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THE PATTERN OF CIRCULATION OF *Diphyllobothrium sebago* (CESTODA: PSEUDOPHYLLIDEA) IN AN ENZOOTIC AREA[1]

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Abstract: In the Rangeley Lakes region of western Maine, where *Diphyllobothrium sebago* (Ward) is enzootic, the spawning of the smelt *(Osmerus mordax)* in late April and early May and the ensuing die-off of the spent fish coincide with the return and reproductive activities of the gulls *(Larus argentatus)*. The gulls feed on the dead plerocercoid-infected smelt, which results in a high infection during the late spring and early summer. Thus, from early July onward, at least until the fall turnover in the lake, a constant source of coracidia is available for the copepod, the first intermediary, which constitutes the chief food of the smelt. The procercoid in the copepod becomes a plerocercoid in the smelt, which serves as a source of infection for the gulls, during either the spring-summer of the next year or of the subsequent year. Epizootiologically, due to the prolonged preservation of the plerocercoids in the fish, the smelt is the natural reservoir. Despite the common occurrence of the plerocercoids in the salmon *(Salmo salar)*, its role as an intermediary is negligible.

INTRODUCTION

For more than a century, descriptive work on life cycles has been of prime importance to parasitologists and biologists. Most life cycle studies are necessarily limited to experimental laboratory conditions, however, which means that they are conducted outside the biotope of the hosts, intermediate(s) and final, and the biotope of the parasite itself. Occasionally, hosts which are foreign or are unimportant in the circulation pattern of a parasite in nature are used in life cycle studies, either unknowingly or intentionally, because they are easier to use in laboratory studies than is the suspected proper host.

The whole process of the larva passing in succession from one host to another in natural conditions is of far greater complexity than the same process taking place under artificial conditions in the laboratory. In addition to methods practicable in experiment, factors have to be considered which are eliminated in the laboratory, such as the influence of the environmental factors on the quantitative occurrence of the suitable hosts, and their interrelationships. The pattern of circulation concept is not new nor original, yet it has been examined critically for few species of heteroxenous parasites.

Meyer and Vik,[10] in a paper on the life cycle of *Diphyllobothrium sebago* (Ward), suggested the possibility that their experimental laboratory findings may not agree with what occurs in nature. Subsequent studies dealing with the hatching of the eggs under conditions simulating those in nature,[9] the intermediary fish hosts,[11] and the final hosts,[12] supplemented by further unreported observations, confirm this possibility.

The purpose of this paper is to summarize previously reported findings, and to collate them with unreported observations in an attempt to show how they are synchronized in maintaining the focus of *D. sebago* in the Rangeley Lakes region.

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The Rangeley Lakes system is a chain of seven coldwater lakes located in the extreme western part of Maine, about 48 km south of the Quebec border. The study was centered on Mooselookmeguntic Lake, which has a small gull rookery, and is not over 27.5 m in depth except for a small area, that extends to 40 m (Fig. 1).

Diphyllobothrium sebago has a three-host cycle, typical of those *Dyphyllobothrium* species which reach maturity in the intestine of fish-eating birds. When a susceptible bird swallows a fish or fish offal containing infective plerocercoids, the larvae develop into adult worms. For obvious ecological reasons, the eggs of helminths in fish-eating birds have a good chance of reaching water. Hatching and development of the eggs occur external to the host after a period in water. If the errant coracidium which emerges is swallowed by a suitable copepod, the parasite develops into a procercoid in the body cavity of the host. When the copepod containing the mature procercoid is swallowed by a susceptible fish, the larva leaves the copepod, penetrates the wall of the fish stomach, and develops into the final larval stage, the plerocercoid. The entire life cycle is, therefore, dependent upon the predator-prey relationships of the hosts.

RESULTS AND DISCUSSION

The Adult Cestode and the Final Host

The herring gull, *Larus argentatus* Pontoppidan, is the final host.[12] Gulls are seasonal residents of the region, arriving from the coast early in April and remaining until about mid - November, when the waters become icecovered. As reported by Vik,[17] from early May onwards the gulls feed almost exclusively on rainbow smelt, *Osmerus mordax* (Mitchill).

The main nesting site is a small unnamed island near Student's Island in Mooselookmeguntic Lake (Fig. 1). Hatching of eggs begins early in June; and after the chicks have left the nesting ground, but before they are able to fly, they remain in the shallow waters around the rookery island. Concurrently, as well as during the breeding season, the older birds tend to congregate in the same area.

The highest incidence of infection of gulls with *D. sebago* occurs during the summer months. The total summer infection was 74 of 110 (67%) birds examined; of 86 gulls examined in June, 66 or 77% were infected. Fewer birds were infected at other times of the year; none during April, 6 of 60 in May, and 4 of 43 during the fall months.[12] The decline in the incidence in the late summer and early fall is due to the short life span of the cestode and the decrease in the available smelt. The prepatent period is about 7 days.

The dispersal pattern of the *D. sebago* eggs by the gulls varies somewhat with the seasonal activities of the hosts. During the breeding season and shortly thereafter, before the chicks are able to fly, the entire gull population tends to remain in the vicinity of the nesting site. After the young of the year have fledged and the flock has left the natal area, the tapeworm eggs have a wider dispersal. Thus, in addition to the egg-laden excrement reaching the inshore waters, incidental to feeding and roosting, it may extend to the greatest depth of the lake.

In the study simulating conditions in nature, Meyer[11] has shown that within 9 to 20 C and at a depth of 27 m the percentage of hatching increases with length of exposure. At 20 C (at 3 m) over 80% of all eggs hatched within 21 days; at 9 C (at 27 m), where no eggs hatched within 21 days and only 15% after 35 days, 50% of the eggs had hatched by 51 days. At the higher temperatures the hatching of eggs is relatively simultaneous, and conversely, at low water temperatures it becomes markedly prolonged.

Thus, beginning about mid-June when the worm eggs seed the warmer waters, where the summer temperature is about 20 C, most of the eggs have hatched within 21 days. Thereafter, in addition to the continuation of the eggs hatching in the inshore waters, the eggs reaching the deeper waters, where the summer temperature is about 9 C, do not start hatching until after 30 days or more. Since it is unlikely that the bottom temperature is lower than 9 C, hatching can be expected to occur beyond the 27 m level.

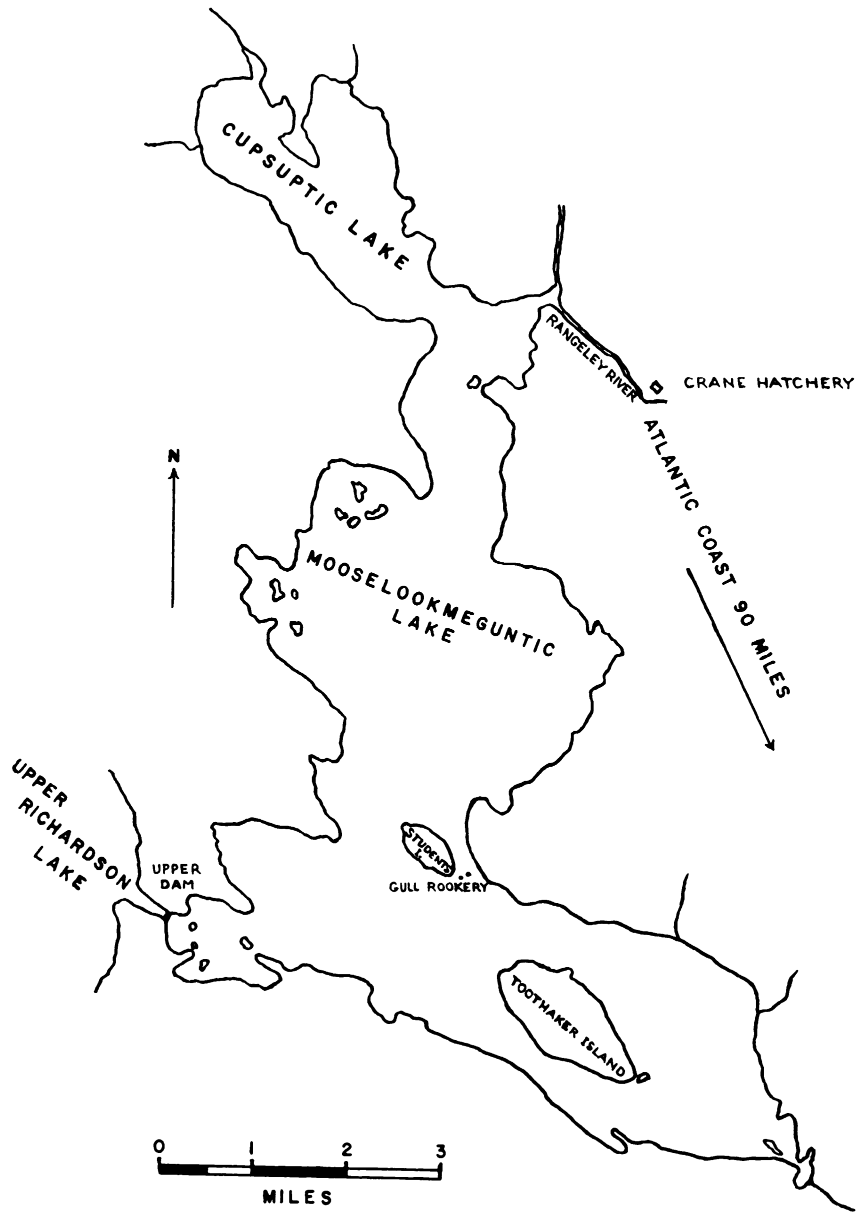

FIGURE 1. Mooselookmeguntic Lake.

The Procercoid and the First Intermediate Host

Meyer and Vik[10] found *Cyclops vernalis* Fischer, *C. bicuspidatus* Claus and *C. scutifer* Sars to be suitable hosts for coracidia. *Cyclops vernalis* occurs primarily in the littoral region of the lake, while *C. bicuspidatus* is chiefly limnetic,[13] as is *C. scutifer* according to Yeaman.[19] Whether the eggs are deposited in shallow or in deeper waters, they will hatch during the summer months; and it appears that there is a juxtaposition in habitat between the coracidia and the required copepods. The role of the various species of copepods in the maintenance of the focus requires further study.

The Plerocercoid and the Second Intermediate Host

When the *Cyclops* containing the infective procercoid is eaten by a smelt, it develops into the final larval stage, the plerocercoid.

During the summer smelts normally occur in the deeper portions of the stratified lakes, but are distributed throughout the entire volume of water during the fall, winter, and spring. Greene,[6] and Gordon[5] found that the food of freshwater smelts consists almost entirely of zooplankton, especially copepods. Insects and fish comprise negligible fractions of the total diet.

Smelts have essentially a 2-year life cycle. They hatch one year, spawn two years later, and then die shortly after spawning. In Mooselookmeguntic Lake spawning takes place in the lake tributaries at night in late April and early May. Large numbers of gravid fish ascend the stream a short distance and select a spawning area in brisk current. Incubation time varies from as few as 5 to 60 days or more, depending upon water temperature, and the current carries the young down-stream into the lake. Following spawning, the spent fish return to the lake, after which there is a heavy smelt mortality that continues into the summer. It is these dead and dying adult smelt, which have a plerocercoid incidence of 4.6%[11], that are the source of the infection for the gulls.

The common occurrence of plerocercoids in landlocked salmon, *Salmo salar* Linnaeus, leads to two interesting speculations: first, what is the source of the larvae, and second, what is the role of the salmon in the circulation of *D. sebago?* Because the salmon, once they cease feeding on insects (Chironomidae and Trichoptera larvae and Ephemeroptera naiads,[1,14,18] feed almost exclusively on smelt[1]) they continue to accumulate the larvae during their entire lives. It is also probable that the larvae will live for several years within the body of the piscivorous fish, which presumably explains the large numbers of plerocercoids in the salmon. The transfer of the *D. sebago* larvae in smelts to salmon has not been demonstrated experimentally, but there is no doubt about this occurring in nature. Hobmaier,[7] Vergeer,[15] Kuhlow,[8] and Vik,[16] have shown that when *Diphyllobothrium* plerocercoids are present in forage fish, such as smelts and sticklebacks, they penetrate the stomach wall of the piscivorous fish (salmonids, burbot, pike) and reestablish themselves in the tissues without a change of form. But despite the common occurrence of the larvae in the salmon,[11] they are not an obligatory link in the life cycle of *D. sebago* and their role as an intermediary is negligible. Except for an occasional salmon dying from some natural cause and the viscera discarded by anglers while fishing, salmon are not normally available to gulls. Thus they generally serve as dead-end hosts.

The plerocercoids of *D. sebago* occur in the kidneys, pancreas, liver, spleen, swim bladder, heart, and gonads of both sexes; the larvae also occur free in the celom, immediately beneath the serosal layer of the body wall; and they occur in the flesh. No part of the fish is always free of plerocercoids.[11]

In addition to interfering with the normal growth of the host as a result of utilizing some of its food material, the nature of the pathogenicity, among other things, is dependent upon the host organ involved and the number of plerocercoids. While epizootic mortalities of Salmonidae are well known,[2] during the nearly 10 years of study no such die-offs attributable to *Diphyllobothrium* plerocercoids were observed among fish in nature or in the rearing pools of the nearby Crane Hatchery.

Based upon available data, the best description of the circulation pattern in the Rangeley Lakes region is: The spawning of the smelt in late April and early May and the ensuing die-off of the spent fish coincide with the return and reproductive activities of the herring gulls. The gulls feed on the dead plerocercoid-infected smelt, which results in a high enzootic infection during the late spring and early summer.

Before the young-of-the-year gulls are fledged they are strictly littoral, which means that the egg-laden excrement is restricted to the shallow waters; after they fledge and disperse with the older birds, the eggs extend to the deeper waters. Thus, from early July onward, at least until the fall turnover in the lake, a constant source of coracidia is available for the copepod, the first intermediary, which constitute the chief food of the smelt. The procercoid in the copepod becomes a plerocercoid in the smelt, which serves as a source of infection for the gulls, during either the spring-summer of the next or of the subsequent year. Epizootiologically, due to the prolonged preservation of the plerocercoid in the fish, the smelt is the natural reservoir.

Chizhova and Gofman - Kadoshnikov[3] described a similar pattern of circulation for *Diphyllobothrium dentriticum* (Nitzsch) in Lake Baikal. The principal final hosts are gulls (species not given), which are 50% or more infected; *Cyclops konesis* var. *baicalensis* Was. and *Epischuria baicalensis* Sars are the principal first intermediaries; and the most important second intermediary is the Baikal omul (*Coregonus migratorius* [Georgi]), of which 80% to 100% are infected. Of the deep lake and the shallow water biotopes, only the latter allows completion of the life cycle of the parasite. In the deep-water the temperature at the bottom throughout the year is near 4 C, which is below that required for the tapeworm eggs to hatch.

Early in the spring the fish begin moving from the deeper portions in Lake Baikal, where they have spent the winter, into the littoral region of the lake for the summer, where the complex of conditions is present which is favorable for the meeting of the hosts and the parasite.

The presence of the omul in the shallow waters coincides with the nesting period of the gulls in the same area, both hosts occurring in great numbers. While inshore the fish are preyed upon by the gulls, the final host of the parasite. The egg-laden feces of the gulls seed the lake, whose shallowness and warm bottom temperatures are favorable to early hatching of the eggs and the meeting of the coracidia with the copepods. Thus, during the summer, when the temperature is most favorable, the necessary hosts (gulls, copepods, fish) converge in the same area of the lake, facilitating the circulation of the parasite.

An examination of the two patterns of circulation of diphyllobothriasis, occurring in widely separated localities, shows that they are similar with respect to the way in which the plerocercoid is passed from the fish intermediary to the gull final host. It is as a result of the synchronized activities of the fish and the gulls, in time and space, that the cycle is completed and the focus maintained. This is but one example which emphasizes the differences between the circulation pattern of a heteroxenous parasite species in nature and the elucidation of its life cycle under laboratory conditions. As additional parasite-host(s) biocenoses are examined critically they can be multiplied almost indefinitely.

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