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AN ANALYSIS OF THE CHANGES IN THE PREVALENCE OF
CAMALLANUS OXYCEPHALUS (NEMATODA: CAMALLANIDAE)
IN WESTERN LAKE ERIE 1, 2

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Distribution of Camallanus oxycephalus was studied in 16 species of fishes in western Lake Erie during the summer and autumn of 1972. This study was compared to studies done in 1927 and 1957. Analysis of the frequency of infection in these fishes indicates that Camallanus has become more abundant in the lake. This increase has occurred since 1957. The increase in prevalence appears related to changes in plankton, benthos and fish communities of the western basin. The importance of host-parasite contact frequency and its relation to parasite population density and regulation is discussed.

Camallanus oxycephalus (Ward and Magath, 1916) is a common and widely distributed nematode parasite of freshwater fish in eastern North America. Despite its abundance, little information concerning the biology of this worm is available. The life history was investigated by Stromberg and Crites (1974). They found that female worms protrude from the anus of fish and release infective first stage larvae into the water. Development continues only if larvae are eaten by copepods. Larvae develop to the infective third stage in the copepod hemocoel and complete development to adulthood when the infected copepod is eaten by a fish. Fish may also become infected by consuming smaller infected fish.

Bangham and Hunter (1939) reported C. oxycephalus for the first time in Lake Erie. Their study, done during 1927, listed 28 species of fish with this parasite. A resurvey of Lake Erie fish parasites done in 1957 (Bangham, 1972) listed 26 species of fish infected with C. oxycephalus. Studies of the population biology and ecology of C. oxycephalus in western Lake Erie (Stromberg, 1973) revealed that the parasite was very abundant. Some species of recreational and commercial value were heavily parasitized. The present study was undertaken to determine 1) if changes in the prevalence of C. oxycephalus have occurred in western Lake Erie and 2) if these changes could be related to documented changes in the biological or limnological characteristics of the lake. Our analysis of changes in the prevalence of C. oxycephalus in Lake Erie is based upon comparison of our data with the data of Bangham and Hunter (1939) and Bangham (1972). The dangers of such a comparison are recognized, but we feel that due to the high visibility and unmistakable appearance of this nematode, earlier data are accurate and comparisons are valid. Our study spanned several years, but data for comparative purposes were restricted to summer and autumn months. This was the survey period of the two earlier studies.

METHODS

Fish were collected from western Lake Erie with otter trawls, poundnets, gill nets, Fyke nets, commercial shore seines, minnow seines and by hook and line. Fish were transported to the laboratory alive or on ice and examined immediately for parasites. Fish were mea-
sured and sexed, and worms were removed and preserved in 70% alcohol for later study. Differences in frequency of infection were compared by calculating a z statistic with the following formula from Freund, et al. (1960):

\[
z = \frac{\sqrt{\theta \left(1-\theta\right) \left(\frac{1}{n_2} + \frac{1}{n_1}\right)}}{\frac{x_1 - x_2}{n_1 - n_2}}\]

where \(x_1\) = number of infected fish

\(n_1\) = number of fish examined

and \(\theta = \frac{x_1 - x_2}{n_1 - n_2}\)

\(z_{a/2} = .025 = \text{level of significance}\)

### RESULTS

Seventeen species of fish were examined for *C. oxycephalus* in western Lake Erie during 1972. Sixteen of these fish were parasitized by the nematode. The 1972 study did not include large mouth bass (*Micropterus salmoides*), bluegills (*Lepomis macrochirus*) or any of the seven species of darters (*Etheostoma, Percina*) previously examined. Table 1 lists species of fish examined in 1972 and the frequency of occurrence of *C. oxycephalus* in 1957 and 1972. It shows clearly that the frequency of occurrence of *C. oxycephalus* was quite high in many of the 1972 fish. Highest frequencies occurred in predatory species (*M. chrysops, Pomoxis spp, S. vitreum*). Low frequencies occurred in plankton feeders with the exception of gizzard shad (*D. cepedianum*) and young of the year freshwater drum (*A. grunniens*).

Comparison of the frequencies of infection between 1927 and 1957 (table 2) revealed a significant decrease in three species; freshwater drum, troutperch (*P. omiscomaycus*) and spot-fin shiner (*N. spilopterus*). The prevalence of *C. oxycephalus* remained unchanged in 14 species. Comparison of the 1957 and 1972 data showed a significant increase of *C. oxycephalus* in 11 species. The frequency of occurrence remained unchanged in 6 species and did not significantly decrease in any. Clearly, the increase of *C. oxycephalus* has been greatest since 1957. Troutperch were the only fish to exhibit a decline in incidence of infection since 1927. This decline occurred between
1927 and 1957. The prevalence of *Camallanus oxycephalus* in troutperch has remained unchanged since 1957. The remaining two species exhibiting declines between 1927 and 1957 showed marked increases in infection in 1972. White bass were the most frequently parasitized fish in all three studies. Although no data for young of the year white bass are available for 1957, direct comparison of the 1972 data with the 1927 data revealed that a significant increase in *C. oxycephalus* had occurred ($z = +2.586$). A similar comparison for yellow perch (*Perca flavescens*) showed that although adult fish are more frequently parasitized, the incidence in young of the year fish has not changed significantly since 1927 ($z = +.498$).

In addition to the increase in incidence of infection of white bass, the data suggest that the intensity of infection has also risen. Bangham and Hunter did not keep precise records of infection intensity, however, they did define three classes of infection intensity. Only 18% of the adult white bass examined in 1927 carried more than 10 worms each, while 45% of the 1972 adult white bass carried over 10 worms each. Thus, the mean worm burden in the adult white bass population appears to have increased.

The magnitude of the changes in prevalence of *C. oxycephalus* in the fish community as a whole is shown in figure 1. This figure compares the sequence of infection frequencies ordered from highest to lowest for each of the three studies. The numbers do not correspond to specific fish, but the graph represents the overall shift of abundance in the nematode population. As with the data in tables 1 and 2, it is clear that no significant change in prevalence of *C. oxycephalus* occurred in the fish community between 1927 and 1957. Curves for 1927 and 1957 are characterized by relatively low frequencies of infection, sloping gradually from a high of about .47 to .01. The 1972 curve represents a large and significant increase in the prevalence of *C. oxycephalus* occurred in the fish community between 1927 and 1957. Curves for 1927 and 1957 are characterized by relatively low frequencies of infection, sloping gradually from a high of about .47 to .01. The 1972 curve represents a large and significant increase in the prevalence of *C. oxycephalus*. Several groups of fish can be defined based upon infection incidence. One species (white bass) occurs at the .90 level, three species (white crappie, black crappie and walleye) occur around .70 and three species (freshwater drum, gizzard shad and yellow perch) occur around .30.
The curve declines sharply after these seven high frequency values through two intermediate frequencies (.40-.20). The remaining seven values are low, occurring around or below .15. The fish exhibiting these low frequencies of infection are all plankton feeders except the catfish and pumpkinseed. The 1927-57 curves, in contrast, have only one species in the high incidence group, three or four species in the intermediate group and the majority (12 species) in the low incidence group.

The frequency of infection of a host by any parasite is at least partially a function of how often the host and parasite contact each other. Another factor of the host-parasite association is how efficiently the parasite transfers environments after it has been contacted by the host. A rise in the incidence of infection will result from an increase in either or both of these factors. Frequency of host-parasite contact is dependent upon such extrinsic factors as population density, food habits and behavior of the organisms. The efficiency of transfer is likely to be affected by intrinsic factors such as host resistance and physiological host-parasite interactions. Although it is possible that the resistance to *Camallanus* in 11 fish populations in Lake Erie has been lowered, it is unlikely that this is the only factor which accounts for the increase in the prevalence of this parasite. This is particularly true for several fish populations which have been highly successful over the last 50 years and showed no signs of stress. No estimation of fish resistance is possible either now or in 1927. Much information is available, however, concerning changes in the western basin of Lake Erie which might affect the frequency of contact between *Camallanus* and its fish hosts (Hartman, 1972; Regier and Hartman, 1973).

Two critical host-parasite contact points occur in the life cycle of *C. oxycephalus*. The first is the contact between the first stage larva and the copepod intermediate host. Because the larvae fall rapidly through a water column, larvae released in the open lake areas are probably exposed to the copepods for only a short period of time. The frequency of host-parasite contact might be greater if the number of copepods in the water column increased. Bradshaw (1964) compared the zooplankton in western Lake Erie for 1939-49-59. He found that copepods did, indeed, increase in density from 70,000/m³ in 1939 to 165,000/m³ in 1959. Un-
fortunately, no data are available to compare the distribution of *Camallanus* in planktonic copepods. Evidence from the infection frequency data supporting the hypothesis that increased copepod density has affected the *Camallanus* population is not decisive. The frequency of *Camallanus* remained unchanged in most planktivorous fishes, while a higher frequency of contact between larvae and copepods should have resulted in an increased flow of the parasite to these planktivorous species. 

The second critical point in the life cycle of *C. oxycephalus* is the contact between infective third stage larvae and the final fish host. This contact is aided by the ability of the worms to pass from smaller infected fishes to larger ones following predation. The increases in the prevalence of *Camallanus* in piscivorous fish suggests that parasite flow through forage fish has been increased. Analysis of the data revealed no increase of *Camallanus* in the principal forage species (*N. hudsonius, N. atherinoides*) found in Lake Erie in 1927 and 1957. The discovery of a high frequency of *Camallanus* in gizzard shad (*D. cepedianum*) in 1972 (table 1) was a particularly significant finding. Although this fish was known from Lake Erie as early as 1848 (Trautman, 1957), Miller (1957) pointed out that it has only become abundant in Lake Erie since the 1950’s. Bodola (1964) noted the rapid rise in abundance of gizzard shad especially in the western basin, since around 1950 and he stated that it had an important effect upon lake ecology. We frequently found shad in white bass and crappie stomachs suggesting that the increase in shad has been exploited by several piscivorous species. 

Changes in the benthic fauna may have indirectly influenced the abundance of *Camallanus* in western Lake Erie. Carr and Hiltunen (1965) recorded a reduction in the *Hexagenia* population by 1965 to less than one percent of the 1930 population level. This reduction in food resource may have forced such generalized feeders as perch, drum and catfish into consuming greater numbers of fish. The concomitant rise of gizzard shad carrying *Camallanus* increased the exposure of the parasite to these fish. 

It appears that the rise in gizzard shad, which occurred roughly during the same time that the *Camallanus* population increased, is a principal factor in the increased prevalence of this parasite in western Lake Erie. Young gizzard shad consume large numbers of cyclopoid copepods (Price, 1960), thus concentrating the nematode larvae and delivering a larger number of parasites to piscivorous fish which feed upon the shad. When the numbers of shad increased, piscivorous species began to consume more shad, which are heavily infected, and thus contacted the parasite more frequently than when they consumed the less infected *Notropis*. Because the incidence of host-parasite contact has increased and the nematodes are concentrated in young shad, the intensity of the infection within individual fishes has probably also risen. Limited evidence of this rise in infection intensity could be seen when the white bass data for 1927 and 1972 were compared. If individual fish carry more nematodes, more nematode larvae are produced and the density of the nematode population increases. 

Crofton (1971a) redefined parasitism based upon a quantitative approach to host and parasite populations. He suggested that the negative binomial distribution was a good fundamental as well as empirical model because it has biological meaning. The fitting of such a distribution implies that parasites can kill their hosts and that host death is a function of the number of parasites in an individual host. This loss of heavily infected hosts is a greater loss to the parasite population but is compensated by the higher reproductive potential of the parasite. Such a relationship has a regulatory effect upon the parasite population (Crofton, 1971b), and the equilibrium levels of host and parasite populations are partially dependent upon the number of parasites required to kill the host. Because the number of parasites found in individual hosts is partially a function of the incidence of host-parasite contact, this contact influences the population level of the parasite. Systems in which host-parasite contact is infrequent may have low parasite population levels, and relatively few hosts will have a lethal
number of parasites. In systems where host-parasite contact is frequent, a larger number of hosts will be adversely affected by the parasite population.

Stromberg (1973) obtained good fits to the negative binomial distribution with his data for *C. oxycephalus* in western Lake Erie fish. Crofton's assumptions about the implication of this distribution may then be applied to the Lake Erie-Camallanus system. Evidence from the analysis of the *Camallanus* population in western Lake Erie suggests that both qualitative and quantitative fluctuations of components in the life history of helminths can have a direct effect upon the density of the parasite population by altering the incidence of host-parasite contact. Pathogenic effects of the parasite, which depend upon the number of parasites in individual hosts, may not significantly influence the host population until the fluctuations alter the distribution of the parasites in the hosts so that lethal levels are frequently encountered.

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LITERATURE CITED


