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Development cycle and some data on the growth of Penilia avirostris Dana in the Sevastopol Bay

By E. V. Pavlova

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E.V. Pavlova

Development cycle and some data on the growth of *Penilia avirostris* Dana in the Sevastopol Bay

Penilia avirostris is one of the representatives of the not so numerous group Cladocera of the marine plankton; it is encountered in the Black Sea during the summer and fall months. Mass development of the Penilia occurs in August and September when it may form up to 50% of the food zooplankton.

The life cycle of the Penilia can be referred to the general scheme characteristic for all Cladocera: during the summer period reproduction of the population occurs by parthogenesis; in unfavorable conditions at the end of the season males appear and formation of eggs begins in the females; after fertilization these eggs are needed for the hibernation period. After the latent period partheno-genetic females hatch again from the hibernating eggs, originating the whole subsequent population.

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During observations of the population of Penilia avirostris in the Sevastopol Bay in the course of three years (1954, 1955, 1956) we succeeded in establishing some details of the cycle of their development.

The first specimens of Penilia started to occur in 1954 at the beginning of July at a temperature of 26° C (Fig. 1). During the whole month of July the population remained very small in numbers (up to 7 specimens per m^3). Rapid development of Penilia in the plankton started in August, producing at the end of August and the beginning of September a maximum quantity i.e. 2118 specimens per m^3. At that time Penilia avirostris was the prevailing form of animal plankton. Up to this period the population consisted only of parthogenetic females and juveniles i.e. females which did not reach yet sexual maturity. At the end of August at a water temperature 19-22°C, males began to appear in very limited quantities (1 male per 100 females). During almost the whole of September the population of females was fairly numerous (448-645 per m^3). Together with females producing parthenogenetic eggs, females appeared which were changing to production of hibernating eggs: this could be clearly noticed by the dark-brown color of their ovaries. At the end of September the quantity of Penilia in the plankton decreased considerably (up to 20 specimens per m^3). At the beginning of October only single specimens were encountered and by 5 October not a single Penilia was caught in the plankton of the bay.

In the following year 1955 Penilia appeared in the last days of July at a water temperature of 25° C i.e. later than in 1954. At the

...3

beginning of August their quantity was reaching 80 specimens per m^3 (Fig. 2). This was the maximum quantity for the year 1955. Up to and including November the population of P. avirostris remained on a low level quantitatively. At the end of November, at a water temperature of 13° C the Penilia disappeared completely from the plankton. The first males appeared, like in the preceding year, 55
at the end of August. Females with hibernating eggs were encountered in the population in October.

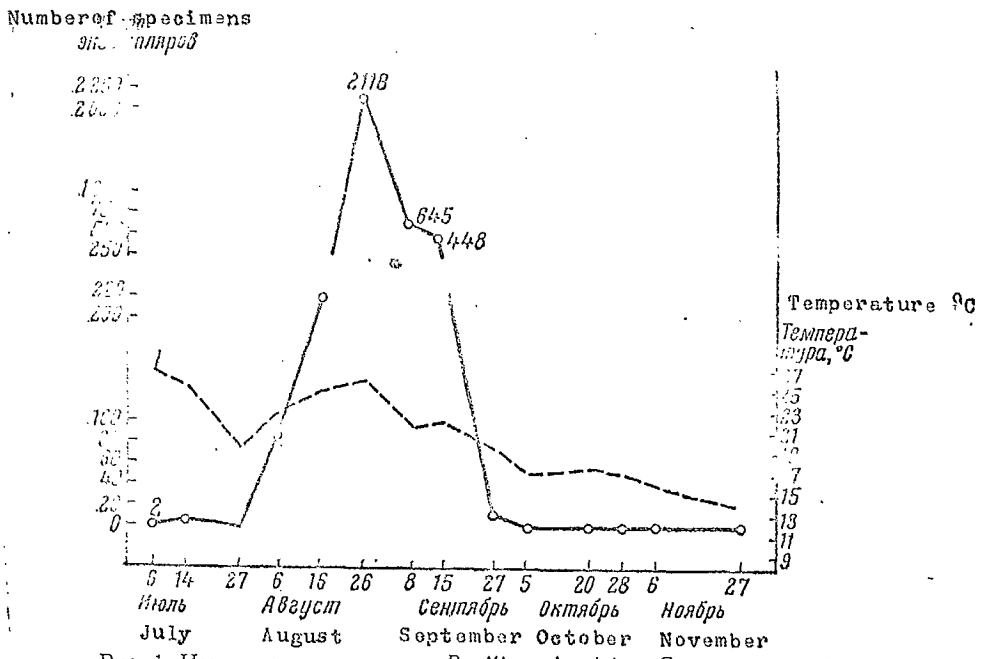

Рис. 1. Изменение численности *Penilia avirostris* в Севастопольской бухте за 1954 год

1 — температура; *2* — число экз.

Fig. 1. Changes of quantities of Penilia avirostris in the Sevastopol Bay in the year 1954
1 - temperature; 2 - number of specimens

The year 1956 was characterized by a short presence of the population of P. avirostris. The small crustacean was encountered

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in the plankton first time in this year in the early days of August at a water temperature of 22°C (Fig. 3). In mid-August the population

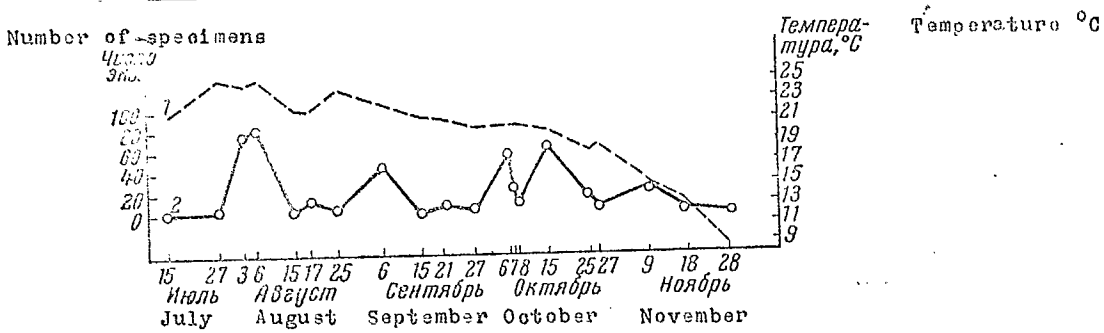

Рис. 2. Изменение численности *Penilia avirostris* в Севастопольской бухте за 1955 год

1 — температура; *2* — число экз.

Fig. 2. Changes of quantities of Penilia avirostris in the Sevastopol Bay in the year 1955
1 - temperature, 2 - number of specimens

grew considerably in numbers and reached its maximum in this year of 358 specimens per m^3. From this moment the quantity of Penilia in the plankton decreased steadily, and already in the first days of September only single specimens were discovered. The disappearamee 56 of the Penilia from the plankton took place at half September at a water temperature 17-18° C. Like in the preceding year, the first males appeared towards the end of August. Females which would change to producing hibernating eggs were not found.

The populations under consideration were different with regard to dates of appearance, length of periods of existence and quantities. In 1954 Peniliae appeared the first time on June 6 at a water temperature 26° C and were encountered during a period of three months. In 1955 they appeared somewhat later on June 26 at a water temperature 25° C and existed for more than four months and in 1956 they came still

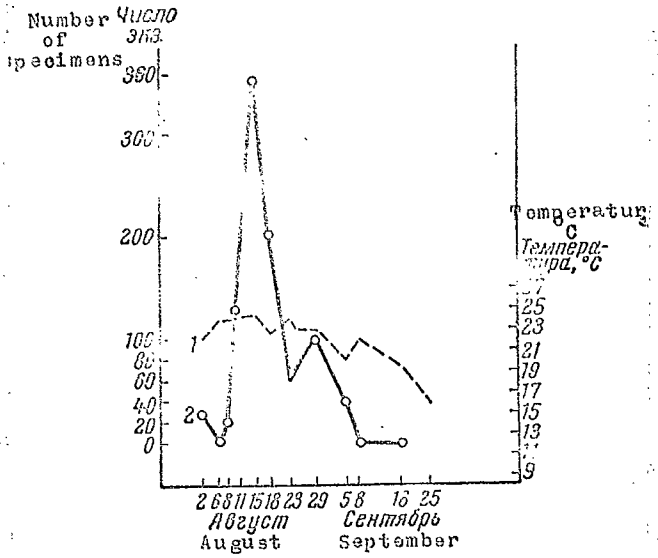

Рис. 3. Изменение численности *Penilia avirostris* в Севастопольской бухте за 1956 год

1 — температура; *2* — число экз.

Fig. 3. Changes in the quantities of Penilia avirostris in the Sevastopol Bay in the year 1956
1 - temperature; 2 - number of specimens

later i.e. on August 1 at a water temperature 22°C and were found in the plankton only for one and a half months. The differing dates of appearance of Penilia in the course of three years depend probably on the establishment of a constant maximum temperature necessary for hatching of the small crustaceans from the hibernating eggs. The length of period of existence of the Penilia in the plankton depends in first place on a uniform decrease of the water temperature in the course of all summer and fall months. Thus the population of 1955 was able to last to November owing to a gentle drop of the temperature from August (24°C) to November (13°C). In 1954 during one month from August to September the water temperature decreased by 9°C (from 26° to 17°C) which caused fast mortality of the population at mid-September.

The problem of quantity variations of Penilia from year to year is a part of the yet unsolved problem of variations in the productivity of the whole black Sea. In the case of P. avirostris of the Sevastopol Bay a clearly expressed direct relationship between quantity variations and temperature changes could not be observed.

In spite of the differences shown between the three populations, it is possible to note common features characteristic for the development cycle of Penilia avirostris.

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The first specimens of the animals appearing as a rule in the July plankton are juveniles and parthenogenetic females of medium size (0.70 mm long) in which the quantity of eggs in the brooding pouches amounts to five on the average. In August, begins a strong development of the population which reaches a maximum at the end of August and the beginning of September. The population consists in 40-60% of juveniles having dimensions 0.49 and 0.56 mm in length. The parthenogenetic females reach maximum dimensions (up to 0.91 and 0.98 mm in length) and produce the largest number of eggs and embryos (8 on the average, 11 maximum). The males appear at the end of August, although in small quantities. At the beginning of September one can find in the plankton single females not able to produce parthenogenetic generations, which have changed to producing hibernating eggs. At the same time females are encountered with hibernating eggs forming;* their largest numbers appear at the end 57
of September and in October. However, till the end of life of the population parthenogenetic females and juveniles remain predominant with regard to quantity. The ratios of all the groups of animals shown in the population of 1955 are given in Fig. 4. Attention is drawn by the very insignificant quantity of females with hibernating eggs (15%) in comparison with the quantity of parthenogenetic ones (60% of the whole quantity of specimens).

*Translator's note:
This sentence is translated verbatim: it seems to be superfluous as it repeats the statement made in the preceding sentence.

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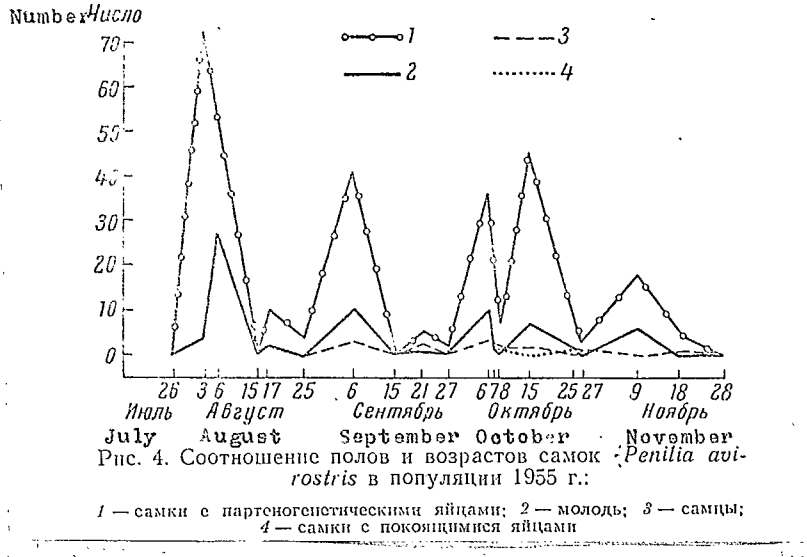

Рис. 4. Соотношение полов и возрастов самок *Penilia avirostris* в популяции 1955 г.:

1 — самки с партеногенетическими яйцами; *2* — молодь; *3* — самцы; *4* — самки с покоящимися яйцами

Fig. 4. Ratios of sexes and of ages of females of Penilia avirostris in the population 1955.
1 - females with parthenogenetic eggs; 2 - juveniles; 3 - males; 4 - females with dormant eggs.

The dimensions of the parthenogenetic females decrease tat the end of September and in October in comparison with August (up to 0.84 and 0.77 mm in length); also the number of mature eggs and embryos decreases (three or four on the average, maximum six). October and November is the period of perishing of the population P. avirostris. From this moment begins the hibernation period during which (8-9 months) only dormant eggs of Penilia are encountered in the Bay of Sevastopol. In July of the following year the cycle begins again.

With the moment when females with dormant eggs appear in the population, some signs of depression can be observed in parthenogenetic females. Apart from a general decrease of body dimensions, which was mentioned earlier, the females deposit in the brooding pouches a smaller number of eggs. In 1954, the average number of eggs in

...8

August was eight and at the end of September three. In 1955 at the beginning of the population development the females deposited on the average six eggs, towards the end the quantity decreases to three or four. A direct relationship between reduction of the number of eggs and decrease of body dimensions of the females towards the end of the life of the population was not noted (Table 1). The quantity of eggs in the brooding pouches of the females of equal body dimensions was different in August and October 1955. As can be seen from the table, females 0.70 and 0.77 mm long gave in August maximum ten, on the average six eggs, and towards the end of the life cycle maximum seven to eight, on the average four to five. Such a decrease of the fertility of P. avirostris between the beginning and the end of the season was observed in all dimensional groups of parthenogenetic females.

When analysing the population of Daphnia magna, Berg (1934) arrived at the conclusion, that the reduction of the quantity of eggs towards the end of the season is not connected with the average decrease of 58
the female's dimensions and that a depression of the population in the change from parthenogenesis to typical sexual reproduction is the cause of it.

...9

Table 1

Change of fertility of females P. avirostris between the beginning and the end of life of the population in 1955

Таблица 1

Изменение плодовитости самок *P. avirostris* от начала к концу жизни популяции 1955 г.

Размеры самок, мм Dimensions of females mm	Number of eggs Число яиц					
	August Август			October Октябрь		
	максимальное maxim.	минимальное minim	среднее median	максимальное maxim.	минимальное minim.	среднее median
0,63×0,28	6	3	5	6	2	4
0,70×0,28	10	1	6	7	1	5
0,77×0,35	10	1	6	8	2	4
0,84×0,35	8	5	6	6	4	5

Some qualitative changes of the parthenogenetic females should also be referred to signs of depression: the eggs become smaller and often as if dispersed over the pouch; females with resorbed eggs and even embryos occur. In the plankton are encountered females covered with infusoria, which impedes movements and filtration and probably proves a general weakness of the organism. All these are features of irreversible physiological changes leading finally to destruction of the population.

In order to clarify the problem of the rate of growth and number of moults of Penilia, an analysis was made of the population in the years 1954 and 1955 and a series of laboratory experiments conducted.

The investigations were conducted in 500 cm^3 vessels tapered downwards which had in the bottom a rubber drain tube with a clamp. In such a vessel it is easy to change the water (every two or three days in our experiments) without causing a trauma by transferring the animals with a pipette, and to drain the sediment forming on the bottom, moult skins and dead animals. The water in which the

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animals were kept was taken from a sea water pipe line and was filtered through a paper filter to remove large particles suspended in the water. The temperature of the water was comparatively stable during the experiments (22-24°C) and corresponded to the temperature of natural conditions; sharp variations in day time and at night were not observed. The experimental vessels were protected against action of direct sunlight. Colorless flagellated algae not larger than 8 μ served as food in the experiments; their cultures were kindly supplied to us by L.A. Lanskaya, employee of the Sevastopol biological station. To determine the body dimensions the experimental animals were picked carefully from the vessel using a wide pipette, placed on a slide glass with a hollow and measured under a microscope by means of a micrometer ocular. The length of the animal's body was measured from the anterior point of the head to the end of the post-abdomen, the width in the middle of the thorax on the dorsal side.

We performed measurements of 520 specimens of females from the natural population of the Sevastopol Bay. Among them most often females were found of some determined dimensions: 0.42; 0.49; 0.56; 0.63; 0.70; 0.77; 0.84; 0.91, mm in length. The dimension 0.98 occurred comparatively rarely. There was an insignificant number of intermediate values among the indicated dimensions. In Fig. 5 is shown the frequency of encountering dimensions of female length. 59 The peaks on the graph correspond to dimensions most often encountered. The presence of such repeated body dimensions made the assumption possible that particularly at those dimensions, being the most steady, occurs the rejection by the animals of the old chitin carapace i.e. that moulting of Penilia avirostris takes place.

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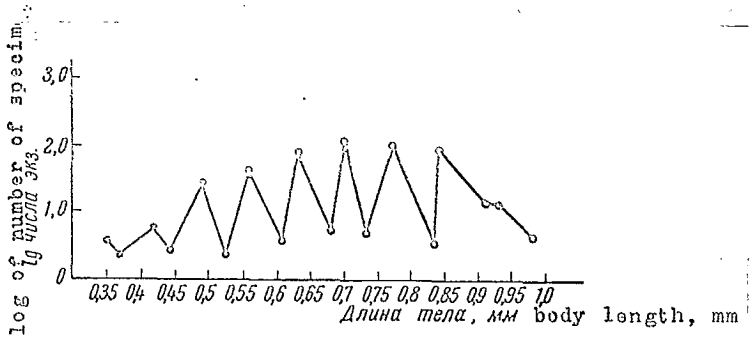

Рис. 5. Частота встречаемости размеров самок *Penilia avirostris* по длине

Fig. 5. Frequency of encountering dimensions of length of the Penilia avirostris

To ascertain the correctness of such an assumption, a series of observations of moults were conducted in laboratory conditions. We did not succeed in observing all the eight successive moults of the same female, because the duration of life of Penilia was much shorter in the experiment, "particularly in individual upkeep"* but in laboratory conditions different females rejected carapaces at all the dimensions enumerated above. All the eight moults are connected with the growth of the animal, as the size of the body increases after each of them. On the average about 48 hours passed from one moult to another. The period up to the third moult is the time of intensive growth, the animal moults in 36 hours. After the third and all the successive moults the length of the period between them increases somewhat (up to 45 hrs.). This probably is connected with the fact that up to the third moult the animal did not yet reach sexual maturity. Only after the third moult the female starts reproduction and bears the first portion of embryos which fact retards the arrival of the next moult. When some impediments to growth and a normal course of the moult are present (e.g. lowering of the temperature of water at night, damage to the bristles of the antennae and tail) the duration of the periods between the moults is extended irrespectively of the age of the female. In such cases moulting did

* Translator's note:
Translated verbatim. I do not get what the author has in mind here. Perhaps keeping the specimen in a test tube separated from others?

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not occur for three or four days and often death of the animal was the outcome, often with preceding resorption of the eggs or embryos in the brood pouch. It can be assumed that under adverse conditions the same occurs to P. avirostris also in the sea.

Knowing the dimensions at which moults of females occur, one can calculate the increment of the body from one moult to another. To calculate the increment to the first moult the average dimension of freshly hatched juveniles and the dimension at which the first moult occurred were taken into account. Their difference is the increment of the body in length. The dimensions in width are the averages of those most frequently encountered for the given length. The results of the calculations are compiled in Table 2. The increment of the body in length is in all cases the same and equals 0.07 mm. The increment in width is equal in females up to the third moult, later it becomes bigger with each moult. This probably depends on the quantity of the embryos born and the stage of their development. The more embryos the female carries in the pouch, the broader is the female. We can compare the data obtained by us only with the unique work on the biology of the P. avirostris from the Adriatic Sea (Steuer 1933). Steuer gives an analysis of the population of Penilia from the channel Di Leme* of samples from August 1932, on the basis of which he shows a graph of the stages of moulting (Fig. 6). As can be seen, there are only six moulting stages (Roman numerals), four of which 60 include animals which did not reach sexual maturity (marked with a plus sign); females in the V and VI stages produce eggs and bear juveniles. Comparing Steuer's graph (1933) with our data we can detect the following differences.

*Translator's note:
Now: Limski Zaliv near Rovinj in Yugoslavia

Table 2

Body increments of females of Penilia avirostris in length and width

Размер тела, мм / Body dimensions, mm	Moults / Линьки I	II	III	IV	V	VI	VII	VIII
Initial body dimensions / Первоначальный размер тела	0,35×0,14	0,42×0,18	0,49×0,21	0,56×0,21	0,63×0,25	0,07×0,25	0,77×0,28	0,84×0,30
Final body " / Конечный размер тела	0,42×0,21	0,49×0,25	0,56×0,28	0,63×0,30	0,70×0,35	0,77×0,39	0,84×0,42	0,91×0,42
Body increment / Прирост тела	0,07×0,07	0,07×0,07	0,07×0,07	0,07×0,09	0,07×0,10	0,07×0,14	0,07×0,14	0,07×0,12

1. According to Steuer sexually mature females go through only two moults instead of five, as follows from our observations.
2. The period up to sexual maturity includes four moults, one more than in the Black Sea Penilia.
3. The Adriatic Peniliae attain larger dimensions than the Black Sea ones (the maximum length of the Adriatic Penilia is 1.09, that of the Black Sea one 0.98 mm).

As far as the first difference is concerned, one can state that the stages between the moults of sexually mature females according to Steuer appear to us to be very spread with a great number of dimensional variations and very large body increments in comparison with the juvenile stages. E.g. the V stage includes body dimensions from 0.70 to 0.86 mm in length, whereas the II stage has from 0.55 to 0.62 mm. This means that the body increment in the first case is twice the increment in the second (0.16 and 0.07). It is difficult to imagine that adult females would have a twice as large body increment than females which did not reach sexual maturity in the period of intensive growth. As has been explained, the body increment of the Black Sea Penilia is the same between any two of the

...14

eight moults and equals 0.07. Therefore we think that the last two stages of moult proposed by Steuer (1933) are cumulative, each consisting at least of two. Steuer's V stage corresponds to two of ours (V and VI), Steuer's VI stage probably covers our three stages (VII, VIII, IX). Since the body increments in Adriatic Peniliae in the first four stages of moult correspond to the increments of the Black Sea ones (calculated from Steuer's graph) the body increments of P. avirostris is probably the same in both seas.

Steuer explains the presence of the I stage of moult by the circumstance that after leaving the brood pouch the juveniles moult immediately. We did not succeed in observing such a phenomenon.

The extension of the juvenile period in the Adriatic Sea in comparison with the Black Sea, together with attaining larger sizes increases considerably the duration of the individual life of the Adriatic Penilia, if we take into account the length of the stages between moults being equal in both seas.

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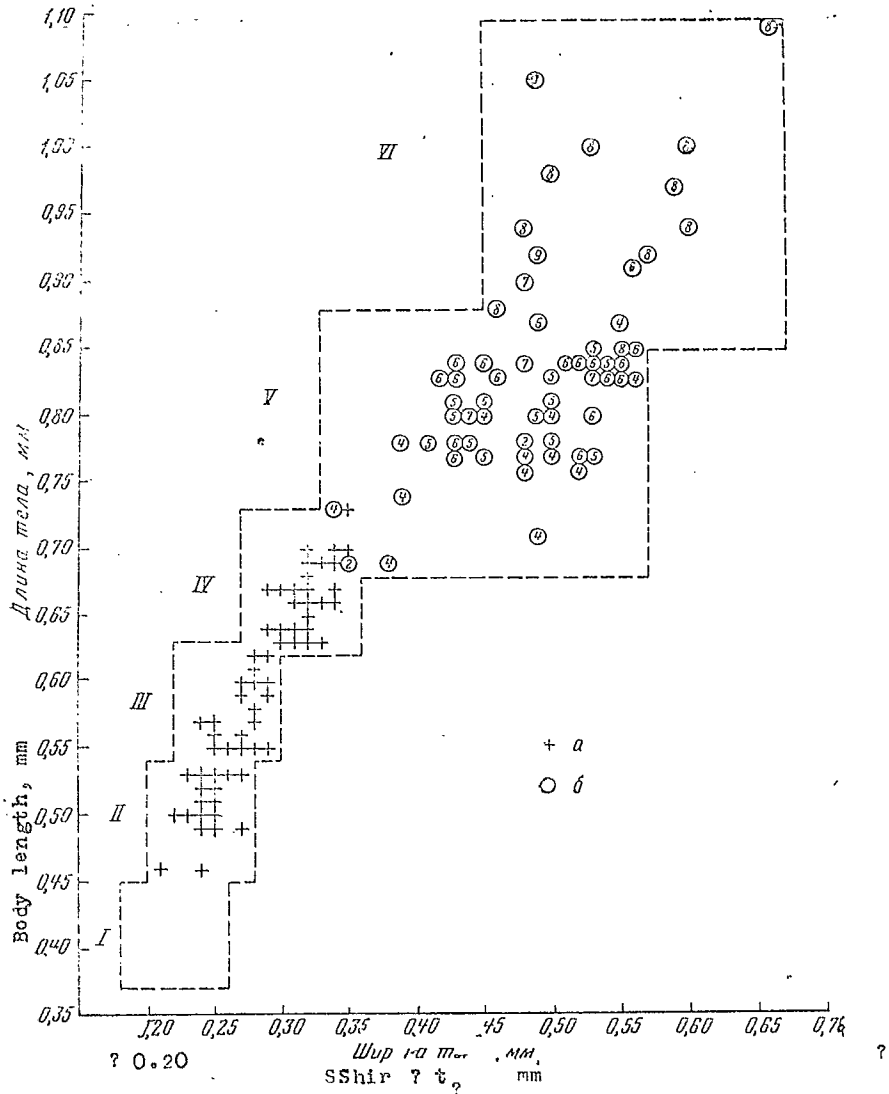

Рис. 6. Анализ популяции *Penilia avirostris* 6 августа 1932 г. из канала Ди Леме (по Штейеру, 1933):

I—VI — стадии линек; *а* — молодь; *б* — взрослые самки (в кружке указано число эмбрионов)

Fig. 6. Analysis of the population of Penilia avirostris of 6 June 1932 in the channel Di Leme* (according to Steuer (1933))

I-VI - stages of moulting; a - juveniles; b - adult females (the number of embryos is shown in circles)

During an inspection of 15 samples of zooplankton from the bay taken from the end of August to the moment of perishing of the population of 1955, 76 males were found, the measurements of which gave the following results:

The prevailing length dimensions - 0.42, 0.49, 0.56, 0.63, 0.70, 0.77 mm;

* See footnote on page 12.

...16

the width of the body increased proportionally to the length from 0.17 to 0.35 mm. These most often encountered body dimensions were taken as border values between two moults. The presence of those dimensional groups confirms in a certain way the existence of five moults of the males of P. avirostris. Up to the I moult the juveniles do not have yet the secondary sexual characteristics of a male: the twin penis and long I antennae. After the first moult the antennae elongate (from 0.112 to 0.255 mm), in the location of the future copulation organs appear small tubercles (0.028-0.07 mm long). With each successive moult the length of the antennae and the penes increases (Table 3). The maximum dimensions of the penes (from 0.21 to 0.308 mm) are observed in males after the V moult; after this moult the antennae exceed the length of the body (0.77 mm).

Table 3

Increase of the length of penes and I antennae of males P. avirostris, following moults

Таблица 3

Увеличение длины пенисов и I антени у самцов *P. avirostris* с линьками

Length of organs, mm / Длина органов, мм	Moults / Линьки I	II	III	IV	V
Penes / Пенисы	0,028—0,07	0,035—0,126	0,07 —0,210	0,112—0,28	0,21—0,308
I antennae / I антенны	0,112—0,266	0,140—0,378	0,210—0,56	0,308—0,658	0,49—0,77

The body increments of the males between two moults are the same as the increments of the females and equals 0.07 mm. Certain variations of the length of penes and antennae correspond to each body dimension of the male; therefore their increments from moult to moult cannot be

...17

shown as one value. It is of interest that after the IV and V moult the growth of the penes and antennae is retarded and stops (at a length of 0.70 mm). Apparently the V and VI stages of moult include fully adult males capable to fertilize the females.

The problem of the duration of the stages between the moults, and consequently the duration of life of the males themselves was not clarified definitely. In experimental conditions the males lived up to five days. Sexually adult males lived in the aquarium three days only.

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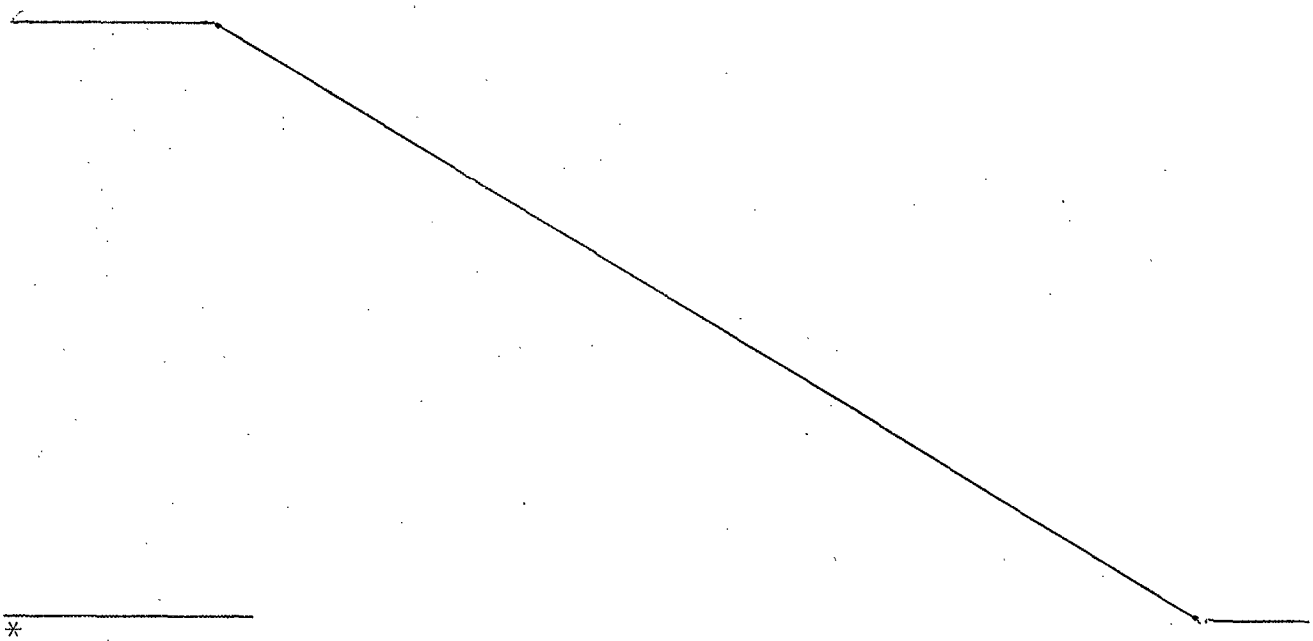

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See note on page 12.