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THE INFLUENCE OF ENVIRONMENTAL FACTORS ON REPRODUCTION
OF FISH PARASITES

By O. N. Bauer.

Laboratory of Fish Diseases, VNIORKh

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parazitov ryb

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Translation by Z. Kabata and L. Margolis

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Investigations of Soviet parasitologists have established the basic principles of the dynamics of the parasite fauna of animals as depending on the age, physiological condition and migration of the host, the season of the year, etc. It has been found for example that with increasing age of the host the parasite fauna becomes richer in species and that, as a result of migration of the host, changes occur in the parasite fauna. However, these general principles are still insufficient to make it possible to determine always and with sufficient accuracy the reasons for the level of abundance of a particular parasite or the reasons for its presence or absence under any concrete conditions.

The general principle of the increase in the parasite fauna with the age of the host does not explain why the abundance of the gill fluke of carp, Dactylogyrus vastator, reaches its peak during the course of the 1-1/2 to 2 months of the life of the young fish and then drops sharply whereas the abundance of another trematode, D. solidus, increases throughout the life of the host. To explain this fact one must study the parasite much more deeply, in particular to explain the influence of the host, i.e., the micro-environment, and the external environment which surrounds the host, i.e., the macro-environment, on the parasite's reproduction, development and growth. Such deeper study of the biology of parasites is impossible without a broad application of the experimental method. The method of complete parasitological examination of animals of various ages, at different times of the year, under different conditions of existence and during different physiological conditions of the host has allowed the establishment of the above principles. By itself, however, it proves insufficient for this purpose and assumes an auxiliary role.

Such study in depth of the biology of the individual parasite species is now being carried out by many Soviet and foreign parasitologists. Naturally, the greatest attention is being paid to the species which are of epidemiological and epizootological importance.

[p. 133] The development of fisheries in natural and artificial bodies of water confronts parasitologists who study the parasites of fishes with a task of great magnitude and responsibility, a task of developing rational methods of controlling the parasites. After all, it is precisely under the conditions of artificial fish culture and of fish husbandry of other types that the danger arises of a great increase in the abundance of a number of parasites which are of no practical importance under natural conditions. At the same time it is precisely under the condition of artificial fish culture that it is possible to apply prophylactic and therapeutic measures, which can be used in natural bodies of water only to a very limited extent.

To develop rational methods of controlling any parasite one must know its biology and its interaction with the external environment which determines its abundance. Unfortunately, the parasites of fishes, even those which are very pathogenic and known as agents of mass epizootics, have been studied very insufficiently from this point of view. Data on this question are very fragmentary. Somewhat more detailed information is available on the biology of the parasites of the pond fishes, mainly carp. The biology of the fishes of the industrial bodies of water have been left almost unstudied. In this paper we intend to collect all these mainly casual and isolated data and if possible to draw conclusions from them.

We shall begin our review with the external environmental factors. It is known that various stages in the parasite's life cycle have various sensitivities to the environmental factors. For this reason the influence of the environmental factors has to be reviewed particularly in relation to the separate stages of the parasite's life cycle.

Of the factors of the external environment, that is, macro-environment, we have taken into account the temperature, salinity, oxygen content, pH, light, and pressure.

For parasites of fish temperature is the main factor of the external environment, influencing them at all stages of their development. In this fish parasites, as well as parasites of other cold-blooded animals, differ greatly from parasites of the warm-blooded animals since the parasitic stages of the latter are usually in more or less constant conditions of temperature, whereas the parasites of fish are exposed to the fluctuations of water temperature at all stages of their development. For each fish parasite it is possible to establish a range within which the increase in temperature speeds up the processes of division (Protozoa), increases the rate of egg deposition (Monogenea), speeds up the embryonic development (all parasitic helminths and Crustacea), growth and maturation of the larval stages (cestodes, nematodes, acanthocephalans) and parthenogenetic generations (Digenea) in the intermediate hosts, growth and maturation of the adults in the definitive host (some Protozoa, all helminths). Various infective stages are also very sensitive to fluctuation in temperature.

Thus, it has been established that the development of Ichthyophthirius multifiliis within the cyst up to the stage of the formation of swimmers takes 10-12 hours at a temperature of 26°, 18-20 hours at a temperature of 20-22°, 23-26 hours at a temperature of 17-18°. At a temperature of 7-8° this process requires 72-84 hours, whereas at 3-4° about six days (I.G. Shchupakov, 1952; O.N. Bauer, 1955). Below 1-2° and above 26° the cysts of Ichthyophthirius perish without forming swimmers. The division of Costia necatrix occurs within the limits of 2-30° (I. Benisch, 1936), but this flagellate divides particularly intensively at 26-28°.

The increase in temperature within certain limits increases the rate of deposition of eggs in monogenetic trematodes. Thus Dactylogyrus vastator, [p. 134] detached from the fish, deposits one egg at least every four minutes at a temperature of 30°; at 19°, every 10 minutes; at 12°, every 13 minutes (E.M. Lyaiman, 1951). The same tendency has been found by I.A. Izyumova (1953), who experimented with D. vastator not detached from the gills of the carp. The increase in temperature above the optimum leads to the formation of a large number of misshapen eggs incapable of further development. Dactylogyrus solidus at a temperature above 15°C deposits mainly imperfect eggs (O.N. Bauer, 1951; O.N. Bauer and N.P. Nikol'skaya, 1954).

In most instances, increase in temperature up to certain limits increases the rate of the embryonic development of the parasite. This fact is now known for many fish parasites. The embryonic development of Hysteromorpha triloba at 19-22° takes 20-25 days. At 26° it takes 17 days, at 37° it takes 6-8 days (E. Huggins, 1954). The larvae of Dactylogyrus vastator at 8° hatch

on the 28th day, at 16° on the 6th-7th day, at 24° on the 4th day (E.M. Lyaiman, 1951). Maturation of the coracidia of Triaenophorus nodulosus at 18-20° takes on the average 7-9 days, whereas at 2-5° it takes 36 days (W. Michailow, 1951). The development of eggs and the emergence of coracidia in all species of the genus Ligula takes 5-6 days at a temperature of 24-28° and 8-9 days at 15-18°. The emergence of coracidia at high temperatures occurs almost simultaneously; with a drop in temperature the period of emergence is extended (M.N. Dubinina, 1953). The drop in temperature considerably extends the period of embryonic development of Contracaecum bidentatum (E.R. Geller and L.A. Babich, 1953), of Camallanus lacustris and of other nematodes. The development of eggs of Argulus foliaceus takes 30-40 days at a temperature of 17-20°; it takes 22-30 days at 20-25° and 15-18 days at a temperature of 25-28° (I.V. Kiselev and V.K. Ivlieva, 1953). A drop in temperature below the minimum arrests the development. For example, the development of eggs of A. foliaceus is arrested at temperatures below 14° (I.V. Kiselev and V.K. Ivlieva, 1953). A lowering of the temperature to 8° arrests the development of eggs of Hysteromorpha triloba, whereas freezing kills them (Huggins, 1954). When the temperature drops to 2° the development of Dactylogyrus vastator is arrested (O.N. Bauer, 1954). According to V. Michailow (1951), the development of eggs of Triaenophorus nodulosus is not arrested even at 2°. They do not perish when kept up to 15 minutes at 1°, but if this period is prolonged beyond 15 minutes they all perish.

For a number of parasites it has been found that active infective stages survive for a longer period at low temperatures. Free-living larvae of Achtheres coregoni live no longer than 1-1/2 days at 20-25°, and up to 7 days at 5° (F. Zandt, 1935). The swarms of Ichthyophthirius remain active for only one day at 25°, the majority of them dying after 12 hours. At 18° they remain alive up to 3 days. Coracidia of Triaenophorus nodulosus perish after several hours at 30°, whereas they live up to 4 days at 15-16° and up to 13 days at 5-10° (V. Michailow, 1951).

The growth and the maturation of the larval stages within the body of the intermediate host are also accelerated by the increase of temperature. The larvae of Cystoopsis acipenseris in amphipods reach infective condition within 14 days at a temperature of 20°, and within 22 days at a temperature of 8° (C. Janicki and K. Rasin, 1929). The period of maturation of larval Leptorhynchoides thecatus in the amphipod Hyalella azteca is about one month at a temperature of 20-25° and two months at a temperature of 13-15° (D. DeGiusti, 1949). The metamorphosis of the onchosphere of Triaenophorus nodulosus into the proceroid in the body of cyclops occurs more rapidly at 15-16° than at lower temperatures (V. Michailow, 1951).

Also within the body of the definitive host the maturation and the growth of parasites [p. 135] occur more rapidly at higher temperatures. For example, Ichthyophthirius reaches maturity in the skin of fish on the 4th day at 28°, on the 6th day at 22-23°, and on the 35-40th day at 8-9°.

On the basis of comparing all the data available one can conclude that among the fish parasites there are species which reproduce and develop most successfully at comparatively high temperatures in the order of 24-26°. To these species belong Ichthyophthirius multifiliis, Dactylogyrus vastator,

Costia necatrix, Argulus foliaceus and several others. In contrast, other species develop and grow most successfully at lower temperatures. To these belong Chilodonella cyprini, Dactylogyrus solidus and others. A great increase in the abundance of a given parasite is possible only at either optimal or near optimal temperature. For example, N.K. Deksbakh and I.G. Shchupakov (1954) note that the epizootics of ligulosis in the lakes of the Urals occur only during hot summers when the incubation of eggs and the hatching of coracidia takes place within the shortest possible time.

Finally it should be noted that closely related species can have different temperature optima. Dactylogyrus vastator and D. solidus can serve as examples.

Salinity. V.A. Dogel and Iu. K. Petrushevsky (1935) have already determined that migratory fishes moving from the sea into rivers to spawn lose the majority of their marine parasites. An assumption has been made that the death of the latter, or at any rate a part of them, occurs under the influence of fresh water. This fact suggests that marine parasites cannot exist and reproduce when the salinity of the water is lowered. As far as the parasites of the freshwater fishes are concerned it is known that many of them are very sensitive to the increase in the salinity of the water and die when it occurs. B.E. Bychowsky (1936) believes that the majority of monogenean trematodes, particularly of the genera Dactylogyrus, Gyrodactylus and Tetraonchus, as well as copepods of the genus Ergasilus, are particularly sensitive to an increase in salinity. V.B. Dubinin (1948), having compared the parasite fauna of fish from the freshwater and brackish water sectors of the river Malyi Uzen', supports this assumption. He notes that among the freshwater parasites one can isolate a group of species capable of withstanding fairly high salinity and these can be regarded as euryhaline species. To this group he refers, in the first place, Diplozoon paradoxum. Further, V.B. Dubinin comments that the freshwater parasites are particularly sensitive to chlorides and sulphates even when these compounds are a part of salt mixtures.

Experimental investigations into the influence of various salt concentrations on different developmental stages of parasites are relatively scarce. According to K. Yanicki (1928) the eggs of Amphilina perish within 12 hours when kept in sea water (38.54 ‰) whereas in the Caspian water (12.85 ‰) they survive for three days and longer. The eggs of Triaenophorus nodulosus perish in water having a salinity of 35 ‰ but are capable of developing successfully in water having a salinity of 5-6 ‰ (W. Michailow, 1951). Diclybothrium armatum, according to our observations, reproduces successfully in solutions of cooking salt up to 20% inclusive. However, in concentrations higher than this it perishes within one to two hours. According to our observations, the increase in the concentration of the cooking salt up to 6-7% causes death of larval Dactylogyrus vastator and D. solidus. Ichthyophthirius multifiliis is very sensitive to high salt content (B.V. Verigin, 1954; O.N. Bauer, 1955). Even 5% solution of cooking salt and of other chlorides and sulphates disturbs normal fission within the cyst. The swimmers, if formed, die rapidly [p. 136] in a 7% solution of cooking salt. Ichthyophthirius is even more sensitive to a mixture of salts. A 6% solution of salts contained in sea water or a mixture of cooking salt and bitter salt prevents the parasite's reproduction.

These latter data as well as our experiments on the influence of salt mixtures on Dactylogyrus vastator (O.N. Bauer and N.P. Nikol'skaya, 1951) support the opinion of V.B. Dubinin (1948) that freshwater parasites are more sensitive to solutions of salt mixtures than to solutions of individual salts.

On the basis of all the material available one can make two conclusions: (1) parasites of fish can be divided into marine stenohaline, freshwater stenohaline and euryhaline. The first two groups are very sensitive to changes in salinity, whereas the third group is able to withstand a fairly considerable variation in salinity and is therefore capable of surviving and sometimes also of multiplying both in fresh and brackish water; (2) parasites of fish are more sensitive to salt mixtures than to solutions of single salts.

The influence of the oxygen content of water on reproduction and development of fish parasites has been almost not studied at all. It has been found that Dactylogyrus vastator develops normally with a sharp deficit of oxygen. In contrast D. solidus is very sensitive to it. When the oxygen content is reduced D. solidus moves to the tip of the gill filament, rapidly deposits numerous eggs, and dies (N.A. Izyumova, 1953). V. Michailow (1951) kept the eggs of Triaenophorus nodulosus in water covered by a thin layer of vegetable oil so as to prevent the absorption of oxygen by water. Under such conditions the eggs of the parasite did not develop and perished. Argulus foliaceus apparently develops more successfully when the oxygen content is lower. In connection with this it is necessary to maintain a good oxygen regime in the waters as one of the conditions which prevent the increase in abundance of this parasite in the ponds and lakes (I.V. Kiselev and V.K. Ivlieva, 1953).

In spite of the scarcity of these data among the parasites of fishes it is still possible to distinguish species which develop successfully only when the oxygen content is normal (Triaenophorus nodulosus, Dactylogyrus solidus), species which develop better under the condition of the oxygen deficit (Argulus foliaceus), and finally species which are relatively indifferent to the oxygen content (Dactylogyrus vastator). In this instance, as in the case of temperature, the members of the same genus can differ in their sensitivity to oxygen content.

The influence of pH of the environment on the reproduction of parasites has been studied even less. It has been suggested in passing that Ichthyophthirius develops poorly under acid conditions (W. Innes, 1953). In contrast, according to the existing observations, Chilodonella cyprini occurs in great numbers on yearling carp in winter ponds with low pH values. This observation calls for experimental testing. Also very necessary are experiments to test the sensitivity of other fish parasites to pH of the environment.

Light, according to the very scanty observations available, differs in its influence on the development of parasites. It has been found that exposure of the larvae of Dactylogyrus solidus and D. vastator (O.N. Bauer, 1951, 1954), and also the swarms of Ichthyophthirius, to sunlight or even to scattered light sharply reduces the life span of these stages. The swarms of Ichthyophthirius remain active in scattered light for no more than 10-12 hours whereas in darkness they remain active up to three days. Fish infected with Chilodonella cyprini are freed [p. 137] from this parasite on exposure to

sunlight. These facts suggest the possibility of using various illuminating appliances of the bactericidal lamp type for the control of some pathogenic parasites.

Light can have an influence on the embryonic development of some parasites. The absence of light retards development of the embryo of Argulus foliaceus, particularly at the point of hatching (I.V. Kiselev and V.K. Ivlieva, 1953). By keeping the eggs of Argulus in complete darkness the authors were able to arrest for 30 days the hatching of larvae which had already begun to hatch. The eggs of Triaenophorus nodulosus develop in darkness slightly more slowly (19 days) than when exposed to light (15 days) (V. Michailow, 1951). Light as a stimulator of the hatching of larvae is also known for the genus Ligula (M.N. Dubinina, 1953) and for some other parasites.

Positive phototaxis has been established for a number of parasite larvae. F. Zandt (1935) notices that the larvae of Achtheres coregoni always try to move towards the strongest light source. By this fact he explains the higher infection of pelagic Coregonus wartmanni with this copepod, when compared with the benthos-feeding demersal whitefish. A positive phototaxis is also known for the coracidia of Triaenophorus nodulosus (V. Michailow, 1951). The same characteristic has been noticed not only in the larvae but also in the adult of Argulus foliaceus. I.V. Kiselev and V.K. Ivlievá (1953) believe that this aids in the search for the host. The fishes which swim in the most highly illuminated parts of the water become infected.

In a number of instances, therefore, light influences the parasite, either increasing or decreasing its abundance.

Parasites are influenced by pressure. In common with their hosts the parasites of the deep-water fishes are adapted to high pressures and perish at ordinary atmospheric pressure. Recently L. Thomas (1952) described Bothriocephalus abyssus from the deep-water fish Echistoma tanneri taken at a depth of 700-800 fathoms. Eggs obtained from the parasite produced coracidia which immediately died at ordinary atmospheric pressure. Sensitivity to changes in atmospheric pressure appears also to be found in freshwater parasites. Thus, according to V. Michailow (1951), the eggs of Triaenophorus nodulosus develop under the pressure of a 1-cm column of water within 7-8 days and under the pressure of a 5-cm column of water in 12 days. At a depth of 10 m the eggs do not develop at all.

Thus the factors of the host's environment exert on the parasite very different kinds of influence. Only under optimal environmental conditions is it possible for the parasite to reproduce and develop normally and consequently for its numbers to increase.

Not of lesser, and in some instances even of greater, importance for these processes is the host itself, the influence of which the parasite experiences only at certain stages of development, i.e. during the time when it remains on the surface of the body or within the fish. The influence of the host, i.e. of the micro-environment, can also be very diverse. Let us examine the influence of the feeding of the fish and of its physiological

There are examples of changes in the tissue associated with the growth of the fish also exerting a significant influence on the parasite which inhabits the tissue. In its vegetative stage Myxosoma cerebralis, the agent of whirling disease of trout, inhabits the cartilage of the young fish. As the cartilage tissue becomes gradually ossified the parasite passes to the stage of sporulation (M. Plehn, 1924). With the gradual ossification of the cartilage the spores appear to perish completely.

A factor of great significance influencing the abundance of the parasite and its reproduction and development is the immunity which develops in the host under the influence of the primary infection. As regards fishes immunity has been studied very little. Evidently, the intestinal parasites either cause no development of immunity or stimulate it only to a very low degree. This has been determined for example [p. 139] for intestinal trematodes of the genus Hamacreadium (O.R. MacCoy, 1930). In contrast, fairly strong super-invasion immunity develops under the influence of coelozoic, histozoic, and some gill parasites. This has been demonstrated experimentally for Benedenia melleni, a parasite of sharks (R. Nigrelli, A.C. Breder, 1943; R. Nigrelli, 1935), and for Ichthyophthirius multifiliis (O.N. Bauer, 1953). On secondary infection with Ichthyophthirius the level of immunity reaches 20 and even higher. The development of immunity has been suggested for acipenserid fishes infected with Amphilina foliaceus (K. Janicki, 1928) and for carp infected with Dactylogyrus vastator (E.M. Lyaiman, 1948) and Neascus cuticola (E.M. Lyaiman and O.D. Sadkovskaya, 1952). However these statements have not been verified experimentally. In any case one can speak here only of a super-infection immunity and not the age immunity which is suggested by E.M. Lyaiman (1948).

It appears that the abundance of many parasites in nature is limited precisely by the existence of immunity. This statement is supported by the instances described in which a parasite has been transported together with a fish which was being acclimatized into a habitat which contained closely related fishes but in which the particular parasite species was absent. The transported parasite, the development of which has not been limited by immunity, can reach tremendous abundance and cause mass mortality among fish. Such was the case of Nitzschia sturionis which was transported to the Aral Sea with the Caspian stellate sturgeon [Acipenser stellatus] and which caused a mass mortality in ship sturgeon [Acipenser nudiiventris] (V.A. Dogel and A.S. Lutta, 1937). In recent times a number of epizootics among fish in pond farms were caused by the introduction of Ichthyophthirius multifiliis with fish transported for stocking (O.N. Bauer, 1955).

The subject of immunity in fish to parasitic diseases is in need of urgent and thorough study which will be of tremendous importance both for theory and for various practices in fish husbandry.

Ending this paper I would like to dwell briefly on yet another factor which is of great importance in the development and reproduction of the parasite. This factor is the density of the fish population. It is known that the higher the density of the population of the hosts, the higher is the abundance of the parasite, since, under the condition of high population density the invasive stage of the parasite has a better chance to come in contact with a host. In

condition, as well as of immunity which it develops, on the abundance of parasites and their reproduction and development.

The character and intensity of the feeding of fish are factors of considerable influence on the reproduction and abundance of parasites in which infection occurs through food. If the intermediate hosts of the parasite are of significant importance in the food of the fish then the abundance of the parasite can be very great. This in turn ensures a considerable increase in its numbers and a high level of infection of the intermediate hosts. The abundance of the parasite can fluctuate [p. 138], depending on changes in the feeding of fish with age and season of the year.

Thus, only beginning with three years of age does the Ladoga whitefish become heavily infected with Echinorhynchus salmonis and Cystidicola, since the intermediate hosts of these parasites, relict amphipods, begin to dominate the diet of the fish only at that age (O.N. Bauer and N.P. Nikol'skaya, 1952). The same Ladoga whitefish is infected with the above parasite less heavily in the northern part of the lake than in the southern part because the relict amphipods occur in the southern part in relatively small numbers. Carp usually become infected with Caryophyllaeus fimbriceps only during the period of early spring when, because of the insufficiency of chironomids, it eats Tubifex, the intermediate hosts of this parasite (W. Wunder, 1939; V.M. Ivasik, 1952), in great numbers.

There are as yet no observations on the influence on parasites of the specific composition of the food. With regards to some intestinal parasites, for example Coccidia, such investigations would be not only of theoretical but also of practical importance.

The decrease in the intensity of feeding or its complete cessation, depending on the physiological condition of the fish (spawning season, wintering), leads either to the gradual dying off of intestinal parasites (many trematodes, non-strobilated cestodes) or to the retardation of the processes of reproduction. The latter is particularly clearly expressed in the phenomenon of destrobilation when the tapeworms lose their strobilae, retaining only the scolex capable of developing a new strobila with the onset of favourable conditions. Such destrobilation has been observed in Proteocephalus osculatus during the wintering period of sheatfish [Silurus glanis] in the hollows of the lower Volga (M.N. Dubinina, 1949), in Eubothrium crassum during the spawning migration of salmon (V.A. Dogel and Yu. K. Petrushevsky, 1935; M.N. Dubinina, 1950) and in other cestodes.

The condition of the fish shows significant influence on the processes of reproduction of some fish parasites. The better the condition of the fish the lower the abundance of the parasite. This has been shown experimentally by A.S. Chechina (1952). Yearling carp with a coefficient condition of 3.965 were infected with Chilodonella cyprini and Trichodina megamicronucleata throughout the entire winter period several times less intensely than the yearling carp with a coefficient condition of 3.489 and living in identical conditions. According to hypothesis suggested by W. Schäperclaus (1935) these parasites develop only on the dystrophic and dying tissue. In poorly fed over-wintering fish the tissues die off more rapidly than in the well nourished fish, thus favouring an increased rate of reproduction of the parasite.

view of that, many parasites, particularly those with a direct development, form invasive stages during the period of the seasonal (spawning, feeding, wintering) grouping of fish.

The relationship between the abundance of the parasite and the density of the fish population assumes special importance in pond rearing of fish. A characteristic feature of such rearing is the unusually high density of fish (by comparison with that in natural waters) which belong most frequently to one, or less frequently two or three, sometimes closely related species. Under such conditions the opportunity arises for a sharp increase in abundance of such parasites which in the natural environment occur very rarely. In fact Costia necatrix, Chilodonella cyprini, Dactylogyrus vastator and many other parasites occur rarely and in low numbers in wild fish and such parasites as Myxosoma cerebralis are generally not known in wild trout. In connection with this, the widely practised procedure in the Soviet pond fishery of increasing the density of fish stocks, if not supported by the corresponding prophylactic measures, favours increase in the abundance of parasites and produces the danger of epizootics. For example, in recent years a gradual increase in the density of the stocks of yearling [p. 140] carp in the winter ponds led to an increase in the abundance of the sporozoans Eimeria and Myxobolus cyprini in a number of fish farms.

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