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STUDIES ON GILL PARASITOSIS OF THE GRASSCARP CTENOPHARYNGODON IDELLA) CAUSED BY DACTYLOGYRUS LAMELLATUS ACHMEROW, 1952

II. EPIZOOTIOLOGY

By

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Dactylogyrus lamellatus infection has been frequently reported since the establishment of grasscarp pond farms (Molnár, 1971), but little information has been presented on the ecology and pathogenicity of the parasite itself.

Bauer and Strelkov (1963) were the first to observe a lethal *D. lamellatus* infection of grasscarp fry. Later Molnár (1966) reported similar outbreaks and described the therapy of dactylogyrosis. Examining the dynamics of *D. lamellatus* infection, Mussellius and Ptashuk (1970) found that the parasite population in the fry-rearing pond tended at first to increase then to fall until it became stabilized at a relatively low level.

As to other *Dactylogyrus* species, epidemiological data have been available primarily on those parasitizing the common carp *(Cyprinus carpio)*. Wunder (1929) and Paperna (1963, 1964) have studied the dynamics and pathology of *D. vastator* infection and Prost (1963) observed the changes caused by *D. extensus* and *D. anchoratus*. Jaczó (1966) and Ivasik (1967) made important observations on the incidence of the above three *Dactylogyrus* species among one-summer cultured carps. Wilde (1937) has investigated the epidemiology of *D. macracanthus* infection in *Tinca tinca* and Musselius (1968) that of *D. aristichthys* infection in the bighead *(Aristichthys nobilis)*. Molnár (1968) carried out similar studies on the phylogenetically distant species *Ancylodiscoides vistulensis*, a gill parasite of the silur *(Silurus glanis)*.

Little is known about the interrelationships between gill parasites and their hosts. Authors concerned with this problem have often noted that reinfection of hosts with an established gill parasitosis is followed by a reduction or even complete disappearance of the infestation rather than by an increase. As a rule this phenomenon has been attributed to immunity, without further scrutiny of the possible specific allergic or other nature of the response. The only species more closely studied in this respect has been *D. vastator*, although it is the least suited for the purpose owing to its special seasonal biological cycle.

Of the authors who have investigated the protective mechanism of the host, Wunder (1929) believed that the proliferative epithelial reaction of the gills is the primary factor in controlling the infection. L'yaiman (1948) attributed the disappearance of *D. vastator* from the host to age resistance, while Bauer (1959) and Vladimirov (1967) have attributed it to acquired (superinvasion) immunity. Paperna (1964) performed similar experiments to Vladimirov's but has been anxious to avoid the term "immunity", using instead the more general term "acquired resistance". Bauer, Musselius and Strelkov (1969) have advanced the theory that the immune response is stimulated by a substance secreted by the larvae rather than provoked by continuous infestation.

Resistance to *D. lamellatus* has not yet been investigated in more detail. Musselius and Ptashuk (1970) have supposed that it might be similar in nature to the acquired immunity to *D. vastator;* in experimentally infected groups of fishes, the peak of the infestation as well as its decline were independent of the season and temperature, i.e., the parasite count of the host tended to decrease regularly after reaching a certain level.

Epizootiological studies of grasscarp dactylogyrosis were carried out in this laboratory to fill certain gaps of knowledge about *D. lamellatus* infection.

Method

The dynamics of *D. lamellatus* infection were followed up over a period of several years. The stricture on interfering with routine operations in the pond farm was a serious drawback, as it prevented regular sampling in most of the ponds. The information emerging from the irregular samplings has therefore been treated as complementary to data obtained from each of the latter 10 fishes were taken as far as possible every seventh day for sectioning in either the freshly killed or formalin-preserved state. All adult and developmental stages harboured by the freshly exterminated specimens were counted, while with formalin-fixed carcases only the adults settled on the gills were counted precisely and the numbers of the developmental stages were estimated roughly as many, few, or very few.

The infection experiments were carried out in aquaria of 30—40 litres volume. One- or two-summer grasscarps (further on referred to as donors) infected with *D. lamellatus* served as the source of infection. The fry to be infected were placed in groups in small mesh-covered wooden boxes floating on the water surface; the each was large enough to admit the *D. lamellatus* larvae.

Eradication of *D. lamellatus* from the fry was accomplished by placing the latter in a 1 ppm Ditrifon bathing solution for two days.

I. Spread of Dactylogyrus lamellatus

The introduction of *D. lamellatus* into Hungary dates back to the first import of 2—3 cm long grasscarp fry from China (SZAKOLCZAI and MOLNÁR, 1964, 1966). At present the parasite occurs in practically all grasscarp ponds of the country.

II. The dynamics of D. lamellatus infection

1. Infestation of the grasscarps during the various stages of breeding

Infection in the fish hatchery is hardly probable, because the larval parasites cannot fix themselves on the gills of larval fishes only a few days old (MOLNÁR 1971). Fry with yolk sac were found to harbour the parasite at 12 days of age at the earliest. As these parasite stages were already fully developed, there is reason to suppose that some of the tens of thousands of fry placed in the aquarium had contracted the infestation as early as 5—7 days of age, viz. at the earliest time demonstrated experimentally.

Acute dactylogyrosis with manifest clinical symptoms was observed on four occasions. In each case the fishes were placed in an experimental nursery pond of 148 m^2 area, at a density of 300 individuals per m^2. The outbreaks, which killed the greater part of the population, developed by the 30th day after transfer to the nursery pond. The 3.5—4.5 cm long young fishes each harboured 80—250 *D. lamellatus* parasites on their gills (Fig. 1). Diseased fishes always carried more than 150 parasites.

Dactylogyrosis of varying severity was observed also in the fingerling ponds, 1600 m^2 in area. At a medium stocking density (90 individuals per m^2) infestation remained at a low level (30—100 parasites per host), but at a high

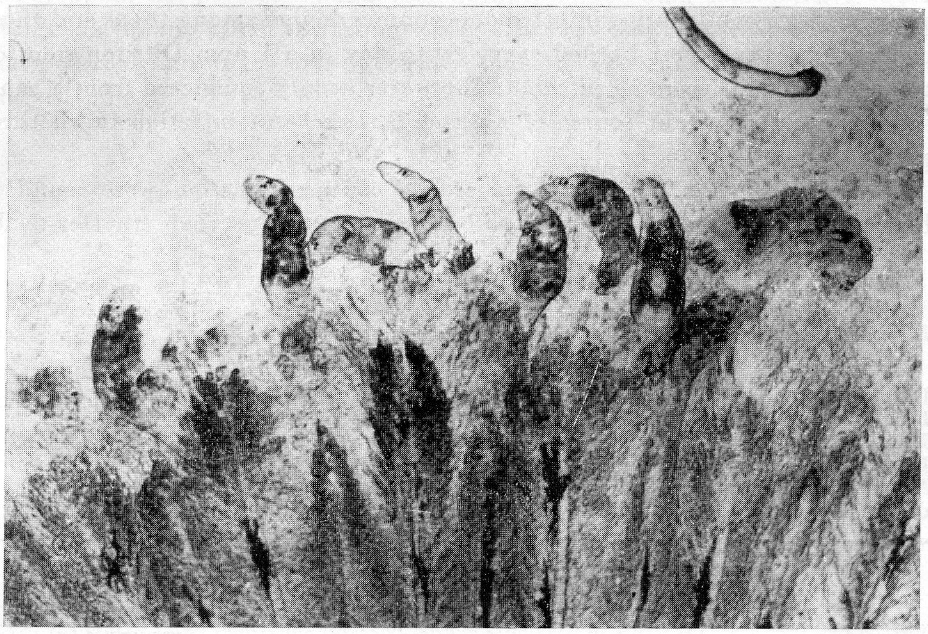

Fig. 1. Dactylogyrus lamellatus individuals on the gills of a grasscarp

population density (200 individuals per m^2) some of the fishes developed clinical dactylogyrosis during the six-week nursery period, each 2—4.5 cm long diseased fish carrying 150—250 *D. lamellatus* individuals.

The degree of infestation usually decreased considerably in the rearing ponds; although all fishes were infested, the number of parasites harboured by any one fish did not exceed 5—30.

Infestation persisted during the winter, but it was of a very low degree; hosts carried only a few parasites and some were even parasite-free, whether transferred to a wintering pond or left in the rearing pond for the season. During spring, parasite counts tended to increase with the rise in temperature, and infestation progressed to clinical disease if the population density was high.

Mother fishes five to seven summers old, kept in stocking ponds as replacement reserves until the end of the spawning season, often became massively infested.

2. *Pond experiments*

Attempts were made to follow up the dynamics of *D. lamellatus* infection of grasscarp fry, in experimental ponds. Three ponds of 172 m^2 area were each stocked with four thousand 20—30 mm long fishes reared free of dactylogyrosis, living at a medium density of 23 per m^2 (Table I). The fishes of the first pond served as controls, those of the second pond were exposed to dactylogyrosis infection by placing infected one-summer donors among them and those of the third pond were bathed every tenth day in a 1 ppm Ditrifon solution to prevent their becoming infected. The water supply conducted from a canal served as a permanent source of natural *D. lamellatus* infection in all three ponds.

Control fishes and those exposed to contact infection were found to harbour *D. lamellatus* parasites as early as nine days after their transfer to the

Table I

D. lamellatus infection of grasscarp fry in three experimental ponds, infected, not infected, and treated every tenth day with a bathing solution

Date of hatching:	4.7.1970
Date of stocking of the ponds:	5.8.1970
Population per pond:	4,000 fry 20—30 mm long
Population density (av.):	23 fishes per m^2
No. of fishes exterminated on each day of examination:	10

Days of examination	Experimental pond No. I		Experimental pond No. II		Experimental pond No. III	
	Control group		Group infected by contact with 50 parasite donors		Group treated by bathing every 10th day	
	*D.l.** adult	*D.l.* larval	*D.l* adult	*D.l.* larval	*D.l.* adult	*D.l.* larval
14.8.	0.2(0—1)	s	18 (3—36)	f	—	—
22.8.	15 (0—32)	f	26 (6—40)	m	—	—
29.8.	8 (2—28)	f	19 (10—28)	m	0.1(0—1)	—
4.9.	5 (2—10)	f	12 (2—34)	m	—	—
12.9.	8 (3—12)	f	6 (2—19)	f	0.2(0—1)	—
19.9.	7 (4—15)	m	9 (2—60)	f	—	—
6.10.	4 (3—6)	m	4 (1—10)	s	16 (14—18)	f
20.10.	3 (2—9)	m	1 (0—7)	f	14 (10—32)	f
5.11.	—	—	1.2(0—5)	13.3(8—20)	37 (12—64)	26 (6—60)
26.11.	—	—	6.2(0—12)	16.6(8—22)	26.8(2—60)	41.5(14—85)
10.12.	—	—	8.3(0—22)	6.6(2—12)	35.6(4—80)	24.1(6—40)

*D.l., *Dactylogyrus lamellatus*; s, some (1—5); f, few (5—10); m, many (10—30) experimental ponds. The degree of infestation was relatively high from the start in the second pond; the parasite counts tended to increase over the subsequent week, then gradually fell. The same process took place also in the control pond, but the parasite counts were lower throughout.

Fishes of the third pond harboured parasites only occasionally, when a longer time had elapsed between the last bathing and examination. If bathing was stopped, the parasite counts rose abruptly, exceeding considerably those established in the other two groups (Fig. 2). Previously parasite-free bathed fishes carried four times more parasites than the control and experimentally infected ones.

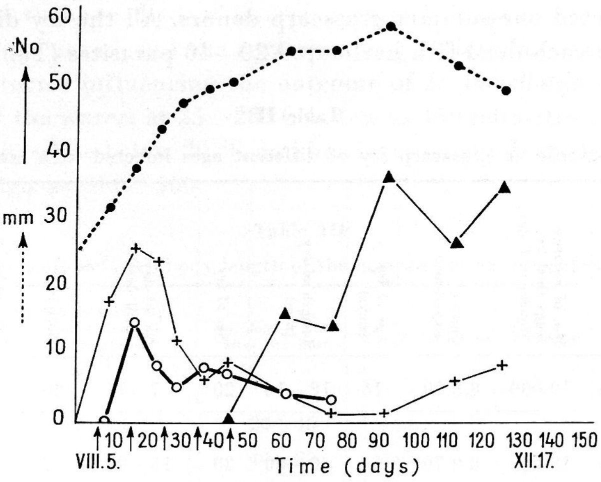

Fig. 2. Dynamics of *D. lamellatus* infection of the grasscarp in three experimental ponds with infected, not infected (control) and medicated populations. ● Average length of fishes in mm; ○ No. of adult *D. lamellatus* parasites on control fishes; ▲ No. of adult *D. lamellatus* parasites on fishes treated with bathing solution every tenth day; + No. of adult *D. lamellatus* individuals on fishes exposed to contact infection by parasite donors; ↑ time of the beginning of bathing treatment

Since the latter two groups differed scarcely in the degree of infestation, the control group was excluded from the further investigations. The remaining two groups continued to behave differently during the autumn: while the parasite counts of the "infected" group became stabilized at a relatively low level, those of the temporarily medicated fishes tended to increase despite the decreasing temperature, so that by the middle of December the 4.5—6.5 cm long fishes each harboured 4—80 adult parasites.

3. *Observations in the aquaria*

In several cases fishes with parasite burden (20—100 parasites per 20 cm long fish) were maintained in aquaria for some years without any change in the degree of infestation.

In other cases a rapid proliferation of *D. lamellatus* infection took place in the aquarium within two to six weeks, and the majority of the fishes died with acute dactylogyrosis within a period of about a fortnight.

One- or two-summer fishes procured from infected ponds for experimental purposes often developed a chronic dactylogyrosis on being maintained in an aquarium for two to five months; some of those which died by the end of this period carried as many as 500—700 *D. lamellatus* parasites on their gills.

4. *Experiments in the aquaria*

Experiment I. Sixteen-day-old fry, 12—14 cm long were placed among massively infected one-summer grasscarp donors. All the fry died 7—11 days after infection; each dead fish harboured 20—40 parasites (Table II).

Table II

Course of dactylogyrosis in grasscarp fry of different ages infected with many or few larvae

No. of experiment	Infective dose	No. of parasite eggs shed by donors in 1 day	Start of experiment	Age of fry (days)	Length of fry (mm)	No. of fry	No. of days until death	Mortality	Days until killed	No. of fry killed	No. of parasites found on gills
1	many larvae	19 000	8.8.70.	16	12—14	20	7—11	20	—	—	20—40
							—	—	7	4	100—300
2	many larvae	18 200	8.9.70.	64	40—60	20	15—20	7	—	—	400—500
							—	—	90	9	20—60
3	few larvae	480	8.8.70.	16	12—14	20	—	—	30	20	2—17
							210—216	3	—	—	510—580
4	few larvae	340	8.9.70.	64	40—60	20	—	—	218	17	5—300

Experiment II. Two-month-old fry, 4—6 cm long, were placed among massively infected donors. Four individuals exterminated after 7 days each harboured 100—300 developing *D. lamellatus* stages. Seven fishes, infected by 400—500 parasites, died by the 15th—20th day after infection. The remaining nine hosts were exterminated three months after infection; three of them were in a very poor condition, already "blackened", and carried 400—500 parasites; the other six were of normal colour and each harboured 20—60 chiefly adult stages of *D. lamellatus.*

Experiment III. Sixteen-day-old fry were placed among donors harbouring parasite populations producing only small amounts of eggs. The fry developed normally during the one-month experimental period and on extermination each was found to carry 2—17 mostly adult stages.

Experiment IV. Two-month-old, 4—6 cm long dactylogyrosis-free fry were placed among poor egg producers and were maintained in an aquarium for seven months (September to March) at 16—18 °C. Three of the 20 young fishes died during the last month of the experiment, each carrying more than 500 *D. lamellatus* stages. On extermination at the end of the experiment some fishes, however, harboured only 5—10 parasites.

III. *Pathogenicity*

Literary data and personal experience suggest that the lethal parasite count depends on the body dimensions of the host. Table III shows the lengths of fishes found to have died of dactylogyrosis in experimental and natural outbreaks in pond farms and the corresponding *D. lamellatus* counts.

Another factor influencing the outcome of *D. lamellatus* infection is the temperature of the water; at 25—28 °C as few as 150 parasites may kill a 3.5—4.5 cm long fish, while below 20 °C and in wintering ponds the lethal counts are as a rule as high as 300—500.

Table III

Relationship between body length of the host and lethal parasite count

Length of grasscarp fry found dead of dactylogyrosis (mm)	Number of parasites per host	Form of dactylogyrosis
12—14	20—40	acute
18—22	40—90	acute
35—45	150—250	acute
40—60	300—600	chronic
70—90	1000—3000	subacute or cronic
100—150	5000—7000	subacute or chronic

Table IV

Correlation between the degree of *D. lamellatus* infection and losses at decreasing oxygen contents of the water

Sequence of the onset of moribund state at decreasing oxygen levels	Number of parasites carried by fishes from pond I			Number of parasites carried by fishes from pond II		
	Adult *D. lamellatus*	Developing *D. lamellatus*	Total	Adult *D. lamellatus*	Developing *D. lamellatus*	Total
First group of moribund fishes (10)	48 (39—64)	104 (50—170)	152 (98—212)	34 (16—44)	54 (12—18)	88 (51—102)
Second group of moribund fishes (10)	39 (22—50)	51 (20—60)	90 (42—115)	5 (1—12)	14 (12—18)	19 (16—25)
Third group of moribund fishes (10)	16 (12—24)	15 (6—30)	31 (21—49)	2 (0—4)	12 (8—14)	14 (9—17)

In experimental studies on the relationship between oxygen depletion and *D. lamellatus* infection, thirty 5.5–6.5 cm long fingerlings were taken from two ponds infected with *D. lamellatus* and transferred to two closed containers, each holding 500 ml water. The fingerlings were removed from the containers in groups of ten, in the sequence of the onset of the moribund state (Table IV). As can be seen from Table IV, the sequence of agony corresponded with the degree of infestation with *D. lamellatus.*

IV. Study of factors influencing the susceptibility or resistance of the grasscarp to D. lamellatus

Experimental and practical observations made in the course of this study unequivocally suggest that in addition to the biological properties of the parasite and its ecological interrelationship with the host, host resistance plays

Table V

Behaviour on reinfection of infected, medicated and not previously infected grasscarp fry in good

Date of hatching 29.7.1970	Group infected from the beginning					Group
	No. of fishes	No. of parasites				No. of fishes
		Adult	Developing	Larval	Total	
Beginning of infection experiment: 11.8.70.	20	—	—	—	—	—
Mortalities up to: 24.8.70.	1	—	—	—	—	—
Fishes bathed: 26.8.70.	—	—	—	—	—	9
Start of challenge: 28.8.1970.	10	—	—	—	—	9
Mortalities from 28.8.70–6.9.70.	1	—	—	—	—	—
Killed on 8.9.70.	9	1 0–3	1.2 0–3	0.4 0–3	2.6 0–9	9

Table VI

Behaviour on reinfection of infected, medicated and not previously infected grasscarp fry in good

Date of hatching: 10.6.1970	Group infected from the beginning					Group
	No. of fishes	No. of parasites				No. of fishes
		Adult	Developing	Larval	Total	
Beginning of infection experiment: 23.6.1970.	20	—	—	—	—	—
Date of treatment with bathing solution: 8.8.70.	—	—	—	—	—	10
Start of challenge: 10.7.1970.	10	—	—	—	—	10
Mortalities from 10.7.70–23.7.70.	3	—	—	—	—	1
Killed on 23.7.70.	7	3.8 1–10	1 0–3	0.3 0–4	5.1 1–12	9

an important role in the fate of the *D. lamellatus* infection. More information was therefore sought about the factors designated in the literature as "age resistance", "acquired immunity", "superinvasion immunity" and "acquired resistance". Some simple experiments were performed to this end.

Experiment I (Table V). Parasite-free grasscarp fry in good nutritional condition were divided into three groups. Fishes of the first and second groups were placed with mildly infected donors when 12 days old. Fifteen days later dactylogyrosis was eradicated from the second group by bathing in Ditrifon solution and the fishes together with those of the non-infected third group were placed in the aquarium holding the first continuously exposed group carrying considerably fewer *D. lamellatus* parasites (av. 2.6) than those of the second (16.4) and third (14.4) groups.

Experiment II (Table VI) was carried out under similar conditions and by the same techniques. On extermination at the end of the experiment, the

condition of health, using as parasite donors fishes producing low numbers of *D. lamellatus* eggs

treated by bathing				Group infected at a later time				
No. of parasites				No. of fishes	No. of parasites			
Adult	Developing	Larval	Total		Adult	Developing	Larval	Total
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	10	—	—	—	—
—	—	—	—	3	—	—	—	—
11.3	4.3	1.8	17.4	7	10	2.8	1.6	14.4
1—24	2—7	0—5	5—36		3—29	0—6	0—7	9—30

condition of health, using as parasite donors fishes producing low numbers of *D. lamellatus* eggs

treated by bathing				Group infected at a later time				
No. of parasites				No. of fishes	No. of parasites			
Adult	Developing	Larval	Total		Adult	Developing	Larval	Total
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	10	—	—	—	—
—	—	—	—	5	—	—	—	—
6.9	2.3	0.3	9.5	5	2	1	0.2	3.2
2—18	0—6	0—2	2—23		1—4	0—2	0—1	1—6

fishes were 26—46 mm long. Again the bathed fishes proved to be the most massively infected (9.5 parasites/fish) while the early and late infected ones carried on average 5.1 and 3.4 *D. lamellatus* individuals, respectively.

Experiment III was performed on 18—22 mm long fishes previously kept in an aquarium for a long period and showing practically no growth during the experiment though being poorly fed. Three experimental groups were treated in the same manner as in Experiment I. Most of the infected and bathed fishes died of dactylogyrosis; the survivors of both groups harboured consider-

Table VII

Behaviour on reinfection of infected, medicated and not previously infected grasscarp fry in poor

Date of hatching: 8.6.1970	Group infected from the beginning					Group
	No. of fishes	No. of parasites				No. of fishes
		Adult	Developing	Larval	Total	
Beginning of infection experiment: 17.7.1970.	40	—	—	—	—	—
Mortalities from 18.7.70—27.7.70.	12	—	—	—	—	—
Date of treatment with bathing solution: 27.7.	—	—	—	—	—	14
Start of challenge: 29.7.—3.8.	14	—	—	—	—	14
Mortalities from 29.7.70.—3.8.70.	11	—	—	—	—	12
Killed on 3.8.70	3	10 0—53	24 16—29	22 8—33	56 43—85	2

Table VIII

Behaviour on reinfection of infected, medicated and not previously infected grasscarp fry in average

Date of hatching: 8.6.1970	Group infected from the beginning					Group	
	No. of fishes	No. of parasites				No. of fishes	No.
		Adult	Developing	Larval	Total		Adult
Beginning of infection experiment: 3.8.1970.	20	—	—	—	—	—	—
Mortalities from 26.8.—30.8. 70.	8	130 (80—240)	162 (70—420)	84 (70—220)	796 (300—220)	—	—
Date of treatment with bathing solution 1.9.70.	—	—	—	—	—	6	—
Beginning of challenge: 3.9.1970.	6	—	—	—	—	6	—
Killed on 8.9.1970.	6	113 (70—230)	122 (50—220)	137 (70—220)	372 (300—400)	6	—
Killed on 6.10.1970.	—	—	—	—	—	—	—

ably more parasites than the fishes of the third group, infected at a later date (Table VII).

Experiment IV was carried out on older 50—70 mm long grasscarp fry reared in surroundings free of *D. lamellatus*. These were placed in an aquarium containing many parasite eggs and larvae, but no donor fishes (Table VIII). Eight of 20 fishes died within the first 30 days after infection; each carried 300—520 *D. lamellatus* stages. Half of the survivors were treated for dactylogyrosis by bathing and two days later they were placed with the rest in the in-

condition of health, using as parasite donors fishes producing large numbers of *D. lamellatus* eggs

treated by bathing				Group infected at a later time				
No, of parasites				No. of fishes	No. of parasites			
Adult	Developing	Larval	Total		Adult	Developing	Larval	Total
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	20	—	—	—	—
—	—	—	—	9	—	—	—	—
—	31 26—37	20 9—31	51 35—68	11	—	2.8 0—8	8.6 2—16	11.4 2—17

condition of health, using as parasite donors fishes producing large numbers of *D. lamellatus* eggs

treated by bathing			Group infected at a later time				
of parasites			No. of fishes	No. of parasites			
Developing	Larval	Total		Adult	Developing	Larval	Total
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—
—	—	—	10	—	—	—	—
276 (120—400)	438 (380—810)	714 (500—1000)	6	—	230 (180—320)	472 (320—740)	702 (500—1000)
—	—	—	4 (21—	27 (21—44)	5 (0—8)	3 (0—16)	35 (33—44)

fected aquarium; the non-infected fishes of the third group were simultaneously transferred to the same aquarium. Five days later the entire lot had to be exterminated because some of the continuously exposed and bathed re-exposed fishes were dying; the degree of infestation was high in all the three groups. The visibly declining fishes (with blackened backs) showed higher parasite counts than the healthier looking ones. Since the time interval between reinfection and extermination was short, no egg-producing parasites had yet developed on the bathed or late-exposed fishes. Four individuals of the bathed and re-exposed group were segregated and observed for one additional month; the parasite counts decreased considerably until they stabilized at a level of 33—44.

Discussion

These studies on the dynamics of *D. lamellatus* infection show that the parasite can occur in pond farms throughout the year and may affect fishes of all ages in all seasons except winter. With the breeding technology adopted in Hungary, the infection is spread primarily by larvae carried in water supplies from canals. Older grasscarps placed in these canals to keep them free of excess vegetation serve as the sources of infection.

The extent of dactylogyrosis in the various types of ponds established for the successive stages of the breeding cycle depends on the breeding technology applied. In those pond farms in which no *D. lamellatus*-free water supply can be provided, even the fry with yolk sac become infected to a greater or lesser extent, depending on the population density and the time of maintenance in the nursery pond. Fishes maintained for long periods in the nursery pond at a high stocking density suffer considerable losses, particularly if the water temperature is high.

Infection can take place by the same way also in the fingerling pond, particularly if the fry are transferred there directly from the hatchery. If the fry with yolk sac are maintained in the nursery pond for the optimal period of 20 days and only then transferred to fingerling or rearing ponds, few *D. lamellatus* parasites can invade them and the stock can be reared without notable losses.

Since *D. lamellatus* multiplies readily at low water temperatures, a high degree of infestation may become established even in the wintering pond if the population density is high.

The number of parasites required to cause a lethal dactylogyrosis depends on the body dimensions of the host, or more precisely on the surface area of the gills, although the temperature and oxygen content of the water play an important role in the fate of the infected fish. The oxygen content is as a rule low at high temperatures, but the oxygen requirement of the fishes increases with the greater intensity of life functions in the warm environment. Fishes with massively invaded gills succumb to oxygen depletion earlier than those less affected by the parasite. The infection experiments in ponds show that when the fish become infected, the parasite count at first rises then gradually falls until it stabilizes at a certain level. This process takes place independently of the temperature, season, or body dimensions of the host, to judge from the behaviour of fish groups infected at different points of time. This is in good accordance with the observations of MUSSELIUS and PTASHUK (1970), who explain the phenomenon by a "superinvasion immunity" of the fishes; the existence of such an immunity cannot, however, be accepted until further proof is forthcoming.

The present experiments in aquaria give no indication of an acquired immunity and the attempts to reproduce the findings of PAPERNA (1964) and VLADIMIROV (1967) yielded the opposite conclusions. Infection of a given degree and for a given period did not protect fishes against reinfection and fish cured of dactylogyrosis by bathing were as susceptible to reinfection as those never infected before. Nevertheless certain observations (Tables V and VI) suggest that a continuous basal infection of the host with *D. lamellatus* protects it against subsequent not too massive exposures and maintains a state of equilibrium in the host-parasite relationship. This so-called "protection by infection" is clearly unrelated to any kind of immune response, because certain non-immune reactions of the host organism, such as cell proliferation, increased mucosal activity or simply increased respiratory movements, may play a substantial role in it.

It appears that the balance of the host-parasite relationship depends primarily on the individual resistance of the host and only secondarily, if at all, on specific protective factors. Well fed and well managed fishes always reach a state of equilibrium with their *D. lamellatus* parasites, with the equilibrium counts varying with the body dimensions of the host. If however the equilibrium between host size and parasite count shifts in favour of the latter, the host either develops a severe dactylogyrosis or dies. Three types of manifest dactylogyrosis can be distinguished according to the mode of infection and symptomatology.

1. *Acute dactylogyrosis*

This affects the one- or two-month-old grasscarp fry during the summer months, when the rapid cyclic development of *D. lamellatus* results in a massive larval invasion of the host within 2—3 weeks. Acute dactylogyrosis was observed under field conditions in 2.5—4.5 cm long fry, but it could be produced experimentally in fishes less than 2 cm long.

The fry normally localize at the bottom of the pond but on infection they seek the surface layers of the water. Some fishes perform compulsive circular movements, often showing their whitish abdominal surface. Moribund and dead fishes float on the water surface, with the abdomen turned upward. Many fishes stay along the sides of the pond preferably around the water inlet; they make no attempt to escape at the approach of human beings and can be caught with the hand. Severely ill fishes have pale, bloodless gills that show grossly visible irregularities surrounded by haemorrhage and covered by copious mucus. Microscopically, many parasites are seen on the broken or merging gill lamellae. Fishes can maintain a good nutritional state despite severe gill damage.

Parasitosis and losses can be rapidly eliminated by treatment with suitable bathing solution.

2. Subacute dactylogyrosis

This affects one- or two-summer grasscarps during the spring if they have been retained too long in the wintering pond. Parasite counts, as low as 5—30 in March, rise to 3000—8000 in April and often become lethal to the 70—150 mm long hosts. In their search for fresh water the diseased fishes move to the sides of the pond or they float in the water surface with abdomen turned upward.

Losses are considerable, amounting sometimes to 40—60% of the stock. There is a marked loss of condition in the non-lethal cases and deaths may still occur after medication.

The severely ill fishes have pale, torn gills covered by copious mucus and invaded by many *D. lamellatus* stages. The most frequent concurrent infection is mycosis, which bears the primary responsibility for the lesions of the gills.

Subacute dactylogyrosis always develops when there is a background of gross feeding errors and management failures. The elimination of the deficiencies is an essential prerequisite of effective medication.

3. Chronic dactylogyrosis

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and may affect

small daily losses

ature, gasping fishes

se make no attempt at

escaping on the appearance of man. The gills are pale and bloodless and harbour many parasites; two-summer fishes may carry up to 8000, five-summer fishes up to 20 000, *D. lamellatus* stages. Chronic dactylogyrosis seldom involves the entire stock; massively infected fishes and fishes carrying only a few parasites are often found in one and the same pond.

SUMMARY

The gill parasite *Dactylogyrus lamellatus* was found to affect grasscarps of all ages and sizes throughout the year. A high stocking density favours its spread, and thus the parasite threatens the populations primarily of the fry-rearing ponds, nursery ponds and wintering ponds.

The fatal outcome of dactylogyrosis depends on the parasite count of the host, but a warm temperature and a low oxygen content of the water accelerate its onset.

Three epizootiologically different forms of *D. lamellatus* infection have been observed in pond farms: acute dactylogyrosis of the fry, and subacute and chronic dactylogyrosis of one- and two-summer grasscarps.

A continuous low-degree infestation with *D. lamellatus* was found to protect the fishes against a not too massive reinfection by larval stages of the parasite. This kind of host-parasite equilibrium seems to depend on the individual resistance of the host.

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