Ecological parasitology

Volume 1
Number 1
1992

SANCT-PETERBURG
PETROZAVODSK

LIFE TABLES OF FISH HELMINTHS AND THEIR ANALYSIS WITH THE CESTODE *PROTEOCEPHALUS PERCAE* (CESTODA, PROTEOCEPHALIDAE), A SPECIFIC PARASITE OF THE PERCH *PERCA FLUVIATILIS*, TAKEN AS AN EXAMPLE

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ABSTRACT. With cestode *Proteocephalus percae*, taken as an example, the populational parameters of the dynamics of fish parasites, which have an annual cycle: survival, mortality, fertility, net reproductive rate, were determined. The principal possibility of using the traditional methods for studying the parasite number for determining the populational parameters was shown.

INTRODUCTION

It is known that many aspects of the populational dynamics can be assessed on the basis of data on changes of its age structure. The variation of the parasite number reflects tendencies in the change of the population density, whereas analysis of ratio between individual age groups allows to determine mortality and survivability. The product of the mean individual fertility of the reproductive part of the population on its number gives an idea of the birthrate, and the sum of the values of the realized fertility for the entire reproductive period - of the net reproductive rate of the population (Odum, 1986). The development of these studies by the conceptual apparatus, traditional for general ecology, becomes of a very common use in studying the biology of fish parasites (Kennedy, 1975; Bauer, 1980; Pronin, Khokhlova, 1987; Ieshko, 1988). In addition, the use of the populational approach to the interpretation of parasitological data makes them more available for a wide circle of biologists.

MATERIALS AND METHODS

The present research was conducted on a typical representative of the Boreal - plain complex cestode *Proteocephalus percae* (Cestoda: Proteocephalidea). The material was collected in 1986-1987 on Lake Rindozero, one of the small water bodies of Southern Karelia. The fish population of the lake is represented by 5 species: roach - *Rutilus rutilus*, perch -*Perca fluviatilis*, ruff - *Gimnocephalus cernua*, pike - *Esox lucius* and burbot - *Lota lota*; only two first species can be considered to be dominant. The populational structure of perch is relatively simple, the stock is dominated by fishes, aged 4+ and 5+ (AD 10-14 sm). As perches from the dominant age classes were mainly infected by cestode *Proteocephalus percae*, and there were no large differences in the distribution and average abundance of parasites (Fig. 1), we used the averaged values of infection of all the fishes studied. In this case the values of the abundance indices (mean intensity) registered are adequate characteristics of the cestode number with the assumption that the host number (n) does not change significantly throughout a year. This assumption is based on studies of P.V.Tyurin, who has shown that natural mortality of perches sharply decreases after they reach sex maturity, and it does not exceed 20%. In small water bodies, where perch is dominant in ichthyocoenosis, the mortality is much lower (Tyurin, 1973). The dates of fish dissection were determined by the biological characteristics of helminth. In the period of open water, from May to July, the fish were dissected at weekly intervals, in August - September - twice a month and in March. 30 fish specimens were examined in each sample, a total of 420 individuals was analyzed.

The helminths found were divided into three developmental stages: immature, mature, but without eggs, and helminths with eggs. At the last stage the helminths with mature and immature eggs were distinguished. The group of immature helminths included plerocercoids, which recently infected the fish and young helminths. They were clearly differentiated by the sizes of the body, scolex and suckers. The division of this group allowed to determine the duration of invasion and rate of immigration. The number of cestodes at each stage was counted.

The length of the helminth was measured. Due to the frequency chosen for field sampling of fishes determination of the developmental stages and sizes of parasites we were able to follow the linear growth and maturation of cestodes living in perch. In this case we did not analyze the mean sizes of helminths found, but the occurrence frequency of individual values of the length for each of the parasite developmental stages distinguished. The correctness of the chosen approach is postulated by the ability of cestodes of the genus *Proteocephalus* to preserve the initial strobile during their whole life (Freze, 1965), and by fairly low abundance of mature helminths at which no competitive relations are observed. The maximum number of mature cestodes - 15 specimens - was found only in one individual.

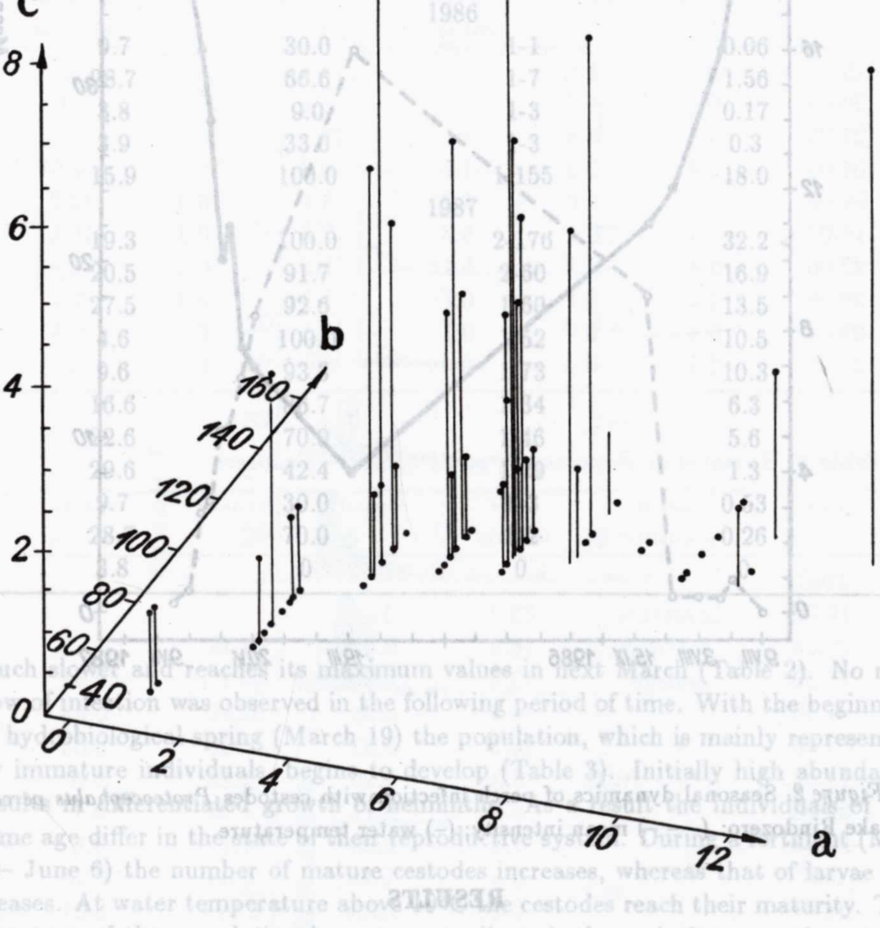

Figure 1. Distribution of *Proteocephalus percae* in Lake Rindozero depending on the age and size of fish. June 14, 1987 (a – age; b – size; c – mean intensity).

The rate of immigration was calculated from the difference between the values of mean intensity of two samples divided on the time interval between them. Specific mortality was determined by similar method. The survival of the helminths is given as portions of the initial abundance in March. The individual fertility was calculated in 22 cestodes with a length of 1-4 cm. On the basis of data obtained the mean fertility of mature helminths was calculated per 1 cm of their length which was then used as the constant.

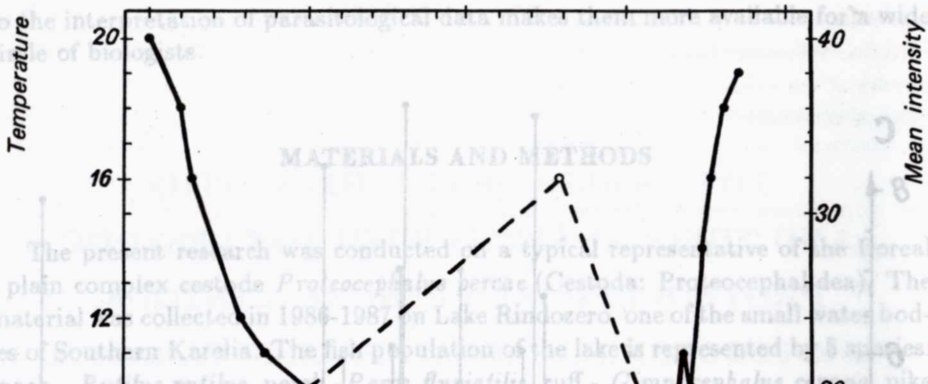

Figure 2. **Seasonal dynamics of perch infection with cestodes *Proteocephalus percae* in Lake Rindozero: (– – –) mean intensity; (–) water temperature.**

RESULTS

Observations of the occurrence and development of *Proteocephalus percae* have shown that in Lake Rindozero the helminth has an annual cycle with the summer - autumn infection of the host, spring maturation and further elimination (Table 1) that is consistent with data of numerous investigations (see Roitman, Tsetlin, 1982). The concrete dates of the helminth development are determined by seasonal changes of water temperature in the lake (Fig. 1,2).

The quantitative values of immigration, survival, mortality and population structure of *P. percae* are given in Tables 2–4. The data presented allow to characterize the dynamics of the populational parameters of helminth at the major stages of its development. The formation of the infection of the final host begins in July. It is extended in time and poorly expressed in summer. The intensive immigration is observed in Autumn. In winter the number of helminth increases

Table 1. *Occurence of P. percae in perch of Lake Rindozero.*

Date	Occurence, %	Ranges min.- max.	Mean intensity, sp.
		1986	
9.7	30.0	1-1	0.06
28.7	66.6	1-7	1.56
3.8	9.0	1-3	0.17
3.9	33.0	1-3	0.3
15.9	100.0	1-155	18.0
		1987	
19.3	100.0	2-176	32.2
20.5	91.7	2-60	16.9
27.5	92.6	1-60	13.5
4.6	100.0	1-52	10.5
9.6	93.3	1-73	10.3
16.6	86.7	1-34	6.3
22.6	70.0	1-46	5.6
29.6	42.4	1-29	1.3
9.7	30.0	1-3	0.53
28.7	70.0	1-2	0.26
3.8	0	0	0

much slower and reaches its maximum values in next March (Table 2). No new flow of infection was observed in the following period of time. With the beginning of hydrobiological spring (March 19) the population, which is mainly represented by immature individuals, begins to develop (Table 3). Initially high abundance results in differentiated growth of helminths. As a result the individuals of the same age differ in the state of their reproductive system. During a fortnight (May 20– June 6) the number of mature cestodes increases, whereas that of larvae decreases. At water temperature above 10^{0}C the cestodes reach their maturity. The structure of the population becomes complicated, the ratio between the groups distinguished changes (Table 3).

Table 2. *Indices of immigration of Proteoceaphalus percae in perch of Lake Rindozero.*

Date	Time interval, days	Temperature, ^{o}C	Mean intensity, sp.	Rate of immigration, sp./day
09.07.86	1	19.0	0.06	–
28.07.86	19	16.6	1.56	+0.08
03.08.86	26	16.0	0.17	–0.09
03.09.86	57	12.0	0.56	+0.009
15.09.86	70	10.5	18.0	+1.45
19.03.87	254	4.0	30.6	+0.06

Table 3. *The structure of population and ratio of the abundance at different stages of P.percae of Lake Rindozero (1987).*

Date	Mean intensity, sp./fish			% of the initial abundance		
	immature	mature	helminths with eggs	immature	mature	helminths with eggs
19.03	30.6	1.6	0	97.5	2.5	0
20.05	10.2	6.7	0	31.7	20.5	0
27.05	6.8	6.6	0	21.1	20.5	0
04.06	1.9	7.1	1.5	5.9	22.0	4.6
09.06	1.0	2.0	7.3	3.1	6.2	22.7
16.06	0.9	0.1	5.3	2.8	0.3	16.5
22.06	0.4	0.1	5.1	1.2	0.3	15.8
29.06	0.4	0.1	0.7	1.2	0.3	2.2
09.07	0.4	0	0.1	1.2	0	0.3
28.07	0.2	0	0	0.6	0	0

Table 4. *Survival of P. percae in perch of Lake Rindozero*

Date,	State of population	Mean intensity	Survival	Mortality	Specific mortality
1987					
19.03	immature	32.2	1	–	–
20.05	mature	16.9	0.52	0.48	0.25
27.05	mature	13.5	0.42	0.1	0.43
4.06	-"-	10.5	0.34	0.12	0.33
9.06	-"-	10.3	0.32	0.02	0.05
11.06	-"-	6.3	0.20	0.12	0.6
22.06	-"-	5.6	0.17	0.03	0.1
29.06	-"-	1.3	0.06	0.11	0.6
9.07	-"-	0.5	0.02	0.04	0.15
28.07	-"-	0.2	0.006	0.014	0.01

Analysis of the size structure of the population has shown that mature individuals developed during winter, eliminate without reaching maturity. The sizes of mature helminths correlate with water temperature. At water temperature of $11-15^0$C (June 9–14) they reach their maximum sizes. The largest of them eliminate. A further rise of temperature is accompanied by maturation of cestodes of smaller sizes. The length of the last mature helminths found on July 9 did not exceed 0.5 cm (Fig. 3).

Development of the population is accompanied by a decline of its number. Approximately half of the helminths (48%) die at the initial stages when mature helminths develop. In the period of their growth there is another 22% decrease of the population, and only a quarter of helminths reach maturity

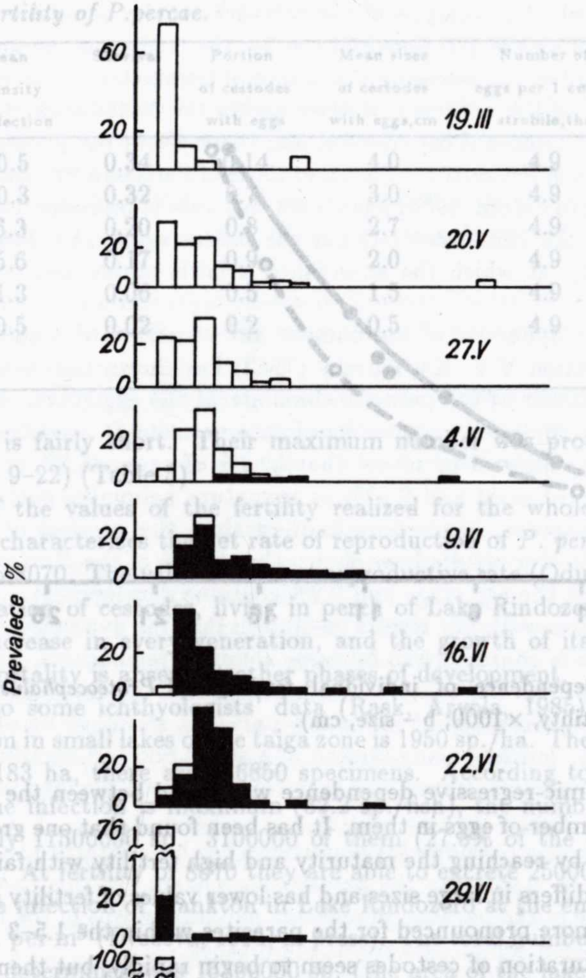

Figure 3. Changes of the size structure of cestodes *P. percae* in perch.

97.5% – (48% + 22%) = 27.5%. Later , when the population is mostly represented by mature individuals, the mortality values decrease. In our opinion, their dynamics is connected with momentary rises or drops of water temperature resulting in increased or decreased mortality of cestodes (Table 4).

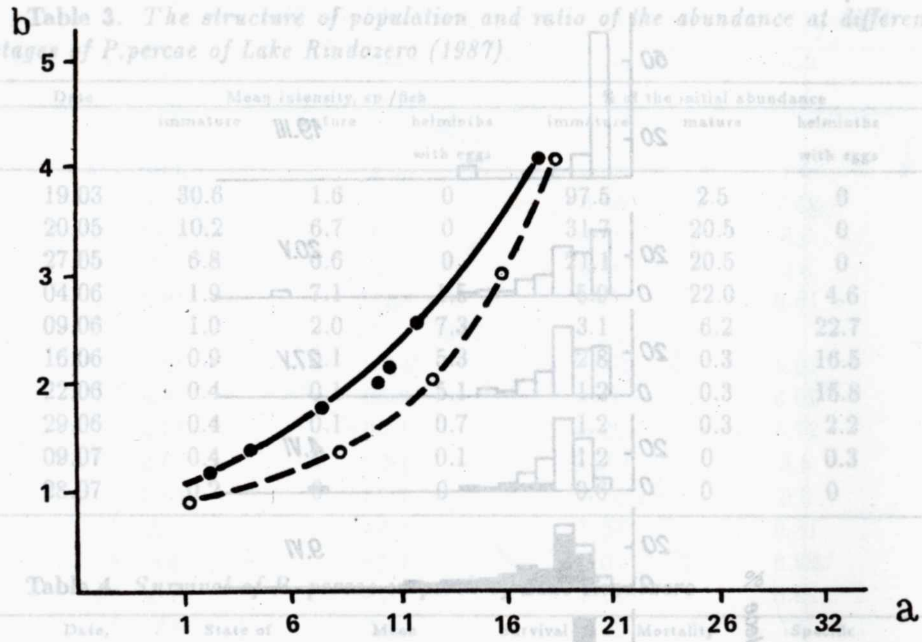

Figure 4. Dependence of individual fertility of *Proteocephalus percae* in Lake Rindozero (a–fertility, ×1000; b – size, cm).

The logarithmic-regressive dependence was found between the length of strobiles and the number of eggs in them. It has been found that one group of cestodes is characterized by reaching the maturity and high fertility with fairly small sizes, while the other differs in large sizes and has lower values of fertility (Fig. 4). These differences are more pronounced for the parasites within the 1.5–3 cm range. The growth and maturation of cestodes seem to begin rapidly, but then an increase of the linear sizes of helminths occurs against the background of excreting mature eggs that results in the apparent decrease of fertility. Knowing the individual characteristics of parasite fertility we determined the mean number of eggs per 1 cm of strobile to be 4900.

Table 5 shows the values characterizing the structure of the mature part of the population and *P. percae* fertility in perch. Our calculations (the product of the mean sizes of mature cestodes with eggs on the average number of eggs in 1 cm of strobile) allow to determine approximate values of fertility, because its accurate determination in natural populations is hardly possible. The fertility realized is the product of the fertility and survival of helminths. Taking into account the fact, that the mature helminths form only a part of the whole population of cestodes registered in perch we calculated their portion in the total number. Knowledge of the population survival at the given time period, the portion of cestodes with eggs, their mean sizes and the number of eggs allows to estimate the realized fertility in the concrete period. According to the data obtained the period of intensive

Table 5. *Fertility of P.percae.*

Date	Mean intensity of infection	Survival	Portion of cestodes with eggs	Mean sizes of cestodes with eggs,cm	Number of eggs per 1 cm of strobile,ths	Realized fertility, ths
04.06	10.5	0.34	0.14	4.0	4.9	0.93
09.06	10.3	0.32	0.7	3.0	4.9	3.29
16.06	6.3	0.20	0.8	2.7	4.9	2.12
22.06	5.6	0.17	0.9	2.0	4.9	1.50
29.06	1.3	0.06	0.5	1.5	4.9	0.22
09.07	0.5	0.02	0.2	0.5	4.9	0.01
						$\sum 8.07$

egg emergence is fairly short. Their maximum number was produced during a fortnight (June 9–22) (Table 5).

The sum of the values of the fertility realized for the whole period of egg emergence (R) characterizes the net rate of reproduction of *P. percae* population, which makes up 8070. The value of the net reproductive rate (Odum, 1986) shows that the population of cestodes, living in perch of Lake Rindozero, should have an 8000-fold increase in every generation, and the growth of its number being unlimited, if mortality is absent at other phases of development.

According to some ichthyologists' data (Rask, Arvola, 1985) the density of perch population in small lakes of the taiga zone is 1950 sp./ha. Then in Rindozero, whose area is 183 ha, there are 356850 specimens. According to these data, in March when the infection is maximum (32.2 sp./fish), the number of helminths is approximately 11500000 sp. 3100000 of them (27.5% of the initial number) become mature. At fertility of 8070 they are able to excrete 25000000000 eggs.

Spontaneous infection of plankton in Lake Rindozero at the end of July – August was 2.2 sp. per m^3 (Evseeva, 1991, in press). The total number of procercoids at the invasion determined was 15700000 sp. (the area of the lake is 1830000 m^2, the average depth 3.9 m).

On the basis of the obtained data we can determine the survival of the parasite from the egg to procercoid stage and then to plerocercoid. Our calculations enabled us to determine the total survival of parasite, which made up. 0.00012 ($0.00063 \times 0.073 \times 0.27$). On this basis, the true reproductive rate of the cestode population *P. percae* in Rindozero or the value of the population increase for one generation equals to 1.005 (0.00012×8070; 8070 - the net rate of reproduction of the cestode population).

DISCUSSION

The populational approach is a qualitatively new level of understanding the regularities of parasite system existence, because biological characteristics of mortality, birth - rate and the age structure of the species have sense only at the populational level. The analysis of the dynamics of the population number in *P. percae* has shown a principal possibility to use the traditional method for studying the parasite number for assessing populational parameters. The reliability of the results is based on the accuracy of determining the boundaries of the population and the spatial - temporal distribution and structure of the parasite population.

The comparison between our data and those of Peris and Pitelka (Peris, Pitelka, 1962: according to Odum, 1986) has shown that rate of reproduction of the cestode population in Lake Rindozero (R) has the values similar to those from natural population (R¡1), at which the abundance is fairly stable and ranges about the mean.

Studying the dynamics of the number and structure of *Dactylogyrus amphibothrium* population V.V. Kashkovsky (1982) has shown that not less than 99% of the initial number of the parasite eliminate at the egg stage. A more detailed analysis of the population parameters of carp parasite *D. vastator* made by V.E. Tomnatik (1988) allowed to reveal that 50.2% of eggs, 48.5% of oncomiracidia, only 0.94% of postlarval and 0.33% of immature helminths survive of the total number of Monogenea. According to these data the survival of mature worms makes up 0.04%. Our results have shown that 99.8% of the *Proteocephalus percae* population die at the egg stage and 0.2% continue development.

The comparison with our results has shown that the dynamics of the number of parasitic species is characterized by some common regularities. First, one should pay attention to high mortality at the preimagional phases of development. The regulation of the mortality of immature parasites seems to be of low efficiency, with the parasite number being limited in a water body. A significant decrease of the survival of helminth larvae and eggs causes serious damage to fish and other hydrobionths.

In this connection considerable importance has been attached to the adult phase of development in stabilizing the parasitising system. In this case studies of the spatial structure of the parasite population and assessment of the heterogeneity of the host population are of paramount importance.

It has been found (Ieshko, 1988) that in the process of host infection and parasite maturation the pattern of their distribution in fish population changes. According to the type of distribution we can distinguish host groups with different susceptibility to infection (Ieshko, 1987; Ieshko, Tomnatik, 1988) and with a different role of maintaining the number of the parasite population (Ieshko, Golitsyna, 1984).

These studies have shown that the success of the survival of the parasite population is dependent on the survival of mature parasites and their fertility which is mainly regulated by the structure of the final host population. The level of the number and distribution of many helminth species depends on the ratio between young and adult fish ages in the population.

Therefore, for water bodies where the first ones (plankton-eating young fishes) are dominant, favourable conditions are created for survival of a large number of parasites, and if the number of old - age groups is higher the level of the parasite number is much lower (Ieshko et al., 1989). In this connection to our opinion many aspects of ecological succession of the parasite fauna are rather with the conditions of survival of preimagional phases of development.

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Таблицы выживаемости гельминтов рыб и их анализ на примере цестоды *Proteocephalus percae* (Cestoda, Proteocephalidae) специфичного паразита окуня *Perca fluviatilis*

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Плотность популяции окуня в малых озерах зоны тайги составляет 1950 экз./га; таким образом, в Риндозере, с площадью 183 га, обитает 356850 экз. Исходя из этих данных, в марте при максимальной зараженности (32,2 экз. на рыбу) численность неполовозрелых цестод приблизительно равна 11,5 млн. экз. Из них половозрелыми становятся 3,1 млн. экз.(т.е. 27,5% от исходной численности). При реализованной плодовитости - 8070, они способны выделить 25000000000 экз. яиц. Общая численность процеркоидов при установленной инвазированности (2,2 экз./м^3) составляет 15700000 экз. По полученным значениям можно определить выживаемость паразита при развитии от яйца до стадии процеркоида, которая равна 0,00063. Выживаемость процеркоидов намного выше, и 0,73 их достигает плероцеркоидной стадии. В процессе созревания выживает лишь 0, 27 часть паразитов. Проведенные расчеты позволили определить общую выживаемость паразита, которая составляла 0,00012. Исходя из этого, реальная скорость размножения популяции цестод *Proteocephalus percae*, или величина, на которую увеличивается популяция при одной генерации, равняется 1.005.