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COPEPOD PARASITES OF FRESH-WATER FISHES AND THEIR ECONOMIC RELATIONS TO MUSSEL GLOCHIDIA.

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Contribution from the United States Fisheries Biological Station, Fairport, Iowa.

INTRODUCTION.

Under an appointment by the Commissioner of Fisheries, during the summer of 1914, at the United States Fisheries biological station at Fairport, Iowa, an extended examination was made of the parasitic copepods which infest our fresh-water fishes in the Mississippi River and its tributaries and of the mussel glochidia which are also parasitic upon fish during their term of metamorphosis. Several of the early American naturalists became interested in the copepods found upon fresh-water fish, and many new species were described. This was especially true of Le Sueur and Dana, and singularly enough the Danish investigator, Krøyer, also obtained a number of American species from fish sent to the Copenhagen Museum. But in every instance the species described were isolated, they were sometimes founded upon single specimens, and many of them have never been seen since their original discovery.

Prof. S. I. Smith published in the Report of the United States Commissioner of Fish and Fisheries for 1872–73 a list of the crustacean parasites of the fresh-water fishes of the United States (p. 661–665). This list included two argulids, one caligid, one ergasilid, six lernæopods, three of which were new to science, and two lernæans, 12 species in all. With true scientific foresight, Prof. Smith stated that the few species he enumerated were "doubtless only a small fraction of those which really prey upon our common fishes," and that his principal object was to "call attention to the subject and furnish a basis for future investigation" (p. 661). But his suggestion did not meet with the response it deserved and beyond the investigations of Smith himself, Packard, Kellicott, Wright, Fasten, and a few others, all widely scattered, no attempt has been made to increase the list up to the time of the present investigation.

About 1895 Mr. R. R. Gurley, at that time in the employ of the United States Bureau of Fisheries, gathered together all the available data with reference to the copepods parasitic upon fresh-water fishes, translating the descriptions given by Krøyer and other foreign investigators and identifying both hosts and parasites amongst the material in possession of the Bureau. He made no attempt to establish new species, but only to bring together all that had been previously described, and he accumulated a manuscript of about 150 pages, which was subsequently turned over to the present author. This has proved of great value on other occasions as well as the present, and Gurley's original identifications and additions to the work of previous authors are acknowledged in the following pages.

The specimens and other material were derived from several sources. First, the work of the biological station involves the handling of large numbers of fish, and several of the regular staff, notably Mr. H. W. Clark, Mr. T. Surber, and Dr. A. D. Howard, have saved such parasitic copepods as they found while examining the gills for glochidia. These were generously turned over to the present author, who had also accumulated a large number of specimens during the surveys of the mussel fauna of various regions of the United States under the auspices of the Bureau of Fisheries.

These collections were augmented during the present investigations by a careful examination of all the preserved gills of fish in the possession of the biological station, of the gills of live fish caught by the regular seining crew or brought to the station for glochidial infection, and of a large number of dead fish caught by local fishermen.

In these different ways, and including chiefly the waters of the Mississippi Valley, the original list has been increased to 46 species, 10 of which are new to science; 1 of Krøyer's and 1 of Le Sueur's species have been rediscovered, and there have been added the larvæ of 4 other species in various stages of development.

During the investigation it early became apparent that certain economic relations existed between the copepod parasites and the mussel glochidia, which are also parasitic on fish. Although the broad fact that parasitized fish do not take or hold glochidia as well as the nonparasitized ones was observed early in the work at the station, nevertheless the existence of particular mutual relations between copepods and glochidia had never been suspected. Of all the authors above mentioned Fasten is the only one who has ever treated the copepods from an economic standpoint, and his excellent papers deal chiefly with the artificial propagation of a single species. It is at once evident, however, that the interrelations between the fish and the two kinds of parasites must exert considerable influence upon the artificial propagation of mussels, as well as upon an intelligent study of the parasitism of the copepods. Accordingly these economical discussions are placed first in the present paper, and the description of the species is left until the last.

RELATIONS BETWEEN THE COPEPODS AND THEIR HOSTS.

As has elsewhere been stated, both by the present author (Proceedings of United States National Museum, vol. 25, p. 654) and by other investigators, it is not probable that the copepod parasites of fresh-water fishes become under natural conditions a serious menace to the life of their host. But it must be remembered that their presence upon the fish is always injurious to the latter and can never be beneficial nor even indifferent.

1. There is a notion prevalent in certain quarters that a limited amount of dirt and vermin is wholesome rather than harmful. It is needless to say that this is erroneous, and that there is no truth also in the idea that a few of these creatures do their host no real harm, but that a considerable number must be present in order to become really injurious. Even a single parasite withdraws from its host enough blood for its own

sustenance. That amount may be small, but it is nevertheless a loss, and it weakens the fish's vitality by just so much. The simple fact that a sufficient number of parasites can weaken or even kill a fish is enough to prove that each one does his share toward that end and is therefore harmful. And here in the Mississippi Valley there are other considerations which tend to greatly increase this influence of parasitism.

2. The parasites, especially the ergasilids, are more numerous upon young fish; one can scarcely examine a young crappie or calico bass 3 to 5 inches in length without finding it infested with *Ergasilus cæruleus*, its particular parasite, and the same may be said of the hosts of the other ergasilids. It is not quite as noticeable in the case of the argulids and lernæopods, although even here the smaller fish are the ones most frequently infested. These young fish are like the young of all animals, including even man. They are growing rapidly; they need all the vital energy they can produce to carry on this growth successfully, and hence they are more susceptible to the injurious effects of parasitism than the matured adult. We thus find a maximum of numbers of parasites at that very stage of development when there is a minimum of resistance on the part of the host, and this greatly increases the influence of the former upon the latter.

3. Again, the parasites are more numerous in the slews and cut-offs (so-called lakes) than in the main river. This is due partly to the absence of a current, thereby enabling the parasite larva to swim about freely, and partly to the crowding together of the parasites and fish, which materially aids the former in their search for the latter; but in these shut-off bodies of water the conditions are not as favorable to the fish as in the open river, especially late in the season. There is not as much food, the water is not as well aerated, and there is a keener struggle for existence. Furthermore, in these slews the young fish far outnumber the older ones; these are the very places to which they resort to escape their enemies. Scarcely a fish can be found in these "lakes" and slews which is free from parasites, and towing reveals the presence of large numbers of parasite larvæ swimming about in search of a host. Thus the parasites attack their hosts not only at the stage of development when they are most susceptible, but also in the places and under the conditions when they are least able to withstand the attack, again greatly augmenting the influence of parasitism.

4. With the time, the place, and the conditions thus favorable to the parasites, the latter respond quickly and show an abnormal increase in development. A far greater number reach maturity than under less favorable conditions; these in turn breed, and the number of larvæ is increased a hundredfold; a considerable percentage find hosts, thus crowding the gills of the young and already weakened fish. In this way parasites that are comparatively harmless under ordinary conditions may, and often do, become a serious menace to the life of the fish.

These considerations are enough to show that the presence of even a few parasites is not a matter of indifference. Fortunately, under ordinary conditions the parasite has an even harder struggle for existence than its host. In this struggle the different kinds of parasites are affected differently, while the ultimate issue is the same for them all.

The ergasilids swim about freely until they reach maturity. The male never becomes a parasite, but completes its life as a free swimmer, while the female seeks a particular host. During this comparatively long free-swimming period both sexes have to contend with many enemies. They are then a part of the plankton and as such have to contribute their share toward the support of all the varied life which feeds upon the plankton. There are many animals which eat copepods and none of them are at all particular as to the species. These free-swimming ergasilids are fully as toothsome as other kinds and are as often eaten. The male never escapes this danger, but the female does when she has once fastened to the gills of a fish. It sometimes happens, however, that when the female is ready to fasten to a fish all the fishes suitable for hosts have left the vicinity. Under such conditions the female parasite must die unless she can swim far enough to find a host.

The argulids swim about freely, even after reaching maturity, especially the males. During this swimming they also become part of the plankton and share in its dangers and vicissitudes. Being external parasites, they are not compelled to find a particular host, for they can remain temporarily upon almost any fish until their true host is found. They are thus much less susceptible to the dangers of the plankton than the ergasilids, and when they have once reached maturity they are thenceforth free from such dangers. Their much larger size also operates in their favor, for they are too bulky to be caught by most of the creatures which eat ordinary copepods.

The lernæopods have but a very short free-swimming period, a few hours at the most, and during that time they, too, are subject to the dangers of the plankton. They must not only survive these dangers but they must also find a particular host within this brief period or they perish; and the same disaster often overtakes them that happens to the ergasilids, namely, when they are ready to attach themselves there are no suitable hosts available.

The lernæids also become a part of the free-swimming plankton at two separate periods in their development. First during the nauplius and metanauplius stages, when they are indistinguishable from all other copepods in the same stages, so far as the dangers of the plankton are concerned. Then they spend the copepodid stages as parasites upon the gills of some fish, apparently any that happens to be available. On leaving this intermediate host they again enter the plankton and swim about freely while a union of the sexes takes place. The male develops no farther, but the female must seek a permanent host, and this time it must be a particular species of fish. During this latter period, therefore, they are in the same condition as the lernæopods and often experience the same trouble, namely, when they are fully developed there are no suitable hosts available.

It follows that the parasites are ordinarily held in check by these means, and if they are to become anything of a menace to the fish there must be peculiar conditions favorable to them and unfavorable to their hosts. The custom practiced by the biological station of seining the fish out of the "lakes" and slews that are likely to go dry and putting them back into the main river is the best thing that could be done to get rid of the parasites. We have just seen that the latter breed rapidly under the conditions obtaining in the slew and that everything works together in their favor. By removing the fish such breeding is at once stopped; all the parasite larvæ and adults left in the slew die, and the new conditions in the main river are such as to keep subsequent breeding within due bounds.

RELATIONS BETWEEN THE COPEPODS AND THE GLOCHIDIA.

We have just discussed the relations between the fish and the copepods, but both copepods and glochidia infest our common fresh-water fishes. Consequently, in view of the efforts which are being put forth by the United States Bureau of Fisheries for the success of artificial mussel propagation it becomes imperative to know whether the habits of these two kinds of parasites are harmonious or antagonistic. Does the presence of copepods upon our common fishes influence in any way their susceptibility to infection by mussel glochidia? This problem can be most intelligently discussed in the form of a series of questions and answers.

I. *Are the fish that serve as hosts for the copepods those which are naturally susceptible to infection by glochidia?*

This question can be best answered by arranging in tabular form a list of the fishes with their glochidia and copepod parasites in parallel columns.

FISH HOSTS WITH THEIR GLOCHIDIA AND COPEPOD PARASITES.

Fish host.	Mussel parasites.		Copepod parasites.		Suggestions.
	On the fins.	On the gills.	On the gills.	On fins and outer body.	
Acipenser rubicundus (rock sturgeon)				Argulus canadensis.	
Ambloplites rupestris (red-eye)		Arcidens confragosus.	Achtheres ambloplitis. Ergasilus centrarchidarum.	Argulus maculosus. Lernæocera cruciata.	
Ameiurus lacustris (fork-tailed cat)				Lernæocera tortua.	
Ameiurus melas (bullhead)			Ergasilus elegans. Lernæocera sp.		Lampsilis anodontoides on gills.
Ameiurus natalis (yellow cat)	Anodonta corpulenta.		Ergasilus versicolor.	Argulus maculosus.	Quadrula glochidia on gills.
Ameiurus nebulosus (bullhead)			Ergasilus versicolor. Lernæocera variabilis. Achtheres pimelodi.	Argulus maculosus. Lernæocera tortua.	Quadrula glochidia on gills.
Amia calva (dogfish)				Argulus americanus. Argulus flavescens.	
Anguilla chrysypa (eel)		Quadrula heros. Arcidens confragosus.			Ergasilus species on gills.[a]
Aplodinotus grunniens (sheepshead)	Anodonta corpulenta. Arcidens confragosus. Quadrula heros.	Lampsilis alata. Lampsilis gracilis. Lampsilis higginsii. Lampsilis lævissima. Lampsilis purpurata. Plagiola donaciformis. Plagiola elegans. Plagiola securis.		Argulus appendiculosus. Lernæocera tenuis.	
Apomotis cyanellus (green sunfish)	Anodonta corpulenta.	Plagiola securis. Quadrula metanevra. Lampsilis sp. Lampsilis ligamentina.	Ergasilus cæruleus. Ergasilus centrarchidarum.		Argulus appendiculosus on outside of body.
Argyrosomus artedi (lake herring)			Achtheres coregoni. Achtheres corpulentus. Salmincola inermis.		Glochidia on gills.
Argyrosomus hoyi (cisco)			Achtheres coregoni. Achtheres corpulentus.		Glochidia on gills.
Catostomus catostomus (red sucker)				Argulus catostomi.	
Chænobryttus gulosus (warmouth bass)		Lampsilis parva. Lampsilis fallaciosa.	Ergasilus centrarchidarum. Ergasilus cæruleus.		
Coregonus clupeiformis (whitefish)			Achtheres coregoni. Achtheres corpulentus.	Argulus canadensis.	
Cristivomer namaycush siscowet (siscowet).			Salmincola siscowet.		

Dorosoma cepedianum (gizzard shad)	Arcidens confragosus. Anodonta corpulenta. Unio gibbosus.		Ergasilus lanceolatus	Argulus appendiculosus	
Erimyzon sucetta (chub sucker)				Argulus catostomi	
Esox lucius (pickerel)		Quadrula plicata		Argulus versicolor	Ergasilus species on gills.[b]
Esox nobilior (muscalonge)				Argulus maculosus	
Eupomotis gibbosus (sunfish)		Quadrula plicata	Ergasilus cæruleus. E. centrarchidarum.	Lernæocera cruciata	Lampsilis glochidia on gills.
Goldfish				Argulus trilineatus	
Ictalurus anguilla (Fulton cat)			Ergasilus versicolor. Achtheres pimelodi.	Ergasilus megaceros (in the nasal Fossæ.)	Quadrula glochidia on gills.
Ictalurus punctatus (channel cat)		Quadrula pustulata	Ergasilus versicolor. Achtheres pimelodi.	Argulus appendiculosus	Anodonta glochidia on fins.
Ictiobus bubalis (smallmouth buffalo)				Argulus appendiculosus	
Ictiobus cyprinella (redmouth buffalo)				Argulus appendiculosus	
Lepisosteus osseus (long-nosed gar)		Lampsilis anodontoides	Ergasilus cæruleus. Ergasilus elegans.	Argulus lepidostei	
Lepisosteus platostomus (short-nosed gar).		Lampsilis anodontoides	Ergasilus elegans. Lernæocera variabilis.	Argulus lepidostei. Argulus mississippiensis.	
Lepisosteus tristœchus (alligator gar)		Lampsilis anodontoides	Ergasilus cæruleus	Argulus ingens. Argulus nobilis (?).	Ergasilus elegans on gills.
Lepomis pallidus (bluegill)[c]	Anodonta corpulenta	Lampsilis recta. Quadrula metanevra solida. Lampsilis ligamentina.	Ergasilus cæruleus. Ergasilus centrarchidarum.	Lernæocera variabilis. Lernæocera pomotidis.	Argulus sp. on outside of body.
Leptops olivaris (mud cat)		Quadrula pustulosa	Achtheres pimelodi. Ergasilus versicolor.	Argulus flavescens	
Micropterus dolomieu (smallmouth black bass).			Achtheres micropteri. Ergasilus centrarchidarum.		Lampsilis glochidia on gills.
Micropterus salmoides (largemouth black bass).	Anodonta corpulenta	Lampsilis anodontoides. Lampsilis ligamentina.	Achtheres micropteri. Ergasilus nigritus. Ergasilus centrarchidarum.	Lernæocera cruciata. Argulus appendiculosus.	
Moxostoma macrolepidotum duquesnei (redhorse).				Lernæocera catostomi. Lernæocera cruciata.	
Oncorhynchus nerka (redfish)			Achtheres ambloplitis. Salmincola falculata. Salmincola californiensis.		Glochidia on gills.
Oncorhynchus tschawytscha (quinnat salmon).			Salmincola beani		

[a] Ergasilus gibbus is recorded by several observers from the European Anguilla anguilla.
[b] Ergasilus sieboldii has been found on the gills of this fish in Europe.
[c] Lepomis auritus (Linn.), common in streams east of the Alleghanies, carries E. centrarchidarum on its gills, but so far as known has never been examined for glochidia.

FISH HOSTS WITH THEIR GLOCHIDIA AND COPEPOD PARASITES—Continued.

Fish host.	Mussel parasites.		Copepod parasites.		Suggestions.
	On the fins.	On the gills.	On the gills.	On fins and outer body.	
Perca flavescens (yellow perch)			Achtheres lacæ.		
Polyodon spathula (spoonbill cat)			Ergasilus sp.[a]		Glochidia on gills.
Pomolobus chrysochloris (skipjack)	Anodonta corpulenta.	Quadrula ebenus. Quadrula heros.	Ergasilus elongatus.		
Pomoxis annularis (crappie)	Anodonta corpulenta. Arcidens confragosus. Quadrula plicata. Unio gibbosus.	Lampsilis ligamentina. Lampsilis recta. Lampsilis ventricosa. Lampsilis lævissima. Lampsilis anodontoides. (?) Lampsilis fallaciosa. Quadrula plicata. Quadrula pustulata. Quadrula pustulosa. Quadrula trigona.	Ergasilus versicolor. Ergasilus cæruleus. Ergasilus centrarchidarum.	Argulus appendiculosus. Argulus canadensis.	Argulus appendiculosus on outside of body.
Pomoxis sparoides (calico bass)	Anodonta corpulenta.	Lampsilis sp. Quadrula trigona.	Ergasilus cæruleus. Ergasilus centrarchidarum.		
Roccus chrysops (white bass)	Anodonta corpulenta.	Lampsilis ligamentina. Quadrula heros. Quadrula plicata.	Ergasilus cæruleus. Ergasilus centrarchidarum.	Argulus appendiculosus.	Argulus appendiculosus on outside of body.
Salvelinus fontinalis (brook trout)			Salmincola edwardsii.		
Salvelinus oquassa (blueback trout)			Salmincola oquassa.		
Scaphirynchus platorhynchus (shovel-nosed sturgeon)		Lampsilis fallaciosa.			Ergasilus species on gills.
Stizostedion canadense (sauger)		Lampsilis ventricosa. Lampsilis higginsii. Plagiola elegans. Plagiola donaciformis. Pleurobema æsopus. Quadrula plicata.	Ergasilus cæruleus. Ergasilus centrarchidarum. Lernæocera sp.	Argulus stizostethii.	
Stizostedion vitreum (wall-eye)		Lampsilis sp.	Ergasilus centrarchidarum.	Argulus stizostethii.	

[a] Marshall and Gilbert, Appendix, Report of Commissioner of Fisheries, 1904, p. 521.

A careful reading of this table shows us:

1. The fish which carry the copepods are also those which serve as hosts for the glochidia.

There are a few exceptions on either side—some fish, like the eel and the shovel-nosed sturgeon, which carry only glochidia, and others, like the dogfish and the bull-head, which carry only copepods. But these are simply the exceptions that prove the rule, and we must also remember that not all the fishes in the list have been thoroughly examined for both copepods and glochidia. Future investigations are very likely to reduce these exceptions and possibly to eliminate them entirely. This is exactly what would be expected, for the temporary parasite, the glochidium, is not so very different in some respects from the permanent parasite, the copepod. The conditions which are favorable to the one would favor the other also, and the conditions which are adverse to the one would be adverse to the other. Hence we may go a step further and affirm:

2. The species of fish which are ordinarily free from copepod parasites do not furnish conditions favorable to infection by glochidia.

The numerous species of buffalofish, carp, suckers, lampreys, minnows, shiners, dace, chubs, and darters are excellent examples. The above table includes all the fresh-water fish at present known to serve as hosts for either copepods or glochidia, and practically none of these fish appear in either list. Nor are they likely to appear in any numbers, for these fish have been as thoroughly examined as any others, but nothing has been found upon them. Lefevre and Curtis mention some of the mechanical factors which tend to render a fish immune to infection by glochidia, such as the smallness of the gill openings, the rapidity of the fin movements, and the texture of the gills. They mention as the most striking instances of immunity the German carp, certain minnows, and the darters, three of the above-named fish. By means of artificial infection they exposed these fish to glochidia, a few of which fastened upon their gills and fins; but these were quickly sloughed off, and none could be carried through the parasitic period. "The disappearance of the hookless glochidia of *Lampsilis* from both gills and fins of the carp * * * suggests rather that there may be some reaction of the host's tissues comparable to the processes which confer immunity against parasitic bacteria in higher vertebrates." (Lefevre and Curtis, Bulletin Bureau of Fisheries, vol. XXX, p. 163.)

We can readily understand how an immunity of this character could operate against the parasitic copepods as well as against the glochidia. Extensive examination in the future may, and probably will, reveal straggling copepods and glochidia, but in such small numbers that they must be regarded as accidental infections. [a]

3. The fish which make the best copepod hosts are also those which are naturally infected with the greatest number and variety of glochidia.

A fish's efficiency as a host may be measured either by the number of any single parasite it harbors, or by the variety of species. In the copepod parasites these two criteria are usually separated and must be considered independently. In the mussel glochidia they are nearly always united, and may therefore be treated conjointly.

Keeping these facts in view, we notice first that the crappie, *Pomoxis annularis*, stands at the head of both lists. It serves as the host of at least 13 species of mussel glochidia, and yields often as many as 500 or 800 specimens of some particular species

[a] *Argulus foliaceus* and *Ergasilus sieboldii* have been found once or twice on the carp (*Cyprinus carpio*) in Europe, while *Lernæocera pectoralis* was reported by Kellicott from the red-fin shiner (*Notropis cornutus*) in the Shiawassee River, Mich.

like *L. ligamentina* or *L. ventricosa*. When artificially infected, each crappie will take from 1,000 to 2,000 glochidia and sometimes even more.

Turning now to the copepods, we find that while it carries on its gills only two species, it is, nevertheless, the worst infected fish in the Mississippi River so far as numbers are concerned. Hardly a crappie examined during the summer season failed to yield specimens of one or both copepods, and frequently the number from a single fish reached into the hundreds and sometimes came close to a thousand. The difference in size between the glochidia and copepods make these numbers closely correspond, and the limit in both instances is apparently determined only by the actual living space on the gills.

The second fish on the list is the sheepshead, *Aplodinotus grunniens*, which serves as a host for 11 species of mussels, and upon the gills of which the number of individual glochidia is usually well up in the hundreds and frequently reaches into the thousands.[a] This is an apparent exception to the rule, for while there is an external *Argulus* parasite to correspond with the few fin glochidia, a careful examination of all the sheepshead gills that were available (about 500) failed to reveal a single copepod; but there are certain facts which profoundly influence our judgment in the present instance.

First, and of the greatest importance, this fish habitually feeds upon thin-shelled mussels, crushing the shells with its powerful pharyngeal jaws. Whenever the shell of a gravid mussel is crushed in this way the gills of the fish necessarily become infected with the glochidia which are set free. *L. lævissima* and *P. donaciformis* are the ones whose glochidia are found in greatest numbers, and these as well as most of the others have papery shells. This method of infection is quite different from that in the crappie and other fish and comes close to being artificial. Furthermore, such infection is practically constant, in fact as constant as the feeding of the fish, and thus the gills are kept loaded with glochidia all the time. The presence of these glochidia prohibits that of the copepods, as will be shown later. The glochidia of the thick-shelled mussels like *Q. heros* are obtained in the usual way and are much fewer in number.

Again we find upon the sheepshead's gills, in addition to the mussel glochidia a trematode ectoparasite, which exists in as great abundance as the copepods upon the gills of the crappie. The presence of these worms may still further explain the absence of copepods.

After the sheepshead comes the sauger with six species of glochidia, the green sunfish with five, the bluegill and white bass with four each, and the gizzard shad, the largemouth black bass, the skipjack, and the calico bass with three each. Of these the bluegill, the white bass, and the calico bass are each infested with the same two species of *Ergasilus* as the crappie, in smaller numbers but still to a considerable degree. The largemouth black bass carries a still smaller number of individual copepods but compensates for it by being the host of five different species. The green sunfish, the gizzard shad, and the skipjack have but a single copepod parasite on their gills, but they are also really the host of but a single kind of glochidium, the others being found in such small numbers that they can be regarded only as accidental infections. Having thus determined that the same fish serve as hosts for both copepods and glochidia, a second question naturally arises:

[a] On the gills of one fish of this species 5,200 glochidia of *P. donaciformis* were found, and upon another fish 10,400 of the same glochidia.

II. *Is there any fellowship between the different species of the two kinds of parasites? Do we find certain species of glochidia associated with the same copepod in a majority of instances?*

This question can also be answered by reference to the table (p. 338), from which we deduce the following:

1. Of the external-fin glochidia *Anodonta corpulenta* is by far the most widely distributed and is always accompanied by an external *Argulus* parasite, usually *A. appendiculosus*. The green sunfish, the calico bass, and the skipjack are apparent exceptions; *Anodonta* glochidia have been found upon them but no *Argulus* copepod. It must be remembered, however, that the glochidia are fastened in the fins and remain there no matter how long the fish may have been kept or how much it may have been handled. On the other hand, the copepod merely clings to the outside surface of the fish and is easily brushed off when alive and practically always falls off when dead. Only a few of these fish have been examined under conditions favorable for finding the copepods, while the conditions are always favorable for finding glochidia.

Such being the case, it seems reasonable to expect that an *Argulus* parasite will be found upon the three fish just mentioned as the result of future examination; but the argument ought to work equally well in the opposite direction, and hence we may look for the future discovery of the glochidia of *A. corpulenta* upon the channel cat, its copepod fellow having been already found.

2. The glochidia found upon the gills of fish may be divided into the two great groups of *Lampsilis* species and *Quadrula* species. Accompanying the former we find *Ergasilus cæruleus* in every instance, except upon the largemouth black bass, where it is replaced by *Ergasilus nigritus*, one of the new species. Accompanying the *Quadrulas* we find *Ergasilus versicolor* upon the catfishes and the skipjack and *Ergasilus centrarchidarum* upon the Centrarchidæ. In this instance the copepods and glochidia are equally well protected, and the only hindrance to their discovery is the lack of fish specimens. Some species of fish are always scarce, while others that may be ordinarily plentiful may be scarce at just the time when they are likely to become infested with the copepods or the glochidia. Hence, while one of the parasites might be well known upon the fish, the other might have escaped notice.

Apparently something of this sort has happened to a few of the catfishes and Centrarchidæ; copepods have been found upon them repeatedly, but thus far no mussel glochidia have been discovered. It would seem reasonable, however, to expect them, and some species of *Quadrula* will probably be found in the future upon the yellow cat, the bullhead, and the Fulton cat, while some species of *Lampsilis* will be found upon the common sunfish, *Eupomotis gibbosus*, the warmouth bass, and the smallmouth black bass.[a]

In connection with the association between *E. centrarchidarum* and *Quadrula* glochidia the following may be suggested:

(*a*) *E. centrarchidarum* is found on the gills of the largemouth black bass, but it is accompanied by *E. nigritus*, one of the new species which evidently takes the place on this host of *E. cæruleus*, the regular associate of *Lampsilis* species. The presence of *centrarchidarum*, therefore, is not to be interpreted as indicating that it is here excep-

[a] Since the writing of this paper two species of *Lampsilis* glochidia have been discovered upon the gills of the warmouth bass and have been inserted in the table on page 338.

tionally associated with *Lampsilis* species but, rather, that *Quadrula* glochidia will be found in the future upon this fish as they have been upon so many of the sunfishes and basses other than the largemouth.

(*b*) Upon the sunfishes it is worth noticing that the two copepods *cæruleus* and *centrarchidarum* occur together, and we should expect such fish to become the natural hosts of both *Lampsilis* and *Quadrula* glochidia. Two of them, the bluegill and the green sunfish, have already yielded both kinds of glochidia, and it would seem probable that future investigation will find both kinds upon the other sunfish where now there is but a single kind.

(*c*) *E. centrarchidarum* is found upon the gills of the wall-eye, which have thus far yielded only *Lampsilis* glochidia; but upon the sauger, another fish of the same genus as the wall-eye, both kinds of copepods and both kinds of glochidia appear. Furthermore, both fishes yield the same species of *Argulus*, so that it does not seem presumptive to suppose that the second species of *Ergasilus* and *Quadrula* glochidia will eventually be found upon the wall-eye, as they have already been upon the sauger.

3. There is a single well-marked instance of individual association between a glochidium and a copepod. *Lampsilis anodontoides*, whose glochidia are practically confined to the gars, is found to be accompanied by a peculiar copepod, *Ergasilus elegans*, another new species, which differs markedly from the others of its genus in the fact that the female remains free swimming for a much longer period. Indeed, it seems probable that they leave the fish's gills after having fastened to them and swim about freely. There are two other new species, *Ergasilus lanceolatus* from the gizzard shad and *E. elongatus* from the spoonbill cat, which are fully as peculiar as *E. elegans* and which may well be the copepod half of other individual associations whose glochidial half has not yet appeared. Furthermore, we may look for *E. elegans* upon the alligator gar, whose gills have already yielded specimens of *Lampsilis anodontoides*.

4. It has long been known that certain species of copepods are confined to particular hosts and are not found upon any others. The table furnishes us several well-marked examples of this: *Argulus mississippiensis* and *A. ingens* are each found upon a single host, and although the two hosts are gars and very closely related to each other the copepods are distinct species. Again, the two species of *Ergasilus* just mentioned, namely, *lanceolatus* and *elongatus*, are each restricted to a single kind of fish and are not likely to be found elsewhere. The same is true of *Ergasilus megaceros* and of *Salmincola oquassa* and *S. edwardsii;* in fact, a good proportion of copepod parasites of both fresh-water and salt water fish show such restrictions.

When we look at the glochidia we find that there are fully as many of them confined to a single host. *Lampsilis alata*, *gracilis*, and *purpurata*, and *Quadrula solida*, *ebenus*, and *trigona* are good examples. Probably further investigations will modify many of these as well as of the copepods, but it is equally probable that some of them will prove to be always solitary. In the case of the glochidia we are not compelled to wait for natural infections, for we can subject a fish to the glochidia of many mussels and determine experimentally whether or not it will make a suitable host for them. In fact, this has been done by Dr. A. D. Howard, who, in the Bureau of Fisheries document no. 801, calls attention on page 36 to what he calls "Restricted infection," which he has demonstrated by actual experiment in the case of *Quadrula pustulosa* upon the channel cat.

Nothing of this sort can be tried with the copepods, since we can not supply larvæ in the right stages of development as we can glochidia. But although our knowledge of both kinds of parasites is rather limited as yet, enough data have been accumulated to show that the two kinds of parasites behave very similarly in regard to their hosts. There is thus a decided similarity between them when each is found by itself upon some suitable host.

III. *Does the actual presence of copepods on a fish's gills exert any influence upon its susceptibility to infection by glochidia?*

In other words, granting that the same fish do serve as hosts for both glochidia and copepods, are the conditions favorable for both at the same time? This is manifestly something which can not be watched under natural conditions, and the only way to answer the question is by artificial infection experiments. Accordingly a hundred crappies, *Pomoxis annularis*, of nearly uniform size (5 to 6 inches long), which had been caught and brought to the station for artificial infection, were carefully examined and 25 were found to be infested with *Ergasilus cæruleus*, while the other 75 were free from them. The entire hundred were then infected in the usual manner and under exactly the same conditions with the glochidia of the black sand-shell, *Lampsilis recta*. After infection the 25 parasitized fish were killed, their gills were removed, and the number of copepods and glochidia on each was counted with the following results:

Fish.	Glochidia.	Copepods.	Fish.	Glochidia.	Copepods.
1	0	350	14	102	87
2	46	150	15	7	393
3	176	121	16	190	36
4	126	140	17	63	310
5	104	78	18	495	8
6	337	7	19	40	196
7	47	253	20	80	112
8	38	218	21	16	372
9	169	142	22	395	10
10	257	44	23	9	403
11	301	63	24	11	396
12	372	30	25	143	134
13	280	31			

The average number of glochidia upon each of the nonparasitized fish was between 1,000 and 1,200. By comparing this with the numbers given in the table we deduce the following:

1. The presence of even a small number of copepods upon the gills of a fish reduces its susceptibility to infection by glochidia to one-third or one-fourth of what it would be if no copepods were present.

Even the gills that contained 10 copepods or less showed the presence of only a few hundred glochidia instead of the thousand or more upon a nonparasitized fish. Such a marked reduction can not be explained by the mere presence of the copepods; they do not occupy enough of the gills to exert any crowding influence, neither are they ever found attached to the tips of the filaments where the glochidia mostly congregate. Manifestly there is room enough for both kinds of parasites without serious crowding; gills that will accommodate 1,200 glochidia with no apparent injury to the fish can certainly find room for more than 400 when only 10 copepods are present.

Lefevre and Curtis say that the stimulus which causes the glochidium to close and thus to fasten itself to the fish is purely a mechanical one (Bulletin Bureau of Fisheries, vol. XXVIII, pt. 1, p. 622). Here again the mere presence of a few copepods upon the gills of a fish could have no effect upon such a stimulus. The respiratory movements of the fish may have considerable to do with it; the crappie's respiration is not very vigorous even at its best, and this is especially true of small fish (Lefevre and Curtis, Journal Experimental Zoology, vol. 9, p. 103).

The irritation due to the presence of parasitic copepods may still further reduce these movements and thus prevent infection by glochidia; but if this were the only cause 10 copepods could hardly produce so large an effect. It would seem as if there must be something further, either chemical or physiological in its action, in order to accomplish the known results. It will not be very easy to prove what this is, but meanwhile the facts remain unaltered that in some way the presence of a very few copepods greatly reduces the fish's susceptibility to infection by glochidia.

2. As the number of copepods upon a fish's gills increases its susceptibility to infection by glochidia diminishes. Naturally a limit is soon reached beyond which the susceptibility has diminished so much that practically there can be no infection at all; this limit for small crappies is about 200 copepods. If more than this number is present, the glochidia are very scattering and are usually below 50 in number. The copepods often increase to 500, and in such instances there are no glochidia, or, if any, their number is expressed by a single digit.

Certain conclusions naturally follow from these facts. The first is that it is obviously disadvantageous to attempt to infect with glochidia fish that are already carrying copepods. A few glochidia will always stick to their gills, but not in sufficient numbers to repay the labor expended. Since the large fish are relatively freer from copepods than the smaller ones, it follows that they make the better hosts. Not only are their gills larger and thus capable of carrying more glochidia, but the latter will fasten to them more readily because of the comparative absence of copepods.

Again, the fish from the main river, whatever their size, make better hosts than those from the slews and "lakes," because they, too, are freer from copepods. This is especially true at those times when the water is very low; during a long-continued drought it would be of little use to try infecting fish caught in such places because they would be so infested with other parasites that very few of the glochidia would fasten to them. The best thing to do with such fish would be to replace them in the main river and trust to taking them again after they had gotten rid of their copepods.

3. It is obviously a poor rule that does not work both ways, and we find that the presence of glochidia is as prohibitive to the copepods as are the latter to the former. This also is something that can not be watched under natural conditions; neither can it be proved by experiment, for we can not supply parasitic copepods as freely as we can glochidia; but it is abundantly sustained by a study of natural infections on the gills of fish taken in the river. There are in the possession of the biological station about 1,000 vials of gills showing natural infection by various glochidia. These were all carefully examined for parasitic copepods under a dissecting microscope, and in not a single instance where the number of glochidia exceeded 300 was there even a single copepod present.

This mutual antagonism between the copepods and glochidia enables us to understand clearly why the sheepshead's gills are never infested with copepods. From the nature of the fish's food, as already explained, its gills are kept crowded with glochidia all the time, and thus the copepods are shut out. This leads to the conclusion that when a fish's gills are artificially infected with glochidia the fish is thereby rendered immune to the copepods. Artificial infection therefore, as regularly practiced at the biological station, not only does the fish no harm but is even positively beneficial.

And this suggests a possible safeguard or remedy for some fish hatcheries. It occasionally happens that parasitic copepods get to breeding in a hatchery in such numbers that they kill the fish. Judging from the cases thus far reported, this seems more likely to occur among trout than among other game fish. The European trout (*Salmo fario* Linnæus) is the natural host of *Margaritana margaritifera*, but our American trout have been examined very little for glochidia. However, if there is any virtue in the conclusions here drawn, the very fact that they are more susceptible than other fish to the copepod parasites indicates that they would make excellent hosts for glochidia. If this be so, an infection with glochidia would be harmless to the fish, but at the same time would render them immune to the copepods. At all events, the experiment is worth trying.

4. The breeding season of the copepods thus acquires especial economic importance with reference to mussel propagation. It is manifest that at the close of a breeding season, when the larval brood of copepods have sought and found their hosts, their numbers will be at a maximum. Consequently this would be the time least favorable to infection with glochidia. On the other hand, the early spring, before the copepods begin to breed, and the intervals between successive breeding periods, would be the most favorable to glochidial infection.

We are not yet sufficiently acquainted with either kind of parasite to be able to make a complete schedule of their times of breeding, but many interesting facts have been ascertained.

Lefevre and Curtis in the Bulletin of the Bureau of Fisheries, volume XXX, page 141, divide mussels into two groups according to the length of the period of gravidity. Those having a long period of gravidity, among which *Lampsilis* species predominate, produce ripe glochidia during the fall and winter and spring months. Those having a short period of gravidity, among which *Quadrula* species predominate, produce ripe glochidia during the summer months. Turning now to the copepods, we find that the ergasilids and argulids have three breeding seasons in the year, the first at the end of May or the beginning of June, the second at the middle or latter part of July, and the third in the latter part of September. We do not yet know all the breeding seasons of the lernæids and lernæopods, but from the material here presented and that obtained from many other investigations it is certain that they also have a breeding season during the middle or latter part of July, and it is probable that there are two other seasons corresponding to those just given.

Comparing the breeding of the copepods with that of the mussels, it will be seen that the winter or early spring is the best time for infection with *Lampsilis* glochidia, since the only copepods then on the fish's gills are such adults as have lasted through the winter. None of the *Quadrula* group produce glochidia early enough to be used for spring infection, and the best months for them would be July and September, just before the second and third copepod breeding seasons; and from what has already been said of the cumulative effects of unfavorable conditions during low water the month of July would ordinarily be preferable to September.

In the paper already referred to Lefevre and Curtis call attention to the desirability of reducing the length of the parasitic period of the glochidium (p. 191), which is inversely proportional to the temperature of the water. Whether the shortening of the parasitic period during the warm summer weather will compensate for the increase in the number of parasitic copepods is a question that can be decided only after careful experimentation. We now know, however, that the presence of these copepods and their periods of breeding are factors that must be given due consideration before the question can be solved.

SYSTEMATIC.

A complete description, fully illustrated with appropriate figures, is given of all the species which are new to science. Of those which have been previously described only such notes are included as are of interest or furnish additional information. The larvæ of a few species were hatched out in the laboratory of the station, and they also are fully described and illustrated, since they add considerably to our previous knowledge of the species. Several parasites were obtained by H. Krøyer, a Danish zoologist, from fish taken near New Orleans and sent to the Royal Museum in Copenhagen. Most of these fish were such as come up the Mississippi River from the Gulf of Mexico, and hence their parasites can not be included amongst the strictly fresh-water species; but they are included in the present list because they are likely to be found in that part of the river.

The parasites of fish in the Great Lakes, the Lake of the Woods in Canada, and of several isolated lakes are also enumerated, since they are all fresh-water forms and really belong with the great fresh-water fauna of the interior of our continent. A few species have been included from west of the Rocky Mountains and east of the Appalachians.

THE ARGULIDÆ.

Argulus canadensis, new species. (Pl. LX.)

Host and record of specimens.—Three fine females were obtained by T. Surber at Le Claire, Minn., from fish caught in the Lake of the Woods. Two were from a species of whitefish, *Coregonus*, while the third was from a rock sturgeon, *Acipenser rubicundus*. The better of the first two is made the type of the new species and has been given catalogue no. 43521, U. S. National Museum. The other has been given catalogue no. 43525, U. S. National Museum, while the specimen from the sturgeon received catalogue no. 43526, U. S. National Museum.

Specific characters of the female.—Carapace elliptical, a little longer than wide, the posterior lobes broad, evenly rounded, and reaching to about the center of the third thorax segment, leaving the two posterior pairs of legs fully visible in dorsal view. Instead of projecting anteriorly the cephalic area is slightly reentrant, ovate, and relatively very small; posterior sinus one-third the length of the carapace, its width posteriorly equal to its length, but narrowed and squarely truncated anteriorly. The supporting rods in the lateral areas of the carapace are peculiarly arranged, meeting at a point far forward and giving the creature a sort of hunch-backed appearance. The respiratory areas are also peculiar, the outer one club-shaped, the large end anterior, while the handle of the club extends backward along the outer margin of the inner area, an arrangement wholly different from anything heretofore described. Abdomen a little more than one-fourth the entire length, its width to its length as 5 to 8; anal sinus cut beyond the center, its sides parallel, lobes narrow-elongate and rather bluntly rounded, papillæ basal. Eyes large and so far forward as to almost touch the anterior margin, but widely separated; sucking disks also far forward and well separated, one-eighth the width of the carapace.

Antennæ small and weakly armed, the terminal joints of the first pair not reaching beyond the lateral claw, the anterior claw minute and nearly straight; second antennæ slender, basal joint enlarged with a small spine on its posterior margin. A pair of large accessory spines behind the antennæ and close to the median line; another pair between the bases of the maxillipeds or slightly posterior to them.

of fresh water are relatively seldom the prey of parasitic Eucopepoda under natural conditions" (p. 828). And he adds: "A study of the literature of the subject confirms our conclusion."

His judgment is based upon the results of this African expedition, during which he says very large numbers of fish were examined, but only two of them were found infested with eucopepods.

While such a conclusion seems inevitable from the data he has given, it must be understood as applying to Africa, and perhaps to that portion covered by these Tanganyika expeditions and not to the world at large. There has been very little work done on the parasites of fresh-water fishes, as has been already shown (p. 333), and no one can say what the future holds in store. It is possible that other portions of Africa are richer in these parasites, and it is certain that the results of the present investigation are not essentially inferior to those obtained from salt-water fishes. It has already been stated (p. 341) that a fish's efficiency as a host may be measured either by the number of any single parasite it harbors or by the variety of species. If we are comparing fresh-water fish with salt-water fish, or the fish from one region in the world with those from another region, we should take into account both the number and the variety. In variety of forms the salt-water fish considerably surpass those from fresh water, but in number of specimens the latter sometimes surpass the former. The present author never has obtained any salt-water fish that could compare with the two crappies in numbers of parasites. Furthermore, in the variety of species found upon any single kind of fish the fresh-water fish present an average fairly comparable with those from salt water. Three and four from the same fish are the general rule rather than the exception. (See table, p. 338.)

And if we were to include the mussel glochidia and all other kinds of gill parasites with the copepods, the salt-water fish would be hard pushed for a victory. Not many salt-water fish can compare with the crappie (*P. annularis*), which harbors 13 species of glochidia, 3 species of copepods, and 3 species of trematode ectoparasites, 19 in all; or with the sheepshead, which acts as the host of 11 species of glochidia, 2 species of trematodes, and two of copepods, 15 in all; or with the sauger, upon which have been found 6 species of glochidia, 2 species of trematodes, and 4 species of copepods, 12 in all. And it must be remembered that these are all natural infestations, which have occurred under perfectly normal conditions. When we come to the abnormal conditions which are favorable to the copepod parasites, then their numbers increase to such a degree that they cause serious epidemics in the breeding ponds and often kill off large numbers of the fish; and since it is fresh-water fish only that are bred in this way it follows that this sort of damage is confined to them and does not occur amongst salt-water fish.

The facts presented in the present paper open up a very fascinating chapter in the book of copepod parasitology, and one that bids fair to become far-reaching in its practical relations; but it must be remembered that we have as yet scarcely made a beginning, and that a vast amount of work is still to be done before we can reach a final solution of the problems. From the facts here presented, however, it would seem as if fresh water presented fully as rich a field to the parasitologist as can be found in the ocean.