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TRANSMISSION TRIGGERS AND PATHWAYS IN *GYRODACTYLUS SPHINX* (MONOGENEA, GYRODACTYLIDAE)

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Transmission Triggers and Pathways in *Gyrodactylus sphinx* (Monogenea, Gyrodactylidae). Dmitrieva E. V. — The ratio between the different ontogenetic stages of gyrodactylids transferred from infected to uninfected hosts was studied. 72% of transmitted individuals have a functional male reproductive system and can reproduce only sexually. Therefore, in *Gyrodactylus sphinx* Dmitrieva et Gerasev, 2000 transmission mainly involves individuals with a functional male reproductive system. It is likely that the sexual maturation of gyrodactylids provides the trigger for migratory behaviour. The restricted occurrence of *G. sphinx* on one host species in nature is a result of innate host specificity. Both the behavioural patterns of *G. sphinx* and physiological parameters of the fish uphold the search for a suitable host.

Key words: Gyrodactylidae, *Gyrodactylus*, transmission, trigger, host specificity.

Пусковой механизм расселения и направление трансмиссии *Gyrodactylus sphinx* (Monogenea, Gyrodactylidae). Дмитриева Е. В. — Проанализировано соотношение особей, находящихся на разных стадиях онтогенеза в части популяции *Gyrodactylus sphinx* Dmitrieva et Gerasev, 2000, мигрирующей на нового хозяина. Среди иммигрировавших гиродактилид доля особей с функционирующей мужской половой системой, способных размножаться только половым путем, составляет 72%. Таким образом, трансмиссия *Gyrodactylus sphinx* осуществляется главным образом за счет особей с функционирующей мужской половой системой. Половое созревание, по-видимому, и является пусковым механизмом миграционного поведения гиродактилид. Узкая встречаемость *G. sphinx* в природе соответствует его врожденной строгой специфичности. По-видимому, особи *G. sphinx* находят подходящего хозяина, ориентируясь по его физиологическим параметрам и благодаря их собственным поведенческим особенностям.

Ключевые слова: Gyrodactylidae, *Gyrodactylus*, трансмиссия, пусковые механизмы, специфичность.

Introduction

Although numerous studies of the biology and ecology of *Gyrodactylus* Dmitrieva et Gerasev, 2000 (Monogenea, Gyrodactylidae) have been conducted, the behavioural triggers involved in the transmission of gyrodactylids and, especially, in the abandonment of a suitable host are as yet unknown. The hypothesis that transmission begins with the accidental detachment of gyrodactylids or an accidental contact of hosts seems dubious, inasmuch as transmission is too important to occur by chance. Known host-parasite systems exhibit a great diversity of specific mechanisms which efficiently enable dispersion of the parasites. Therefore, it seems rather questionable to assume that gyrodactylids have not developed similar mechanisms. Looking at data on the biology of *Gyrodactylus*, it appears reasonable to suppose that the development of the male reproductive system may be the trigger for their migratiory behaviour. In oviparous monogeneans cross-transmission induced by sexual maturation is common. For example, sexually mature gill-parasitic monogeneans, such as *Ancyrocephalus paradoxus* and some species of both *Dactylogyrus* and *Diplectanum*, move along the gill forming aggregations of individuals prior to fertilization (see *inter alia* Oliver, 1976; Izumova, Zharikova, 1982; Gerasev, Starovoitov, 1988; Dorovskikh, Matrokhina, 1991). *Entobdella solea,* the early stages of development of which take place on the upper surface of the its host, migrate to the lower surface of the fish on reaching sexual maturity (Kearn, 1963).

In order to validitate this hypothesis, the composition the ontogenetic stages in the population of gyrodactylids migrating from infected hosts to uninfected ones was analysed.

Material and methods

Gyrodactylus sphinx Dmitrieva et Gerasev, 2000 parasitizes the Black Sea blenny, *Blennius sphinx* Valenciennes. Four ontogenetic stages of the worm (fig. 1) were distinguished based on the development of the

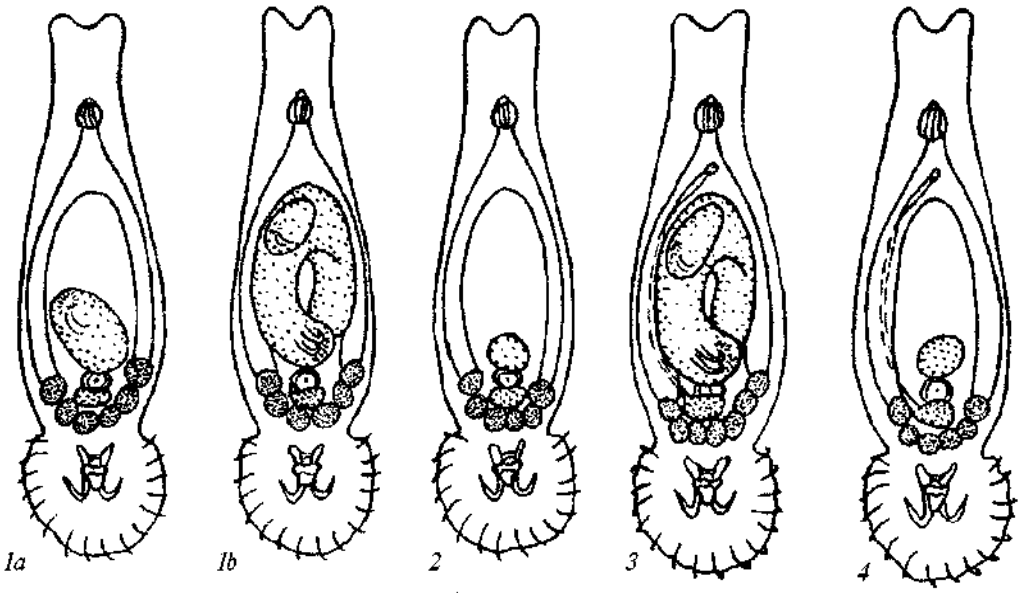

Fig. 1. Ontogenetic stages of gyrodactylids according to the development of reproductive system and embryo: *1* — new born (*1a*) pre-first birth individuals (*1b*); *2* — immediately post-first birth individuals; *3* — pre-second or pre-third birth individuals; *4* — post-second or post-third birth individuals.

Рис. 1. Стадии онтогенеза гиродактилид, определяемые по степени развития репродуктивной системы и эмбриона: *1* — новорожденная (*1a*) перед отрождением первого потомка (*1b*) особи; *2* — особь сразу же после отрождения первого потомка; *3* — особь перед отрождением второго или третьего потомка; *4* — особь после отрождения второго или третьего потомка.

male reproductive system and embryo using data presented by Harris (1985): *1* — the new-born (*1a*)/pre-first birth (*1b*) individuals, which have an advanced embryo, have no penis and can reproduce only asexually; *2* — the immediately post-first birth individuals, which have an embryo consisting of several cells and no penis. At this stage the male reproductive system is still under development, thus the second embryo is formed without fertilization, although the following one will definitely be the result of fertilization; *3* — the pre-second and pre-third birth individuals, which have a penis and an advanced embryo. The latter could result from both asexual (if it is the second embryo) and sexual (if the third embryo) reproduction, but subsequently they will reproduce only sexually; *4* — the post-second or post-third birth individuals, which have a functional male reproductive system and a uterus either empty or containing a very small embryo. These individuals also reproduce only sexually.

Two specimens of the host (*B. sphinx*) infected with *G. sphinx* and one uninfected were placed in an aquarium filled with 1 litre of the seawater at a temperature of 16°C. Average initial intensity of infection was 8 worms per host. Seven replicates were performed, each lasting for 10 days. Transmitted gyrodactylids were

Table 1. Ontogenetic stages of *Gyrodactylus sphinx* transmitted from infected fish to uninfected fish and the transmission rate

Таблица 1. Стадии онтогенеза особей *Gyrodactylus sphinx*, иммигрировавших на незараженного хозяина и скорость трансмиссии

Replicate	Initial infection of 2 fishes	Day										Average per day
		1	2	3	4	5	6	7	8	9	10	
1	7, 9	0	0	3s*	4s, 2s	2s, 3s	2s	3s	4s	0	0	0,8
2	10, 12	0	2s	3s, 3s	4s	2s, 4s	3s	4s	4s	4s	0	1
3	10, 8	0	3s	3s, 4s	2s, 4s	2s, 4s	2s	3s	4s	0	0	1
4	10, 7	0	0	2s	2s	4s	3s	4s	4s	0	0	0,6
5	9, 8	0	0	3s	3s, 2s	4s, 3s	4s	0	4s	0	0	0,7
6	10, 7	0	0	2s, 2s	3s, 4s	4s, 4s	3s	0	3s	0	0	0,8
7	7, 8	0	0	2s	3s	2s	0	3s	4s	0	0	0,5
Average:	8										Average:	0,8

* The stages of gyrodactylid ontogenesis: 1s — the pre-first birth/new-born individuals; 2s — immediately post-first birth individuals; 3s — the pre-second or pre-third birth individuals; 4s — the post-second or post-third birth individuals.

immediately detached from the host and their developmental stages determined. The blennies were examined daily. The resulting data are presented in table 1.

Other experiments were carried out in order to determine the host specificity of *G. sphinx*. In the first experiment *B. sphinx*, the typical host of *G. sphinx*, were placed an aquarium with other fish species (*Blennius pavo* Risso, *B. sanguinolentus* Pallas, *Neogobius melanostomus* (Pallas)) from the same natural habitat. Seven replicates were performed: 1 — fishes were examined after 1 day of exposure to the parasite; 2 — after 2 days; 3 — after 3 days; and so on. In another experiment, several *G. sphinx* were placed on specimens of *B. pavo* and *B. sanguinolentus*, which were then examined hourly. The longest exposure time in this experiment was 5 hours. The experiment was replicated 5 times.

Results and discussion

A sum total of 54 gyrodactylids transferred to a new host, with a mean rate of transmission from infected to uninfected host of 0.8 per day. The first ontogenetic stage was not found among the transmitted gyrodactylids. The proportion of immediately post-first birth individuals with a second embryo and in which the male reproductive system is under development (2nd stage) was 28%; the remainding 72% were those with a functional male reproductive system and a sexual reproduction mode (third and fourth stages) (tabl. 2).

Such a population structure of developmental stages among the transmitted gyrodactylids cannot be the result of the accidental detachment of worms, because accidental detachment is equally likely for all developmental stages. Furthermore, these experimental results differ from those known for these stages in gyrodactylid populations. For example, half the *Gyrodactylus turnbulli* Harris, 1986 population consists of the pre-first birth worms, and the proportion of post-second and post-third birth worms is less than 2%; and populations of *G. arcuatus* Bychowsky, 1933 and *G. gasterostei* Glaser, 1974 include 55% pre-second birth individuals and only 5% of post-second and post-third birth worms (Harris, 1985, 1988, 1993). Among the transmitted individuals of *G. sphinx* there are no the pre-first birth worms, whereas the post-second and post-third birth worms (4th stage) comprise almost 40%, i. e. 6 times as many as normally occurs in the population. (fig. 2). Therefore, the migration of this stage cannot be accidental and may well result from behavioural changes associated with sexual maturity.

Moreover, data on the distribution of these stages among gyrodactylids recovered from sediment (Harris, 1988) agrees with our data from transmitted forms. High values of the portions of third and fourth stages found in sediment (fig. 3) have been explained by Harris as exclusively the result of age-specific mortality. However, direct evidence is not available, because all worms are found alive. Furthermore, both our data and that of Scott and Anderson (1984) indicate that detached gyrodactylids can move successfully to a new host. It is likely that mature gyrodactylids are more abundant in sediment than on fish through active migration from their hosts.

The ratio between the ontogenetic stages of *G. arcuatus* on the gills and on the skin (Harris, 1993) agrees with the model of gyrodactylid transmission presented here. The percentage of "on-skin" gyrodactylids with a functional male reproductive system is several times greater that on the gills (fig. 4). This disparity can hardly be explained by

Table 2. The percentage of the ontogenetic stages of *Gyrodactylus sphinx* in specimens transmitted to various uninfected fish

Таблица 2. Процент особей разных онтогенетических стадий *Gyrodactylus sphinx*, иммигрировавших с зараженных рыб на незараженных

Stage	Replicate							Total ± Sx, %
	1	2	3	4	5	6	7	
2s	37.5	20	30	33	14	25	40	28.5 ± 9.4
3s	37.5	30	30	17	43	37.5	40	33.6 ± 8.8
4s	25	50	40	50	43	37.5	20	37.9 ± 11.6

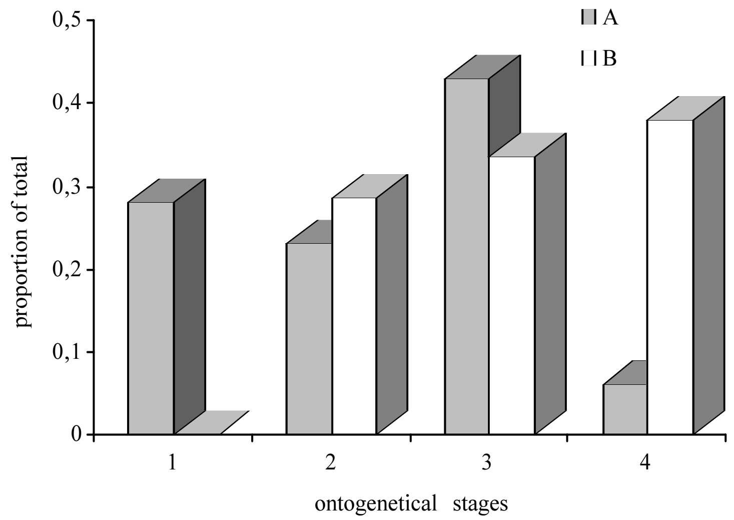

Fig. 2. Ratio between the ontogenetic stages (see fig. 1) in the entire population of Gyrodactylus sphinx (A) and between individuals which have migrated to a new host (B).

Рис. 2. Соотношение особей, находящихся на разных стадиях онтогенеза (см. рис. 1), во всей популяции Gyrodactylus sphinx (A) и среди особей, иммигрировавших на нового хозяина (B).

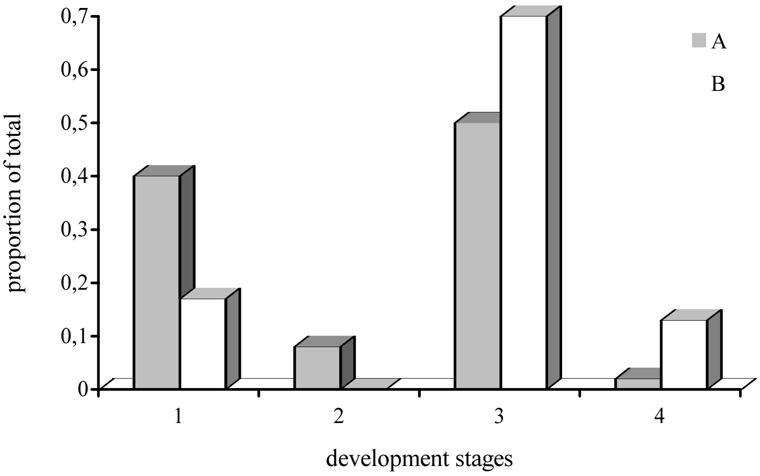

Fig. 3. Ratio between the ontogenetic stages (see fig. 1) of Gyrodactylus turnbulli on the skin of Poecilia reticulata (A) and in sediment (B) (using data from Harris, 1988).

Рис. 3. Соотношение особей Gyrodactylus turnbulli, находящихся на разных стадиях онтогенеза (рис. 1), на коже Poecilia reticulata (A) и в осадке (B) (использованны данные из работы П. Харриса, 1988).

age mortality, and is more likely due to the displacement of sexually mature worms from fish gills to the skin prior to transmission to a new host.

We suggest that the searching behaviour of gyrodactylids is induced by the physiological changes which accompany the development of the male reproductive system.

The transmission of sexually mature organisms from host to host aids the survival of the species. Asexual reproduction leads to the gyrodactylid stock on one host consisting of several asexual clones of the same species. Cross-fertilization between these closely related individuals increases the risk of the homozygosity of recessive characters. Therefore, the immigration of mature parasites to other hosts helps maintain heterozygosis in the population and increases genetic diversity, which also promotes the survival of the species in general.

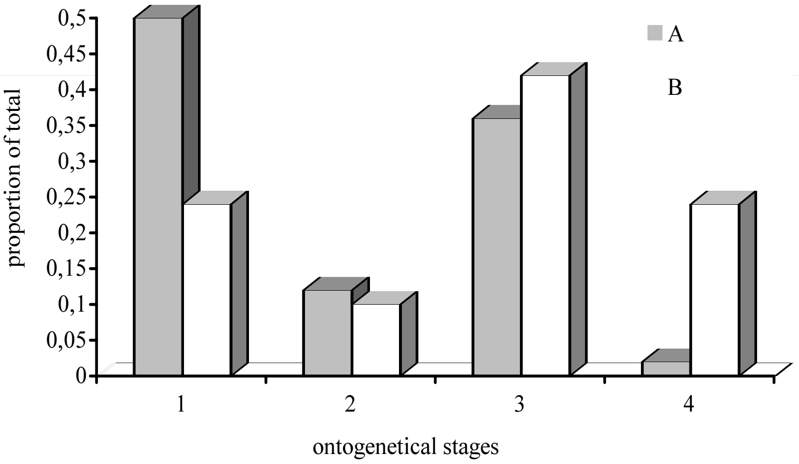

Fig. 4. Ratio between ontogenetic stages (see fig. 1) of Gyrodactylus arcuatus on the gill (A) and on the skin (B) of Gasterosteus aculeatus (using data from Harris, 1993).

Рис. 4. Соотношение особей Gyrodactylus arcuatus, находящихся на разных стадиях онтогенеза (рис. 1), на жабрах (A) и коже (B) Gasterosteus aculeatus (использованны данные из работы П. Харриса, 1988).

Bakke et al. (1992) have described different transmission pathways for gyrodactylids and have pointed out that worms behaviour is an essential component of the dispersal strategy of these worms. In order to clarity the specific mechanism of transmission used by *G. sphinx* in the Black Sea coastal environment, a number of experiments were carried out. In nature this species is found only on one host, *Blennius sphinx*. Under experimental conditions, *G. sphinx* did not leave its natural host and move to other fish species placed in the same aquarium. When these gyrodactylids were mechanically transferred to atypical hosts, they detached within a few hours, which clearly indicates a strictly physiological mechanism for maintaining the presence of *G. sphinx* on its appropriate host. Therefore, this gyrodactylid species does not apparently use a transport host as an aid to transmission in its natural environment. On the other hand, this species has a behavioural mechanism which enables an efficient search for a suitable host. All of the detached worms were found on the bottom and walls of the aquarium and ignored all macrophytes. This behaviour is congruent with the behaviour of its host, the blenny, which prefers to locate on the substrate and away from macrophytes.

Thus, *Gyrodactylus sphinx* transmission is undertaken by individuals with a functional male reproductive system, and the trigger for their migratory behaviour may be sexual maturation. The narrow occurrence of this monogenean in nature totally coincides with its innate host specificity. In their search for a suitable host these worms are abetted by physiological parameters of the host and by their own behavioural patterns.

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