growth practically ceases.

The presence of eggs of Haliplidae in the egg-capsules in spring was considered to be fortuitous. Some of them could be identified as *Haliplus ruficollis* (de Geer).

Possible stimuli for the oviposition under natural conditions are discussed.

7. REFERENCES

- BACKMANN, G., 1943. Der Lebenslauf der Organismen nebst kritischen Betrachtungen zu meiner Wachstumstheorie. Z. Altersforsch., vol. 4, pp. 237—290.
- BAILY, J. L., 1931. Some data on growth, longevity and fecundity in *Lymnaea columella* Say. Biol. Gen., vol. 7, pp. 407—427, figs. 1—16.
- BENTHEM JUTTING, W. S. S. VAN, 1933. Mollusca. A. Gastropoda Prosobranchia et Pulmonata. Fauna Nederl., part 7, 387 pp.
- , 1952. Weekdieren, part 2. Wat leeft en groeit, vol. 36, 139 pp.

- BLOCH, S., 1938. Beitrag zur Kenntnis der Ontogenese von Süßwasserpulmonaten, mit besonderer Berücksichtigung der Mitteldarmdrüse. Rev. Suisse Zool., vol. 45, pp. 157—220, 24 figs.
- BONDESEN, P., 1950. A comparative morphological-biological analysis of the egg capsules of freshwater pulmonate gastropods. Natura Jutlandica, vol. 3, pp. 1—208, 9 pls.
- BOYCOTT, A. E., 1936. The habitats of fresh-water mollusca in Britain. J. Anim. Ecol., vol. 5, pp. 116—186, 63 figs.
- BRACKETT, St., 1940. Studies on schistosome dermatitis. VII Notes on the biology of the snail hosts of Schistosome cercariae in Wisconsin and epidemiological evidence for the life cycles of some avian schistosomes. Amer. J. Hyg., vol. 32, pp. 85—104.
- BRETSCHNEIDER, L. H. 1946. Development of *Limnaea stagnalis* L. a. Mechanism of oviposition. In: M. W. WOERDEMAN and CHR. P. RAVEN, Experimental embryology in the Netherlands 1940—1945. Monogr. Progr. Res. in Holland during the war. New York & Amsterdam.
- BROWNEE, K. A., 1949. Industrial experimentation. 4th ed., 194 pp., London.
- CHEMIN, E., 1926. Les mollusques d'eau douce. Enc. Prat. Nat., vol. 24, pp. 1—185, 15 pls., 47 figs.
- CLESSIN, S., 1877. Deutsche Excursions-Mollusken-Fauna, vol. 3, pp. 289—432.
- CORT, W. W., D. B. MC MULLEN, L. OLIVIER, and St. BRACKETT, 1940. Studies on schistosome dermatitis. VII Seasonal incidence of *Cercaria stagnicola* Talbot, 1936, in relation to the life cycle of its snailhost, *Stagnicola emarginata angulata* (Sowerby). Amer. J. Hyg., vol. 32, sect. D. Helminthology, pp. 33—69, 1 map, 8 graphs, 3 tables.
- CORT, W. W., L. OLIVIER, and D. B. McMULLEN, 1941. Larval trematode infection in juveniles and adults of *Physa parkeri* Currier. J. of Parasit., vol. 27, pp. 123—141.
- CRABB, E. D., 1931. The origin of independent and of conjoined twins in fresh-water snails. Roux' Arch. Entw. Mech., vol. 124, pp. 332—356.
- DEWITT, R. M., 1954. Reproduction, embryonic development, and growth in the pond snail, *Physa gyrina* Say. Trans. Am. Micr. Soc., vol. 73, pp. 124—137, 3 figs.
- DYBOWSKI, W., 1900. Beobachtungen über das Wachstum der *Limnaea stagnalis* L. Nachr. Bl. D. Malak. Ges., vol. 32, pp. 111—114.
- EHRMANN, P., 1933. Mollusken. Brohmer—Ehrmann—Ulmer, Tierw. Mitteleuropas vol. 2, prt 1, 264 pp., 13 pls.

- FELIKSIK, St., 1939. Über Biologie und Morphologie der Mantelschnecke, *Radix glutinosa* (O. F. Müller). Zool. Jahrb. (Syst.), vol. 72, pp. 17—70, 23 figs.
- GERMAIN, L., 1931. Mollusques terrestres et fluviatiles II. Faune de France, vol. 22, pp. 479—897.
- GIARD, A., 1908. Un nouveau Rotifère (*Proales ovicola*) parasite des pontes de mollusques d'eau douce. Feuille J. Nat. Paris, vol. 38, p. 184.
- GLASCOTT, L. S., 1893. A list of some of the Rotifera of Ireland. Sci. Proc. Roy. Dub. Soc., vol. 13 (n.s.) pp. 29—86, 5 pls.
- HAZAY, J., 1881. Die Mollusken-Fauna von Budapest III, Biologischer Theil. Zur Entwicklungs- und Lebensgeschichte der Land- und Süßwasser-Mollusken. Malak. Bl., (n.s.) vol. 4, pp. 43—224, 7 pls.
- HENDRIKSEN, K., 1930. Vandkalve- og Hvirvlerlarverne. In: V. Hansen, Biller VIII (Halipidae, Dytiscidae and Gyrinidae). Danmarks Fauna, vol. 34, pp. 150—226.
- HICKMAN, J. R., 1929. Life-histories of Michigan Halipidae (Coleoptera). Pap. Mich. Ac. Sci., Arts and Letters, vol. 11, pp. 399—424.
- HOLZFUSS, E., 1914. Selbstbefruchtung einiger Süßwasserschnecken. Nachr. Bl. D. Malak. Ges., vol. 46, pp. 67—73.
- KAMPS, L. F., 1937. De Chineesche Wolhandkrab in Nederland. Thesis, 112 pp.
- KEVAN, D. KEITH MC E., 1943. Study of an introduced North American freshwater mollusc, *Stagnicola catascopium* (Say). Proc. Roy. Soc. Edinb., section B (biol.), vol. 61, pp. 430—461, 10 graphs, 20 figs.
- KUIPER, J. G. J., 1947. Bijdrage tot de kennis der zoetwaterweekdieren van het natuurmonument Naardermeer. Basteria, vol. 11, pp. 2—53, 11 figs., 6 pls.
- KÜNKEL, K., 1908. Vermehrung und Lebensdauer der *Limnaea stagnalis* Lin. Nachr. Bl. D. Malak. Ges., vol. 40, pp. 70—77, 2 tables.
- LAMEERE, A., 1895. Faune de Belgique I, animaux non insectes. Bruxelles, 640 pp.
- LEHMANN, R., 1873. Die lebenden Schnecken und Muscheln der Umgegend Stettins und in Pommern. 328 pp., 22 pls.
- LÖHNER, L., 1924. Zur Kenntnis der oligodynamische Metall-Giftwirkungen auf die lebendige Substanz. II. Mitteilung. Über den Einfluss der Wasserkupferung auf Haemocyanin-tiere. Pflüger's Arch. Ges. Phys., vol. 203, pp. 524—532.

- LUTTERMOSER, G. W., 1943. A note on the life cycle of *Australorbis glabratus* (Say, 1818) Pilsbry, 1934, a snail intermediate host of *Schistosoma mansoni*. J. of Parasit., vol. 29, p. 231.
- Maandelijks overzicht der weersgesteldheid in Nederland, vol. 47, 48, 49, 50 and 51 (1950, 1951, 1952, 1953 and 1954). Edition no. 94a, Koninklijk Nederlands Meteorologisch Instituut.
- MACAN, T. T., 1949. A key to the British fresh- and brackish-water Gastropods. Freshw. Biol. Ass., Sci. publ. vol. 13, 45 pp.
- MANDAHL—BARTH, G., 1949. Bløddyr III: Ferskvandsbløddyr. Danmarks Fauna, vol. 54, pp. 1—249.
- MOQUIN—TANDON, A., 1855. Histoire naturelle des Mollusques terrestres et fluviatiles de France. Paris, vol. 2, pp. 1—416.
- MORRISON, J. P. E., 1932. Studies on the life history of *Acella baldemani* ("Desh." Binney). Trans. Wisc. Ac. Sci. Arts and Letters, vol. 27, pp. 397—414.
- NIEUWENHOVEN, L. M. v., S. J., and J. LEVER, 1946. The egg-laying stimulus. In: M. W. WOERDEMAN and CHR. P. RAVEN, Experimental embryology in the Netherlands 1940—1945. Monogr. Progr. Res. in Holland during the war, New York & Amsterdam, 1946, pp. 65—72.
- NEKRASSOW, A. D., 1929. Vergleichende Morphologie der Laiche von Süswassergastropoden. Z. Morph. Oek. Tiere, vol. 13, pp. 1—36, 26 figs.
- ODHNER, N. Hj., 1929. Die Molluskenfauna des Tåkern. Sjön Tåkerns Fauna och Flora, no. 8, 127 pp., 7 pls., K. Sv. Vet. Akad.
- OLDHAM, C., 1930. Fecundity of *Planorbis corneus*. Naturalist, London, pp. 177—179.
- PELSENEER, P., 1920. Les variations et leur hérédité chez les mollusques. Mém. Acad. Roy. Belg., (2e), vol. 5, pp. 1—821.
- , 1926. Périodicité diurne dans la ponte, chez les mollusques. Ann. Soc. Roy. Zool. Belgique, vol. 57, pp. 34—38.
- , 1935. Essai d'éthologie zoologique d'après l'étude des Mollusques. Acad. Roy. Belg., (Sciences), Publ. Fond. Agathon de Potter no. 1, Bruxelles, 662 pp.
- PFEIFFER, C., 1821. Naturgeschichte deutscher Land- und Süswasser-Mollusken. Weimar 1, 134 pp., 8 pls.
- PRECHT, H., 1936. Zur Kopulation und Eiablage einiger Planorbiden. Zool. Anz., vol. 115, pp. 80—89, 2 figs.
- RAVEN, CHR. P., and L. H. BRETSCHNEIDER, 1942. The effect of centrifugal force upon the eggs of *Limnaea stagnalis* L. Arch. Néerl. Zool., vol. 6, pp. 255—278.

- ROSS, I. C., and A. C. MCKAY, 1929. The bionomics of *Fasciola hepatica* in New S. Wales and of the intermediate host *Limnea brazieri* (Smith). Bull. Council Sci. and Ind. Res., Australia, no. 43, pp. 1—62, 13 figs.
- SCHODDUYN, R., 1925. Observations biologiques en Microaquarium. Ann. Biol. Lac., vol. 14, pp. 39—47.
- STEVENS, J., 1912. Note on *Proales (Notommata) gigantea* Glascott, a Rotifer parasitic in the egg of the Water-snail. J. Quekett Micr. Cl., (2), vol. 11, pp. 481—485, pl. 24.
- TAKI, I., 1931. Some ecological observations on *Lymnaea (Radix) japonica* Jay. Venus vol. 2, English summary pp. 286—288.
- THIEL, M. E., 1929. Zur Biologie unserer Süßwasser-Muscheln. Z. Morph. Oek. Tiere, vol. 13, pp. 65—117.
- TINBERGEN, L., and J. VERWEY, 1945. Zur Biologie von *Loligo vulgaris* Lam. Arch. Néerl. Zool., vol. 7, pp. 213—286.
- VAN CLEAVE, H. J., 1935. The seasonal life history of an amphibious snail, *Fossaria modicella*, living on sandstone cliffs. Ecology, vol. 16, pp. 101—108.
- VENMANS, L. A. W. C., 1949. Malacologische aantekeningen. 1. Legfels van *Physa fontinalis* (L.). Basteria, vol. 13, pp. 43, 44.
- WALTON, C. L., 1918. Liverrot of sheep, and bionomics of *Limnaea truncatula* in the Aberystwyth area. Parasitology, vol. 10, pp. 232—266, 5 figs.
- WALTON, C. L., and W. N. JONES, 1926. Further observations on the life history of *Limnaea truncatula*. Parasitology, vol. 18, 144—147.
- WESENBERG—LUND, C., 1939. Biologie der Süßwassertiere. Wirbellose Tiere. Vienna, 791 pp.
- WESTHOFF, V., 1949. Landschap, flora en vegetatie van de Botshol nabij Abcoude. Uitgave Stichting Commissie voor de Vecht en het Oostelijk en Westelijk Plassengebied, Baambrugge 1949, pp. 1—102.
- WHITEHEAD, H., 1935. An ecological study of the invertebrate fauna of a chalk stream near Great Driffield, Yorkshire. J. Anim. Ecol., vol. 4, pp. 58—78, pl. 3, 4 figs.
- WIERZEJSKI, A. 1905. Embryologie von *Physa fontinalis* L. Z. Wiss. Zool., vol. 83, pp. 502—507.
- WILCKE, J., 1953a. Wilde planten in 1940—1951. Landbouwk. Tijdschr., vol. 65, pp. 216—217.
- , 1953b. Wilde planten in 1952. Ibid., vol. 65, pp. 761—762.
- WINCKWORTH, R., 1931. On the growth of *Pappia undulata* (Veneridae). Proc. Malac. Soc. London, vol. 19, pp. 171—174.

- WINSOR, CH. P., and A. A., 1932. Polyvitelline eggs and double monsters in the pond snail *L. columella* Say. Biol. Bull., vol. 68, pp. 400—404.
- WREDE, W. L., 1927. Über die Abwehrreaktion von *Physa*. Zool. Jahrb. (Allg. Zool. u Phys. Tiere), vol. 44, pp. 315—322.

After the manuscript of this paper had been finished Mr. R. M. DEWITT kindly sent me reprints of his papers on *Physa gyrina* Say. I regret having been unable to discuss most of his results. One of his papers was mentioned above; the following are additional references:

- DEWITT, R. M., 1954. Reproductive capacity in a pulmonate snail (*Physa gyrina* Say). Amer. Nat., vol. 88, pp. 159—164, 1 fig.
- , 1954. The intrinsic rate of natural increase in a pond snail (*Physa gyrina* Say). Ibid., vol. 88, pp. 353—359, 2 figs.
- , 1955. The ecology and life history of the pond snail *Physa gyrina*. Ecology, vol. 36, pp. 40—44.