

DYNAMICS OF EGG PRODUCTION OF THE CESTODE DIPHYLLOBOOTHRIUM DENDRITICUM (NITZSCH, 1824) (CESTODA: PSEUDOPHYLLIDEA) AND THE CONCEPT OF FECUNDITY IN HELMINTHS

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Abstract. The dynamics of egg production of the tapeworm *D. dendriticum* has been estimated experimentally in nestlings of the herring gull *Larus argentatus* per day and per reproductive period. Numbers of eggs in strobilae have been estimated for the maturation period. Mean egg production of one tapeworm per day (10.42 ± 2.72 mln) is two orders of magnitude as high as the maximal number of eggs in a mature strobila (0.206 ± 0.007). It is proposed to estimate the coefficient of reproduction intensity as the ratio of egg output per unit of time and maximum egg numbers in a mature strobila.

The development of research into population ecology of parasites requires an estimation of their population numbers at all phases of the life cycle. For parasites with a simple cycle and also for hemipopulations of parasitic phases of parasites with a complex development cycle this task is being solved on the basis of data on the structure and number of host populations in concrete ecosystems and on the distribution of parasites in a host population (Bauer 1984). For freshwater ecosystems similar studies have been carried out to determine the population structure of trematodes of the genus *Diplostomum* at all phases of the life cycle (Shigin 1980), and to estimate the absolute number of plerocercoids and imaginal phase of the cestode *Triaenophorus nodulosus* (Pronin and Khokhlova 1986) and the change in the numbers of *Acantocephalus lucii* in a population of *Asellus aquaticus* (Serov 1986).

A weak link in the study of the parasite population structure has been the estimation of the numbers of their hemipopulations at all free-living stages (eggs, coracidia, miracidia, cercariae) caused by the lack of counting methods. The first step in studying these stages with regard to the populations has been to estimate the numbers of eggs or larvae laid by the parasite. It appears that the knowledge of the reproductive potential of parasitic animals in general and helminths in particular is extremely scanty and has been elucidated for a very small number of species. A most detailed study has been made of the effect of many factors on the egg output in monogeneans per day under experimental conditions (Kearn 1986). However, their egg output for the entire reproduction period has been established only for *Polystomum integerrimum* (Bychowsky 1957) and *Dactylogyrus amphibothrium* (Kashkovskii 1982). Therefore the knowledge of the fecundity and dynamics of the egg output in *D. dendriticum* was required for the study of the structure of natural foci of diphylobothriosis and estimation of its numbers at all development stages in the ecosystem of Lake Baikal. A study of the egg output dynamics of *D. norvegicum*, that is a synonym *D. dendriticum* (Halvorsen 1970), has been performed by Braten (1966) in the experiment with golden hamsters. However, this laboratory model is ecologically inadequate to the life cycle of *D. dendriticum* in nature.

The data collected for many years on the distribution of *D. dendriticum* in fish-

eating birds of the Chivyrkuisky Bay and of its numbers have shown that about 90 % of hemipopulation of the tapeworm at the imaginal phase were found in the herring gull (Pronin et al. 1984). Analogous data on fish-eating colonial birds of the entire Baikal allowed us to estimate the total number of helminths in the definitive hosts in various nesting periods. It has been found that on the whole 93–95 % of adult hemipopulation of *D. dendriticum* is concentrated in herring gulls. Evidently this part of the hemipopulation of the tapeworm must provide the main amount of eggs laid in the water body. Therefore, primarily its egg production should be estimated.

MATERIALS AND METHODS

The estimates of *D. dendriticum* fecundity in the herring gull have been carried out in the Chivyrkuisky Bay (base of the Institute of Biology, Buryat Branch, Siberian Department of the USSR Academy of Sciences) and in the delta of the Selenga River (Ornithological Station of the Irkutsk University). For that purpose some experiments have been undertaken to study the establishment of plerocercoids of the tapeworm in gulls and the egg output dynamics. Nestlings of gulls were taken from their colonies in the Chivyrkuisky Bay one day after hatching. During the experiment, the nestlings were fed on filleted fishes (Cyprinidae and Percidae) which are not infected with diphylobothriids in Baikal Lake. Older nestlings were preliminarily dehelminthized with fern extract that gave 100 % result. This was followed by a coprooviscopic control using Kato method. The nestlings were infected by feeding capsules with plerocercoids of the tapeworm taken from the Baikal omul (*Coregonus autumnalis migratorius*). In various experiments, the nestlings were given 20, 10, or 1 capsule. The establishment of the plerocercoids was determined by the dissection of nestlings 3, 5, 7, 10, 14, 20 days p.i. The number of eggs in the strobila of tapeworms was estimated with the method of direct counts in the homogenate of single proglottids from 4 sites calculating it per number of segments in every site and summing up the values obtained. The observations on the egg-laying were made by a coprooviscopic control with Kato method beginning from the 3rd day after infection. Circadian hatching rhythm and daily egg output of the tapeworm were estimated by weighing all excrements on analytic balance at an interval of 2 h and by calculating the number of eggs in the smears with Kato method, the average mass from every portion of excrements being 4 mg. The data on *D. dendriticum* fecundity in herring gull only have been used in this work.

RESULTS

The experiments on the establishment of plerocercoids of tapeworm in nestlings of herring gull giving every nestling 20 capsules have shown that 5 days after infection the nestlings of the herring gull had 4–10 helminths (20–50 % of the number consumed, on the average $32-37 \pm 7-10$ %). The tapeworms were at various development stages. During that period only one strobila reaches the maturity in the intestine of every nestling which is 8–10 % of the number of helminths that have survived in all nestlings. About 70 % of the tapeworms had maturing strobilae and about 15 % were in the latent state at the plerocercoid phase. Further ratio of mature and maturing tapeworms changes according to the number of the remaining helminths, but the eggs are normally produced only by one specimen.

Thus the physiological age of most tapeworms is not determined by the duration of their occurrence in the definitive host. Therefore, the estimates of the egg numbers in the strobilae of tapeworms are given with the reference to their size and state of reproductive organs (Table 1), but not with the reference to the periods from the moment of infection. These data show that the total number of eggs increases regularly with the development of strobila and is directly related both to its length (correlation coefficient $r = 0.53 \pm 0.10$, $P = 0.999$) and to the number of mature segments in the strobilae ($r = 0.33 \pm 0.12$, $P = 0.95$). The maximal mean number of eggs (206.9 \pm 7.5 thousand) is observed in strobilae before the eggs are laid and in the

Table 1. The total number of eggs in strobilae of *Diphylobothrium dendriticum* of different sizes from nestlings of herring gull in experiment 5–20 days after infection

Characteristic of strobila	Length of strobila in mm		Number of segment		Total number of eggs in strobila in thousands	
	limits	M \pm m	limits	M \pm m	limits	M \pm m
Juvenile (n = 5)	65–158	124 \pm 22	100–370	224 \pm 50	0.03–3.3	1.3 \pm 0.7
Maturing (n = 14)	200–334	271 \pm 19	276–600	401 \pm 20	9–158	33.1 \pm 4.0
Mature (n = 23)	400–590	503 \pm 13	340–744	538 \pm 27	44–374	152 \pm 8.0
Sexually mature (n = 10)	600–899	714 \pm 32	445–760	609 \pm 38	64–358	206 \pm 77.0

beginning of egg-laying. In the “old” strobilae completing the production, the number of eggs is sharply reduced. A high coefficient of linear correlation between the number of larvae and body length of female of the nematode *Camallanus lacustris* ($r = 0.75$) has been shown by Tseitlin (1976). A direct relationship of the body size and daily egg output is known for the monogenean *Eutobdella solea* (Kearn 1986) and other helminths.

After an initial infection of nestlings with 10 and 20 capsules with plerocercoids of *D. dendriticum* the egg-laying began 5–6 days p.i. A regular periodicity of numbers of the eggs laid was observed with maxima 8–9, 14–16, 20–21 days p.i. with intervals of 5–7 days. Thus in the nestling N 25 infected with 20 capsules the maximal numbers were observed 8, 16, 20 days p.i. When it was dissected 22 days after beginning of the experiment, 8 tapeworms were found. Only one of them had a mature strobila producing 29.0 cm long eggs. Three strobilae were maturing (body length 12.0, 15.5, and 17.0 cm) and 4 were juvenile (length 3.0, 4.2, 7.0, 8.2 cm). At a longer observation on egg-laying in 12 nestlings to which 10–20 capsules were fed, the duration of production in 8 nestlings did not exceed 29 days p.i. In one nestling, the egg-laying finished 39 days p.i., in another one 66 days p.i. When they were dissected in 1–3 days after negative results in coprooviscopic test had been obtained, the tapeworms were not found. No release of segments of parts of strobila with excrements was observed. In two nestlings that received 20 capsules each, the eggs were laid periodically during 74 days p.i. At the dissection on 2 September 1985 each appeared to have one strobila of *D. dendriticum*. Most segments were without eggs. Some parts of strobila (2–6 segments) began splitting along the emptied uteri. It is obvious that in *D. dendriticum*, the resorption of strobila occurs after the reproduction, as has been observed in ligulids (Dubinina 1966). Before the dissection of these nestlings, a day-long observation on the egg output was carried out. It was 0.4 and 4.2 mln eggs per day. Thus at the initial stage, when the nestlings received 10–20 capsules with plerocercoids of tapeworm, it appeared impossible to determine either individual life duration of *D. dendriticum* in the definitive host or reproductive period duration of a single individual.

A long delay of *D. dendriticum* development in the definitive host at multiple infection has already been observed in experiments and immature strobilae with “primary” segments were found only several months after infection (Wardle and

McLeod 1952). However, causes of this phenomenon have not yet been analyzed (Freze 1977). In Freze's opinion the long delay in ontogenesis of this tapeworm is the result of superinfection, whereas the presence of "primary" and "secondary" strobila is not a permanent characteristic of ontogenesis in diphylobothriids and does not reflect the stages of their development, but it is an adaptive morphogenetic response related to a change of their habitat during the migration to different parts of intestine.

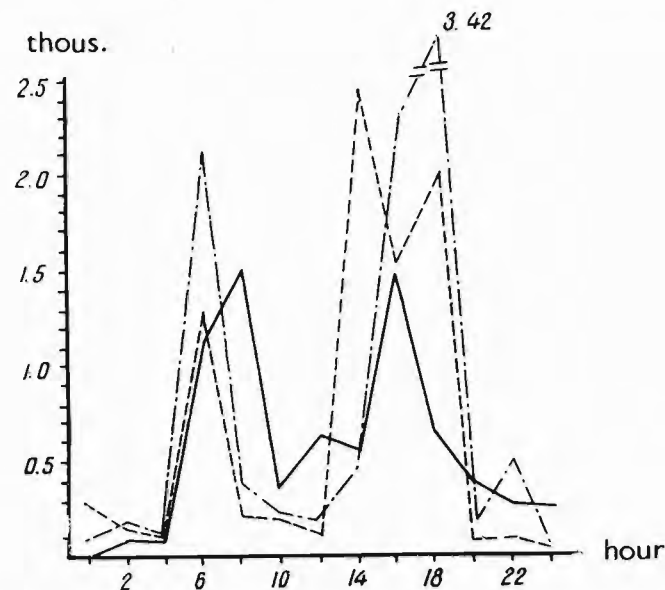


Fig. 1. Daily rhythm of egg production of *Diphylobothrium dendriticum* determined by the number of eggs in a smear with the Kato method in three experimentally infected nestlings of the herring gull.

Objective data on the life span and reproduction of diphylobothriids might have been obtained in experiments with guaranteed infection with one helminth developed from a plerocercoid of a certain size and age. We have carried out experiments infecting gull nestlings with only one capsule; but as one capsule may contain one as well as two plerocercoids of *D. dendriticum* (Pronin 1981), the nestlings in these experiments may have been infected by one or two specimens. Of 13 nestlings, that had received one capsule of tapeworm each, 8 became infected (61.5%). The egg-laying began 5–10 days, mainly 6–7 days p.i. Different rates of maturation of the tapeworms probably depend on the size and age of the plerocercoids given to them. In most nestlings (6 out of 8), the egg-laying was completed 13–15 days p.i. Further coprooviscopic tests gave negative results, i.e. the reproductive period of *D. dendriticum* is 7–10 days long. In two nestlings, the egg-laying lasted 18–20 days after infection, with two maxima of production intensity. One may assume that infection with two helminths was involved in these two cases.

A distinct rhythm in egg production of tapeworms was observed during the daytime (Fig. 1). A minimal number of eggs was laid at the night time. The first period of intensive egg-laying was observed after 4 a.m. with a maximum peak at 6 a.m. Then the number of eggs in smear decreased by an order of magnitude. The second period

of intensive egg-laying began after 2 p.m. with a maximum from 4 p.m. This periodicity of egg production of tapeworms during 24 hours obviously depends on the daily rhythm of metabolism of helminths that in its turn depends on the daily rhythm of metabolism of host and its feeding activity in natural conditions. For the tapeworm this is of great biological importance, since it provides egg dispersal during hours of host's activity (search for food, feeding), but not during periods of gulls rest in colonies on the coasts during night or day time. Obviously such circadian rhythm of physiological processes of tapeworm is genetically fixed and is revealed even under experimental conditions, although it may be slightly shifted in time. It is probably related to circadian rhythm of mitotic activity in adult of *D. dendriticum* that has been described earlier (Wikgren et al. 1970).

The number of eggs produced by a tapeworm per day varies greatly throughout the reproductive period (Fig. 2). During the first three days from the beginning of

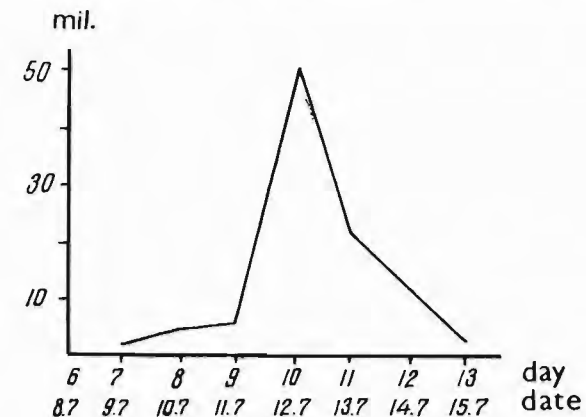


Fig. 2. Dynamics of mean daily egg production of *D. dendriticum* in a nestling of the herring gull during the non-reproductive period.

reproduction the daily egg output increases slowly with a subsequent sharp maximum (50.7 mln/day) on the 4th day and then gradually declines by the 7th day to the initial level of 2.5 mln. The total 7-day egg output of a tapeworm, whose dynamics of egg production is shown in Fig. 2, has been 99.45 mln, a half of the maximum egg output per one day. A similar parabolic pattern of reproduction intensity was observed by Bychowsky (1957) in the monogenean *Polystomum integerrimum*. The annual period of polystome reproduction lasts 12–13 days when it lays 200–2500 eggs; the egg production rate increases from several dozens up to hundreds of eggs per day and then reduces. A maximum egg production per day may be 900–1500 eggs (from 40% up to 60% of the total egg production per the reproductive period). Such dynamics of egg production may be typical of many helminths with a short reproductive period. Thus the first branch of the parabola is distinctly traced in the intensity of egg production of monogenean *Dactylogyrus vastator* according to the data of experimental observations of Izyumova (1956). These parabolas terminate in the point of maximum, which is related to the extreme environmental conditions for the host and parasite. Anderson (1976) used Miles's data to publish a parabolic graph of egg production of the trematode *Transversotrema patialense* during the reproductive period that lasts 9 weeks.

The total egg production of one tapeworm per reproductive period in various nestlings of herring gull in the experiment ranged within 60 to 100 mln and was 73.74 ± 3.73 mln on the average. Probably this figure can be adopted as the working one for calculating the egg production of a tapeworm hemipopulation in herring gull on Baikal Lake, the mean daily egg production of one tapeworm being 10.43 mln. A single-day observation on the egg production in spontaneously infected nestlings of herring gull from colonies has also shown considerable fluctuations of egg output per day from 1.0 to 19.7 mln and they did not coincide with the maximum intensity of egg production.

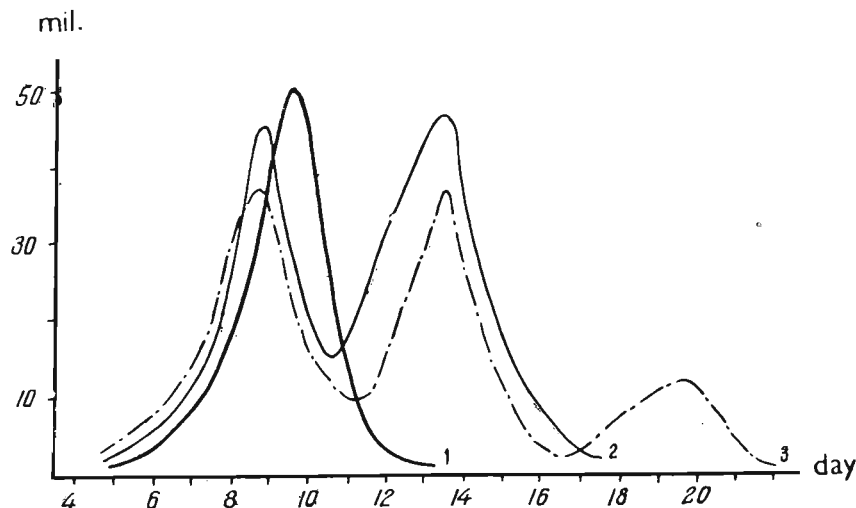


Fig. 3. A scheme of dynamics of egg production of *D. dendriticum* at different infection intensities: 1 — with one helminth, 2 — with two helminths, 3 — with three helminths.

As has already been mentioned, when nestlings of gulls were infected by several tapeworms, a periodicity of egg production intensity was observed, which is determined by consequent maturation and reproduction period in several helminths in the intestine of one gull. In case of infection with two tapeworms, at first only one helminth produces eggs with the same parabolic dynamics of daily egg production as in case of infection with one helminth. Perhaps products inhibiting the maturation of the other one are released. After one of the helminths has completed the egg production, it is resorbed and another helminth begins to produce eggs. The intensity of daily egg production of the second helminth has the same egg-output dynamics as that of the first one, with an analogous maximum 14–15 days p.i. At increasing infection intensity the number of such parabolic waves of egg production increases accordingly and the life span in the definitive host of tapeworms that have reached maturation period in the second, third turn increases. A principle scheme of egg output at different initial intensities of infection is shown in Fig. 3. Thus the maximal life span of tapeworms attains 74 days, as has been found in two herring gulls infected experimentally with 20 capsules each mentioned in the beginning of this paper. Obviously in those cases up to 10 helminths survived, that reached maturity, laid eggs, and were eliminated by the host in turn. The life duration of some helminths up to egg production increased, but not the duration of the reproductive period.

Thus the observations have shown that despite different life spans in the obligatory and definitive hosts (from 15 to 74 days) depending on the initial intensity of infection, *D. dendriticum* has a relatively short reproductive period, during which it produces an enormous amount of eggs.

In golden hamster, under experimental conditions *D. dendriticum* commences the egg production only 5–7 days p.i. with a parabolic pattern of egg output during the initial period (Braten 1966). However, the life span of tapeworm in a noncharacteristic host is extended and fluctuates within the limits of 61 to 273 days. The above-mentioned author did not present any figures on the daily egg production of tapeworm in hamsters. However, judging from the diagrams of egg numbers in the day amount of excrements it varied from 0.2 to 2 mln eggs with repeated oscillation changes during the reproductive period. By the 6 diagrams given by Braten (1966) one can determine approximately that the total egg production was 25 to 250 mln eggs. Evidently, the host factor has a profound influence on the intensity of metabolic processes in helminths, though the reproductive potential, of the species, in spite of the high individual heterogeneity, can be realized also in an atypical host with essential variation of length of the reproductive period.

CONCLUSION

A high fecundity is regarded as a characteristic feature of most of the parasitic animals (Dogiel 1962; Schulz and Gvozdev 1972; Kennedy 1975). However, there are no accurate data on the fecundity and clear view of fecundity of parasites, particularly of helminths (Roytman 1981). Fecundity is frequently understood, even in general handbooks and manuals on parasitology, as the number of eggs in reproductive organs of a parasite. Apart from the concept of “fecundity” and egg production, terms as individual, real, factual, potential fecundities, etc. are used. Evidently, in parasitology the general concept of fecundity should correspond to its general biological meaning as the number of eggs (or larvae in case of viviparity) produced by an organism per one reproductive period or for lifespan. Therefore, the quantitative equivalent of fecundity means the estimate of egg output of animal per reproductive period or per lifespan. However, the concept of “fecundity” should not be identified with “egg production”. Fecundity is the result. Egg production means the process and result per given period of time. In our opinion, individual fecundity should be regarded in a specific sense as fecundity estimated for a concrete individual, and in population counts, the mean individual fecundity should be estimated as the quotient of a sum of individual fecundities and number of individual whose fecundity is determined and whose sample shows the structure of the mature part of parasite hemipopulation. In this case, it is not worthwhile to use the concept “population fecundity”, since it is substituted by “mean individual fecundity” (MIF) of x-hemipopulation and fecundity of a population as the product of MIF by the number of its mature individuals. Evidently, for parasites not dispersing all eggs and larvae at a time, “fecundity” should not be judged by the number of eggs and germinal balls in reproductive organs. However, “potential” fecundity in the sense considered in the work by Serov (1984) is the MIF of *Acanthocephalus lucii*, whereas Tseitlin's data (Tseitlin 1987) on the number of larvae in females of *Camallanus lacustris* should be identified neither with the potential fecundity as the above-mentioned author does, nor with the individual one.

At the same time, MIF of the population does not characterize peculiarities of the reproductive potential of the species, since the duration of the reproductive period

is different in different species. Similar numbers of eggs (larvae) can be produced in different species per several days in one and per several months or a year in another, and we have to speak of their similar fecundity. Therefore, it is worthwhile to compare "fecundity" of different species by the egg output per equal periods of time (day, hour). To characterize the intensity (rate) of reproductive process it is suggested to use the ratio of the number of eggs laid per unit of time (N_t) and mean maximum number of eggs in reproductive organs (n) of mature parasites. This index can be called reproduction coefficient K_r . It should be estimated primarily for the whole reproductive period. For example, for *D. dendriticum* it is equal to $73.7 \cdot 10^6 : 2.0 \cdot 10^5 = 3.68 \cdot 10^2$. Using this coefficient, individual fecundity can be estimated at first approximation in this case data are provided on the number of eggs in parasites $N = K_r \cdot n$. Accordingly, the daily reproduction coefficient can be calculated. For *D. dendriticum* $K_r = 10.4 \cdot 10^6 : 2.0 \cdot 10^5 = 0.52 \cdot 10^2$.

ДИНАМИКА ЯЙЦЕПРОДУКЦИИ ЦЕСТОДЫ *DIPHYLLOBOOTHRIUM DENDRITICUM* (NITZSCH, 1924) (CESTODA, PSEUDOPHYLLIDEA) И ПОНЯТИЕ ПЛОДОВИТОСТЬ У ГЕЛЬМИНТОВ

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Резюме. Изучена динамика яйцепродукции *Diphyllbothrium dendriticum* у птенцов серебристой чайки *Larus argentatus* в течение суток и за репродуктивный период (РП). За РП левтец выделяет от 60 до 100 млн. яиц, более половины которых может продуцироваться за одни сутки. Среднесуточная яйцепродукция лентца ($10,42 \pm 2,72$ млн.) на два порядка больше максимальной численности яиц в зрелой стробиле ($0,206 \pm 0,007$). Обсуждаются понятия плодовитость и яйцепродукция у паразитических животных. Предложено определять коэффициент интенсивности репродукции (K_r) по отношению величины продукции яиц за единицу времени к максимальной численности яиц в зрелой стробиле.

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