THE UNIVERSITY OF MANITOBA

METAZOAN PARASITES FROM WHITEFISH, CISCO AND PIKE FROM SOUTHERN INDIAN LAKE, MANITOBA: A PREIMPOUNDMENT AND DIVERSION ANALYSIS

by

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ABSTRACT

Intensity, prevalence and dominance of parasites, as well as the diversity and similarity of the parasitofauna of the lake whitefish (*Coregonus clupeaformis* Mitchill), the lake herring or cisco (*C. artedii* Leseur) and the northern pike (*Esox lucius L.*) were studied at Southern Indian Lake (S.I.L.), Manitoba. Amphipod vectored parasites were less important and copepod vectored parasites were more important in S.I.L. than reported for other systems. Abundance of parasite species was altered by host age and season. Geographical location affected the ranking of parasite abundance but no differences in parasite abundance was observed in different sexed fish. Plerocercoids of *Triaenophorus crassus* Forel in whitefish and cisco, and *Diphyllobothrium sp.* in pike exhibited nonrandom distribution in host musculature and could not be explained entirely by relative muscle mass or asymmetry of fish intestinal tracts. Condition of cisco and whitefish was modified by presence of *T. crassus* plerocercoids. This study presents data prior to impoundment and diversion of current, and predicts changes in the parasitofauna of these fish species.

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I. INTRODUCTION

Considerable information is available on the parasite fauna of a variety of freshwater fish species (Hoffman 1967). Usually these reports deal with one species of host or one species of parasite in complex ecological systems. Leong (1975) is the first to attempt a comprehensive overview of the interaction of a community of fish and their parasites. The system which he chose was a large, deep lake with a large scale introduction of an exotic fish species. Although this system illustrated parasite flow, modification of parasite abundance by host age, host sex and season, the system was probably unstable because of the short association of the introduced host species.

Southern Indian Lake (S.I.L.), in northern Manitoba is a relatively stable, shallow, mesotrophic freshwater lake. It has a well established commercial fishery and for this reason three economically important fish species were chosen for study; namely the lake whitefish, *Coregonus clupeaformis* (Mitchill); lake herring or cisco, *C. artedii* LeSueur and the northern pike, *Esox lucius L.* These species are hosts for two stages of the life cycle of the economically important cestode, *Triaenophorus crassus* Forel, 1868. Furthermore, because impoundment and diversion, major ecological changes, were about to occur in S.I.L.

this was a unique opportunity to establish base-line data for long term comparisons. Recent work (Petersson 1971a) suggested that these changes would result in an increase in *T. crassus* and a decrease in the value of whitefish catches.

In order to develop a comprehensive overview of parasites in a large lake one must know the parasitofauna, fish age, sex, diet and water temperature. All of these factors are extremely important in predicting adequate sample size to evaluate if sample size is adequate to give an acceptable representation of the lake.

Finally, few comprehensive studies of fish parasites have been undertaken in Manitoba. In fact most parasite records come from a study by Dechtiar (1972) of Lake of the Woods, an atypical aquatic environment for Manitoba. The objectives of the present study were:

1. To determine the parasitofauna of these three fish species, percentage of hosts infected, number of parasites in an infection, size of the parasite population, dominance of parasite species, and diversity and similarity of parasites.
2. To determine the effects of the following modifying factors on these parasites: (a) age (b) season (c) food habits (d) sex (e) location.
3. To determine what constituted the sample size necessary for an adequate representation of the parasitofauna of the host species.

4. To determine how representative our sampling was, particularly with reference to *T. crassus*.
5. To determine the distribution of *T. crassus* and *Diphyllobothrium sp.* plerocercoids in the musculature of their respective intermediate hosts.
6. To determine if *T. crassus* plerocercoids significantly alter fish condition.
7. To predict changes in the parasitofauna of these fish species with lake impoundment and diversion of current.

II. LITERATURE REVIEW

a) PARASITE SURVEYS

Although the north temperate region of North America including Manitoba has been incompletely surveyed for fish parasites, several surveys of Ontario, British Columbia and the maritimes have been completed. Fish of the Coregoninae and Esocidae have been surveyed in other continents and have a parasite fauna not unlike that of comparable North America fishes. Most intensive studies on coregonid parasites other than that of *Triaenophorus crassus* were done in the U.S.S.R. and in the Scandinavian countries. For convenience these surveys are included in Appendix I.

b) GENUS *TRIAENOPHORUS*

The genus *Triaenophorus* is circumpolar in distribution. Cooper (1918) first reported it from North America and subsequently Hjortland (1927) reported it from Minnesota. Nicholson (1928) reported *Triaenophorus* from Manitoban cisco though little of its biology was known. Lawler and Scott (1954) reviewed the geographic distribution of the genus in North America. Distribution in Eurasia was studied by Uzmunn and Hesselhost (1957) and Michajlow (1962). *Triaenophorus* species were studied in Norway (Vik, 1959) and Lake Mälaren, Sweden (Lawler, 1969b).

Three species; *T. crassus*, *T. nodulosus* Pallas, 1760 and *T. stizostedionis* Miller, 1945 were known when Kuperman (1968) described three others; *T. amurensis*, *T. orientalis* and *T. meridronalis* from fish of the Amur basin and southern reservoirs of the U.S.S.R. These latter three species are unreported from North America and are not included in this literature review.

Review of the biology and control of the North American species of *Triaenophorus* were prepared by Doan (1950a, 1050b), Kennedy (1951b), Miller (1952, 1954) and Lawler (1955; 1956; 1959a, 1959b; 1960; 1961a; 1965). Kuperman (1973) produced the most recent review of the taxonomy and bionomics of the genus.

Procercoid larva of *T. crassus* infect copepods (primarily *Cyclops*). These are eaten by plankton feeding fish, cisco (*C. artedii*) and to a lesser extent whitefish (*C. clupeaformis*) and the plerocercoid larvae develops in host musculature. When infected cisco and whitefish are eaten by the definitive host, pike (*E. lucius*) mature worms develop in the pike intestine.

T. nodulosus also infects copepods and becomes a plerocercoid in plankton feeding intermediate, usually burbot (*Lota lota* L.) or perch (*Perca flavescens* Mitchill). Plerocercoids develop in the visceralorgans and mesentaries. Pike are the definitive host and the last link in the cycle.

T. stizostedionis infect copepods which are eaten by trout-perch (*Percopsis omiscomaycus* (Walbaum)) and develops in the visceralorgans and mesentaries. Walleye (*Stizostedion vitreum* (Mitchill)) are the definitive host.

All three species of *Triaenophorus* mature in the spring and deposit eggs which hatch releasing a ciliated coracidia which are in turn eaten by copepods.

Plerocercoids of *T. crassus* were also found in the sea and arctic lamprey (McLain, 1951; Guilford 1954, and Buchwald and Nursall, 1969) and the sockeye salmon (Margolis 1963). Besides the burbot and the yellow perch, plerocercoids of *T. nodulosus* were reported from the white perch, *Roccus americanus* (Gmelin) (Tedla and Fernando 1969a), and the European perch (*Perca fluviatilis* *L.* (Chubb 1964).

Many authors have studied the biology of these three cestode species. Procercoids of these cestodes in their copepod hosts were studied at Heming Lake (Watson, 1963; Lawler, 1961b; Watson and Lawler 1961, 1963, 1965; Lawler and Watson 1963; and Watson and Price 1960). Miller (1945a, 1945b, 1945c) studied the biology of these species in their vertebrate hosts in Lesser Slave Lake, Alberta. Lawler (1950b, 1950c; 1952; 1953;

1968; 1969a) studied the biology of *T. nodulosus* in its intermediate hosts (perch and burbot) and its definitive host (pike) (Lawler 1955). Chubb (1963) also studied the bionomics of *T. nodulosus* in pike.

In 1932, Nicholson established that *Triaenophorus tricuspidatus* Bloch, 1779 (= *crassus*) was non-pathogenic to man. Newton (1932) initiated studies of its biology inwestern Canada. He described the effect of host age and of season on the numbers and distribution of plerocercoids in the musculature of whitefish. In the 1950's inspectors of the U.S. Food and Drug Administration began to refuse heavily infected fish at the Canada/U.S.A. border. Adverse economic effects on the canadian fisheries promoted much of the subsequent research on *T. crassus*. Ekbaum (1936, 1937) first described the hatching of eggs of this cestode. Surveys of cisco and whitefish in Lake Winnipegosis, Lake Manitoba (Doan 1945a, 1945b), Nesslin Lake (Wheaten and Rawson 1949a), Southern Indian Lake (Sunde 1963, 1965) and many other commercial lakes were initiated to locate lakes with low infection levels of *T. crassus* and thus avoid American rejection of fish exports.

Although candling and selection of fish from lakes and regions of lakes with low infections reduced rejection of fish shipments, methods were sought to reduce *T. crassus* infections. Control was attempted by removing the pike from Heming Lake (Doan 1949; Kennedy and Doan 1949; Lawler 1950a, 1950d; 1951a; 1959a; 1961a), Lake Winnipeg (Kennedy and Doan 1949) and Square Lake, Alberta (Miller 1950). Removal of the pike significantly reduced *T. crassus* infection in whitefish but the method was expensive. Similarly cisco, thought to be important in maintaining heavy infections in whitefish, were selectively removed from Lesser Slave Lake (Miller 1948), Mosher Lake (Wheaton and Rawson 1949b), and Lake Winnipeg (Kennedy (1950, 1951a). Results were positive but not economically feasible. Experiments to control coracidia were unsuccessful (Miller and Watkins 1946; Miller 1949; Libin 1950a, 1950b, 1951).

Other work on *T. crassus* by Kennedy (1948) and Oakland (1949) established statistically sound methods of classifying *T. crassus* infection levels in lakes. Keleher (1950) studied differences in *T. crassus* parasitism of different species of cisco in Lake Winnipeg. Miller (1945b) examined the effect of this cestode on the growth of cisco and whitefish. Welch (1950, 1951, 1952) investigated the relationship between limnological factors and *T. crassus* infections in lakes in the Thunder Bay district. Lawler (1951d) stocked Wapum Lake with whitefish in an attempt to observe the establishment of *T. crassus* but stocking was not successful.

Taxonomic studies of cisco revealed differences in the *T. crassus* infections of different species (Lawler 1951b, Keleher 1952). Keleher (1953) studied the factors resulting in differential infections of Lake Winnipeg cisco.

Although interest in *T. crassus* declined since the 1960's, research continues. Margolis (1963, 1967) successfully used this species as a biological tag to separate spawning stocks of the sockeye salmon. Research was conducted into the detection (Budde 1965, Freese 1970) and the nutritional effects (Crampton 1960) of plerocercoids in whitefish fillets. Petersson (1971a) found that lake impoundment in Sweden raised *T. crassus* infection levels in coregonids.

c) MODIFYING FACTORS

i) Host Age

Many authors studied changes of parasite fauna with host age. This effect was observed in *T. crassus* infections (Newton 1932, Welch 1952, Miller 1952). Hine and Kennedy (1974) found *Pomphorhynchus laevis* (Zoega) Müller, 1776 accumulated in aging dace, *Leuciscus leuciscus* L. while changes in this parasite's distribution within the host also occurred. Bibby (1972) found the acanthocephalan *Neoechinorhynchus rutili*

(Müller, 1780) decreased in abundance with age of *Phoxinus phoxinus L.* The copepod, *Ergasilus centrachidarum* Wright, tended to increase in abundance with bass age for three years than declined (Cloutmann and Becker 1977). Awachie (1966) found *Cyathocephalus truncatus* (Pallas, 1781) peaked in prevalence in three year old trout though incidence did not change. Parasites within the same host reacted differently to changing host age. Shotter (1973) found some parasites of whiting (*Odontogadus merlangus L.*) like the cestode *Grillotia trinaceus* Guiart, 1924, the monogean *Diclidophora merlangi* (Kuhn in Nordm., 1832), the digeneans, *Hemiurus commonus* Odhner, 1905 and *Derogenes varicus* (Mueller, 1784) Looss, 1901 and nematode *Contracaecum elavatum* Raillet et Henry, 1912 increased in incidence and intensity with host age while the digeneans *Stephanostomum pristis* (Deslongchamps, 1824) and *Lecithaster gibbosus* (Rud., 1802) Lüke, 1901, metacercaria of *Cryptocotyle lingua* (Crepl., 1825) Fischoeder, 1903 and the copepod *Clavella uncinata* Müller decreased with host age.

Miller (1952) found that cisco accumulate *T. crassus* plerocercoids and whitefish do not. He suggested that this stemmed from dietary differences affecting uptake rates of infected copepods. Petersson (1971a) thought this explained why whitefish with high gill raker counts and not those with lower counts accumulated plerocercoids of *T. crassus* with age.

Change of diet with age of brown trout resulted in reduced infections of *Crepidostomum metoecus* (Braun, 1900) and *C. farionis* (O.F. Müller, 1784) Nicoll, 1909 (Awachie, 1968). Bauer and Nikol'skaya (1957) and Rumyantsev (1973) found that differences in fish diet and fish distribution in a lake could account for parasite changes in fish of different ages.

More *Discocotyle sagittata* (Leukart, 1842) Diesing, 1850 were found in older trout (Thomas 1964, Paling 1965). Paling (1965) found two generations of monogenea on older trout (on the basis of size) and suggested this accounted for the higher numbers on these fish.

Leong (1975) pointed out that age affects parasite species differently in different hosts or in different geographical locations. Complexity of whitefish and coho parasite faunas decreased with age while that of cisco peaked in middle-aged fish (Leong 1975).

Changes in host diet, host physiology (resistance) and/or host geographical location are the primary explanations for changes in parasite abundance with age.

ii) Season

Seasonal changes in abundance were observed in many species of fish parasites. Midsummer increase of *T. crassus* plerocercoids in the intermediate host following a decrease of mature worms in pike in the spring were observed by many authors (Ekbaum 1937, Newton 1945, Miller 1945b and Welch 1952). Connor (1953) found *Proteocephalus stizosthethi* Hunter and Bangham 1933 from walleye followed a seasonal cycle of incidence.

Timing of maximum and minimum abundances differed greatly among parasite studies. Many parasites had autumnal peaks. Bauer and Nikol'skaya (1957) found *Discocotyle*, *Proteocephalus spp.* and *Chlormyxum coregoni* Petrushevski and Shulman, 1958 infected whitefish more in autumn. Hopkins (1959) found that numbers of *Proteocephalus filicollis* Rudolphi in *Gasterosteus aculeatus L.* increased in July. This increase peaked in autumn and was followed by a stable period caused by conditions favourable to parasites. By midwinter, conditions were less favourable and the numbers declined until the spring reinfection (Hopkins 1959). Awachie (1966) found *C. truncatus* became established in brown trout in late autumn, matured in late winter and early spring, and disappeared by late summer. Other parasites exhibited late summer or autumnal minima. Brown trout were heavily infected by *Crepidostomum metoecus* and *C. farionis* in February, incidences fell throughout. *Echinorhynchus salmonis* Muller, 1784 in perch peaked in late winter and fell to zero by fall (Tedla and Fernando 1969b). Kennedy (1968) found *Caryophylleus laticeps* (Pallas, 1781) infected dace during December, incidence rose until mid-winter, remained constant until spring, then declined and disappeared in August. Other parasites had peaks of abundance in the spring or summer. Paling (1965) found that *D. sagittata* invaded trout from April to November with peaks in July or August (somewhat earlier than the autumn peak of this species in the U.S.S.R., Bauer and Nikol'skaya 1957). Burreson and Olson (1974) found two hemuirds increased in incidence and intensity during the spring and summer then decreased in July or August. Shotter (1973) found parasites of Whiting peaked in summer and early autumn with juvenile digeneans being most apparent at this time. Kennedy and Hine (1969) found infection of dace by *Proteocephalus torulosus* (Batsch) was initiated in winter, increased to steady levels in late spring, then declined and terminated in summer. Not all parasites have demonstrated seasonal cycles. Although Kennedy and Hine (1969) and Kennedy (1969) demonstrated the seasonality of some dace parasites such as *P. torulosus* and *C. laticeps*, Hine and Kennedy (1974) were unable to do so with *Pomphorhynchus laevis*. They suggested this resulted from physiological differences of these parasites.

Many explanations for seasonal cycles have been proposed. Hopkins (1959) suggested that these cycles resulted from the net influx and outflux of parasites. Temperature is the variable most frequently used to explain these fluctuations. Rawson and Rogers (1972, 1973)attributed the seasonal abundance of monogenea on largemouth bass and bluegill to water temperature changes. Cloutman and Becker (1977) found the abundance of the copepod, *Ergasilus centrarchidarum*, declined sharply with decreasing temperature and egg production ceased below 17°C. Eure (1976a) found that decreased water temperature in southern latitudes stimulated migration of *Proteocephalus ambloplitis* (Leidy, 1887) within largemouth bass while increased water temperature in northern latitudes caused the same effect. Temperature may have affected individual parasite species differently. The life cycles of *P. filicollis* reported by Hopkins (1959) in stickleback and that of *P. torulosus* in dace differ and Kennedy and Hine (1969) suggested that the latter is better able to establish and to grow at colder temperatures. Tedla and Fernando (1969b) observed seasonal changes in several parasites of perch and suspected that water temperature was the stimulus. They felt that within the host, parasites were less affected by low winter temperatures. Influence of diet or breeding cycle of the perch could not be detected (Tedla and Fernando 1969b). Awachie (1968) observed the timing of parasite cycles of *Crepidostomum* in its intermediate host (*Gammarus*) and in the trout and speculated that water temperature was the controlling stimulus. Stromberg and Crites (1975) found the growth of the nematode *Camallanus oxycephalus* Ward and Magath, 1916 in the white bass increased as water temperature rose. Seasonal timing was important in maximizing the efficiency with which the copepod intermediate was infected (Stromberg and Crites 1975).

Some authors thought temperature modified host activity (feeding and diet). Bibby (1972) attempted to explain seasonal parasite changes of minnows *Phoxinus phoxinus* by temperature induced changes in host activity. Cold, "hibernating" winter minnows consumed relatively few parasites compared with actively feeding summer hosts (Bibby 1972). Temperature could not explain seasonal changes in the parasite fauna of *Coregonus albula L.* in the U.S.S.R. (Rumyantsev 1973). Kennedy (1972) explained this phenomenon by a study of temperature effects on *Pomphorhynchus laevis* in goldfish. He suspected that temperature exercised a major control in the flow of parasites through both non-seasonal and seasonal endoparasitic fish host systems but in different ways and to varying degrees. A quantitative mechanism might explain why parasites exhibited a seasonal cycle in one locality and not in another (Kennedy 1972) Anderson (1976) used mathematical modelling to show that seasonal variation of *C. laticeps* was due to the combined effects of a temperature dependent mortality rate and fluctuations in host-feeding activity. Moravec (1970) explained the seasonal cycle of the nematode *Raphidascaris acus* (Bloch, 1779) in brown trout by changes in host diet. He could not rule out other factors such as temperature. Eure (1976b) felt that seasonal abundance of *Neoechinorhynchus cylindratus* (Van Cleave, 1913) Van Cleave, 1919 was due to changes in the fish feeding behavior and annual temperature regimes. Bauer and Nikol'skaya (1957) attributed greater seasonal changes in younger whitefish to the seasonal variability of their plankton food source compared to the uniform amphipod diet of older fish.

Still other authors felt that temperature changes acted on parasites via host hormones or the host immunological system. Cushing (1942) demonstrated reduced fish antibody production at lower water temperatures. Maturation cycles of *C. laticeps* in dace did not appear to be initiated by water temperature changes but possibly by host hormone levels (Kennedy 1968). Kennedy (1969) observed that if dace spawned a month earlier than normal, the seasonal cycle of *C. laticeps* was shifted by the same period of time. Kennedy and Hine (1969) suggested that water temperature modified host resistance and might explain the seasonal cycle of *P. torulosus* in dace. Leong (1975) found whitefish and cisco parasite communities had maximum diversity in January and decreased to April. He explained greater abundance of several parasite species in winter by temperature reduced host resistance.

iii) Food Habits

Many authors suggested dietary differences explained changes in the parasite fauna of fish with season, host age and sex. (see corresponding sections) Rumyantsev (1973) found infection of *C. albula* was influenced by its plankton diet which contained the intermediate hosts of its dominant cestode parasites. Older fish began to feed on benthic amphipods (*Pontoporeia affinis* Lindström, 1855) and were then infected with parasites vectored through them. Hine and Kennedy (1974) found that warmer summer water temperatures increased consumption of the intermediate amphipod host of the acanthocephalan *Pomphorhynchus laevis* by dace, and resulted in higher levels of parasitism. Dechtiar and Loftus (1965) found *Cyathocephalus* infections of perch and cisco in winter resulted from the increased consumption of infected amphipods (*Pontoporeia*) at this time. Cannon (1973) demonstrated our present lack of knowledge of the relationships between fish diet and helminth incidence by showing that sexual differences in parasite incidences might be explained by host size differences which affected food intake. Leong (1975) found correlations between diet and parasite fauna were obscured because 1) the importance of food items as intermediate hosts varied, 2) digestion rates varied 3) host specificity and 4) parasites modified intermediate host behavior (increased susceptibility to predators).

Parasites may be used as indicators of diet. Lawler (1970) reported that Bauer (1948) found a similarity in the ectoparasites of plankton and benthic feeding forms of coregonids. Benthic feeding hosts had more trematodes and fewer cestodes unlike plankton feeding forms, which suggested the possibility of parasites as indicators of diet.

Petersson (1971a, 1971b) showed that the number of gillrakers in coregonids can result in different diets and hence different levels of parasitism. Lake impoundment modified the diet of some coregonids altering their cestode fauna (e.g. T. *crassus* levels) (Petersson 1971a)

iv) Host Sex

Many parasite studies (Leong 1975, Rumyantsev 1973 and others) have not indicated differences in the parasite fauna of fish due to host sex. Welch (1952) observed no differences in *T. crassus* infections of different sexed whitefish. Bibby (1972) found sex had no apparent effect on the worm burden of the minnow *Phoxinus phoxinus*.

These differences, nevertheless, could be observed in some studies. Hicks and Threlfall (1973) found sexual differences in the parasite fauna of eighty-one Atlantic salmon (*Salmo salar L.*). Females had a higher prevalence of *Bunodera luciopercae* (Müller, 1776) and *Diplostomulum spathaceum*, (Rudolphi, 1819) Braun, 1893 and a lower prevalence of *Eubothrium crassum* (Bloch, 1779) than males. They observed no such differences with these parasites in four other species of fish studied. Shooter (1973) found male and female whiting were equally infected with most parasite species but the copepod *Lernaeocera* occurred only in females. Kennedy (1968) found female dace acquired and lost *Caryophyllaeus laticeps* before, and generally had heavier worm burdens than male dace.

Some authors explained sexual differences by host hormone and size differences. Paling (1965) found male brown trout harbour twice as many *D. sagittata* as female trout and more were infected. He speculated that infective oncomiracidia may have a sex preference and that because sexual bias occurred only during the years when the host is fertile this may indicate that sex hormones were involved. Eure (1976b) found no sexual differences in the number of *Neoechinorhynchus cylindratus* harboured by either sex of bass except during the spring (females preferred). Cannon (1973) found that sexual size differences in perch caused differing diets which might account for the greater number of *Proteocephalus pearsei* La Rue, 1914 and *Leptorhynchus thecatus* (Linton, 1891) in the larger females.

v) Geographical Location

Most locational differences in the parasite fauna of fish were discovered in an effort to find biological tags for marine fish stocks. Margolis (1963, 1967) found sufficient differences in the internal parasites of Pacific salmon to trace the origin of stocks in the North Pacific. Successful separation of fish stocks by parasitological indicators has been achieved with flounders (Gibson 1972), the swordfish (Isles 1971), the smelt (Kilambi and DeLacy 1967), the Atlantic salmon (Pippy 1969a, 1969b) and other species.

Shotter (1973) tried to explain different infections of whiting at different geographical locations by salinity differences that might suppress some parasites and not others. Hicks and Threlfall (1973) attributed geographical differences in the parasite fauna of the Atlantic salmon, the brook trout and the lake trout to differing habitats such as landlocked habitats and those habitats accessible to the marine environment or to slight differences in the behavior, feeding and/or migrations of the hosts in the different areas sampled. They added that differing availability of intermediate hosts may also have affected parasite distribution.

Much of the research to separate freshwater fish stocks has involved *T. crassus*. Lawler (1970) reported that Petersson (1969) could separate spring from autumn spawning ciscoes living sympatrically in Lake Oren by different degrees of *T. crassus* infection. Petersson (1969) demonstrated that infections differed between whitefish spawning in rivers and those spawning from the Baltic coast though both lived sympatrically in the Baltic. Welch (1952) found headwater lakes drained by rapids or falls were protected by these barriers from the entry of fish infected with *Triaenophorus* and as a result were infection free. Lawler (1969) found pike from shallower areas had lower incidences of *T. crassus* in Lake Mälaren, Sweden. Oakland (1949) found that a distance of 9 miles yielded samples of whitefish with significantly differing levels of *T. crassus* infections. Sunde (1963) found such differences in S.I.L. in areas differing by less than 2 miles. Welch (1952) found whitefish from open areas of Lake Nipigon, Ontario has lower intensity infections of *T. crassus* than those whitefish from sheltered bays.

d) PLEROCERCOID DISTRIBUTION

Few studies have examined the distribution of plerocercoids within the musculature of fish.

Distribution of *Diphyllobothrium spp.* in the musculature of pike has not been studied. Several authors have studied the distribution of *T. crassus* in the musculature of whitefish and cisco in an effort to reduce the amount of musculature needed to inspect fish efficiently.

Newton (1932) found the orientation of plerocercoids was random but their distribution was not. He found 80% were in the anterior epaxial muscle, 10% in the posterior epaxial and the remaining plerocercoids were in the hypaxial musculature. He did not separate plerocercoids on the right from those on the left of the fish. Welch (1952) also found an anterior preference. He found 54% of plerocercoids were on the right of the fish and suggested as did Miller (1945, 1952) that as the stomach was to the right of the midline, larvae emerge here. Miller (1952) found cysts were rare distal to the anus and heavy in the flesh bordering the body cavity from which they migrate. He found that the right/left cyst ratios for Lesser Slave Lake (1.30) and Square Lake (1.23) were somewhat higher than that found by Welch (1952). Freese (1970) used ultrasonic detectors to find the exact location of muscle cysts of *T. crassus*. He found that epaxial muscle was more infected near the surface which he attributed to the migration of cysts to the surface. Based on three lakes his right/left cyst ratio was 1.5.

e) CONDITION

Condition or fish health has usually been assumed to be best when a fish has a high weight to length ratio. Many studies of the condition of parasite infected fish involved those dead, dying or severly stressed.

Several studies were undertaken on parasitized fish that superficially seemed normal. Meakins and Walkey (1975) and Lester (1971) found that during routine and maximum activity infected fish consumed more oxygen than uninfected fish. They postulated the respiratory rate of infected fish might explain their surface swimming behavior. Arme and Owen (1970) observed a host response to plerocercoids of *Ligula intestinalis* (L., 1758) in the body cavity. Sweeting (1977) showed implanted *Ligula* caused atrophy of fish musculature and resulted in reduced swimming performance which increased predation. He also observed distension of the abdomen, inhibition of gonadal development, decreased liver size, proliferation of connective tissue, changes in the blood cell spectrum, and levels of serum proteins. Bauer and Nikol'skaya (1957) found that the acanthocephalan *Echinorhynchus* (= *Metechinorhynchus*) *salmonis* caused mucosal damage and inflammation in the whitefish. They found heavy infections reduced the nutritional state of the fish. Results of parasite infection can be more subtle. Klein, Olsen and Bowden (1969) failed to establish physiological differences except lower hemoglobin and hemocrit levels between uninfected Rainbow trout and those infected with *Crepidostomum farionis*. Miller (1945d) found that cysts of *T. crassus* caused a slight decrease in the growth rate of whitefish and cisco. This effect was reduced in older fish which had acquired a resistance. Growth decreased with increased infection and was more suppressed in whitefish than cisco which were the natural host (Miller 1945d).

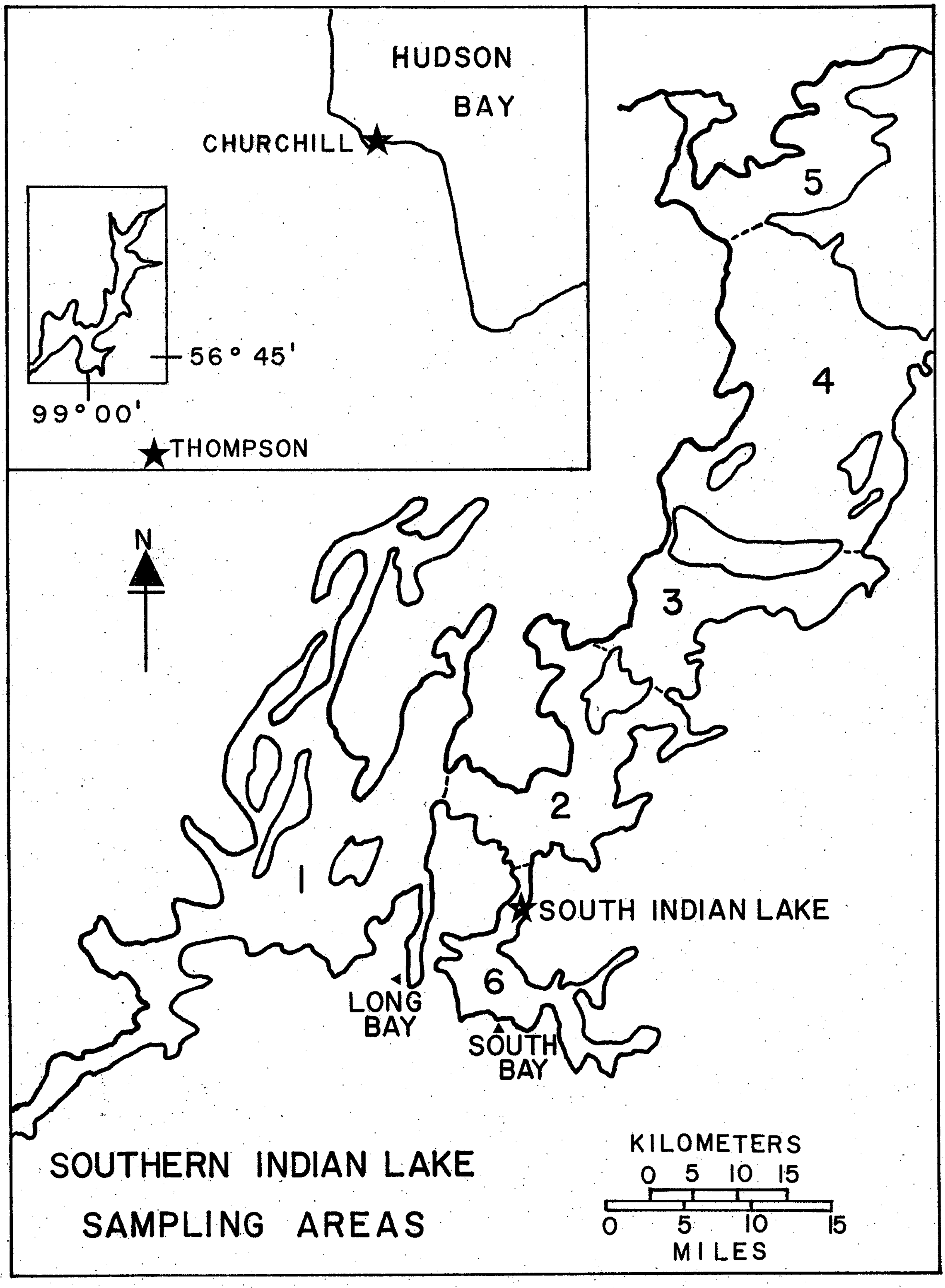
The effect of fish parasites on fish have been reviewed several times. Vik (1963) reviewed the effects of *Diphyllobothrium dendriticum* (Nitzoch, 1824), *C. truncatus* and *Triaenophorus robustus* (= *crassus*) Olsson, 1892 on the production and utilization of host species. Hoffman (1973) described how effects of parasites on fish productivity can be demonstrated. He found that one of these effects is the reduction of the growth rate and the condition factor (weight over length cubed) of parasitized fish. Chubb (1973) reviewed the effects of parasites on freshwater fish in Britain.

III. STUDY AREA

Southern Indian Lake (S.I.L.) (99°00',56°45') is a large (surface area, 2250Km^2) shallow (mean depth, 9.2 m), riverine lake located about 100 Km (60 miles) north-west of Thompson, in Northern Manitoba. (Fig. 1) With a maximum length of 140 Km (85 miles) and maximum width of 30 Km (20 miles) it is the largest lake on the Churchill River System (Hecky, Harper and Kling 1974). During the ice free period from late May (mid June in the extreme north) to early October, the lake remains isothermal and well oxygenated. As the Barrington River supplies only 10% of inflowing water, the lake can be considered an extended portion of the Churchill River passing to Hudson Bay. Hecky (1975) described the morphometry and chemistry of S.I.L. in greater detail.

Hecky et al. (1974) outlined the major taxonomic phytoplankton groups in order of importance as: Diatomeae, Cyanophyta, and Chrysophyceae. The diatom *Melosira* dominated the lake in the spring and autumn, while small surface blooms of *Anabena* and *Aphanizomenon* also occurred in midsummer. Hecky et al (1974) found the increase and decrease of diatoms controlled the relative abundance of all algae.

Figure 1. Map of northern Manitoba showing location of Southern Indian Lake and sampling areas.



SOUTHERN INDIAN LAKE SAMPLING AREAS

Patalas and Salki (1974) found a diverse fauna of zooplankton. Fifteen copepod species and 15 cladocerans were identified of which 25 were true pelagic species and 5 were littoral.

Hamilton (1974) found that the average density of benthic macroinvertebrates was substantially greater than densities in most shield lakes of the region. Benthic fauna in order of importance were: the amphipod *Pontoporeia affinis*, Chironomidae or midges, and Sphaeriidae (fingernail clams). Gastropods were rare except in the extreme south of the lake (6, Figure 1).

Fish species present included the lake whitefish, northern pike, yellow walleye, sauger, perch, cisco, goldeye, burbot, two suckers and several cyprinids (Ayles and Koshinsky 1974) (App. II). They found that whitefish were abundant in the central and northeastern areas of the lake and suggested that the population was underexploited. Sauger was abundant only in the southern areas, out of the main current. Other species were more uniformly distributed throughout the lake.

IV. HOST SPECIES

This section is composed of biological observations from the literature and wherever possible from my general observations of whitefish, cisco and pike in S.I.L.

Whitefish are opportunistic feeders and change food size and type with the increase of their intergill-raker distance. As fry, they feed on plankton (Hart 1931). Diet of fry in the present study was primarily *Diaptomus* and *Cyclops*. Kliewer (1970) found that the size of food increased as gill raker spacing increased. In this study, the diet of whitefish of age three years or more was primarily amphipods, sphaeiriids, gastropods, chironomids and ephemeroptera larvae (Append. X).

It has been often observed that whitefish move to deeper water in July and August in response to warming water (Scott and Crossman 1967). In contrast, whitefish were often caught in shallow water during this period in the present study. These whitefish had eaten large quantities of amphipods which possibly indicated, food, not temperature may be the major factor which determined their distribution. During spawning water temperature was important and stimulated spawning sometime in October when temperatures dropped from 3°

to 2°C (Weagle and Baxter 1973). They also found that whitefish spawned in S.I.L. at depths from 1.5 to 6.8 meters over rocks and boulders.

Diets of young and adult cisco were similar in S.I.L. Young cisco consumed large quantities of *Cyclops*, *Diaptomus* and other zooplankton. Larger, mature cisco also fed on insect larvae and fry of percid fishes. Cued by declining water temperatures, cisco spawn in the autumn in shallow areas (Scott and Crossman 1973).

Pike were voracious, opportunistic predators and fed mainly on cisco, whitefish, white sucker and burbot in S.I.L. They were particularly abundant in shallow areas and spawned in May in the shallow weedy bays and streams around S.I.L.

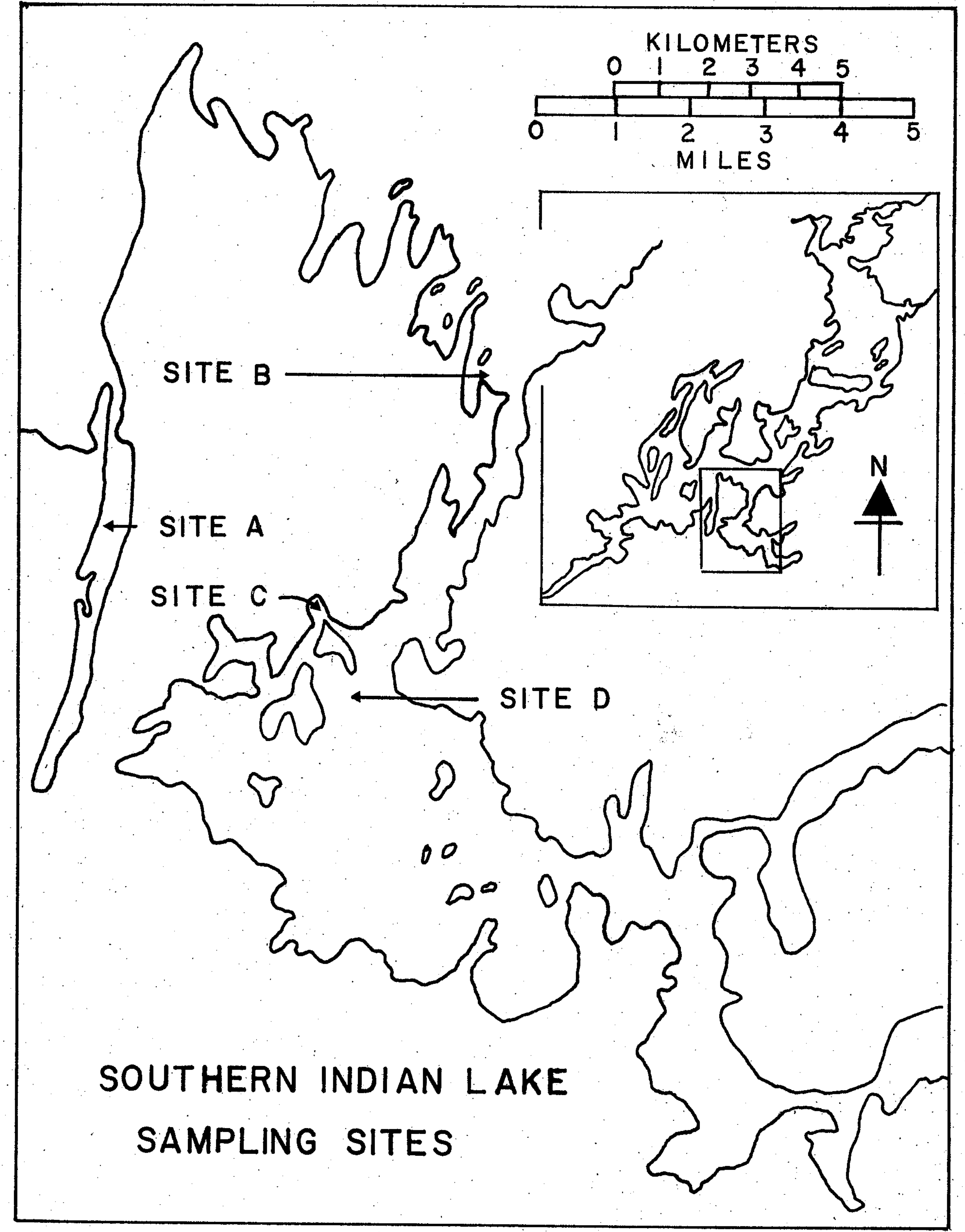
V. MATERIALS AND METHODS

Gillnets were used to obtain samples except during the spring of 1976. At this time seining and spawning traps were used to supplement samples. Seven sizes of gillnet mesh: ½", 1½", 2", 2 3/4", 3½", 4¼" and 5¼" were used to catch fish.

Sampling commenced June, 1975 and continued until mid September, 1975 and focused on areas 2 and 6 (Fig. 1). Collection of fish from these areas was continuous during these months except when samples were being collected from the extreme northern areas (4 and 5, Fig. 1) or other lakes in the diversion system. Samples were rarely taken from the same geographic location during this first summer and a variety of depths were sampled.

Further samples were obtained from site A (see figure 1) in October; from sites B and D in January; and from sites A, B and D in March of 1976. During May, 1976 sampling sites were situated on a stream to the east of Area 6. By the end of May regular sampling of sites A through D had begun. Each site was sampled at least once weekly using gillnets. Most fish were necropsied within 5 hours of removal from nets and some were stored frozen and examined later immediately upon thawing.

Figure 2. Map of the southern portion of Southern Indian Lake showing sampling sites.



SOUTHERN INDIAN LAKE
SAMPLING SITES

Round weight, fork length, sex and maturity were determined for each fish. Scales and pelvic fin rays were taken for aging. External surfaces were examined macroscopically for ectoparasites. All organs were removed, separated, and studied immediately.

Cestodes were relaxed in cold water and killed with hot F.A.A. Trematodes were relaxed, flattened under coverslips and killed with F.A.A. Other parasites were relaxed, and killed as follows: acanthocephalans with refrigerated tap water; nematodes using hot glacial acetic acid; Crustacea and leeches in 70% ethanol. All parasites were stored in 70% ethanol prior to staining and only Crustacea were not previously fixed in F.A.A.

Trematodes were stained with hemotoxylin or acetocarmine (Humason 1972). Cestodes and acanthocephalans were flattened and stained in acetocarmine. Nematodes and smaller crustaceans were cleared in glycerine and ethanol then examined in temporary mounts.

Stomachs of specimens were examined for food items. These were identified and the most dominant food items noted. Percentage of host stomachs containing a food item was used to determine its dietary importance.

Terminology of analysis is defined as follows; abundance or parasite population size was calculated as the product of prevalence (percent of sample infected) and the intensity (mean number per infected fish, $\overline{N}$) (Leong 1975).

Abundance of a parasite species in a host species, divided by the sum of abundances of all parasite species in that host species, is Pi, the proportion of parasite i. This proportion of parasite i expressed as a percentage is the dominance of that parasite in the host.

Dominance indices for each species of parasite in the "community" of the three host species were also calculated. In addition, a weighted dominance index for each species of parasite was calculated using weighting factors assigned by the ratio of their host species in catch records (Append. III).

Intensity values were transformed by taking their natural logarithm to reduce the effect of sample size on sample variation and the transformed values are used graphically in sections 2 C i and ii.

To compare parasite fauna diversity, the Shannon-Weaver (1949) index of diversity, the reciprocal of Simpson's (1949) index, and Hurlburts' (1971) index of evenness were calculated (see appendix II).

Indices of similarity of parasite fauna in different hosts were calculated by summing the lesser of the two abundances for parasites occurring in both host species and expressing this as a percentage of the abundance of all parasites in these two species.

Comparison of parasite fauna in different geographical locations involved nonparametric tests of ranking differences using Kendall's tau (Siegel 1956).

Statistical analysis employed an IBM 360/70 computer using A.P.L. and S.P.S.S. programs available through the University of Manitoba computer center.

VI. PARASITE FAUNA

Autopsies of 3,202 fish of the three species; whitefish, cisco and pike were done to reveal parasites. Host autopsies included 571 whitefish, 446 cisco and 444 pike which were autopsied completely, and in addition, 985 whitefish and 756 cisco which were examined only for the muscle plerocercoids of *T. crassus*.

Autopsy of these three species revealed 29 species of parasites; 2 monogeneans, 4 trematodes, 9 cestodes, 4 nematodes, 3 acanthocephalans, 1 annelid, 1 mollusc and 5 crustaceans.

Whitefish had a wide range of parasites (Table 1). Of the 19 species of whitefish parasites found, only those with prevalences of over 10% were considered important. Whitefish parasites based on prevalence are listed in Table 1 in decreasing order.

Tetracotyle intermedia Hughes, 1928 was the most prevalent parasite and had the most intense infections (average of 37.7 metacercaria per infected fish). Other parasites which exhibited high intensities were: *C. truncatus* (30.1), *Proteocephalus exiguus* LaRue, 1911 (22.6), *Spinitectus gracilis* Ward and Magath, 1916 (19.0), *Cr. farionis* (17.0), *D. spathaceum* (13.3) and *M. salmonis* (12.7) (Table 1).

Table 1. Whitefish parasites

Parasite	Prevalence (% infected)	Intensity	Abundance	Dominance
**Tetracotyle intermedia*	75.5	37.74	28.50	39.11
Proteocephalus exiguus	75.2	22.63	17.02	23.34
**Diplostomulum spathaceum*	56.7	13.29	7.53	10.33
**Triaenophorus crassus*	49.7	2.27	1.12	1.54
Metechinorhynchus salmonis	37.6	12.72	4.79	6.57
Cystidicola farionis	33.2	6.19	2.06	2.83
Discocotyle satittata	29.1	2.16	0.63	0.86
Raphidascaris sp.	23.0	3.63	0.84	1.15
Cyathocephalus truncatus	21.8	30.09	6.28	8.55
Crepidostomum farionis	14.4	17.02	2.46	3.38
Ergasilus nerkae	14.2	5.58	0.79	1.08
Salmincola extumescens	14.0	1.18	0.16	0.22
Salmincola extensus	4.0	1.30	0.05	0.00
Argulus canadensis	3.5	1.60	0.06	0.00
**Spinitectus gracilis*	3.0	19.00	0.57	0.78
Piscicola milneri	0.7	1.00	0.01	0.00
**Diphyllobothrium sp. I*	0.2	1.00	0.00	----
Neoechinorhynchus cylindratum	0.0	2.25	0.00	----
Pomphorhynchus bulbocolli	0.0	1.00	----	----
			72.87	100.00

* larval forms

Dominance of a parasite species depended on its prevalence and its intensity. High prevalence and intensity resulted in the high dominance values of *T. intermedia* (39.1% of all whitefish parasites were this species), *P. exiguus* (23.3%), *D. spathaceum* (10.3%), *C. truncatus* (8.6%) and *M. salmonis* (6.6%) (Table 1).

Cisco harboured 18 species of parasites, many shared with whitefish. Table 2 lists the parasites in descending order of prevalence. Generally intensity of parasite infection was less than whitefish (Table 1 and 2).

Proteocephalid species, *P. filicollis* and *P. exiguus*, had a combined intensity of 36.6 per infected cisco. Other parasites with high intensities were: *S. gracilis* (10.2), *D. spathaceum* (8.1), *T. intermedia* (5.5), *Ergasilus nerkae* Roberts, 1963 (5.0) and *C. truncatus* (4.0) (Table 2).

Cestodes, *P. filicollis* and *P. exiguus*, were the most numerous parasites of cisco and represented 47.9% and 31.9% respectively of the total numbers of parasites in cisco. Of lesser importance based on dominance values were *D. spathaceum* (5.4%), *T. intermedia* (4.1%) and *T. crassus* (3.6%) (Table 2).

Based on prevalence values only eight of the 18 species of pike parasites were present in over 10% of pike autopsied (Table 3). The two most prevalent parasites were *Proteocephalus pinguis* LaRue, 1911 (96.2%) and *Tetraonchus monenteron* (Wagener, 1857) Diesing, 1858.

Table 2. Cisco parasites

Parasite	Prevalence (% infected)	Intensity	Abundance	Dominance
**Triaenophorus crassus*	63.5	2.19	1.39	3.55
Proteocephalus filicollis	51.2 }	36.65	18.76	47.91
Proteocephalus exiguus	34.2 }		12.53	32.00
**Tetracotyle intermedia*	29.1	5.53	1.61	4.11
**Diplostomulum spathaceum*	26.1	8.14	2.13	5.44
Ergasilus nerkae	20.9	4.98	1.04	2.66
Raphidascaris sp.	14.3	2.58	0.37	0.94
Discocotyle sagittata	11.9	2.00	0.24	0.61
**Spinitectus gracilis*	6.8	10.22	0.69	1.76
Metechinorhynchus salmonis	6.7	2.57	0.17	0.43
Argulus canadensis	3.1	2.36	0.07	0.18
Cyathocephalus truncatus	2.7	4.00	0.11	0.28
Contracaecum brachyurum	1.1	2.80	0.03	0.08
Salmincola extensus	0.9	1.00	0.01	0.03
**Diphyllobothrium sp. I*	0.7	1.00	0.01	0.03
Piscicola milneri	0.4	1.00	0.00	0.01
Crepidostomum farionis	0.2	2.50	0.00	0.01
Pomphorhynchus bulbocolli	0.0	1.00	0.00	----
			39.16	100.00

* larval forms

Table 3. Pike parasites

Parasite	Prevalence (% infected)	Intensity	Abundance	Dominance
Proteocephalus pinguis	96.2	70.38	67.71	30.03
Tetraonchus monenteron	94.8	129.17	122.45	54.34
Triaenophorus crassus	72.5	14.55	10.55	4.68
Contracaecum brachyurum	65.5	15.96	10.45	4.64
**Diphyllobothrium sp. II*[Ψ]	54.8	3.42	1.87	0.83
Raphidascaris sp.	46.6	10.89	5.07	2.25
Triaenophorus nodulosus	33.1	15.52	5.14	2.28
Centrovarium lobotes	16.4	12.90	2.12	0.94
Crepidostomum farionis	0.2	1.86	0.00	---
Piscicola milneri	0.0	1.00	0.00	---
Cyathocephalus truncatus	0.0	5.00	0.00	---
Metechinorhynchus salmonis	0.0	1.00	0.00	---
**Spinitectus gracilis*	0.0	1.00	0.00	---
Ergasilus luciopercarum	0.0	1.00	0.00	---
**Glochidia (Pelecypoda)*	0.0	25.00	0.00	---
Glaridacris catostomi	0.0	5.00	0.00	---
Salmincola extensus	0.0	1.00	0.00	---
Argulus canadensis	0.0	1.00	0.00	---
			225.36	100.00

* larval forms

[Ψ] probably D. latum

Pike parasites are listed in order of prevalence in Table 3.

T. monenteron exhibited high intensity of infections with a mean of 129.2 monogeneans per infected pike. Intensity was also high in the following parasites: *P. pinguis* (70.4), *Contracaecum brachyurum* (Ward and Magath, 1917) (16.0), *T. nodulosus* (15.5), *T. crassus* (14.6) and *Centrovarium lobotes* (MacCallum, 1895) (12.9). Larval clams (glochidia) occurred on the gills of only one of the 444 pike surveyed but had an intensity of 25.0 (Table 3).

Pike parasites with the highest dominance values were *T. monenteron* and *P. pinguis* which were respectively 54.3% and 30.0% of the total numbers of all pike parasites. Lower dominance values were found for *T. crassus* (4.7%) and *C. brachyurum* (4.6%) (Table 3).

When the three host species and all their parasites were considered, two pike parasites dominated the "community." These were the monogenean, *T. monenteron*, and the cestode, *P. pinguis*, with unweighted dominance values of 36.3 and 20.1 respectively (Table 4). Parasites of whitefish and cisco also with high dominance values were: *P. exiguus* (8.8) *T. intermedia* (8.9) and *P. filicollis* (5.6). The cestode, *T. crassus* (3.9), common to both the coregonids (as a plerocercoid) and pike (as an adult) was also important based on dominance values (Table 4).

Table 4. "Community" parasites

Parasite	Unweighted dominance		Weighted dominance (for Site A, Fig.2)	
Tetraonchus monenteron	36.29		49.03	
Proteocephalus pinguis	20.07		27.11	
Proteocephalus exiguus	8.76		2.57	
**Tetracotyle intermedia*	8.92		2.49	
Proteocephalus filicollis	5.56		1.64	
Triaenophorus crassus	3.13	3.91	4.22	4.45
**Triaenophorus crassus*	0.74		0.23	
Contracaecum brachyurum	3.11		4.19	
**Diplostomulum spathaceum*	2.86		0.84	
Cyathocephalus truncatus	1.89		0.56	
Raphidascaris sp.	1.87		2.14	
Triaenophorus nodulosus	1.52		2.07	
Metechinorhynchus salmonis	1.47		0.43	
Crepidostomum farionis	0.73		0.21	
Centrovarium lobotes	0.62		0.85	
Cystidicola farionis	0.61		0.18	
**Diphyllobothrium sp. II*	0.55		0.75	
Ergasilus nerkae	0.54		0.16	
**Spinitectus gracilis*	0.37		0.10	
Discocotyle sagittata	0.26		0.00	
Salmincola extumescens	0.05		0.00	
Argulus canadensis	0.04		0.00	
Salmincola extensus	0.02		---	
Piscicola milneri	0.00		---	
**Diphyllobothrium sp. I*	0.00		---	
**Glocidia (Pelecypoda)*	0.00		---	
Glaridacris catostomi	0.00		---	
Neoechinorhynchus cylindratum	0.00		---	
Ergasilus luciopercarum	0.00		---	
Pomphorhynchus bulbocolli	0.00		---	
	100.00		100.00	

* larval forms

To obtain weighted dominance values of Table 4 the catch records available for site A (Fig. 2) were examined. The ratio of pike/cisco/whitefish caught in this area was 4.6/1/1. As net selectivity of one species over another was unknown this ratio was used without further adjustment to produce the weighted dominances. Parasite dominances were weighted in favour of pike parasites and caused no major changes as pike parasites, *T. monenteron* (49.0% of all parasite numbers) and *P. pinguis* (27.1%) continued to have the highest dominance values (Table 4). Coregonid parasites *P. exiguus*, *T. intermedia* and *P. filicollis*, lost most of their relative dominance to pike parasites. Instead higher dominance values were recorded for: *T. crassus* (4.4%) and *C. brachyurum* (4.2%) (Table 4).

Although each host species yielded approximately the same number of parasite species, their indices of diversity differed (Table 5). As the indices of diversity indicate, whitefish had the most diverse fauna (S.I. = 4.4), cisco intermediate (S.I. = 3.0), and pike the least (S.I. = 2.6). Although pike parasite fauna contained as many species as those of cisco and whitefish, two of its parasites, *T. monenteron* and *P. pinguis* together contained over 80% of all parasites found in this host (Table 3). The great dominance of these two species in the total fauna reduced diversity (Table 5). Although the dominance values of cisco parasites were more equal than those of pike, their diversity was lower

Table 5. Diversity and similarity of parasite fauna

Indices of diversity

HOST	No. of Species	Shannon-Weaver (H´)	Reciprocal Simpson's (SI)	Evenness (E)
Whitefish	19	1.73	4.44	0.58
Cisco	18	1.44	2.96	0.50
Pike	18	1.24	2.56	0.42

Indices of similarity (%)

	Whitefish	Cisco
Cisco	39.0	
Pike	2.7	5.0

than whitefish. This is due to the high dominance values for the two proteocephalid species *P. filicollis* and *P. exiguus*, which together made up 80% of all cisco parasites (Table 2). In contrast, the two most dominant species of whitefish parasites, *T. intermedia* and *P. exiguus* made up only 61% of whitefish parasites (Table 1).

Parasite fauna of the two coregonid fishes were more similar than either were with pike (Table 5). This strong similarity was due to the high dominance values for *P. exiguus* in both hosts. Greater abundance values of the nematode *C. brachyurum* and the cestode *T. crassus* in cisco than in whitefish (Tables 1 and 2) accounted for the greater similarity of pike fauna with cisco, than whitefish (Table 5).

Based on dominance values the major parasites in this host"community"were mature forms (Table 6). Cestodes were the most dominant type of parasite, including 7 species and 41.1% of the total numbers. Although there were 5 species of crustaceans and one species of larval clam included in the "others" category, their numbers and hence their dominance index was very low (Table 6).

Table 6. Breakdown of parasite fauna into classes

	Sum of dominance indices	No. of Spp.	Percent of total
Adult parasites	86.9	23	79
Monogeneans	36.7	2	7
Trematodes	1.4	2	7
Cestodes	41.1	7	24
Nematodes	5.6	3	10
Acanthocephalans	1.5	3	10
Others	0.6	6	21
Larval stages	13.1	7	24
To fish	1.2	2	7
To birds	11.9	4	14
Others	0.0	1	3

Discussion

Amphipod vectored parasites were not prevalent and numerous whitefish parasites in this study, unlike the literature (Table 7). Bauer and Nikol'skaya (1957) found *Echinorhynchus* (= *Metechinorhynchus*) *salmonis* was the most numerous parasite of whitefish. Leong (1975) found that this parasite made up 80% of all the numbers of whitefish parasites. Bangham (1955) and Dechtiar (1972) found it to be the second most prevalent parasite of whitefish (Table 7). *Cyathocephalus truncatus*, vectored by the same amphipod hosts, was also a major parasite of whitefish in the literature (Table 7). Dechtiar (1972) found it the most prevalent whitefish parasite. Leong (1975) found this cestode had the second highest dominance value. This cestode was also prevalent in surveys by Bauer and Nikol'skaya (1957) and Bangham (1955). Another amphipod vectored parasite, the nematode *Cystidicola stigmatura* (= *C. farionis*) was also one of the major parasites in many studies (Table 7). It was prevalent in studies by Bangham (1955), Bauer and Nikol'skaya (1957), Dechtiar (1972) as well as having the third highest dominance value in Cold Lake whitefish (Leong 1975). By contrast, these amphipod vectored parasites, though major parasites, did not play such a major role in the parasite fauna of whitefish in the present study (Table 1).

Table 7. Literature values for whitefish parasites

Author	Location	Host	No. Examined	Parasite	Prev. *	Int. & (Range) *	Abund. ⊞	Domin
Bauer and Nikol'skaya 1957	Lake Ladoga U.S.S.R.	*Coregonus lavaretus* (whitefish)	15*	*Echinorhynchus salmonis* (=*Metechinorhynchus salmonis*)	100%	60	60	
				Cystidicola farionis	67	16.1	10.8	
				Diplostomulum spathaceum	13	0.38	4.9	
				Tetracotyle intermedia	60	6.5	3.9	
				Proteocephalus exiguus	40	6.4	2.6	
				Discocotyle sagittata	73	3.3	2.4	
				Achtheres extensus (=*Salmincola extensus*)	33	0.4	0.1	
				Cyathocephalus truncatus	27	0.4	0.1	
				Diphyllobothrium sp.	7	0.2	0.0	
				Salmincola extumescens	13	0.13	0.0	
				Ergasilus sieboidi	13	0.13	0.0	
				Raphidascaris sp.	7	0.07	0.0	

Table 7. Continued

Author	Location	Host	No. Examined	Parasite	Prev.	Int. & (Range)	Abund.	Domin.
Hicks and Threlfall 1973	Coastal Labrador	*Coregonus clupeaformis*	27	*Diplostomulum spathaceum*	67%	19(2-98)	12.7	
				Proteocephalus sp.II	40	7(1-20)	2.8	
				Proteocephalus sp.I	13	9(4-17)	1.2	
				Proteocephalus tumidocollus	7	10(3-17)	0.7	
				Salmincola extensus	13	2(1-3)	0.3	
				Discocotyle sagittata	7	2(1-3)	0.1	
				Crepidostomum farionis	3	1	0.0	
Bangham and Hunter 1939	Lake Erie	*Coregonus clupeaformis*	9	*Proteocephalus exiguus*	67			
Bangham 1955	Lake Huron & Manitoulin Is.	*Coregonus clupeaformis*	99	*Diplostomulum sp.*	71			
				Echinorhynchus salmonis (=*Metechinorhynchus salmonis*)	69			
				Proteocephalus exiguus	65			
				Cyathocephalus americanus (=*C. truncatus*)	40			
				Triaenophorus crassus	18			
				Cystidicola stigmatura (= *C. farionis*)	13			
				Spinitectus gracilis	8			

Table 7. Continued

Author	Location	Host	No. Examined	Parasite	Prev.	Int. & (Range)	Abund.	Domin.
				Proteocephalus laruei	2%			
				Diphyllobothrium sp.	1			
Bangham 1940	Algonquin Park Lakes	*Coregonus clupeaformis*	10	*Proteocephalus laruei*	90%			
				Ergasilus sp.	70			
				Crepidostomum cooperi	20			
				Spinitectus gracilis	10			
Dechtiar 1972	Lake of the Woods, Ont.	*Coregonus clupeaformis*	15	*Cyathocephalus truncatus*	100	(11-50)		
				Metechinorhynchus salmonis	60	(11-50)		
				Proteocephalus laruei	27	(11-50)		
				Discocotyle sagittata	20	(11-50)		
				Tetracotyle intermedia	80	(1-10)		
				Triaenophorus crassus	53	(1-10)		
				Cystidicola stigmatura (=C. farionis)	47	(1-10)		

Table 7. Continued

Author	Location	Host	No. Examined	Parasite	Prev.	Int. & (Range)	Abund.	Domin.
				Diphyllobothrium sp.	30	(1-10)		
				Proteocephalus exiguus	13	(1-10)		
				Diplostomulum sp.	13	(1-10)		
				Achtheres corpulentis (=Salmincola extumescens)	7	(1-10)		
Leong 1975	Cold Lake Alberta	*Coregonus clupeaformis*	836	*Metechinorhynchus salmonis*				79.6
				Cyathocephalus truncatus				9.7
				Cystidcola stigmatura (= farionis)				4.6
				Discocotyle sagittata				1.3
				Proteocephalus exiguus				1.1
				Ergasilus nerkae				0.3
				Salmincola extensus				0.3
				S. extumescens				0.2
				Diplostomulum spathaceum				0.007
				Crepidastomum farionis				0.0009
				Diphyllobothrium sp.				0.0005

*Based on 4$^+$ Aged Fish ⊞Calculated from literature

Based on relative dominance values, metacercaria of trematodes *T. intermedia* and *D. spathaceum* and the cestode *P. exiguus* were the most important parasites of whitefish in this study. These three were the most numerous parasites after the two amphipod vectored parasites *E. (=M) salmonis* and *C. farionis* (based on my calculated abundance values) from a study of Russian whitefish (Bauer and Nikol'skaya (1957). *D. spathaceum* was the most prevalent and abundant parasite though *T. intermedia* and *P. exiguus* were not reported by Hicks and Thelfall (1973). Similarly *Diplostomulum sp.* and *P. exiguus* were reported by Bangham (1955), but are the first and third most prevalent parasites at SIL. *Tetracotyle intermedia*, *P. exiguus* and *Diplostomulum sp.* are major parasites of Lake of the Woods whitefish, but ranked after the amphipod vectored and other parasites in prevalence and intensity (Dechtiar 1972). By contrast with the present study, only *P. exiguus* and *D. spathaceum* and not *T. intermedia* are reported from Cold Lake whitefish and these have low dominance values (Leong, 1975). Bangham and Hunter (1939) only reported *P. exiguus* from Lake Erie whitefish. Bangham (1940) did not find the three major parasites from the present study or the three amphipod vectored parasites from Algonquin Park whitefish.

T. crassus was a major parasite of whitefish in this study and in the studies of Bangham (1955) and Dechtiar (1972), but was conspicuously absent from those of Bauer and Nikol'skaya (1957), Hicks and Threlfall (1973), and Leong (1975). The monogenean *Discocotyle sagittata* was a major whitefish parasite in this study and those by Bauer and Nikol'skaya (1957), Hicks and Threlfell (1973), Dechtiar (1972) and Leong (1975). In contrast, Bangham (1940, 1955) and Bangham and Hunter (1939) failed to report this parasite.

Other major parasites from my study are in order of dominance values *Raphidascaris sp.*, *Crepidostomum farionis*, *Ergasilus nerkae* and *Salmincola entumescens* (Table 1). Only *Crepidostomum farionis* was unreported by Bauer and Nikol'skayer (1957) although they found *Ergasilus siebodi* Nordmann, 1832, not *E. nerkae*, on Russian whitefish. Of these four, Hicks and Threlfall (1973) found only *Cr. farionis*. Parasites of the genus *Ergasilus* and *Crepidostomum* were reported from Algonquin Park whitefish by Bangham (1940), but the latter parasite was represented by *C. cooperi* Hopkins, 1931 and not *C. farionis*. Dechtiar (1972) reported *Achtheres corpulentis* Kellicott, 1882 from Lake of the Woods whitefish which has subsequently been placed in the genus *Salmincola* by Kabata (1969). All but *Raphidascaris sp.* were reported from Cold Lake whitefish though the other three were relatively minor parasites based on their dominance values (Leong 1975). In contrast to the present study, Bangham and Hunter (1939) and Bangham (1955) did not report any of these four (Table 7).

The whitefish parasite fauna of S.I.L. differs from that reported from whitefish elsewhere in the literature, by the greater relative importance on the basis of prevalence and intensity of the copepod vectored parasites (*Proteocephalus spp.* and *T. crassus*) and the trematode metacercaria (*D. spathaceum* and *T. intermedia*) than the amphipod vectored parasites (*M. salmonis*, *C. truncatus* and *Cy. farionis*). All studies reported from the literature except those of Hicks and Threlfall (1973), Bangham and Hunter (1939) and Bangham (1970) (the latter two are inconclusive because of low sample size) found the amphipod vectored parasites were generally the most prevalent and of highest intensity (Table 7).

Copepod vectored cestodes; *T. crassus*, *Proteocephalus filicollis* and *P. exiguus* are the most important parasites of cisco in this study on the basis of prevalence and intensity (Table 2). Species of *Proteocephalus* were within the three most important parasites in studies by Bangham (1940, 1955), Bangham and Hunter (1939), Dechtiar (1972) and Leong (1975) (Table 8). More than one species of *Proteocephalus* were reported from cisco by each of the above studies except Bangham (1940) who had a small sample. Although *T. crassus*

Table 8. Literature values for cisco parasites

Author	Location	Host	No. Examined	Parasite	Prev.	Int. & (Range)	Abund.	Domin
Dechtiar 1972	Lake of the Woods, Ont.	*Coregonus artedii*	52	*Argulus canadensis*	23	(11-50)		
				Cyathocephalus truncatus	19	(11-50)		
				Proteocephalus laruei	6	(11-50)		
				Discocotyle sagittata	42	(11-50)		
				Proteocephalus exiguus	35	(1-10)		
				Triaenophorus crassus	33	(1-10)		
				Metechinorhynchus salmonis	29	(1-10)		
				Diphyllobothrium sp.	23	(1-10)		
				Cystidicola stigmatura (=*C. farionis*)	15	(1-10)		
				Tetracotyle intermedia	10	(1-10)		
				Spinitectus gracilus	8	(1-10)		
				Ergasilus sp.	6	(1-10)		
				Proteocephalus spp.				50.3
				Ergasilus nerkae				16.1
				Ergasilus auritus				10.4
				Metechinorhynchus salmonis				9.8
				Proteocephalus filicollis				9.3
				Discocotyle sagittata				1.5

Table 8. Continued

Author	Location	Host	No. Examined	Parasite	Prev.	Int. & (Range)	Abund.	Domin.
				Cyathocephalus truncatus				0.9
				Cystidicola stigmatura (=*C. farionis*)				0.1
				Diphyllobothrium sp.				0.1
				Crepidostomum farionis				0.09
				Salmincola extensus				0.003
Bangham and Hunter 1939	Lake Erie	*Coregonus artedii*	78	*Proteocephalus exiguus*	"dominant"			
				Proteocephalus wickliffi	present			
				Cystidicola stigmatura (=*farionis*)	1.3%			
Bangham 1955	Lake Huron Manitoulin Is.	*Coregonus artedii*	79	*Proteocephalus laruei*	90%			
				Triaenophorus crassus	77			
				Diphyllobothrium sp.	68			
				Diplostomulum sp.	61			
				Salmincola inermis	24			
				Echinorhynchus salmonis (=*Metechinorhynchus salmonis*)	13			
				Discocotyle salmonis (=*D. sagittata*)	11			
				Proteocephalus exiguus	11			
				Argulus sp.	5			
				Cystidicola stigmatura (=*C. farionis*)	4			
Bangham 1940	Algonquin Park lakes	*Coregonus artedii*	16	*Ergasilus caeruleus*	94%			
				Proteocephalus laruei	25			

was the most prevalent cisco parasite in this study, it was the second in Lake Huron cisco (Bangham 1955), third most in Lake of the Woods cisco (Dechtiar 1972) and was unreported by Bangham and Hunter (1939), Bangham (1940) or Leong (1975) (Table 8). As with whitefish, metacercaria of *T. intermedia* and *D. spathaceum* were major cisco parasites in the present study. From the literature *Diplostomulum sp.* is reported from Lake Huron cisco (Bangham 1955) and *T. intermedia* only from Lake of the Woods cisco (Dechtiar 1972), the latter with low prevalence.

Other major parasites of cisco from the present study were *E. nerkae*, *Raphidascaris sp.* and *D. sagittata*. Of these, only *Discocotyle salmonis* (=*D. sagittata*) was reported from Lake Huron cisco (Bangham 1955). Only the genus *Ergasilus* was represented in Algonquin Park cisco (*E. caeruleus* Wilson, 1911) (Bangham 1940). *D. sagittata* was a major parasite of cisco reported by Dechtiar (1973) and Leong (1975). *E. nerkae* was reported by the latter as the cisco parasite with the second highest dominance value, whereas, in the former it was reported as a minor parasite. Bangham and Hunter (1939) report none of the three (Table 8).

The amphipod vectored parasites, *M. salmonis*, and *C. truncatus*, played minor roles, and *Cystidicola farionis* was not found in cisco from my study though, they were relatively major parasites in other studies.

Echinorhynchus salmonis (=*M. salmonis*) and *Cystidicola stigmatura* (=*C. farionis*) were reported by Bangham (1955), the former as a major cisco parasite based on prevalence. All three amphipod vectored species were major cisco parasites in Lake of the Woods (Dechtiar 1972), but while Leong (1975) reported all three, only *M. salmonis* could be considered a major parasite based on dominance values.

It appears that the major differences between the parasite fauna of cisco from S.I.L. and that of the literature is the relatively minor role played by the amphipod vectored *M. salmonis*, *C. truncatus* and *Cy. farionis*, while copepod vectored cestodes *T. crassus* and *Proteocephalus sp.* play a relatively major role in this study.

P. pinguis and *T. monenteron* are the two most important parasites of pike from this study based on prevalence and intensity (Table 3). These were commonly major parasites of pike in other surveys. (Table 9) Dechtiar (1972) and Threlfall and Hanek (1970) found that *T. monenteron* was the major parasite of pike on the basis of intensity. This monogenean was also found by Hunter and Rankin (1939) and Arai and Chein (1973). In contrast, it was unreported by Bangham and Hunter (1939) or Bangham and Adams (1954) who reported only *P. pinguis*. Leong (1975) reported *P. pinguis* but as a minor parasite based on its dominance value.

Table 9. Literature values for pike parasites

Author	Location	Host	No. Examined	Parasite	Prev.	Int. & (Range)	Abund.	Domir
Hunter and Rankin 1939	A Connecticut Lake	*Esox lucius*	11	*Proteocephalus pinguis*	10-49%			
				Centrovarium lobotes	present			
				Tetraonchus monenteron	present			
				Spinitectus gracilis	present			
Threlfall and Hanek 1970	Labrador	*Esox lucius*		*Tetraonchus monenteron*		110 (35-250)		
				Proteocephalus pinguis		20 (6-45)		
				Proteocephalus sp.		4 (1-10)		
				Raphidascaris sp.		1		
Bangham and Adams 1954	Mainland B.C.	*Esox lucius*	2	*Proteocephalus pinguis*	100%			
Bangham and Hunter 1939	Lake Erie	*Esox lucius*	8	*Proteocephalus pinguis*	88%			
Bangham 1955	Lake Huron and Manitoulin Is.	*Esox lucius*	66	*Proteocephalus pinguis*	91%			
				Gyrodactyloidea	56			
				Contracaecum brachyurum	53			
				Triaenophorus crassus	48			
				Diplostomulum sp.	39			
				Echinorhynchus salmonis (=*Metechinorhynchus salmonis*)	29			

Table 9. Continued

Author	Location	Host	No. Examined	Parasite	Prev.	Int. & (Range)	Abund.	Domin.
Arai and Chien 1973	Southern Alberta	*Esox lucius*	21	*Tetraonchus monenteron* (Only monogenea studied)	33	3.4(1-9)	1.1	
Dechtiar 1972	Lake of the Woods, Ont.	*Esox lucius*	23	*Tetraonchus monenteron*	70%	> 50		
				Contracaecum brachyurum	96	(11-50)		
				Triaenophorus crassus	70	(11-50)		
				Triaenophorus nodulosus	48	(11-50)		
				Proteocephalus pinguis	87	(1-10)		
				Metechinorhynchus salmonis	39	(1-10)		
				Diplostomulum sp.	30	(1-10)		
				Tetracotyle sp.	18	(1-10)		
Leong 1975	Cold Lake Alberta	*Esox lucius*	62	*Proteocephalus spp.*				44.9
				Triaenophorus nodulosus				35.4
				Metechinorhynchus salmonis				19.1
				Proetocephalus pinguis				0.4
				Neoechinorhynchus strigosum				0.07
				Triaenophorus crassus				0.05
				Raphidascaris sp.				0.05

This cestode was a major parasite for Hunter and Rankin (1939), Bangham (1955), Threlfall and Hanek (1970) and Dechtiar (1972 (Table 9).

T. crassus, a prevalent and abundant parasite of pike in this study, was reported as a prevalent parasite from only studies by Bangham (1955) and Dechtiar (1972). Leong reported it had a low dominance value in Cold Lake, Alberta (Table 9).

Next in order of prevalence in the present study was *Contracaecum brachyurum*. This nematode was reported only as prevalent by Dechtiar (1972) and Bangham (1955) (Table 9).

Diphyllobothrum sp. II which has high prevalence and intensity in pike in this study, was not reported in any of the above studies of pike parasites. Other major pike parasites in this study, based on prevalence and intensity, were *Raphidascaris sp. Triaenophorus nodulosus* and *Centrovarium lobotes* (Table 3). Of these *T. nodulosus* was reported as a major parasite only by Dechtiar (1972) and Leong (1975) while the latter and Threlfall and Hanek (1970) reported *Raphidascaris sp.* as a rare parasite. *Centrovarium lobotes*, a prevalent parasite in the present study, was only reported by Hunter and Rankin (1939) but no quantitative measure was presented.

Major differences between reports of pike fauna from the present study and that of the literature are the relatively high dominance values of *T. crassus*, *C. brachyurum* and *Raphidascaris sp.* in the literature and not in this study. Based on dominance values from this study these parasites are minor parasites compared to *P. pinguis* and *T. monenteron* which were commonly major pike parasites in other studies.

When weighted dominance values are considered, the parasites of pike dominate the parasite community of these three hosts species not simply because of the relative importance of pike in the catch records (weighting the weighted dominances values in favour of pike), but because of their high prevalences and intensities (Table 4). Had weighting factors for the weighted dominance calculations been available from catch records for other areas of the lake, the results might have been slightly different. Pike are disproportionately abundant in Area 1 (Fig. 1) when compared with the lake as a whole. If catch ratios had been available for the lake, the weighted dominance values would be closer to those of the unweighted values. No attempt is made to use the weighted dominance values to represent the whole lake, but simply to indicate relative dominance of parasites of these three host species in Area 1 based on apparent host ratios.

It should be stressed that dominance values used in this study, and by Leong (1975) are based solely on the estimated size of the parasite population and do not attempt to weight the importance of parasites using their biomass or their potential effect on the host species.

In contrast to the parasite community of Cold Lake (Leong 1975), the acanthocephalan, *M. salmonis* was not the dominant parasite species in the present study. In this regard his study was more like those of Bangham (1955) and Dechtiar (1972). Instead, in the present study, the pike monogean *T. monenteron* and several *Proteocephalus* species made up 71% of the numbers of parasites of whitefish, cisco, and pike combined (Table 4). This may be due to a relatively smaller population of the amphipod intermediate hosts (*Pontoporeia affinis*) of *M. salmonis* in the more northern, shallower S.I.L. environment. Abundance of this acanthocephalan in Cold Lake might result from the availability of many salmonid definitive hosts (whitefish, cisco, coho and trout). This could explain why amphipod vectored parasites were more major parasites of whitefish and in S.I.L. cisco than in other systems reported in the literature.

Unlike the study by Leong (1975) indices of parasite diversity could not be correlated to the number of each host species examined. Diversity as measured by these indices was not significantly increasing with the addition of more samples indicating it is unlikely that even rare parasitic species of these hosts remained undiscovered. Ranking of the diversity of fish species was the same for each of the three indices indicating that only one type may be necessary for evaluation.

Parasite diversity of S.I.L. cisco was lower than that of the same species from Cold Lake, Alberta (Table 10). Whitefish parasite fauna on the other hand, was more diverse as measured by the indices in Appendix III, than that of Cold Lake. Pike parasite fauna from this study was more diverse by the Simpson's and Evenness indices, but less diverse when the Shannon Weaver indices were compared with those of Cold Lake (Table 10). *M. salmonis* dominated the whitefish fauna of Cold Lake to the point that it limited diversity and this may explain why diversity was less than the present study. Domination of S.I.L. cisco fauna by species of *Proteocephalus* explains the lesser diversity when compared with Cold Lake cisco.

When parasites are assigned to major classes in this study (Table 6), and compared with those of Leong (1975) (Table 11) some basic differences emerge. Adult parasites, particularly monogeneans and cestodes, were more dominant in the present study. Cestodes and monogeneans amount to 77.8% of all parasites at S.I.L. (Table 6) and only 13.9% of Cold Lake parasites (Table 11). Acanthocephans which amount to 53.1% of Cold Lake

Table 10. Indices of diversity from Leong (1975)

	Shannon-Weaver		Simpsons's		Evenness	
Fish species	SIL*	CL	SIL*	CL	SIL*	CL
Whitefish	1.73	0.83	4.44	1.55	0.58	0.30
Cisco	1.44	1.52	2.96	3.24	0.50	0.55
Pike	1.24	1.08	2.56	2.75	0.42	0.52

SIL*-Southern Indian Lake (present study)

CL -Cold Lake (Leong 1975)

Table 11. Breakdown of parasite fauna from Leong (1975) into classes

	Sum of dominance indices	No. spp.	Percent of total
Adult parasites	78.44	32	70
Monogeneans	4.1	2	4
Trematodes	0.12	4	9
Cestodes	9.8	12	26
Nematodes	2.87	5	11
Acanthocephalans	53.14	3	7
Others	8.41	6	13
Larval stages	21.56	14	30
To fish	16.07	9	19
To birds	5.49	5	11

parasites amounted to only 1.5% in the present study. Larval parasites of Cold lake fish utilize fish (16.1%) and birds (5.5%) to complete their life cycles. Larval parasites S.I.L. fish pass mostly (11.9%) to birds and much less so to fish (1.2%) (Tables 6 and 11). This suggests that birds, primarily gulls are most important in the completion of larval parasite life cycles than fish in S.I.L. in contrast to Cold Lake larval parasites.

VII. MODIFYING FACTORS

a) HOST AGE

Parasites show patterns of abundance with host age. Dogiel (1961) recognized three patterns; namely, abundance independent of age, an increasing function of age, and a decreasing function of age. Leong (1975) identified a fourth pattern that of a peak of abundance in middle age. Observations in the present study indicates two additional patterns exist, relatively independent of age. One in which abundance is constant from fish less than one year old to the oldest, and another pattern in which an increase in abundance from 0 to 1 year old fish is followed by a constant abundance level. Patterns shown by the common parasites of whitefish, cisco and pike are summarized in Table 12.

Only *P. filicollis* from cisco and *P. pinguis* from pike were independent of age when fish less than one year of age were considered. The crustacean, *E. nerkae*, from whitefish was the only parasite that decreased in abundance with host age, though it peaked in abundance in middle-aged cisco (Table 12). The rest of the abundant species were independent of age once established in young fish, increased with host age or

Table 12. Patterns of major parasite abundance with host age

Patterns	Whitefish	Cisco	Pike
Independent		*Proteocephalus filicollis* *exiguus*	*Proteocephalus pinguis*
Independent once established	**Triaenophorus crassus*		*Raphidascaris sp.*
	Raphidascaris sp.		*Centrovarium lobotes*
	Discocotyle sagittata		
	Crepidostomum farionis		
Increase	**Tetracotyle intermedia*	**Tetracotyle intermedia*	**Diphyllobothrium sp. II*
	**Diplostomulum spathaceum*	**Diplostomulum spathaceum*	
	Metechinorhynchus salmonis	**Triaenophorus crassus*	
	Cyathocephalus truncatus		
	Cystidicola farionis		
Decrease	*Ergasilus nerkae*		
Peaked at Age(s)	*Salmincola extumescens*	*Discocotyle sagittata*	*Triaenophorus crassus*
	Proteocephalus exiguus	*Raphidascaris sp.*	*Triaenophorus nodulosus*
		Ergasilus nerkae	*Tetraonchus monenteron*

* larval forms

reached a maximum (s) during the middle of the host's life. Major trematode parasites of whitefish and cisco, *T. intermedia* and *D. spathaceum* increased with host age (Fig. 3). Dominant cestodes from whitefish peaked in abundance in middle aged fish in contrast to abundance of cestodes of cisco and pike, *P. filicollis* and *P. pinguis* respectively, which were completely independent of host age. Abundance of the cestode *T. crassus* was independent of host age once established in whitefish, increased with host age in cisco and peaked in abundance in middle-aged pike (3 to 5 yrs). *T. nodulosus* peaked in abundance in young pike (0 to 3 years of age).

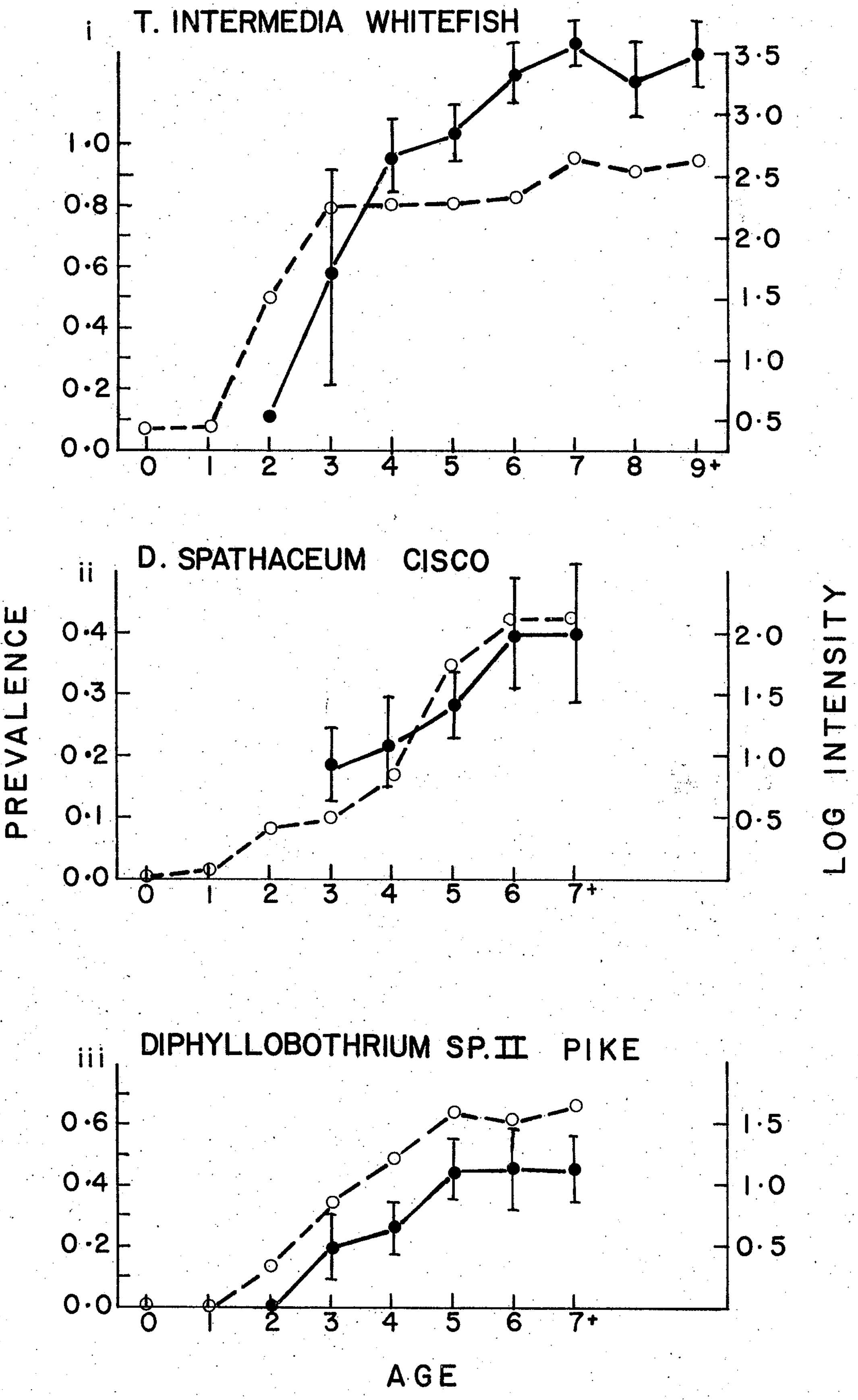
Plerocercoids of *Diphyllobothrum sp. II* increased in abundance with pike age (Fig. 3iii, Append. II). Abundance of *Raphidascaris sp.* while independent of host age, once established in whitefish and pike, peaked in middle-aged cisco (Fig. 8). While *D. sagittata* also peaked in abundance in middle-aged cisco, abundance was independent of whitefish age once established (Fig. 3ii, iii). Increased abundance of *T. intermedia*, *D. spathaceum* and *Diphyllobothrium sp. II* with host age resulted in both increased intensity and prevalence (Fig. 3). Major increase in abundance of *T. intermedia* in whitefish occurred between 2 and 3 years of age (Fig. 3i). Increase in abundance of this species in cisco was more gradual and constant (Append. V).

Figure 3 (i,ii, and iii). Prevalence and log intensity of some major larval parasites with host age. (Append. IV, V, and VI)

O---------O prevalence

●———————● log intensity

(± standard error)


i
T. INTERMEDIA WHITEFISH
1·0
0·8
0·6
0·4
0·2
0·0
3·5
3·0
2·5
2·0
1·5
1·0
0·5
0
1
2
3
4
5
6
7
8
9+
ii
D. SPATHACEUM CISCO
PREVALENCE
0·4
0·3
0·2
0·1
0·0
LOG INTENSITY
2·0
1·5
1·0
0·5
0
1
2
3
4
5
6
7+
iii
DIPHYLLOBOTHRIUM SP.II PIKE
0·6
0·4
0·2
0·0
1·5
1·0
0·5
0
1
2
3
4
5
6
7+
AGE

The trematode *D. spathaceum* increased constantly in abundance in cisco (Fig. 3ii), but decreased in 7 year old whitefish before continuing to increase (Append. IV). Plerocercoids of *Diphyllobothrum sp. II* increased in abundance from the initiation of infection at age 1 year but slowed its increase after 5 years (Fig. 3 iii).

All three of the amphipod vectored whitefish parasites (*Cy. farionis*, *M. salmonis* and *C. truncatus* increased with host age (Fig. 4). Increasing abundance of *Cy. farionis* resulted from both increased prevalence and intensity whereas that of *M. salmonis* resulted primarily from increased intensities while prevalence began to fluctuate after 3 years of age (Fig. 4i, ii). Increased abundance of the cestode *C. truncatus* resulted from increased prevalence while intensity was stable after 5 years (Fig. 4iii).

T. crassus responded differently to increasing age of whitefish, cisco and pike (Fig. 5) after an initial rise in prevalence from 31% to 54% between whitefish of their 2nd and 3rd years, prevalence stabilized. Intensity of this cestode in whitefish is constant throughout the fish's life (Fig. 5i). Resulting abundance of *T. crassus* in whitefish is constant after initial establishment (Append. IV). Increased abundances of this parasite in cisco results from increased intensity (Fig. 4ii) as prevalence values

Figure 4 (i, ii, and iii). Prevalence and log intensity of amphipod vectored whitefish parasites with host age. (Append. IV)

O--------O prevalence

●————● log intensity

(± standard error)

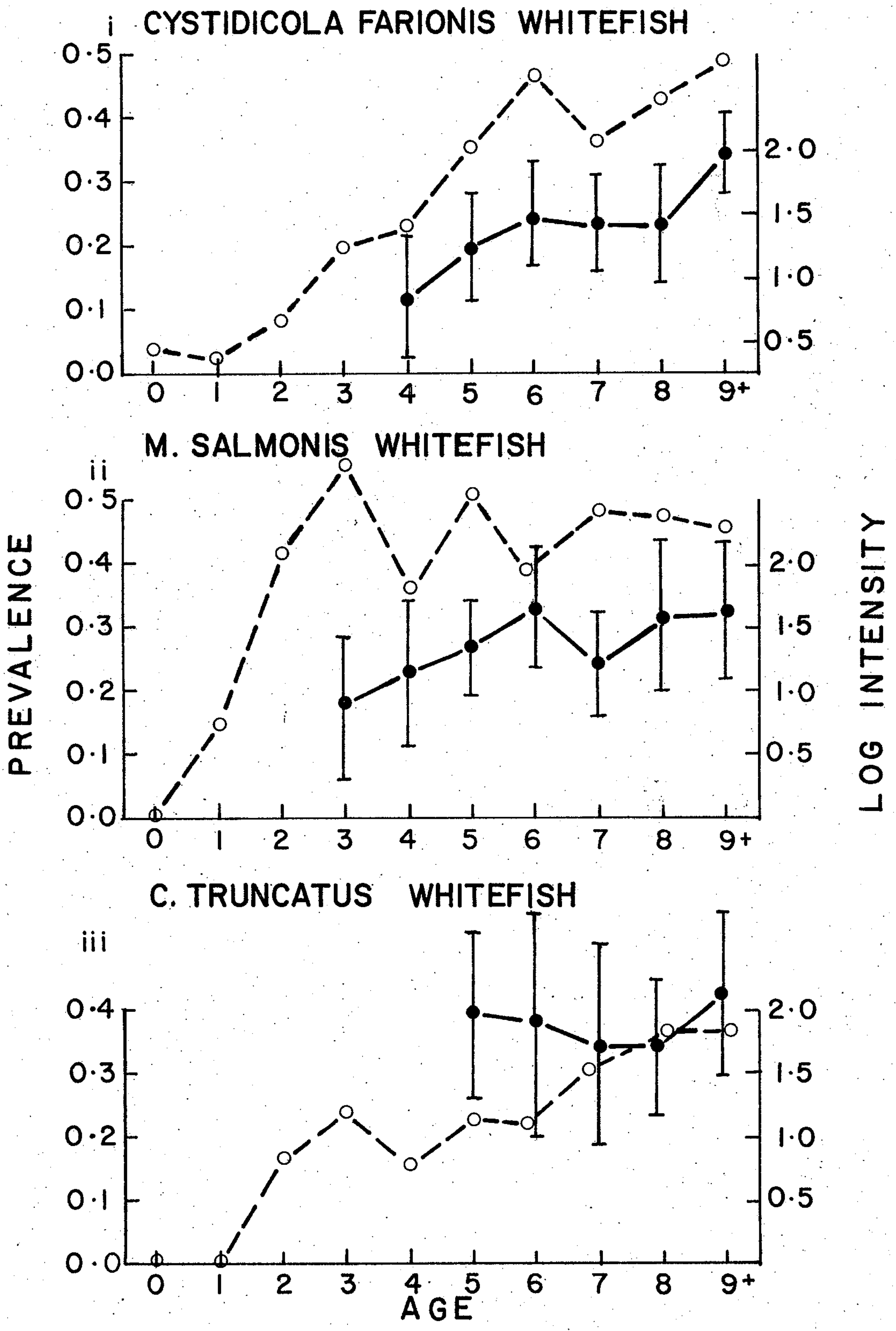
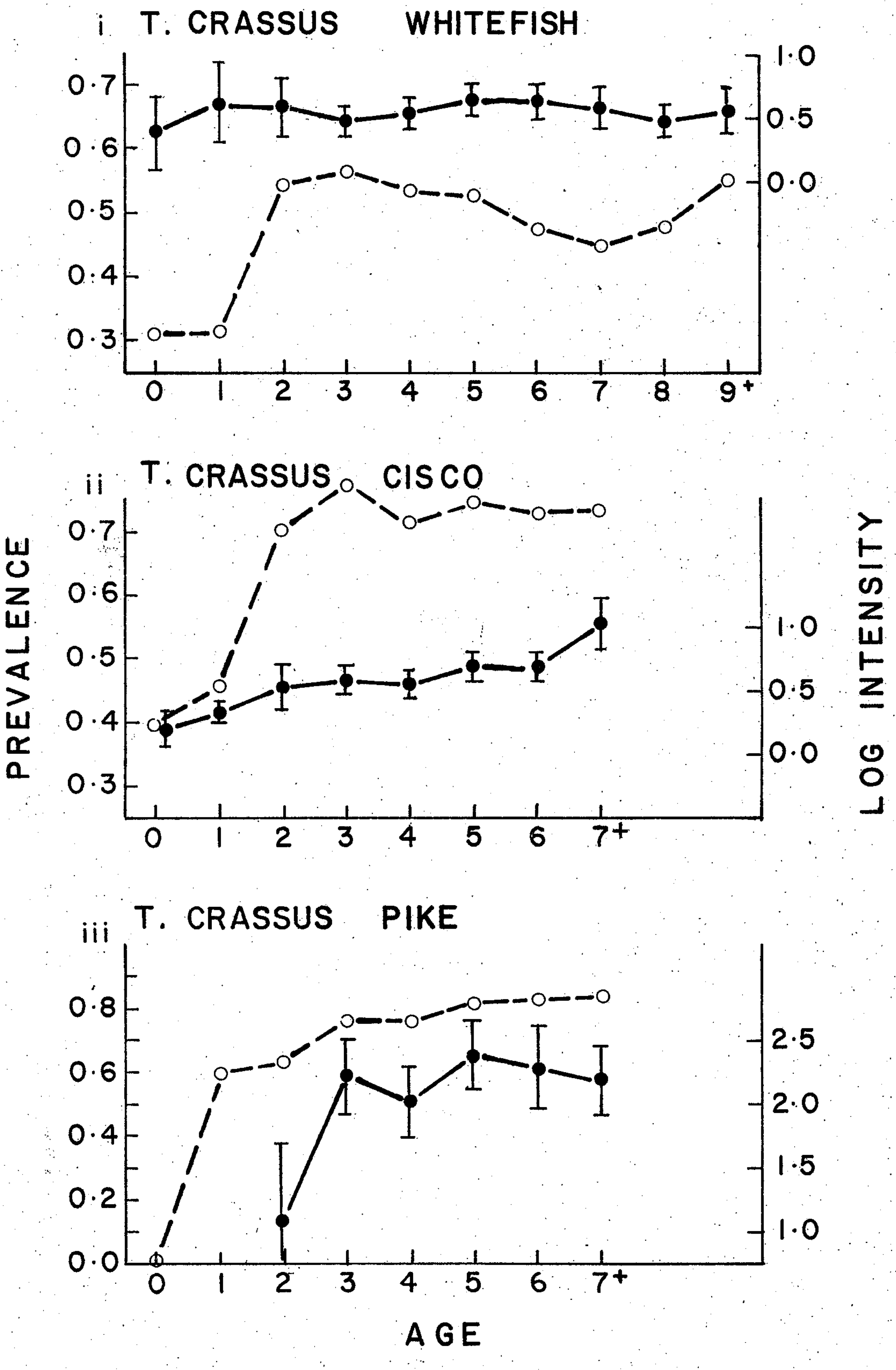

i CYSTIDICOLA FARIONIS WHITEFISH
ii M. SALMONIS WHITEFISH
iii C. TRUNCATUS WHITEFISH
PREVALENCE
LOG INTENSITY
AGE
0·0
0·1
0·2
0·3
0·4
0·5
0·5
1·0
1·5
2·0
0
1
2
3
4
5
6
7
8
9+

Figure 5 (i, ii, iii, and iv). Prevalence and log intensity of *Triaenophorus* with host age. (Append. IV, V, and VI)

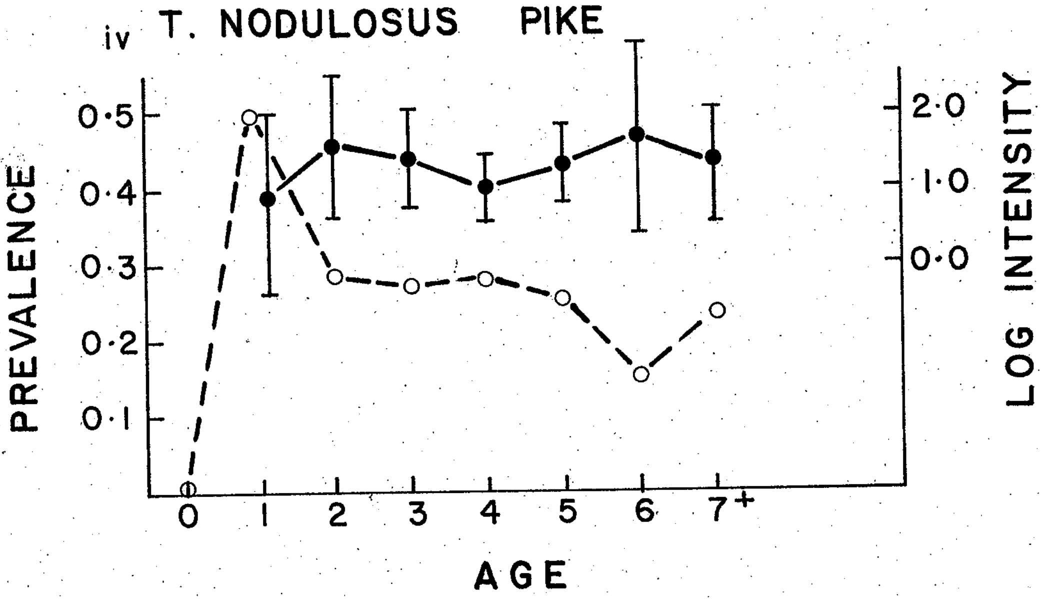
O---------O prevalence

●————● log intensity

(± standard error)



i T. CRASSUS WHITEFISH
0·7
0·6
0·5
0·4
0·3
1·0
0·5
0·0
0 1 2 3 4 5 6 7 8 9+
ii T. CRASSUS CISCO
0·7
0·6
0·5
0·4
0·3
1·0
0·5
0·0
0 1 2 3 4 5 6 7+
iii T. CRASSUS PIKE
0·8
0·6
0·4
0·2
0·0
2·5
2·0
1·5
1·0
0 1 2 3 4 5 6 7+
PREVALENCE
LOG INTENSITY
AGE


iv
T. NODULOSUS PIKE
PREVALENCE
0·5
0·4
0·3
0·2
0·1
LOG INTENSITY
2·0
1·0
0·0
0
1
2
3
4
5
6
7+
AGE

remain constant after a rise of 24% between the cisco's first and second year. Peak of abundance of *T. crassus* in pike resulted from the constant levels of prevalence after the fish's 2nd year (following a rise of 60% during the pike's first year) while intensity levels rose to a maximum at 3 and 5 years of age and then dropped (Fig. 5iii). Maximal abundance occurred at 5 years of age (Append. VI).

Abundance of *T. nodulosus* in pike peaked at 2 years (Append. VI), prevalence was at maximum at 1 year of age, following an increase of 50% and intensity was at its highest at 2^+ and 6^+ years (Fig. 5iv).

Differing responses of proteocephalid species to host age are shown in Figure 6. Abundance of *P. exiguus* in whitefish peaked at 3 years due to increased intensity and prevalence. After 3 years intensity declined and stabilized while prevalence continued to decline resulting in maximal abundance at 3 years (Fig. 6i, Append. IV).

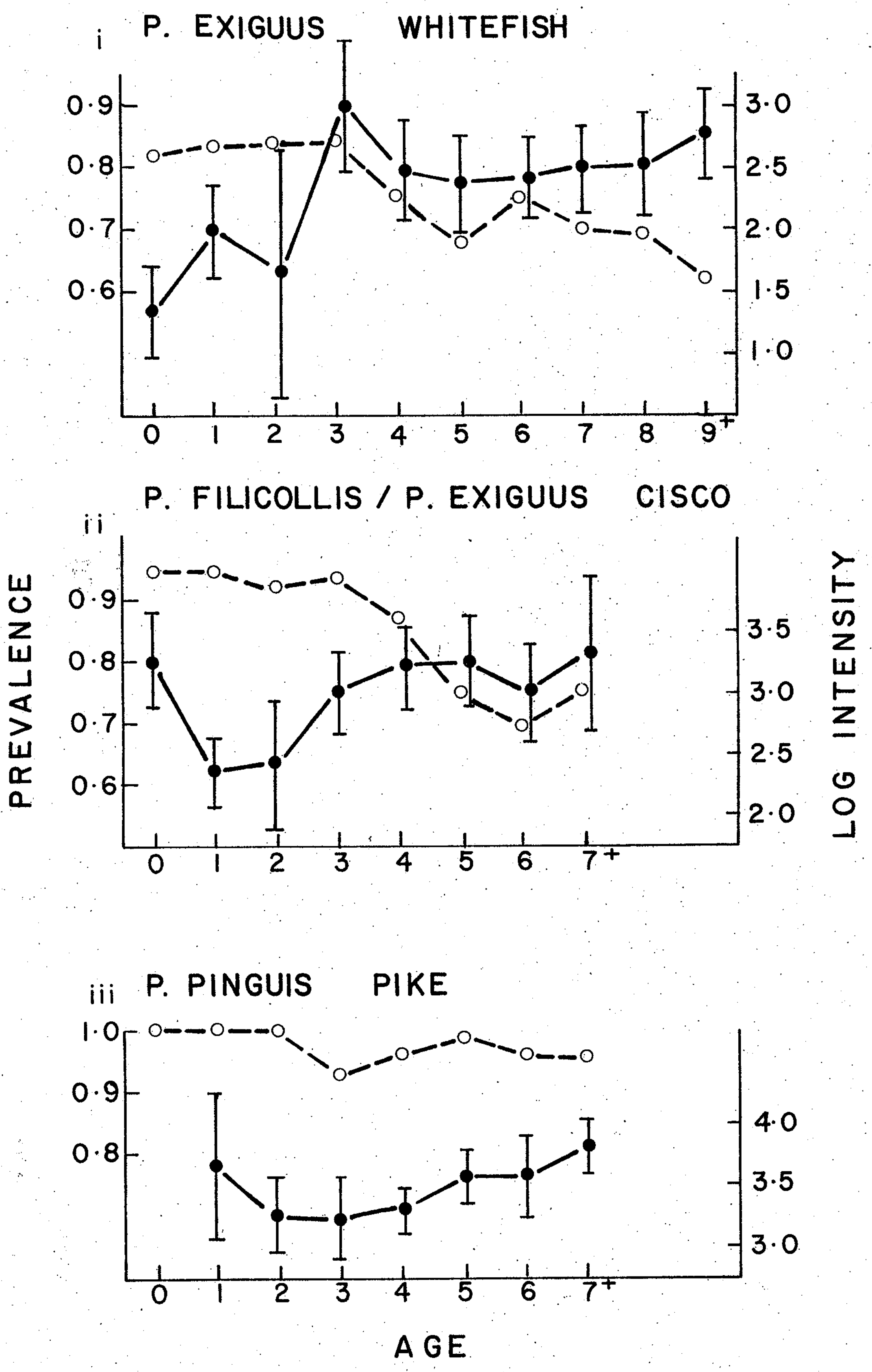
P. filicollis (with a component of *P. exiguus*) in cisco and *P. pinguis* in pike were independent of host age. In cisco this resulted from a rise in intensity to a peak in fish of 5 years while prevalence correspondingly dropped during this period (Fig. 6ii). The product of intensity and prevalence or abundance remained relatively stable except for somewhat lower values for cisco of 1 and 2 years of age which resulted from low intensity (Append. V). Constant values of

Figure 6 (i, ii, and iii). Prevalence and log intensity of proteocephalid species with host age. (Append. IV, V, and VI)

O--------O prevalence

●———● log intensity

(± standard error)


i
P. EXIGUUS WHITEFISH
0·9
0·8
0·7
0·6
3·0
2·5
2·0
1·5
1·0
0
1
2
3
4
5
6
7
8
9+
P. FILICOLLIS / P. EXIGUUS CISCO
ii
0·9
0·8
0·7
0·6
3·5
3·0
2·5
2·0
0
1
2
3
4
5
6
7+
PREVALENCE
LOG INTENSITY
iii
P. PINGUIS PIKE
1·0
0·9
0·8
4·0
3·5
3·0
0
1
2
3
4
5
6
7+
AGE

P. pinguis abundance resulted from relatively constant intensity and prevalences (Fig. 6iii and Append. VI).

The trematodes *C. lobotes* from pike and *Cr. farionis* from whitefish maintained their abundance independent of host age after establishment. Maximal prevalence of *C. lobotes* (29%) occurred in 2 year old pike after which prevalence declined, then subsequently rose (Fig. 7i). Intensity fluctuated and abundance that resulted was constant except for drops at 4 and 6 years of age corresponding to low values in the fluctuating intensity (Append. VI). Although only prevalence values are available for *Cr. farionis* these values become relatively constant after establishment of the parasite at 5 years of age (Fig. 7ii).

Abundances of *Raphidascaris sp.* in whitefish and pike were independent of host age, but once established this value peaked in cisco of 3 years (Fig. 8). Prevalence of *Raphidascaris* was constant after an increase of 20% from whitefish of 2 to 3 years of age. Intensity was relatively constant though fluctuating abundance values did not show a discernable pattern with age (Append. IV). The same was true for *Raphidascaris* from pike though initial increase of prevalence was 60% during the first year after which values exhibited less fluctuation than with cisco (Fig. 8 iii and Append. VI). Abundance of *Raphidascaris* from cisco exhibited three peaks at 3, 5

Figure 7 (i and ii). Prevalence and log intensity of some major trematodes with host age. (Append. IV and VI)

O--------O prevalence

●———● log intensity

(± standard error)

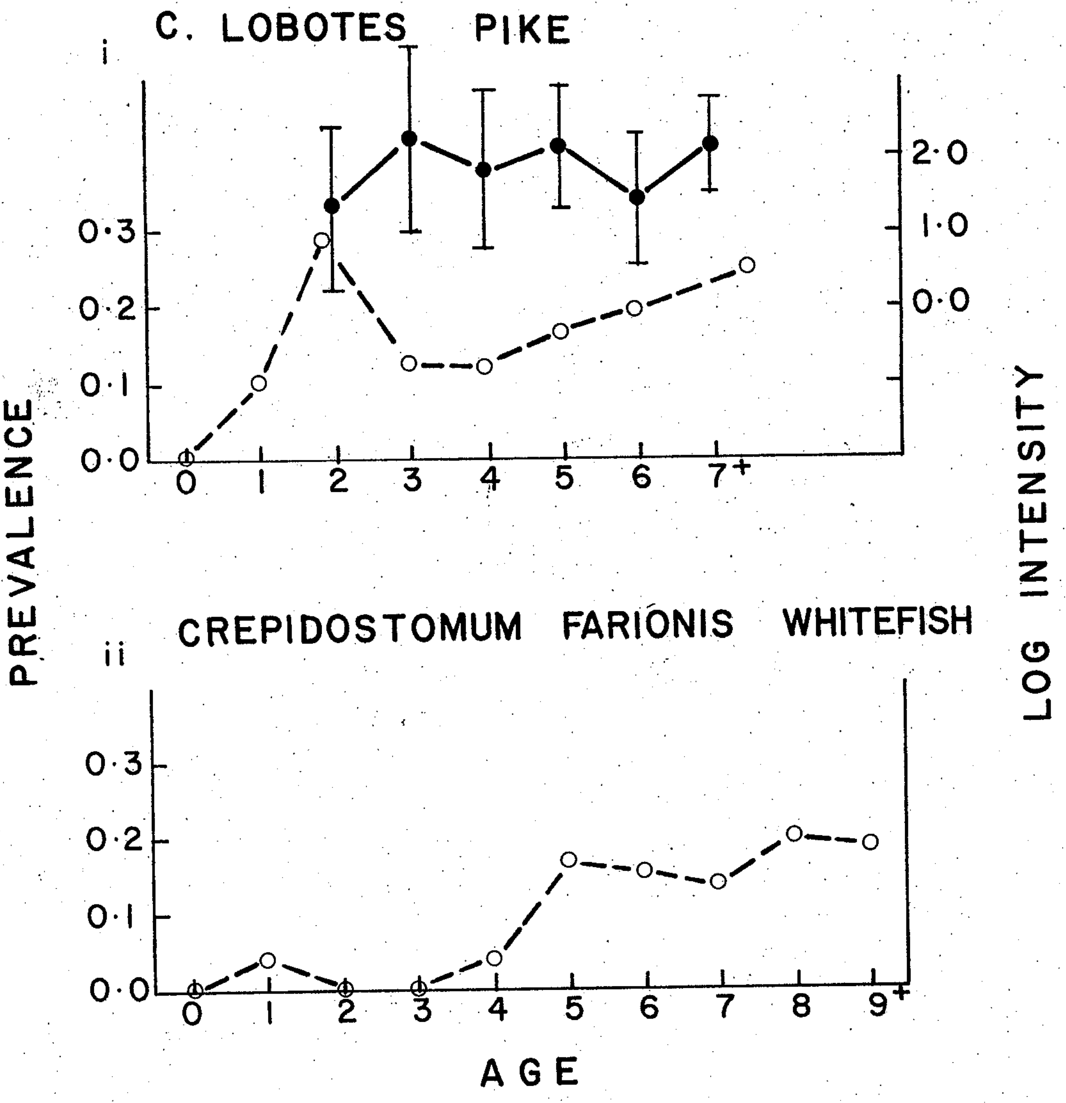
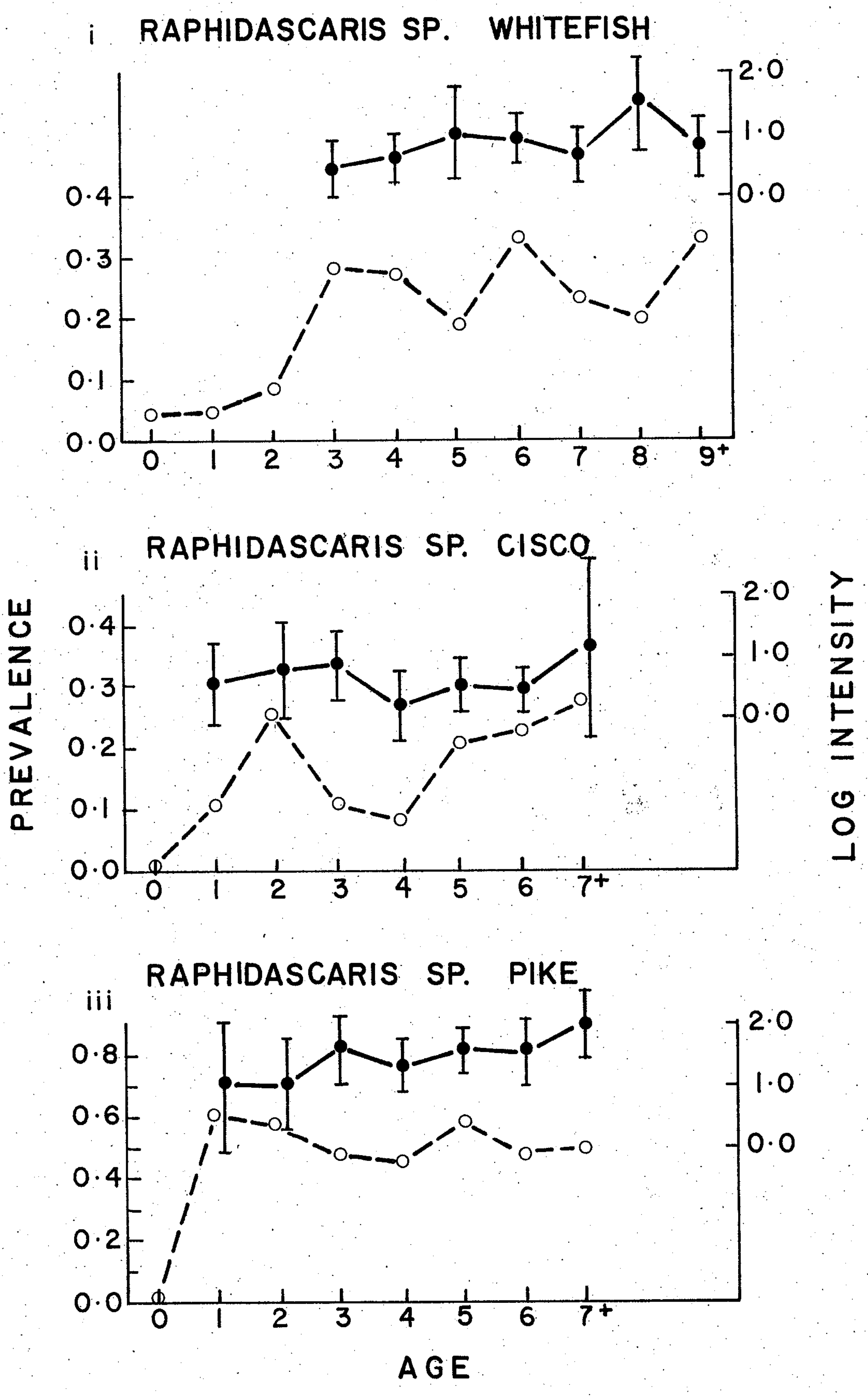
i
C. LOBOTES PIKE
0·0
0·1
0·2
0·3
2·0
1·0
0·0
0
1
2
3
4
5
6
7+
ii
CREPIDOSTOMUM FARIONIS WHITEFISH
0·0
0·1
0·2
0·3
0
1
2
3
4
5
6
7
8
9+
PREVALENCE
LOG INTENSITY
AGE

Figure 8 (i, ii, and iii). Prevalence and log intensity of *Raphidascaris sp.* with host age. (Append. IV, V, and VI)

O---------O prevalence

●————● log intensity

(± standard error)


i RAPHIDASCARIS SP. WHITEFISH
ii RAPHIDASCARIS SP. CISCO
iii RAPHIDASCARIS SP. PIKE
PREVALENCE
LOG INTENSITY
AGE
0·0
0·1
0·2
0·3
0·4
0·6
0·8
0·0
1·0
2·0
0
1
2
3
4
5
6
7
8
9+
7+

and 7 years of age, all of which resulted from increased prevalence and intensity at these ages (Fig. 8 ii). Greatest peak of abundance occurred in fish of 7 years of age and older (Append. V).

Trematodes which showed peaks of abundance were *T. monenteron* from pike and *D. sagittata* from cisco. Although intensity of *T. monenteron* continues to rise, prevalence peaked at 4 years (Fig. 9i, ii), a resultant peak of abundance occurred at 6 years of age (Append. VI). Prevalence and intensity of *D. sagittata* peak in cisco at 5 and 6 years of age (Fig. 9iii). In contrast *D. sagittata* in whitefish has no apparent pattern of abundance once established (Fig. 9ii). Changes in abundance resulted from greatly fluctuating prevalence values while intensity remained relatively constant (Append. IV).

The gill crustacean, *E. nerkae* from cisco peaked in abundance at 3 years of age as a result of peaked prevalence, while intensity values peaked in fish of 4 years of age (Fig. 10i). Although only prevalence values are available for this parasite from whitefish these values decreased with host age from a maximum at 1 year (27%) to the absence of the parasite in fish of 9 years of age and older (Fig. 10 ii). In contrast, *S. extumescens* another whitefish gill copepod peaked in prevalence at 8 years of age and is absent to age 4 years (Fig. 10iii).

Figure 9 (i, ii, and iii). Prevalence and log intensity of monogenean trematodes with host age. (Append. IV, V, and VI)

O--------O prevalence

●———● log intensity

(± standard error)

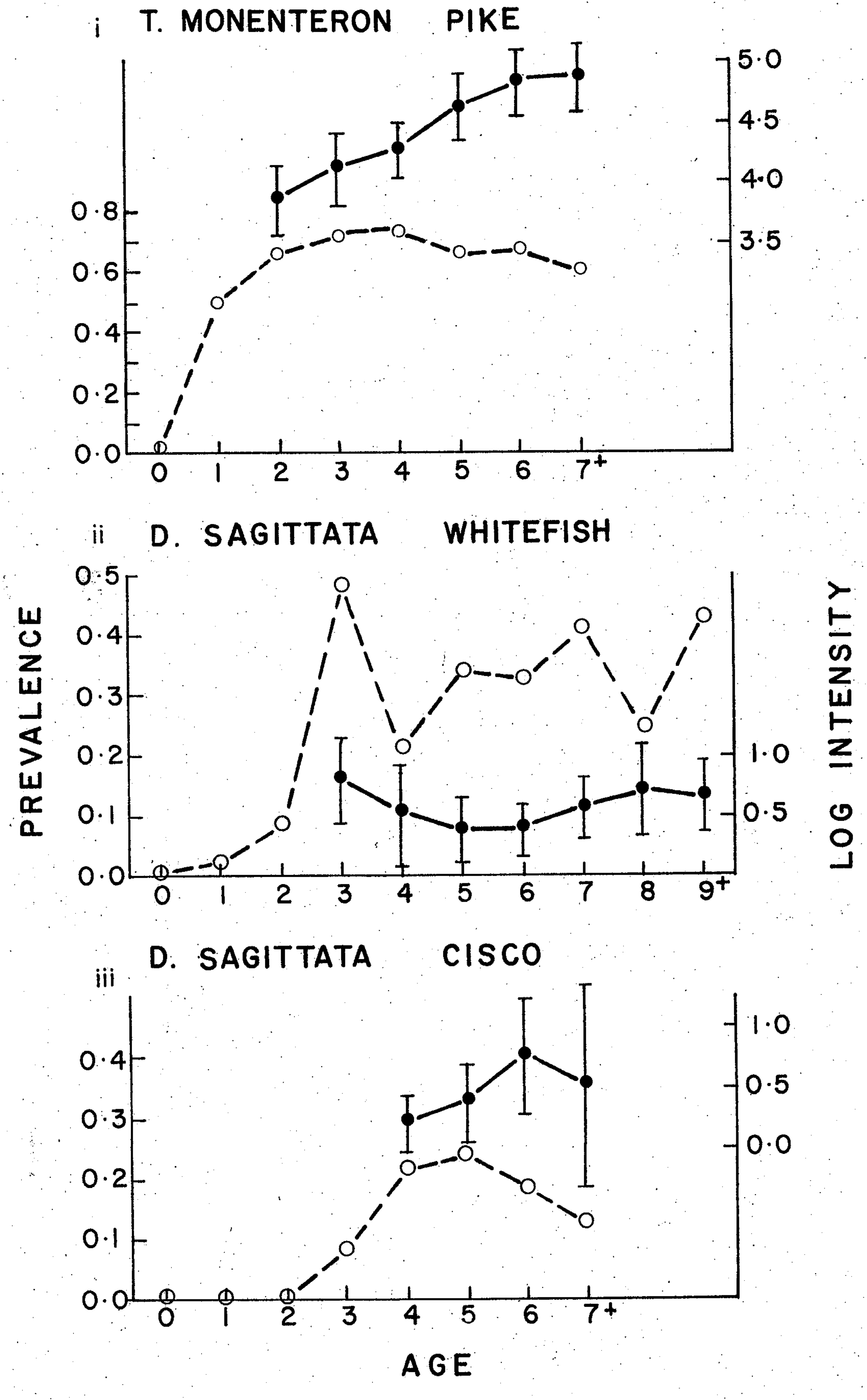
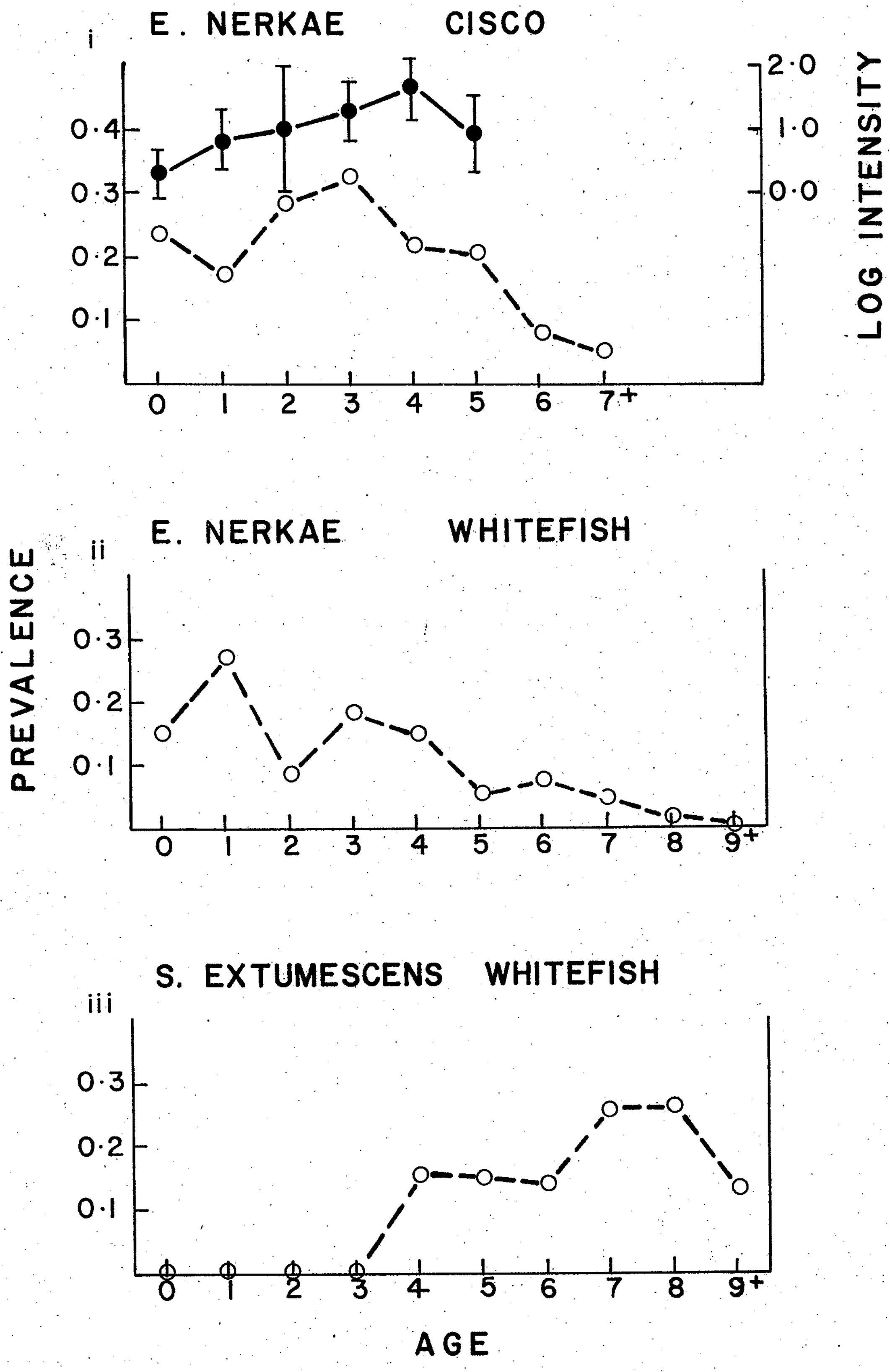

i T. MONENTERON PIKE
0·0
0·2
0·4
0·6
0·8
3·5
4·0
4·5
5·0
0
1
2
3
4
5
6
7+
ii D. SAGITTATA WHITEFISH
0·0
0·1
0·2
0·3
0·4
0·5
0·5
1·0
0
1
2
3
4
5
6
7
8
9+
PREVALENCE
LOG INTENSITY
iii D. SAGITTATA CISCO
0·0
0·1
0·2
0·3
0·4
0·0
0·5
1·0
0
1
2
3
4
5
6
7+
AGE

Figure 10 (i, ii, and iii). Prevalence and log intensity of major gill copepods with host age. (Append. IV and V)

O--------O prevalence

●————● log intensity

(± standard error)


i
E. NERKAE CISCO
0·4
0·3
0·2
0·1
2·0
1·0
0·0
LOG INTENSITY
0
1
2
3
4
5
6
7+
ii
E. NERKAE WHITEFISH
PREVALENCE
0·3
0·2
0·1
0
1
2
3
4
5
6
7
8
9+
iii
S. EXTUMESCENS WHITEFISH
0·3
0·2
0·1
0
1
2
3
4
5
6
7
8
9+
AGE

Discussion

Changes in the abundance of parasite species have been explained by host diet (Miller 1952, Awachie 1968, and others), host distribution (Bauer and Nikol'skaya 1957, Rumyantsev 1973), host surface area (Dogiel 1961), host behavior (Dogiel 1961), or by combinations of these factors. The effect of host age on parasite species was different in different hosts or in different geographical locations (Leong 1975).

Cisco in the present study accumulated *T. crassus* with increasing age while whitefish did not. Miller (1952) suggested that this resulted from dietary changes in whitefish which decreased the uptake rate of the infected copepods. Petersson (1971) found coregonids with high gill raker counts (like cisco) and not those with lower counts (whitefish) accumulated *T. crassus* with age due to their greater intake of plankton. In this study plankton formed a substantially greater portion of the diet of young cisco (63%) then of whitefish (15%). As these species age, plankton decreased in their diets but plankton continued to form a higher proportion of cisco's diet (21%) than whitefish (2%) (Table 14 Sec. 2 ciii). Greater ingestion of plankton including the intermediate host *Cyclops* would explain the accumulation of plerocercoids in cisco and not in whitefish. Miller (1952) suggested that these muscle cysts may survive 3 to 4 years. Intake of infected copepods must simply replace dying pleroceroids in whitefish while adding to their numbers in cisco.

Paling (1965) found that older trout harboured more *D. sagittata* because they carried two rather than one generation of the monogeneans. Thomas (1964) found *D. sagittata* increased in intensity in brown trout until the oldest fish studied (5 years old). Leong (1975) found that this pattern with *D. sagittata* in Cold Lake cisco. Paling (1965) found that numbers reached a maximum in trout of 6 years and decreased through to fish of 9 years of age. The pattern of *D. sagittata* abundance shown by my data was similar to the latter, but peaked in cisco of age 5. Leong (1975) found a similar pattern to Paling (1965) with whitefish and not with cisco. Abundance of *D. sagittata* in whitefish in my study remained independent of age once established. Leong (1975) proposed that lower numbers of *D. sagittata* in older whitefish may have been due to 1) stronger gill ventilating currents, 2) larger gill filaments and 3) behavioral changes associated with aging. Leong (1975) suggested that the adaptation of clamp size to a growing host is finite and resulted in the ultimate loss of the monogenean. Constant intensity levels at S.I.L. suggested that though loss of monogenean may occur, reinfection maintains intensity levels.

Leong (1975) found that the abundance of *Cr. farionis* increased with coho age and reached a maximum in middle-aged cisco. He did not report age effects for this parasite in whitefish or explain the patterns of its abundance in other salmonids. This parasite maintained constant levels of abundance once established in S.I.L. whitefish (Fig. 7 ii). In contrast, Awachie (1968) found that as brown trout age, dietary changes reduced infections of *Cr. farionis*. The insect portion of whitefish diet in this study remained constant with age (35 to 39%) and as the infective metacercaria were found in mayfly larvae (Hoffman 1967), the intake of infected intermediates remained constant. This explains the independence of abundance and host age once the whitefish is old and large enough to eat mayfly larvae (about 2 years of age).

Leong (1975) found an increased abundance of *C. truncatus* with whitefish and cisco age. My data suggest an increase in whitefish which can be explained by increased ingestion of benthic foods (amphipod intermediates). Percentage of whitefish eating amphipods increased by 16 to 18% after 4 years of age at S.I.L. (Table 14). Observations in this study agree with those of Halvorsen and McDonald (1972) and Leong (1975) that this cestode occurs most often in the more anterior caeca (longer and closer to the bile duct opening).

In larger whitefish where the caeca are larger, more worms may occupy each caeca. Caecal size may be a factor which determined abundance of the cestode. Leong (1975) suggested that caecal number may also be important, but I have no evidence that this varied with host age.

Abundance of *M. salmonis* and *Cy. farionis* was probably related to increased consumption of amphipods by whitefish. Caecal size may have been a factor influencing the increased abundance of the caeca inhabiting *M. salmonis*, but not the swimbladder nematode *Cy. farionis*. Hine and Kennedy (1974) found that like *M. salmonis*, the acanthocephalan *Pomphorhynchus laevis* accumulated with age in dace though Bibby (1972) found that the acanthocephalan, *Neoechinorhynchus rutili*, decreased with host age.

Leong (1975) found that *E. nerkae* decreased in abundance with the age of whitefish, cisco and coho, while *E. auritus* peaked in abundance in middle-aged cisco and increased with coho age. He explained these different patterns of abundance as different immune responses to different species. Ergasilids were more abundant in older cisco than older whitefish probably because dietary changes occurred in whitefish (plankton to benthos) which located them out of the infected surface waters (Leong 1975). Observations in this study indicated *E. nerkae* decreased with whitefish age and peaked in abundance in cisco of middle-age at S.I.L. Decreases in whitefish might be explained by dietary changes or by increased gill ventilation or by increased gill size. Cisco may be able to accumulate *E. nerkae* only as long as they were below a critical size (reached at 3 years of age) while they fed in the surface waters where nauplii are located. After gill filament diameter or gill current become too great, accumulation ceased as new *E. nerkae* no longer established and established ones die.

Peak of abundance of the monogean, *T. monenteron*, on pike gills might also have resulted from gill size and ventilating currents which prevented establishment once the fish reached a critical size. It is possible that by 6 years of age declining prevalence reduced abundance due to the death of original monogeneans without recruitment.

Peak of abundance of *S. extumescens* found in the inner opercular face of whitefish in this study may be explained by the failure of new nauplii to establish themselves once a critical gill current is reached and/or changes in feeding location. Once this happens (age 8) abundance no longer increases but decreases. Leong (1975) found *S. extensus* had a peaked abundance but offered no explanation.

In this study the abundance of *P. exiguus* peaked in whitefish at 3 years of age while Leong (1975) found a peak in middle age hosts. My observations indicate this corresponded to the oldest whitefish which are eating appreciable amounts of plankton, including *Cyclops* the intermediate host. Subsequent change of diet to a benthic mode explains the drop in prevalence. In contrast, I found the abundances of *P. filicollis* and *P. pinguis* were independent of cisco and pike age respectively. This may be explained in part by the continued planktonic feeding of cisco. However, both older cisco and pike consumed plankton rarely once there was too great a separation between their gill rakers At this point the continued abundance of *Proteocephalus* in these species probably resulted from ingestion of plerocercoids contained in the intestines of fish eaten. Cisco reduced their plankton consumption by 40% as they age but increased their fish diet by 7.5% at the same time (Table 14, Sec. 2ciii). Many plerocercoids might be ingested with a fish, thus maintaining abundance levels.

The independence of abundance of *Raphidascaris sp.* with age of whitefish and pike once infections are initiated may be explained by host diet. Whitefish began to acquire *Raphidascaris* at 3 years of age, when they began to feed on mayfly larvae (an intermediate). The nematode larvae which whitefish pick up are enclosed in cysts on their gut surface. As the insect (mayfly) portion of whitefish diet remained constant with age and the encysted nematodes did not survive long (40% of cysts contained dead larvae), the abundance remained constant as a result. At one year of age pike reached a size which enabled them to ingest infected mayfly nymphs. These nematode larvae apparently matured in the pike intestine. As the pike grew its intake of infected whitefish and cisco increased and of infected mayfly larvae decreased correspondingly. The net result was a relatively stable abundance of this nematode in pike. The three peaks of abundance of *Raphidascaris sp.* occurred in cisco and corresponded to: (1) a period of optimal fish size for the ingestion of infected mayfly larvae (3 years old) (2) a period when both mayfly larvae and some infected fish were consumed (5 years old) and (3) a period when cisco could begin to ingest infected fish but eat less mayfly larvae (7 years of age and older).

Abundance of *C. lobotes* in this study was independent of age once established in pike. When pike are large enough to eat trout-perch containing metacercaria (2 years of age), the rate of intake must be almost equal to the yearly loss of this trematode resulting in constant abundance levels.

Metacercaria of *T. intermedia* (pericardium) and *D. spathaceum* (in eye) had increasing abundances after their initial appearance in whitefish and cisco. *T. intermedia* had become established by 2 years of age in whitefish and a year later in cisco. This was true of *D. spathaceum* in 2 year old whitefish and cisco.

Metacercaria of these species are long lived and dead specimens were never found in this study. This longevity combined with continued exposure resulted in increasing abundances. Exposure is apparently increased in older whitefish when they begin to feed on benthic fauna. Significantly more whitefish ($p < .05$) feeding on benthos and in close proximity to the bottom were infected with these two species of trematode. This explains the faster increase of abundance of these species in whitefish than in cisco, which apparently do not feed near the bottom. This agrees with observations by Lester and Huizinga (1976) of cercaria of *Diplostomum adamsi* Lester and Huizinga, 1976 which settle to the bottom but swim rapidly upwards when light intensity decreases. It is possible cercaria would penetrate benthic feeding fish like whitefish in the area.

Longevity and continued infection resulted in the increasing abundance of *Diphyllobothrium sp. II* once established in 2 year old pike. Plerocercoids are apparently long lived and the possibility of infection through accidental ingestion of plankton must be great enough to slowly increase abundance.

Cestodes, *T. crassus* and *T. nodulosus*, peaked in abundance in pike at S.I.L. Miller (1943) found *T. nodulosus* predominantly in pike less than 3 pounds whereas *T. crassus* was predominantly in larger pike.

Although *T. nodulosus* was always less abundant in pike in S.I.L. it was nearly equal to *T. crassus* in fish of 2 years of age when the peak of abundance of the latter occurs. By age 5 years, when the peak of *T. crassus* abundance occurred *T. nodulosus*, was much less abundant. This can be explained by the pike's consumption of the intermediate hosts involved. From my observations small pike eat many trout-perch and perch (intermediates for *T. nodulosus*) but less whitefish and cisco (intermediates for *T. crassus*). As a result *T. nodulosus* is more abundant in pike less than 3 years of age. As the pike grew they consumed more and more coregonids and the abundance of *T. crassus* increased when the pike reached a large size (7 years of age and older) it was beginning to eat larger whitefish and cisco, but ate less often. As a result abundances of *T. crassus* again decreased.

Dietary changes probably are the primary reason for changes in endoparasite abundance with age while host location in the lake (as a result of feeding) and/or factors; physiological (host resistance), morphological (gill size, gill current, surface area) may explain changes in the abundance of exoparasites.

b) SEASON

Parasites show patterns of seasonal abundance. These patterns are represented here by five general patterns; namely, those independent of season, and those reaching maximum abundance in each of the four seasons. Parasite species may have more than one month or season with a peak of abundance but are categorized here based on their period of maximum abundance. Patterns shown by the major parasites of whitefish, cisco and pike are summarized in Table 13.

Only *Diphyllobothrum sp. II* in pike shows no seasonal changes in abundance. Five of the major parasite species were most abundant in winter. An equal number of species were most abundant in summer. Of the major parasite species six reached maximal abundance in the spring and three in the autumn (Table 13).

Of the major parasites of whitefish and cisco, *P. exiguus* and *P. filicollis* peaked in abundance in the spring. *T. crassus* peaked in abundance in the spring in whitefish and in the summer in cisco. *T. intermedia* had its highest abundance values in winter while the metacercaria of *D. spathaceum* was at its maximum in summer. Major pike parasites *P. pinguis* and *T. monenteron* reached maximum abundances in the winter and summer respectively.

Table 13. Patterns of major parasite abundance with season

Pattern	Whitefish	Cisco	Pike
Independent			**Diphyllobothrum sp.II*
Highest in Winter (Jan. - April)	*Cystidicola farionis* **Tetracotyle intermedia*	*Raphidascaris sp.* **Tetracotyle intermedia*	*Raphidascans sp.* *Triaenophorus crassus* *Proteocephalus pinguis*
Highest in Spring (May - June)	*Proteocephalus exiguus* *Crepidostomum farionis* **Triaenophorus crassus*	*Proteocephalus filicollis* *exiguus*	*Centrovarium lobotes* *Triaenophorus nodulosus*
Highest in Summer (July - Sept.)	*Discocotyle sagittata* **Diplostomulum spathaceum*	*Discocotyle sagittata* **Diplostomulum spathaceum* **Triaenophorus crassus* *Ergasilus nerkae*	*Tetraonchus moneneron*
Highest in Fall (Oct. - Dec.)	*+Raphidascaris sp.* *Metechinorhynchus salmonis* *Cyathocephalus truncatus*		

* larval forms

Although intensity and prevalence of *Diphyllobothrum sp. II* fluctuated monthly, their product was relatively stable which indicated that the number of these plerocercoids was not affected by season (Fig. 11, Append. IX).

Seasonal effects on abundance of *T. crassus* was observed in all its vertebrate hosts. As this cestode accumulated with cisco age, the results were divided into two age groups (those under 5 years of age and those 5 years and older) for the purposes of seasonal study. Peak abundance of *T. crassus* in whitefish occurred in May while those of younger and older cisco occurred in August and July respectively (Fig. 12 i-iii, Append. VII & VIII). At these times, peaks of prevalence and intensity produced maximal abundance values. By September to October, *T. crassus* abundances were much reduced as a result of decreased prevalence and intensity values (Fig. 12 i-iii). In contrast, this cestode reached maximum abundance in its definite host, the pike, in January after which the net effect of changes in prevalence and intensity resulted in a constant reduced value (Fig. 12 iv, Append. IX).

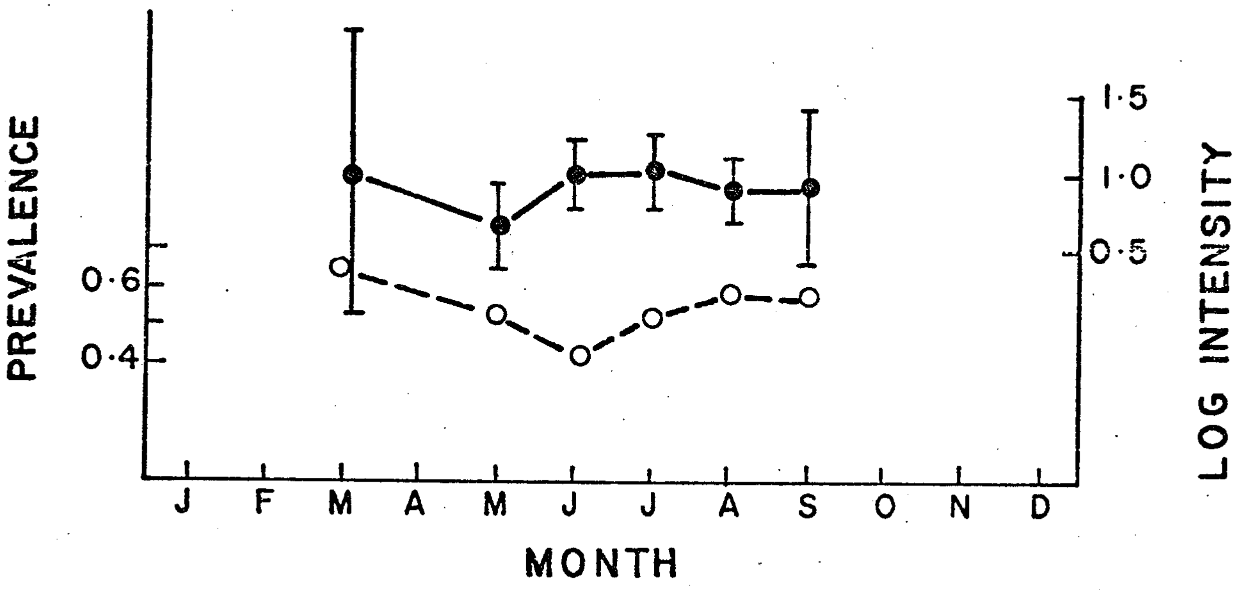
Abundance of proteocephalid species in whitefish and cisco reached maxima in May and June respectively followed by a slow decrease in abundance as summer progressed (Fig. 13i). In contrast, *P. pinguis* in pike reached maximal abundance in January (Fig. 13ii,Append.IX) then,

Figure 11 (i, ii, and iii). Prevalence and log intensity of *Diphyllobothrium sp.* II in pike with month. (Append. IX)

O--------O prevalence

●————● log intensity

(± standard error)



DIPHYLLOBOTHRIUM SP. II PIKE

Figure 12 (i, ii, iii, and iv). Prevalence and log intensity of *Triaenophorus crassus* in its host with month. (Append. VII, VIII and IX)

O--------O prevalence

●————● log intensity

(± standard error)

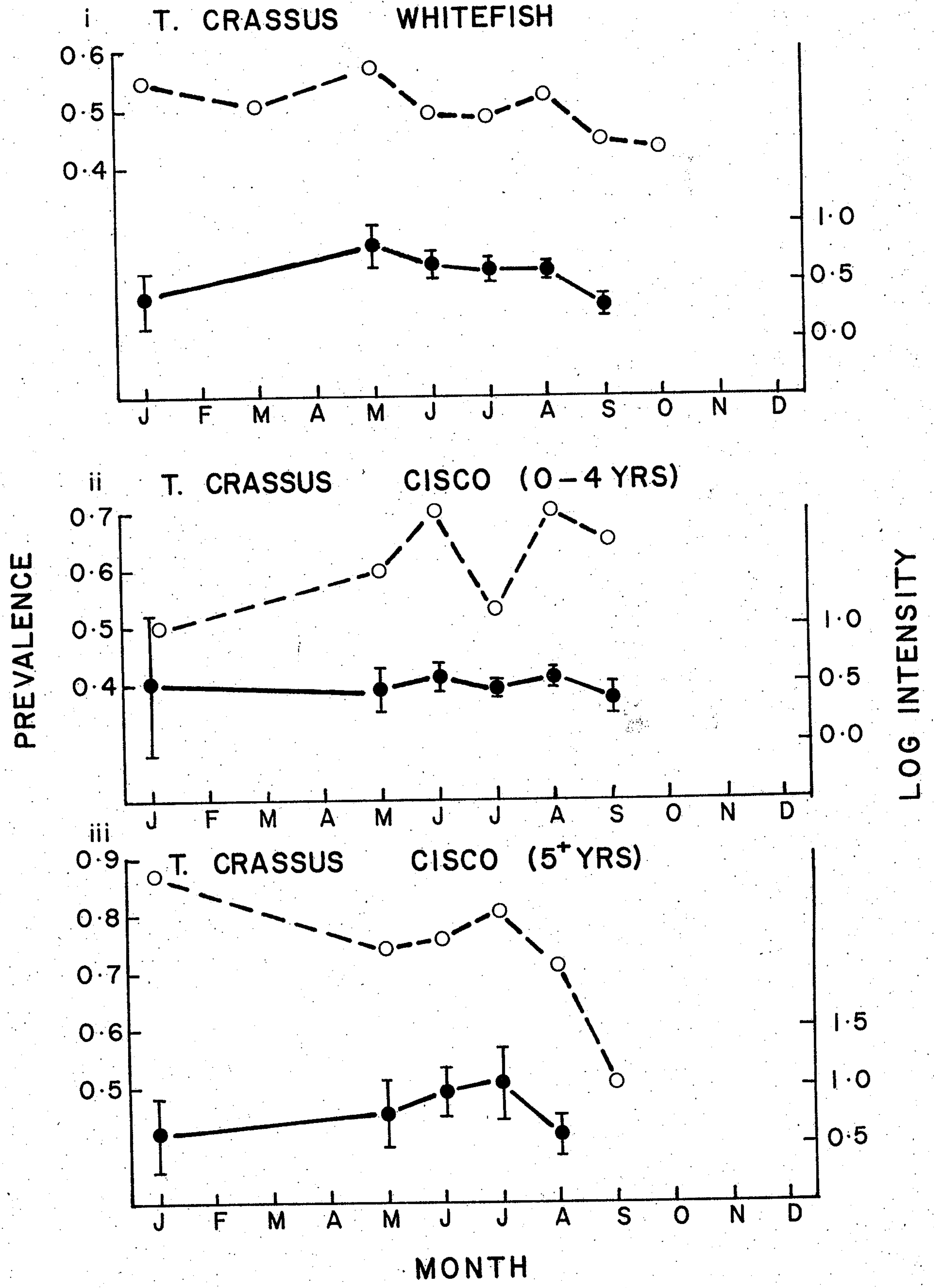
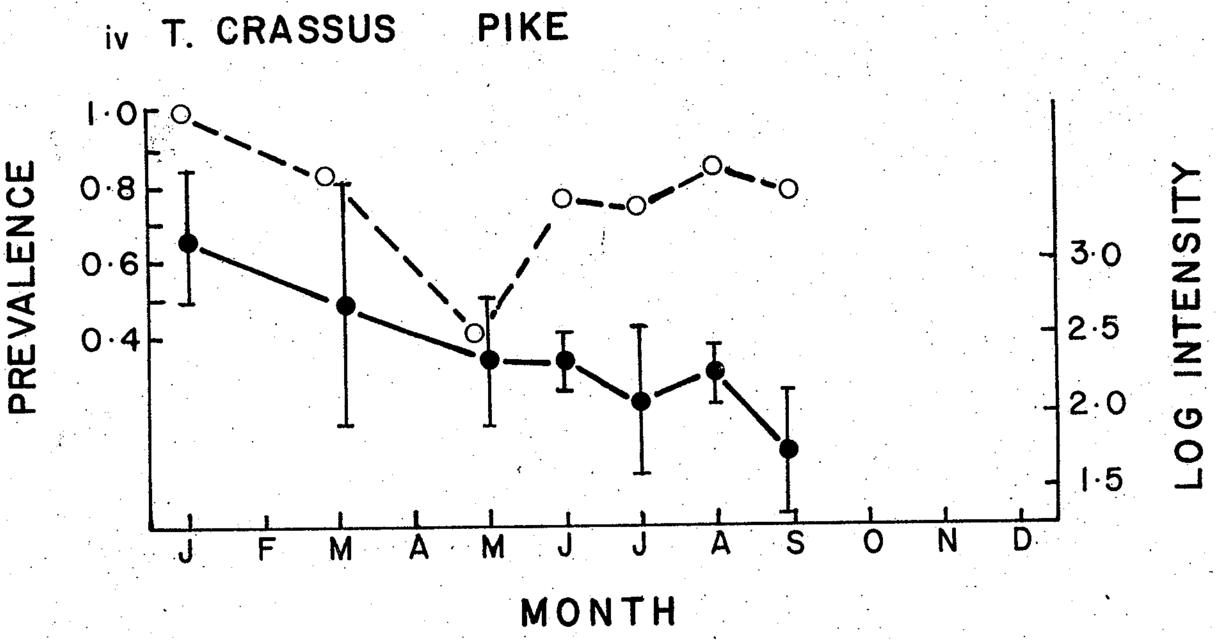

i
T. CRASSUS WHITEFISH
0·6
0·5
0·4
1·0
0·5
0·0
J F M A M J J A S O N D
ii
T. CRASSUS CISCO (0–4 YRS)
0·7
0·6
0·5
0·4
1·0
0·5
0·0
J F M A M J J A S O N D
iii
T. CRASSUS CISCO (5+ YRS)
0·9
0·8
0·7
0·6
0·5
1·5
1·0
0·5
J F M A M J J A S O N D
PREVALENCE
LOG INTENSITY
MONTH

Fig 12

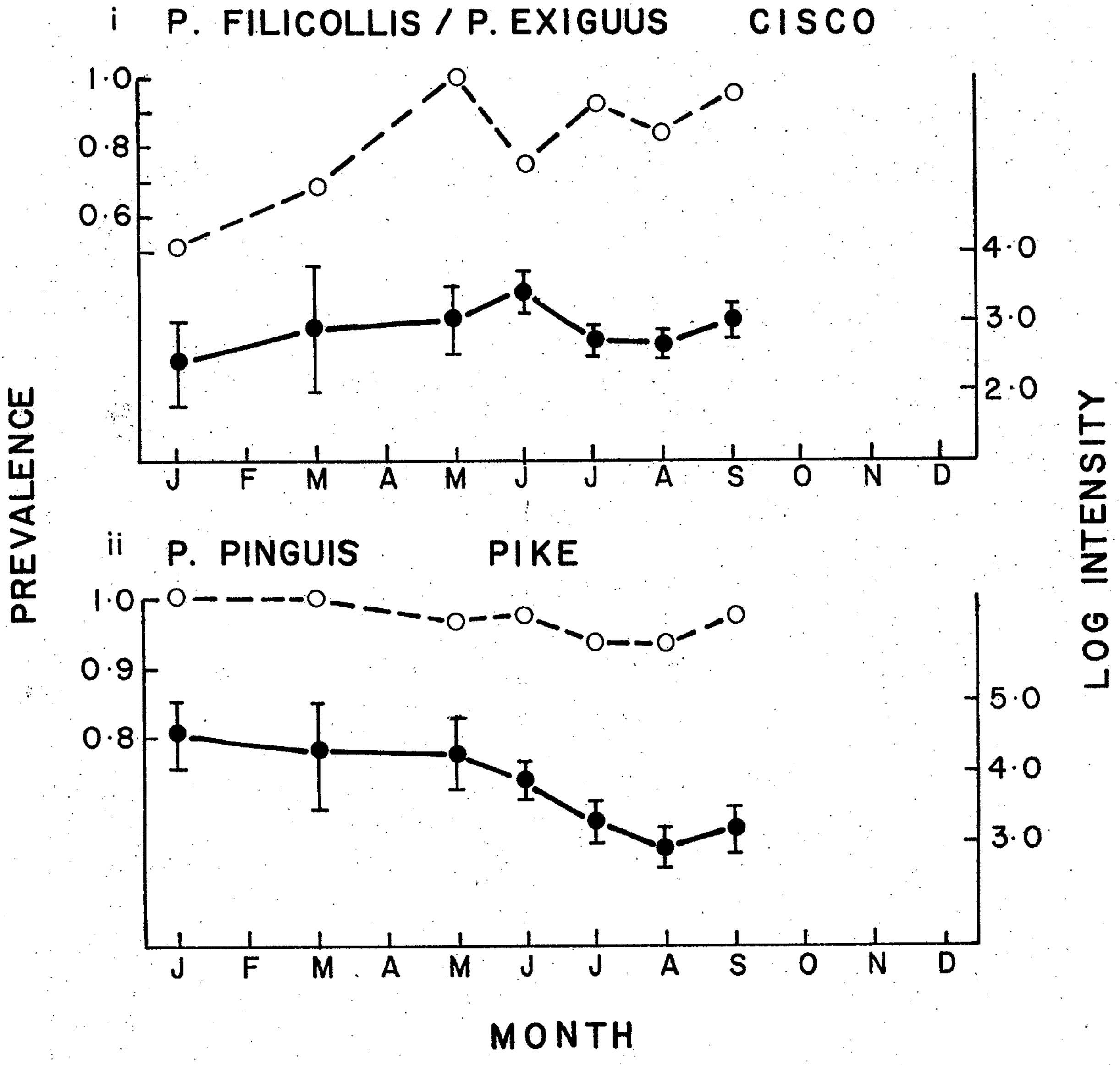


iv T. CRASSUS PIKE

Figure 13 (i and ii). Prevalence and log intensity of proteocephalid species in its hosts with season. (Append. VIII and IX)

O---------O prevalence

●————● log intensity (± standard error)


i P. FILICOLLIS / P. EXIGUUS CISCO
1·0
0·8
0·6
4·0
3·0
2·0
J F M A M J J A S O N D
ii P. PINGUIS PIKE
1·0
0·9
0·8
5·0
4·0
3·0
J F M A M J J A S O N D
PREVALENCE
LOG INTENSITY
MONTH

as with *P. exiguus* and *P. filicollis* abundance declined until September and then increased again.

Differences in the seasonal cycle of *Raphidascaris sp.* from whitefish and pike are apparent in Figure 14. Encysted nematodes of this genus from whitefish reached maximal abundance in autumn as prevalence and intensity increased from minimal spring values (Fig. 14i). *Raphidascaris* free in the gut of pike reached maximal abundance in March as a result of peaks of intensity and prevalence. Another smaller peak in the abundance of this nematode in pike occurred in July (Fig. 14i,Append.IX).

Similarities in the seasonal abundances of whitefish parasites vectored by amphipod intermediate hosts can be observed in Figure 15. Maximal abundance in *M. salmonis* and *C. truncatus* in whitefish occurred in the autumn, while minimal values for these two species occurred in the summer (Fig. 15 i & ii,Append.VII). Throughout the year changes in the prevalence of these species was paralleled by changes in parasite intensity. The amphipod vectored nematode, *Cy. farionis* reached maximal abundance in winter (Fig. 15 iii,Append.VII). Abundance was lowest in the summer as with *M. salmonis* *C. truncatus*, but resulted almost exclusively from a decrease in prevalence (Append. VII).

Differences exist between the seasonal cycles of abundance for the major parasites of whitefish and cisco, the metacercaria of *T. intermedia* and *D. spathacaecum*. Although these two species of trematodes were at

Figure 14 (i and ii). Prevalence and log intensity of *Raphidascaris sp.* in its hosts with season. (Append. VII and IX)

O--------O prevalence

●————● log intensity

(± standard error)

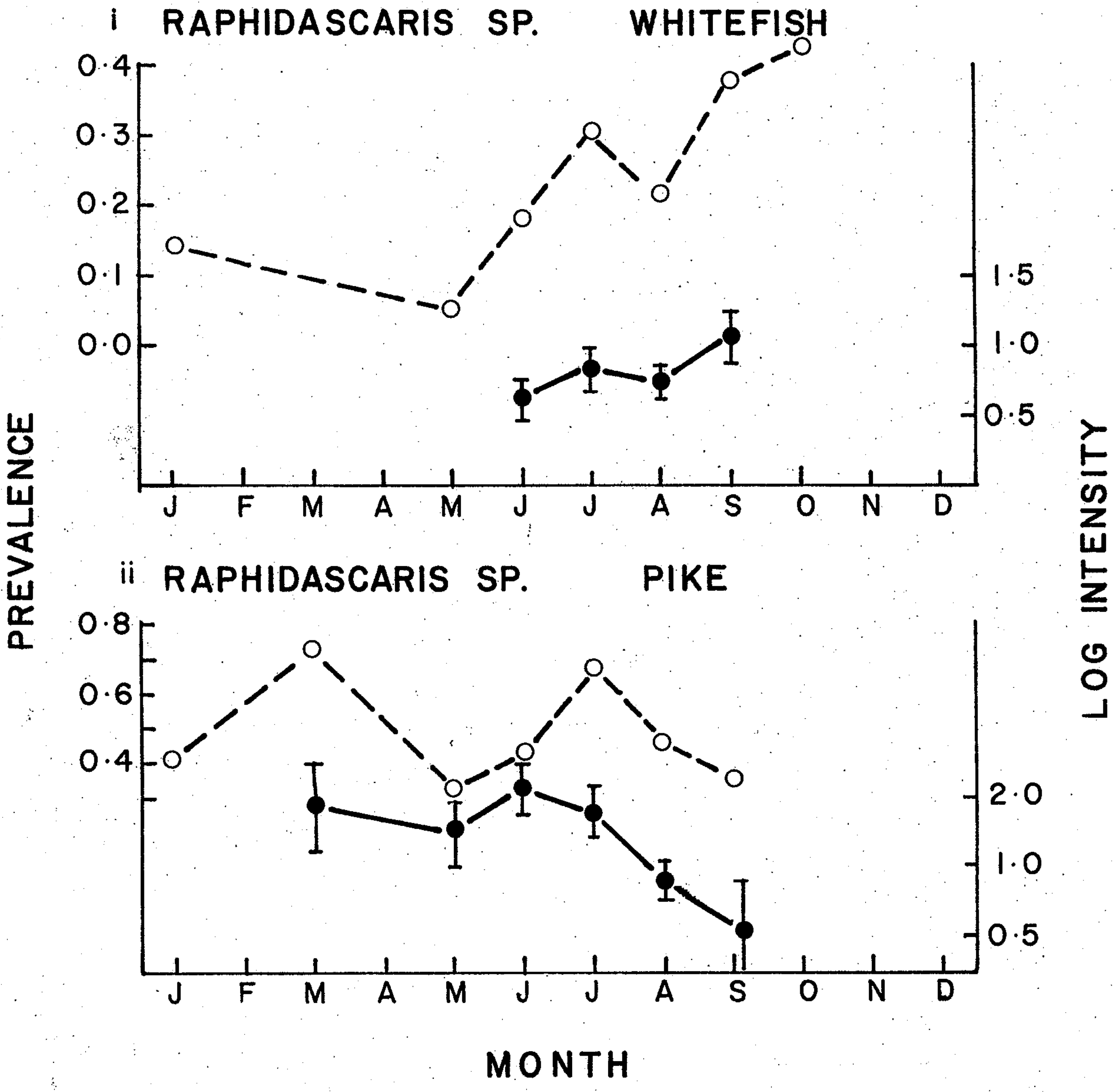
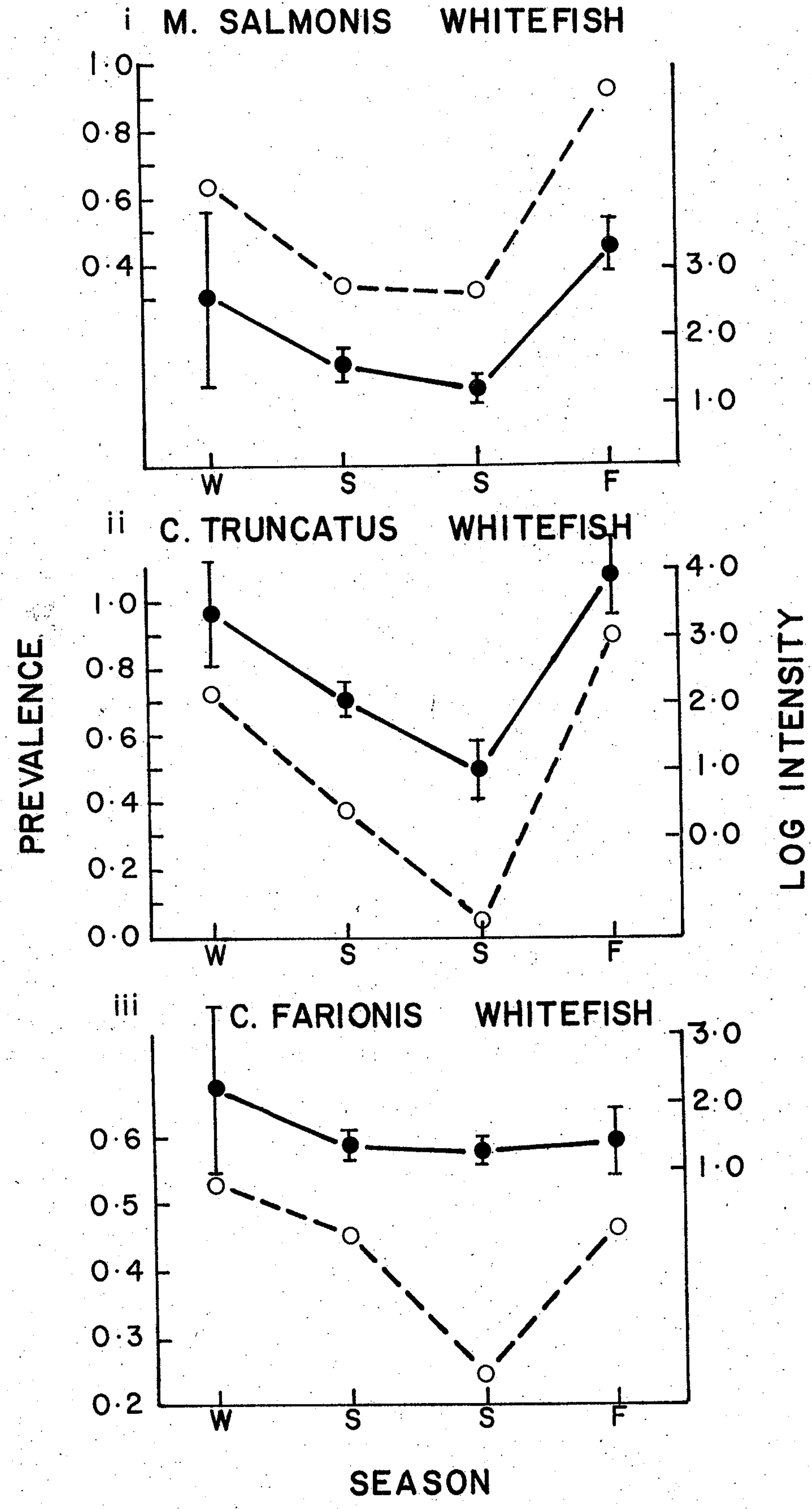

i RAPHIDASCARIS SP. WHITEFISH
0·4
0·3
0·2
0·1
0·0
1·5
1·0
0·5
J F M A M J J A S O N D
ii RAPHIDASCARIS SP. PIKE
0·8
0·6
0·4
2·0
1·0
0·5
J F M A M J J A S O N D
PREVALENCE
LOG INTENSITY
MONTH

Figure 15 (i, ii, and iii). Prevalence and log intensity of amphipod vectored whitefish parasites with season. (Append. VII)

O--------O prevalence

●————● log intensity

(± standard error)



i M. SALMONIS WHITEFISH
ii C. TRUNCATUS WHITEFISH
iii C. FARIONIS WHITEFISH
PREVALENCE
LOG INTENSITY
1·0
0·8
0·6
0·4
0·2
0·0
0·5
0·3
4·0
3·0
2·0
1·0
0·0
W
S
S
F
SEASON

minimal abundance in both host species in July, the maximal abundance of T. *intermedia* occurred in March while that of D. *spathacaeum* took place in June in both cisco and whitefish (Fig. 16, Append. VII and VIII).

The gill monogenean, D. *sagittata* from whitefish and cisco; and the monogenean T. *monenteron* from pike, reached maximal abundances in July (Fig. 17, Append. VII and IX). Abundances of both these parasites dropped to minimum values preceding and following this midsummer peak.

Another gill parasite, E. *nerkae* reached maximal abundances in summer (August) when increasing prevalence values and decreasing intensities resulted in maximal parasite population size (Fig. 18, Append. VII).

Figure 16 (i, and ii). Prevalence and log intensity of trematode metacercaria with month. (Append. VII and VIII)

O--------O prevalence

●————● log intensity

(± standard error)

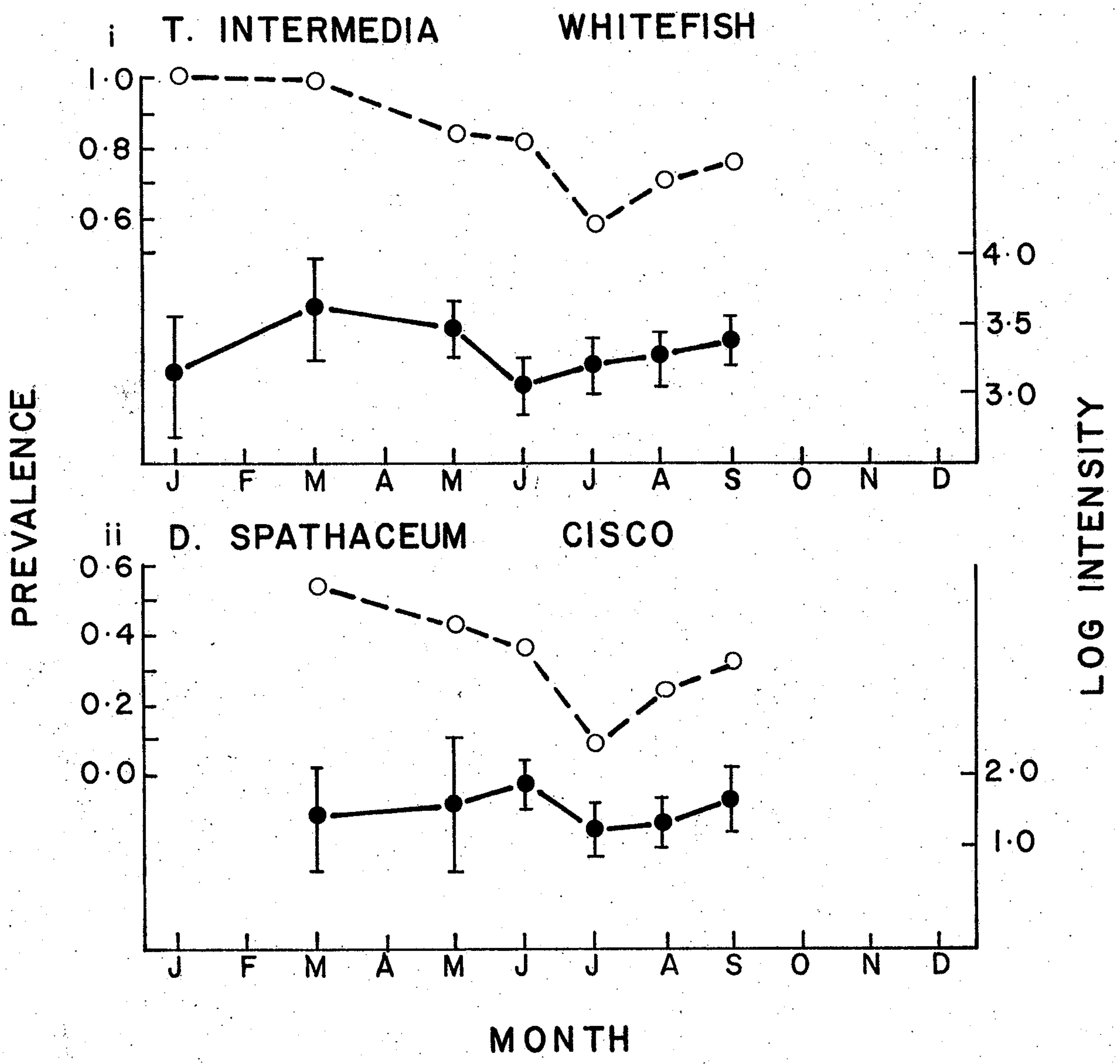

i T. INTERMEDIA WHITEFISH
1·0
0·8
0·6
4·0
3·5
3·0
J F M A M J J A S O N D
ii D. SPATHACEUM CISCO
0·6
0·4
0·2
0·0
2·0
1·0
J F M A M J J A S O N D
PREVALENCE
LOG INTENSITY
MONTH

Figure 17 (i and ii). Prevalence and log intensity of monogenean gill parasites with month. (Append. VI and IX)

O---------O prevalence

●————● log intensity

(± standard error)

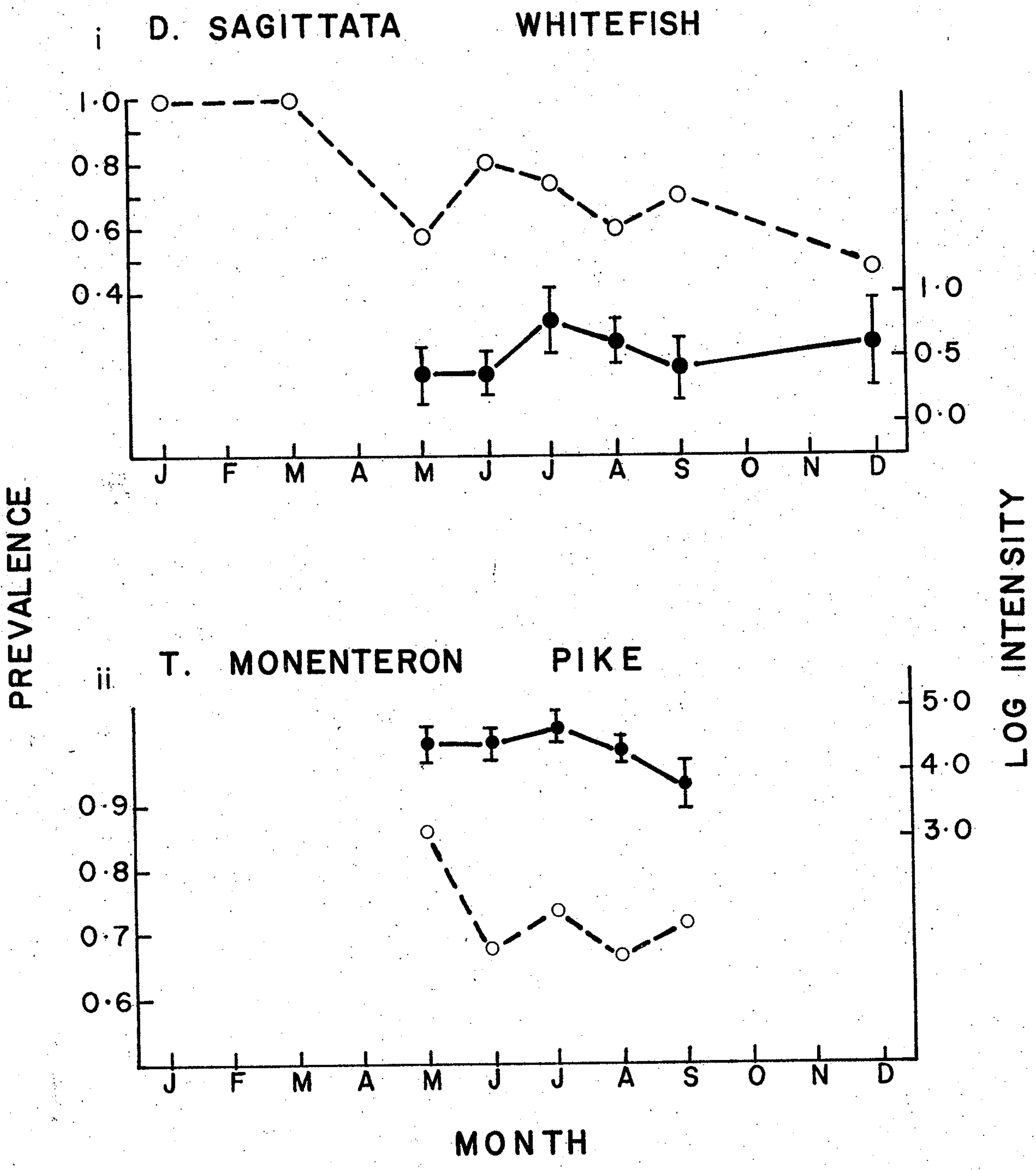
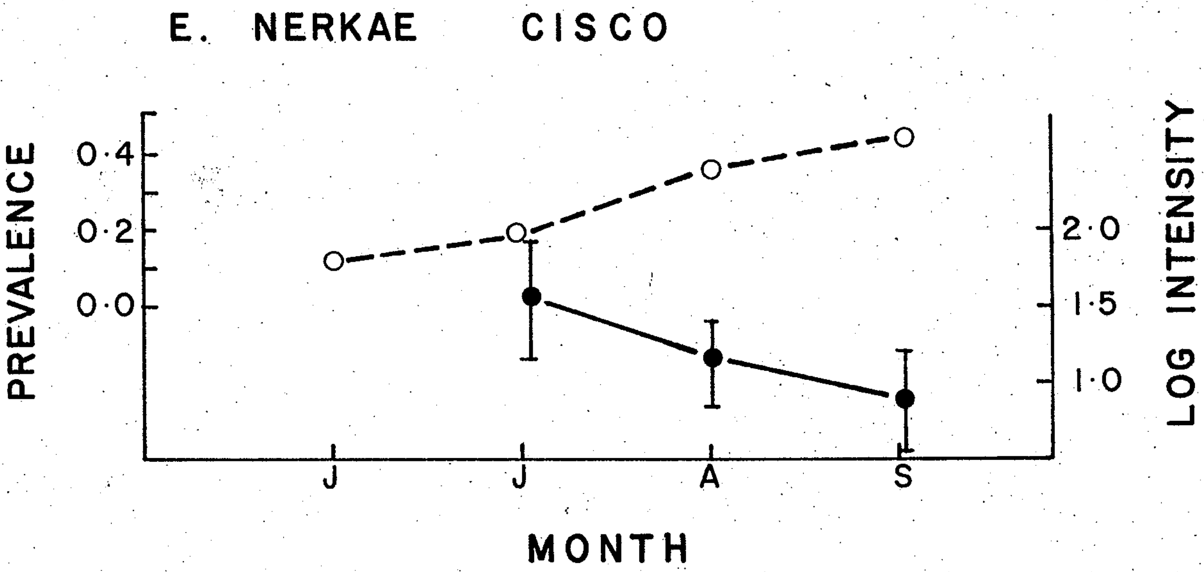

i
D. SAGITTATA
WHITEFISH
1·0
0·8
0·6
0·4
1·0
0·5
0·0
J
F
M
A
M
J
J
A
S
O
N
D
PREVALENCE
LOG INTENSITY
ii
T. MONENTERON
PIKE
5·0
4·0
3·0
0·9
0·8
0·7
0·6
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

Figure 18. Prevalence and log intensity of *Ergasilus nerkae* with month. (Append. VIII)

O---------O prevalence

●————● log intensity

(± standard error)


E. NERKAE CISCO
PREVALENCE
0·4
0·2
0·0
LOG INTENSITY
2·0
1·5
1·0
J
J
A
S
MONTH

Discussion

Seasonal changes in water temperature have been used to explain the seasonal cycle of abundance in fish parasites (Awachie 1968; Rawson and Rogers, 1972, 1973; Cloutman and Becker 1977; Hopkins 1959; Tedla and Fernando 1970 and others). Seasonal timing stimulated by water temperature was shown to be effective in maximizing the efficiency with which the intermediate host is infected (Stromberg and Crites 1975). Other authors showed that water temperature acts to affect parasite abundances by modifying host activity such as feeding (Bibby 1972, Anderson 1976). Changes in host diet was used to explain seasonal cycles (Moravec 1970, Eure 1976b). Temperature was eliminated as a causal agent by Rumyantsev (1973). Other workers believed that water temperature may act only secondarily on parasite abundance by controlling host breeding cycles (hormones) (Kennedy 1969) and host immune response (Kennedy and Hine, 1969, Leong 1975).

It is generally accepted that water temperature, host diet, host activity and host immunology control seasonal cycles of parasite abundance but these factors may act in different ways and to varying degrees on different parasite species and on the same parasite in different hosts.

Leong (1975) found *Cystidicola farionis* from Cold Lake whitefish attained maximal abundance values in the winter and minimal values in late summer with maturation occurring in the spring and summer. In this study, maximal values of abundance also occurred in the spring when many small larvae of these species are present in the swimbladders of whitefish. Minimal abundance values also occurred during the summer. Leong (1975) explained winter abundance peaks by a decrease in the activity of the host immune system due to low water temperatures. This could also explain abundance peaks at S.I.L.

Acanthocephalan *M. salmonis* (vectored by amphipod hosts) had a winter abundance peak in perch and dropped to zero by autumn (Tedla and Fernando 1970). Leong (1975) demonstrated that a peak of abundance in this parasite in December in young whitefish and in July and December in older whitefish but observed little seasonal variation in cisco. He used temperature controlled changes in host immunity to explain winter peaks in abundance. In this study maximal abundance of this species in whitefish was in late fall. Lower water temperatures at this time could have resulted in lower host immune responses.

Awachie (1966) found that the amphipod vectored cestode *C. truncatus* established in brown trout in late autumn; matured in late winter and early spring; and disappeared by late summer. Leong (1975) found that the abundance of *C. truncatus* peaked in whitefish in early winter and in summer, and used temperature controlled host resistance as an explanation. A similar interpretation may explain the late fall peak in abundance of *C. truncatus* in S.I.L. although an obvious summer peak of abundance was not observed as reported by Leong (1975).

Seasonal changes in *T. crassus* were reported by several authors. A period existed in the late spring or early summer when whitefish and cisco begin to feed on infected *Cyclops*. Approximately one month later the number of plerocercoids in the musculature of these fish increased dramatically (Miller 1945, 1952; Lawler 1951). Following this increment period some authors did not detect a decrease in cestode numbers (Miller 1945, 1952; Lawler, 1951) but Newton (1932) found an autumnal decrease which he suggested was due to the host's immunological system. Peaks of *T. crassus* abundance occurred in spring in whitefish and in late summer in cisco at S.I.L. The earlier peak of abundance in whitefish may be due to a faster rate of encystment of plerocercoid, perhaps, due to a greater immune response in the whitefish than in cisco (the natural host). Such encystment would allow earlier detection of new plerocercoids in the musculature. Reduction of *T. crassus* abundance in the autumn in whitefish and cisco corroborates Newton's (1932) findings and may be explained by a strong host immunological response. By early fall water temperatures (16°C) were only slightly lower than those of summer maximums (19°C) and consequently temperatures probably had not affected fish immunity.

Ekbaum (1932) reported that *T. crassus* matured in the intestine of the pike in February. Miller (1952) found maximal numbers in the late autumn and winter and following release of eggs in early May he found the mature worms were lost without replacement from mid May to mid June. Maximal abundance of *T. crassus* in the present study occurred in pike in January, and though minimal abundance occurred after release of eggs by gravid worms in early May, the period of "relatively *T. crassus* free pike" reported by Miller (1952) did not occur. Not all of these cestodes are lost but destrobilization might account for the effect observed by Miller (1952) and others. Spawning pike do not feed, and without the influx of *T. crassus* plerocercoids from infected whitefish and cisco, replacement would be delayed until after the spawning period when active feeding is resumed.

Bauer and Nikol'skaya (1957) found *Proteocephalus* numbers in whitefish increased in autumn. Hopkins (1959) found numbers of *P. filicollis* peaked in *Gasterosteus aculeatus* in autumn. Proteocephalid numbers often peaked in abundance in the spring. Connor (1953) found *P. stizosethi* in walleye and Kennedy and Hine (1967) found *P. torulosus* in dace peaked in numbers in the spring.

Abundance of *P. filicollis* peaked in Cold Lake cisco in August with minimal values in winter (Leong 1975). He also found *Proteocephalus sp.* plerocercoids reached maximal abundance in January in whitefish and April in cisco. Leong (1975) found abundance of *P. exiguus* in whitefish in Cold Lake was highest in May then declined through until the winter. *Proteocephalus* from whitefish and cisco from the present study reached maximal abundances in May and June respectively which indicates the component of *P. exiguus* present with *P. filicollis* in cisco appears to obscure their reported autumn abundance peak. Peak of abundance of *P. exiguus* from whitefish and cisco in the spring resulted from a diet of infected copepods in the proceeding months, though most *Proteocephalus* in these fish matured quickly and were gravid by spring. This suggests that a spring peak was due to gradual accumulation, following a loss of many gravid cestodes which occurred in early summer. Peak abundance of *P. pinguis* from pike in July may be related to water temperature and host response.

Brown trout were found most heavily infected by *Cr. farionis* in February, then incidences fell through summer to their minimal values in September (Awachie 1968). He speculated that water temperature synchronized the cycle of this parasite in trout and its intermediate host (*Gammarus*). Spring abundances in S.I.L. were many times those of winter suggesting that if such coordination of life cycles is maintained, the biology of trout and *Gammarus* in Awachie's study (1968) must differ from the biology of whitefish and *Gammarus* in the present study or that seasonal availability of the mollusc hosts may be important. Diet of whitefish during the early spring consisted mainly of *Gammarus*. The resultant peak of abundance could then be explained by seasonal changes in diet.

Bauer and Nikol'skaya (1957) found *D. sagittata* numbers were higher on whitefish gills in autumn. Paling (1965) found invasion in April to November and a late summer peak. Leong (1975) found peaks of abundance from late summer to early winter in whitefish and cisco respectively. An early winter abundance peak in cisco was explained by low water temperatures reducing host resistance. The midsummer (July) peak of abundance of this monogenea in whitefish and cisco found in the present study is difficult to explain on the basis of host resistance as it occurred during warmer water temperatures. Perhaps, host activity or host distribution within the lake varies. Movement of fish might have resulted in a different population of fish being sampled.

Gill monogenean, *T. monenteron* of pike also peaks in abundance in the summer. A temperature induced immunological response would be strong at this time and explanation of the summer abundance maximum necessitates other factors. It is possible that following spring spawning, pike had a reduced resistance which allowed monogenea to increase in abundance.

Becker (1977) found numbers of *E. centrarchidarum* declined sharply with decreased temperature. Leong (1975) found that *E. nerkae* peaked in abundance in late summer while another cisco gill crustacean, *Ergasilus auritus* Markevich, 1940, peaked in April and May and to a lesser extent in September and October. These two species apparently had seasonal cycles which reduced interspecific competition. In the present study *E. nerkae* also peaked in abundance in late summer (August), though the explanation of interspecific competition can not be accepted as only one of these species infects cisco at S.I.L. Host activity must allow accumulation of the copepods until dropping water temperatures somehow reduce the establishment of nauplii and/or cause the death of established crustaceans.

The peak of abundance of *Raphidascaris sp.* in whitefish in the autumn and in cisco, and pike in the winter in the present study, could be related to low water temperatures during these periods or by changes in host diet. Moravec (1970) explained the seasonal cycle of *Raphidascaris acus* in brown trout by changes in host diet. He failed to rule out other factors such as water temperature. *Raphidascaris sp.* occurring in cisco and pike originate from encysted larvae in fish such as whitefish. Peak abundance in piscivorous species (pike and cisco) might follow the peak in species such as whitefish and a period of time for the increase in numbers to move up the food chain.

An increment period or peak of abundance does not occur with plerocercoids of *Diphyllobothrum sp. II* from pike as it did with those of *T. crassus* in whitefish. There is no autumnal decline as with *T. crassus*. Ingestion of infected copepods apparently occur for most of the year without any immunological control when water temperatures increase. Definitive host of this parasite is probably the herring gull, *Larus argentatus* and this might remove at least part of the life cycle from control of water temperature though complete seasonal stability cannot be explained.

Metacercaria of *T. intermedia* in whitefish and cisco peaked in abundance in the winter (March) possibly indicating that host immunity probably plays a role in the seasonal cycle. In contrast, metacercaria of *D. spathaceum* which occur in the immunologically more tolerent eye of these hosts peaked in June indicating that proximity of the host to the source of cercaria (snail) may be more important than the reduction of host response when water temperatures are low.

Pike parasites *C. lobotes* and *T. nodulosus* both had maximal abundances in the spring. Both are vectored by minnows and smaller fish species. Diet of post spawning pike consisted mainly of shiners (intermediates for *C. lobotes*) and perch (intermediates for *T. nodulosus*), both of which were found in shallow areas, in the vicinity of spawning sites. Diet must be the major factor that controlled these spring abundance peaks.

Although reduced host resistance may explain the peaks of abundance of parasite species during late fall, winter and early spring (periods of low water temperature); it does not explain peaks at other seasons. Effect of temperature as a stimulus affecting host diet, activity and distribution in the lake can not be overlooked and appears to be the main explanation for peaks of abundance during warm water periods. Although such factors as intermediate host or definitive host availability may be the only cause of spring or summer peaks of abundance, these factors cannot escape the modifying effects of water temperature.

c) FOOD HABITS

Changes in the abundance of parasite species with season, host age and sex can often be explained by changes in host diet (Sec. VII a, b and d). Host diet was studied in order to explain differences in the abundance of parasite species.

Major food items of whitefish were pelecypods, gastropods, chironomid larvae, amphipods and ephemeroptera larvae (Append. X). Cisco fed mainly upon zooplankton (mainly *Cyclops* and *Diaptomus*) ephemeroptera larvae, trichoptera larvae, chironomid larvae and small fish (Append. XI). Major pike food items are fish (mostly Percidae) and trichoptera larvae (Append. XII).

Whitefish diet was studied here within restricted age groups when diet changed significantly ($p < .01$) with host age. Major foods of young whitefish were chironomid larvae which made up 20% of all identifiable food items, zooplankton (principally *Cyclops*, *Diaptomus* and *Daphnia*) which make up 15%, gastropods (15%), pelecypoda and hydrachellidae each with 14% of identifiable food items (Append. X). In mature whitefish (5 to 7 years of age), however, pelecypoda made up 20%, gastropods 18%, chironomid larvae 12% and trichoptera larvae 11% of identifiable food items (Append. X). Older whitefish (8 years and older) had a diet similar to that of mature whitefish with 20% pelecypods, 18% amphipods, 15%

gastropods and chironomid larvae each and 9% ephemeroptera larvae (Append. X).

Diet of cisco also significantly changed with age ($p<.01$). The identifiable diet of younger cisco (0 to 4 years of age) consisted of 63% plankton, 9% trichoptera larva, 8% ephemeroptera larvae, 8% chironomid larvae and 3% fish (Append. XI). Older cisco (5 years old and older) had a diet which consisted of 25% ephemeroptera larvae, 21% plankton, 20% trichoptera larvae and 11% fish (Append. XI).

Diet of pike did not change with age. Identifiable food items were 61% various fish species, 9% trichoptera larvae, 8% ephemeroptera larvae and 5% odonata larvae and amphipods each (Append. XII).

Changes in whitefish diet with age are summarized in Table 14. Although insects had a consistent role in the diet (35 to 39%), plankton decreased in importance (15 to 2%), and benthic fauna increased from 35 to 52% of their diet. As their intake of *Cyclops*, *Diaptomus* and other plankton decreased; amphipods such as *Pontoporeia*, gastropods, and pelecypods became more important. Basically it was a change from a planktonic feeding mode to one in which benthic feeding predominates.

Cisco dietary changes are summarized in Table 14. As cisco increase in age the insect component of diet incresed from 32.8 to 60.6%, fish from 3.4 to 10.9% while the plankton portion of the diet decreased from 62.6 to 21.2%. Although plankton continued to play a major role

Table 14. Summary of changes in diet, diet similarity and diversity with age.

WHITEFISH	0-4 yrs	5-7 yrs.	8^+ yrs.
Insecta	35.2*	36.9	38.8
Plankton	15.3	1.2	2.9
Benthic	34.2	50.0	52.5
Simpson's Index	8.14	10.07	10.34

CISCO	0-4 yrs.	5^+ yrs.
Insecta	32.0	60.6
Plankton	62.6	21.2
Fish	3.4	10.9
Simpson's Index	3.82	4.14

PIKE	0-4 yrs.	5^+ yrs.
Anthropods	29.8	26.3
Fish	66.3	47.0
Simpson's Index	3.51	4.11

Similarity of Diet

	Whitefish	
48.8		Cisco
27.7	34.1	Pike

*percent of stomachs containing food item in the diet of cisco as they age (unlike whitefish), fish and insects become the major food of older fish. Cisco continue to feed on plankton but, when older, fed mainly on food items too large for young cisco to catch.

Diet of pike changed little with age. Arthropods (principally insects) remained constant (26 to 30%) as did the fish component (57 to 66% of recognizable food items).

As these three fish species age their diet became more diverse as reflected by increasing values for Simpson's index (Table 14). Whitefish diet was more diverse than that of cisco which was slightly more diverse than that of pike.

When similarity of diet was calculated the diet of whitefish was more similar to that of cisco (48.8%) than to that of pike (27.7%). Cisco were more similar in diet to pike (34.1%) than whitefish were (Table 14).

Discussion

Diet of whitefish in this study was similar to that reported by other authors (Forbes 1888, Hart 1931, Reckahn 1970 and others). It is generally accepted that the mode of whitefish feeding changes from a planktonic to a benthic form. Kliewer (1970) found that as gillraker spacing increased as the fish aged, larger food items were taken. This change in size did not preclude consumption of planktonic food (Kliewer 1970). By three years of age the diet of whitefish in this study was essentially the same as those over ten years old. Reckahn (1970) found that within a year of hatching whitefish had begun to feed on foods characteristic of adults. Amphipods were less important in the diet of S.I.L. whitefish then gastropods and pelecypods. This was more similar to the feeding of whitefish reported by Bajkov (1930) from Lake Manitoba and Lake Winnipegosis than from Lake Winnipeg.

Entomostracans were the principal food taken by cisco (present study). Cisco unlike whitefish fed on plankton to a large degree at all ages. Dobie (1966) found cisco were principally pelagic feeders. Diet of cisco from other lakes as reported by Nelson and Hasler (1942), Rimsky-Korsakoff (1930), Fry (1937), Langford (1938) and others was similar. None of these authors suggested a significant portion of the diet of older cisco consisted of fish as the present study indicated. Scott and Crossman (1973) suggested that cisco may eat their own eggs and have occassionally eaten small minnows.

Pike when young fed on aquatic insects but by 50 millimeters in length, fish became the predominant food item (Scott and Crossman 1973). They report pike will eat virtually any living vertebrate available to them within the size range they can engulf. Lawler (1965) found that fish and insects formed the bulk of pike diet at Heming Lake, Manitoba. Most studies like the present have concluded that changes in the diet of pike with age was mostly in the size of fish consumed. Thus younger pike would live on fry and minnows while older pike could consume larger fish such as suckers, perch and coregonids.

Changing diets of these fish species may have produced many of the changes in parasite abundance with age (Sec. IIIa). Rumyantsev (1973) found age differences in diet explained changing parasite prevalences. Lawler (1970) reported that Bauer (1948) found benthic feeding coregonids had more trematodes and fewer cestodes than plankton eating forms. When older whitefish in the present study began to feed on benthic amphipods (*Pontoporeia affinis*), the abundance of *M. salmonis*, *C. truncatus* and *Cy. farionis* vectored through these increased. Differences in diet explain why younger pike have higher abundances of *T. nodulosus* (vectored by minnows and smaller fish) and smaller abundances of *T. crassus* (vectored by comparatively larger coregonids) then they do when they were older and could consume larger fish.

Prolonged plankton diet of cisco (compared with whitefish) explained why they accumulated plerocercoids of the copepod vectored *T. crassus* while the latter does not.

The order of decreasing parasite fauna diversity (Table 5) was whitefish, cisco and pike. This was the similar to decreasing diversity of diet (Table 14). It appears that with a more diverse diet an expected increase in parasite diversity occurs. Whitefish feed on plankton and benthic foods, cisco plankton and fish, and pike feed only on fish. These different types of foods vectored different parasites. As whitefish become benthic feeders they stayed in close proximity to the bottom and were possibly exposed to trematode cercaria released by molluscs. Addition of several trematodes (*T. intermedia*, *D. spathaceum etc.*) to their fauna increases their diversity. Leong (1975) found no correlation between the diversity of foods and of parasites. He explained it by four factors 1) importance of food items as intermediate hosts varied 2) digestion rates varied 3) host specificity of parasites varied and 4) parasites modified intermediate host behavior (increased susceptibility to predation).

In the present study there also existed a relationship between the similarity of diet (Table 14) and similarity of parasite fauna (Table 5). Similarity of diet between the coregonids, cisco and whitefish, resulted in similar parasite fauna. Parasites exhibited very little host specificity between these two species of fish, and as a result when their diets were similar the resulting parasite fauna was similar. Consumption of the amphipod intermediate host by both hosts make it hard to postulate the reason for the presence of *Cy. farionis* in whitefish and its total absence in cisco. The amphipod *Gammarus* may prove to be the intermediate for this nematode for unlike *Pontoporeia* which vectors *M. salmonis* and *C. truncatus* to both fish hosts, *Gammarus* is eaten only in quantities by whitefish.

Although many authors used diet to explain seasonal changes in parasite abundances, food analysis on a seasonal basis in this study was not possible. As water temperature increased fish fed more and digestion rate, like other biochemical processes in poikilothermic animals, increased. As a result food items rarely eaten may be identifiable at lower water temperatures, but commonly eaten food items may be digested so quickly at summer temperatures that they are unrecognizable soon after consumption. Seasonal differences in digestion rates are apparent in temperate lakes and prevents accurate seasonal analysis.

Differences in diet with season and fish age may explain the changes in the abundances of parasites that are eaten in intermediates hosts. Changes in the mode of feeding (planktonic to benthic) may also change the abundance of external parasites or parasites which pass the fish surface (trematode cercaria).

d) HOST SEX

Abundance of major parasites of whitefish, cisco and pike was studied to observe if differences existed between different sexes of host. No parasites exhibited a sexual bias.

Discussion

Differences in the abundance of parasite species in male and female hosts appears to be the exception and not the rule. Although Paling (1965) Kennedy (1968), Shooter (1973) and others have reported sexual differences other authors such as Welch (1952), Bibby (1972), Rumyantsev (1973) and Leong (1975) have not.

No one seems to have been able to explain why one parasite in a host can show sexual differences and not others, or why a parasite exhibits a sexual preference in one host species and not another.

Although major parasites were studied during every season and in hosts of every age in this study, no sexual differences in abundance occurred indicating that these parasites (in these hosts) did not have a sexual bias.

e) GEOGRAPHICAL LOCATION

In an effort to establish sampling locations that could separate future effects of lake impoundment from those of impoundment and current diversion, four sites were chosen as figure 2 illustrates. Sites B and D would be exposed to changing water currents in addition to water level increases, while sites A and C were narrow-necked bays which would not be influenced by current diversion. In order to test the similarities of parasites found at these sites the abundances of the major parasites were ranked and tested for significant differences using Kendall's T nonparametric correlation. Values for *T. crassus* and *T. intermedia* in whitefish and cisco from areas 4 and 5 (Fig. 1) were included for comparison with the four southerly sites. This was undertaken to evaluate the degree of representation of these sites of the whole lake parasite community (Append. XIII and XIV).

Abundances of major whitefish parasites and their ranking at each site appear in Append. XIII. The three most abundant parasites *T. intermedia*, *P. exiguus* and *D. spathaceum* did not change in ranking. Major differences in ranking resulted from the high abundance value for *M. salmonis* in site B giving it a rank of 4, while it ranked 9, 10.5 and 9 at sites A, C and D respectively. Although *E. nerkae* ranked 4th in sites

A and C (areas of restricted current) it ranked 9.5 and 11 at B and C respectively (Fig. 2). Abundance of *Crepidostomum farionis* was low in site C and ranks 10.5 while it ranked, 5 and 4 in A, B and D respectively. Ranking of the four sites, however, were not significantly different. Correlations of ranking appear in Table 15. The most similar ranking was between B and D while the least similar was B and C which were less than two miles apart (Fig. 2).

Ranking of abundances of major cisco parasites appear in Append. XIV. Although the most abundant parasite *P. filicollis* and the least abundant *D. sagittata* had identical rankings, other parasites had slightly differing rankings. Noticeable differences in ranking was the abundance of *E. nerkae* in site A with a rank of 2, while at sites B, C and D (Fig. 2) it ranked 6, 4 and 5 respectively. *D. spathaceum* ranked 2 and 3 at sites B and D while it ranked only 4 and 5 at sites A and C. Differences of ranking was significantly different between sites A and B (Table 15). Parasite ranking of site C was equally similar with site A and B and the parasite ranking of site D was equally similar with A, B and C.

Ranking of major pike parasites was similar and the ranking of the three most abundant parasites *T. monenteron*, *P. pinguis* and *T. crassus* at each of the four sites was identical (Append. XV). The most noticeable difference was the ranking of 4 for *T. nodulosus*

Table 15. Kendall's nonparametric correlation of parasite ranking at sampling locations

Whitefish:

	B	C	D
A	.59	.68	.56
B		.44	.83
C			.47

Cisco:

	B	C	D
A	*.43	.62	.71
B		.62	.71
C			.71

A ≠ B

Pike:

	B	C	D
A	.90	.90	.52
B		.81	.62
C			*.43

C ≠ D

*Ranking Significantly Different, $p < .05$

at site D while it ranked 7th at A, B and C. In contrast, *C. lobotes* ranked 7th at site D while it ranked 5, 6 and 4 at sites A, B and C respectively. Differences in ranking was significant between C and D which were less than one mile apart (Table 15). Most similar were sites A and B and sites A and C.

Abundance of *T. crassus* in whitefish and cisco at areas 4 and 5 was comparable to that in sites A, B, C and D. Although abundance of *T. intermedia* in cisco was comparable to these southern sites, that of whitefish was considerably higher.

Discussion

Although much research has been done on the separation of marine fish stocks using parasite indicators by many authors (Margolis 1963, 1967; Gibson 1972; Isles 1971; Pippy 1969a, 1969b; and others) little work has been done with freshwater species. Differences in parasite infections were explained by salinity (Shotter 1973), differing habitats which resulted in slightly different host behavior, feeding and or migrations (Hicks and Threlfall 1973). The latter authors also explained differences by unequal distribution of intermediate hosts. Lawler (1970) reported that Petersson (1969) separated stocks of cisco by degrees of *T. crassus* infection. Lawler (1969) found shallower areas of Lake Mälaren, Sweden had lower incidences of *T. crassus*. Oakland (1949) and Sunde (1963) found differing levels of *T. crassus* infections in areas separated by less than 9 and 2 miles respectively. *T. crassus* larvae are long lived and should be a more sensitive biological tag than parasites that appear and disappear seasonally.

No areas were different when the ranking of major whitefish parasites were analysed. This was as expected because of the close proximity of the sampling sites (Fig. 2) and the similarity of whitefish age distribution at the four sites.

Differences in the parasite fauna of cisco at sites A and B resulted from the greater abundance of *E. nerkae* at site A. Site A does not have a current unlike site B. Other basic ecological differences undoubtedly also exist. Cisco at site A also tended to be younger than at site B and as *E. nerkae* tended to decrease in abundance with host age this explains most of the difference.

Major differences in ranking of pike parasites between sites C and D resulted from higher abundances of *T. nodulosus* at C and lower abundances of *C. lobotes* at site C. Cyprinids which vector the metacercaria of *C. lobotes* were in much greater abundance at site C and explains the greater abundance of the mature trematodes in pike here. Plerocercoids of *T. nodulosus* are vectored by perch and young burbot (Lawler 1968, 1969a). Burbot were most abundant in site D but perch were almost absent from both locations. It is possible that differences in the availability of intermediate hosts might explain the greater abundance of *T. nodulosus* at site D.

It appears that though some parasites such as *T. crassus* may have similar abundances in widely separated parts of the lake, abundances of other parasites like *T. intermediate* in whitefish may be more representative of a smaller area. Such differences may result from an unequal distribution of intermediate host for some parasites (such as snails) and not others (copepods) or the relative abundance of host fish species. Although not a complete comparison of these two parts of the lake, it does draw attention to the danger of generalizing from sampling site(s) to a large lake.

Generally most differences in sampling sites which did not differ greatly in proximity or depth can only be explained by differences in intermediate hosts or by differences in the age class structure of host species.

VIII. MUSCULAR DISTRIBUTION OF PLEROCERCOID CESTODES

Plerocercoids of *T. crassus* and *Diphyllobothrium sp.* II are located in the musculature of their intermediate hosts (whitefish or cisco) and the pike respectively. These plerocercoids were not evenly distributed in the musculature and a comparison was made between their distributions.

Prevalence of plerocercoids of *T. crassus* was highest in the right anterior epaxial muscle of whitefish. Cestodes were much more prevalent in the right side, the upper muscle and the anterior end of the whitefish. In intensity was significantly higher ($p<0.01$). Ratio of *T. crassus* plerocercoids on the right/left side was 1.31 (Table 16).

Similarly plerocercoids of *T. crassus* also had higher intensity in the right anterior epaxial musculature of cisco, however, unlike the corresponding higher prevalences of plerocercoids in the anterior and epaxial muscle, the plerocercoids were more prevalent on the left side and not the right. Although ratio of intensity of plerocercoids on the right/left side of cisco was 1.24 and was significant ($p<0.05$), cestode abundance was actually higher on the left side (Table 16).

Table 16. Distribution of cestode plerocercoids in host musculature

Position in Musculature	*T. crassus* Whitefish	*T. crassus* Cisco	*Diphyllobothrium* Pike
Anterior	0.78 (.44) [0.96]	0.61 (.58) [1.07]	0.79$^{\Psi}$ (.37) [0.82]
<			
Posterior	0.21 (.18) [0.22]	0.13 (.22) [0.25]	0.73 (.40) [0.83]
Epaxial	1.23 (.48) [1.64]	0.88 (.62) [1.49]	1.17 (.50) [1.61]
<			
Hypaxial	0.23 (.06) [0.07]	0.15 (.07) [0.08]	0.39 (.09) [0.13]
Right	0.55 (.35) [0.61]	0.41* (.47) [0.71]	0.62 (.32) [0.59]
<			
Left	0.42 (.32) [0.49]	0.33 (.64) [0.89]	0.87 (.44) [1.05]

*Significant at $p < .05$

ΨNot significant

all others significant $p < 0.01$

A (B) [C] a = prevalence, b = intensity c = abundance

Distribution of plerocercoids of *Diphyllobothrium sp. II* in pike exhibited no anterior/posterior bias. Intensity and prevalence was greater in epaxial and left musculature of pike (Table 16). Ratio of plerocercoid intensity left/right was 1.40.

Discussion

Although several studies of the distribution of *T. crassus* plerocercoids are reported (Newton 1932; Welch 1952; Miller 1945, 1952) no such study has been done on the distribution of plerocercoids of *Diphyllobothrium*. Newton (1932) found the orientation of *T. crassus* plerocercoids in whitefish was random but their distribution was not. He found 80% of plerocercoids in the anterior muscle, 10% in the posterior epaxial and remaining plerocercoids in the hypaxial musculature. He did not study a right/left bias. Welch (1952) found an anterior and right preference in whitefish. He found 54% of cysts found were on the right side and suggested as did Miller (1945, 1952) that as the stomach was to the right of the midline, cestode larvae emerged and were encysted here. Miller (1952) found the majority of plerocercoids anterior to the anus and around the body cavity (their point of origin). His right/left ratios for Lesser Slave and Square Lake were 1.30 and 1.23 respectively. These were somewhat higher than those of Welch (1952). Freese (1970) used ultrasonic detectors to accurately locate plerocercoids of *T. crassus* in whitefish. His right/left ratio was 1.5. He also found epaxial muscle was more infected near the surface which he attributed to migration of cysts under muscle pressure.

Ratio of the abundance of *T. crassus* plerocercoids in the right/left of whitefish from this study was most similar to that of Square Lake. Although no explanation for the variability of this lateral bias in the distribution of this cestode in whitefish has been proposed, it may be that these values are characteristic for stocks of whitefish. Differences could be based on host physiology or anatomy or on some difference in the parasite itself at these different locations. It is less difficult to explain anterior and epaxial biases, merely on the basis of relative muscle mass. Anterior and epaxial musculature are more extensive then are their counterparts and could be expected merely on a chance basis to contain more plerocercoids.

Lateral distribution of *T. crassus* in cisco was unusual because of the significantly different ($p < .05$) but opposite biasis of cestode intensity and prevalence. It may be that for some inexplicable reason stomach and/or pyloric region positioning is such that more plerocercoids enter the left side of the host (in contrast to whitefish), but somehow survival rate on this side is less than that of the right.

The elongate shape of pike explains the lack of any anterior bias in the distribution of *Diphyllobothrium*. With anterior and posterior muscle masses nearly equal, change infection results in an equal distribution. The greater epaxial muscle mass explains the significantly higher abundances here then in the hypaxial muscle.

It was not possible to distinguish a left/right asymmetry of the position of the pike stomach. Buckle (1971) did not describe such asymmetry though he worked on the anatomy of the pike alimentary system. Intestinal asymmetry may exist and have produced right/left abundance differences.

Little explanation can be offered for the unequal distribution of cestode plerocercoids in the musculature of fish other than unequal muscle mass and asymmetrical positioning of the stomach/intestine from which the plerocercoids leave.

IX. *TRIAENOPHORUS CRASSUS* AND HOST CONDITION

Plerocercoids of *T. crassus* were approximately 1.5 by 0.75 centimeters as they occur encysted in the musculature of whitefish and cisco. With such a large parasite size relative to host size particularly in young fish, and with several plerocercoids usually occurring within the musculature of an infected host, some type of adverse effect on the host would be expected.

To investigate the effect of *T. crassus* upon infected whitefish and cisco, the ratio of host weight to host length and to host length cubed were calculated as indices of host condition. The latter value was less sensitive to changes in host condition and will not be discussed further. Condition values representing the weight/length ratio for different aged whitefish and cisco appear in Table 17.

Whitefish infected with plerocercoids of *T. crassus* were generally shorter and weighted less except fish younger than one year old. These changes were not proportional and infected whitefish were generally thinner or lighter for their lengths than uninfected whitefish. This was true for all but the 0 and 2 year old fish. These differences in condition were significant in fish 8 and 9 years and older ($p < .10$ and .05 respectively) (Table 17).

Table 17. Effect of *Triaenophorus crassus* plerocercoids on host condition

condition = weight/length

	Whitefish			Cisco		
Age	uninfected		infected	uninfected		infected
0	1.00	<	1.05	1.01	>	0.91 *
1	1.88	>	1.84	1.27	<	1.31
2	3.17	<	3.38	2.28	<	2.31
3	5.52	>	5.00	3.93	<	4.09
4	8.13	>	7.64	5.52	<	5.75
5	12.12	>	11.98	7.88	<	8.09
6	16.88	>	16.04	9.25	<	9.64
7 (+)	20.90	>	20.10	10.71	<	12.75 *
8	24.35	>	22.58 **			
9 (+)	27.21	>	25.69 *			

* Significant < .10

** Significant < .05

In contrast, infected cisco were heavier and longer. These changes were not proportional and infected fish generally had heavier bodies for their length. Again the fish aged 0 were an exception and were significantly lighter per unit body weight ($p < .10$) than their uninfected counterparts. In contrast, infected cisco of 7 years and older had significantly more body weight per unit length ($p < .10$) and were in better condition than uninfected fish of the same age (Table 17).

Discussion

Several authors showed changes in the physiological condition of infected fish such as increased oxygen consumption (Lester 1971, Meakins and Walkey 1975). Sweeting (1974) found that implanting the plerocercoids of *Ligula* into fish caused changes in swimming behavior, atrophy of organs and an immunological response. Besides mucosal damage Bauer and Nikol'skaya (1957) found *M. salmonis* reduced the nutritional state of the fish. Petersson (1971a) was unable to demonstrate changes in the weight/length ratio of infected whitefish at various ages. Miller (1945b) found that the presence of *T. crassus* in whitefish and cisco caused slight decreases in the growth rate (more so in weight than length). He found less of an effect in what he termed the resistant older fish. This condition change was increased with increased infection and was more pronounced in whitefish (incidental hosts) than cisco (natural host) (Miller 1945b).

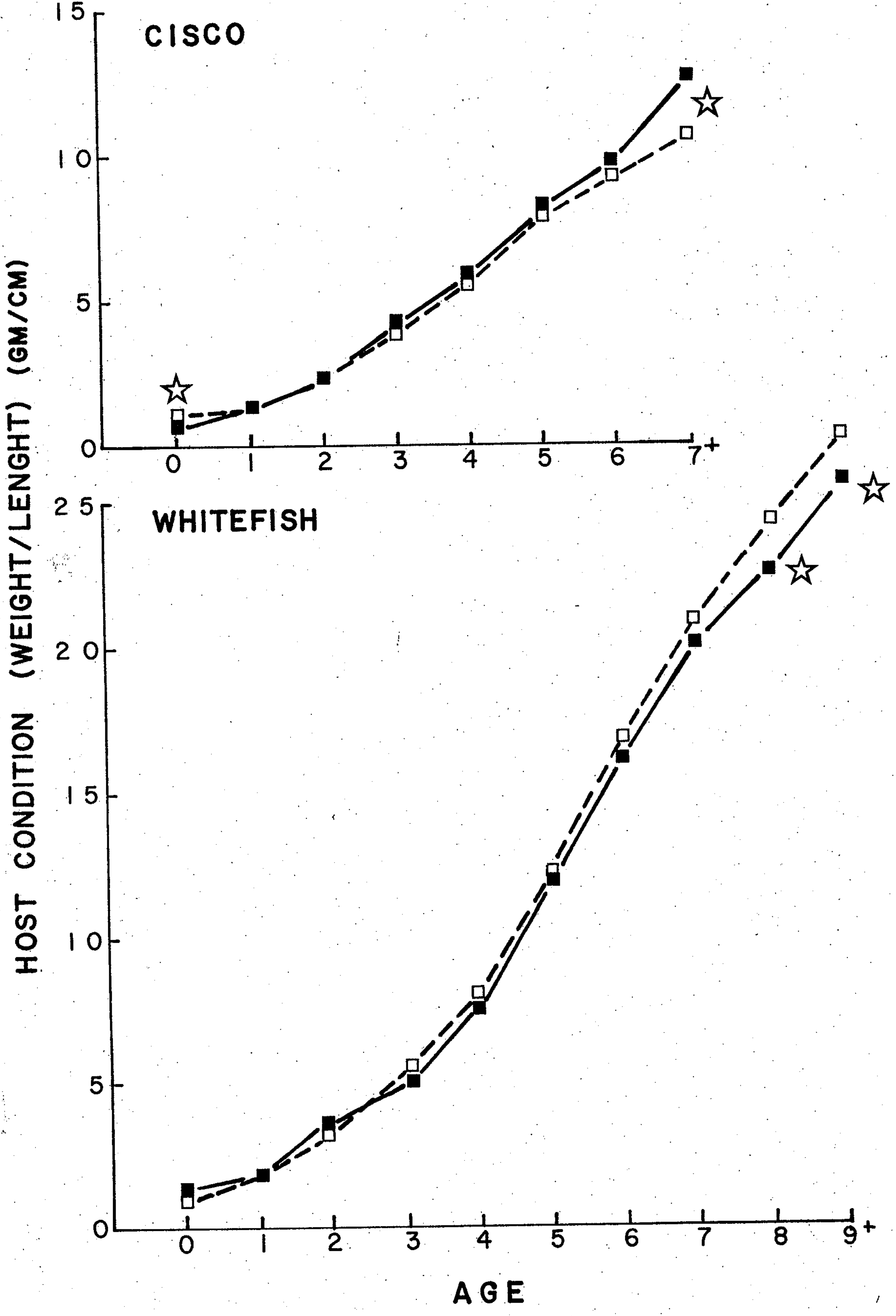
Condition of infected whitefish decreased with respect to uninfected whitefish until by 8 years of age their condition was significantly worse (Fig. 21). Effect of *T. crassus* in the muscle would appear to slow the weight gain of whitefish relative to their growth in length. The longer this retardation of weight gain is in effect, the greater the resultant effect. Whether this is competition for nutrients between the plerocer-

Figure 19. Effect of *Triaenophorus crassus* plerocercoids on host condition.

□ uninfected

■ infected

☆ significant difference $p < .1$



CISCO
WHITEFISH
HOST CONDITION (WEIGHT/LENGHT) (GM/CM)
AGE
15
10
5
0
25
20
15
10
5
0
0
1
2
3
4
5
6
7+
0
1
2
3
4
5
6
7
8
9+

coid and host tissues or simply an adverse effect due to a more active immune response to the parasite cannot be answered. Plerocercoids which are fully encysted and walled off probably do not have much of a biochemical exchange with the surrounding host tissue though this cannot be easily tested. Young of the year whitefish and cisco that eat more plankton could be expected to gain weight more quickly nourished by this rich food source. If the extra plerocercoids they consume as a result do not have an immediate adverse effect they can be expected to be in better condition. Such an immediate effect might explain the greater weight/length ratio of infected young of the year whitefish. In contrast, cisco of the same age appeared to be adversely affected by plerocercoids consumed with plankton and their condition is reduced. Older cisco, however, did not appear to be adversely affected by *T. crassus*. Feeding on plankton, cisco grow more quickly and their growth does not appear to be retarded by plerocercoids. As a result infected cisco of 7 years of age and older are significantly better condition. Effect of plerocercoids on young cisco and not older year classes could have two explanations. The plerocercoid are larger in relation to fish size in younger cisco and as plerocercoids were only recently picked up they are frequently not encysted. Non-encysted plerocercoids might stimulate a greater immune response or take up more nourishment from the host. As the fish grows most plerocercoids are found encysted and walled off and the effect of increased plankton in the diet might become more positive than negative.

It is possible that if infection levels in S.I.L. cisco and whitefish increase that the condition of whitefish and possibly cisco would be more adversely affected by the cestode presence.

X. GENERAL DISCUSSION

The parasite fauna of whitefish, cisco and pike have been qualitatively and quantitatively described as they exist before impoundment and current diversion of S.I.L. The parasite fauna of this host "community" is dominated by pike parasites and not amphipod vectored salmonid parasites as Leong (1975) and others found elsewhere. In addition within the salmonid species surveyed, amphipod vectored parasites were second to trematode metacercaria and copepod vectored cestodes.

The various patterns of abundance caused by age and season are influenced by host diet. It is the single most important factor affecting changes in abundance of parasites with different host age, season, host sex and location. Water temperature is possibly also an important causal agent of changes in parasite abundance with season and age.

Parasite diversity of the host species in this study was not related to increasing sample size and this indicated an adequate sample size had been taken. Changes of parasite abundance with host age and abundance can cause samples taken at one period in time or those which include only limited age groups of fish to be unrepresentative of the parasitofauna of the lake. Samples should preferably be taken on at least a monthly basis including all age groups. The present study suggests that such monthly samples should include at least 15 specimens from each study species per location. Stations used in the present study were similar and could be combined to provide an adequate sample size of greater than 60 per month of each species.

Although the parasite fauna of the four sampling sites were similar the data cannot be unconditionally used to extrapolate to the whole lake. It is evident that parasites like *T. crassus* did not vary much in abundance over large distances while *T. intermedia* did, even though these were both larval parasites with a long life span and thus were good biological tags.

Distribution of cestode; plerocercoids in the musculature of their hosts revealed that the patterns could not be explained simply on the basis of relative muscle mass or intestinal asymmetry.

Plerocercoids significantly reduced host condition in older whitefish and young cisco and the explanation must be the relative consumption of plankton and adaptation to the encysted parasite.

S.I.L., is a unique opportunity to study the parasite fauna of several fish species as their environment becomes modified by lake impoundment and current diversion.

Many aspects of lake chemistry and biology have been studied concurrently by workers at S.I.L. and the changes they have predicted are already occurring. The lake level will be raised over 3 meters through control of the lake's principal outlet at Missi Falls (Fig. 2) and a diversion channel will be created from South Bay (Area 6, Fig. 2) to the Rat River system to the south. Effects on lake biology will be due to both current diversion and lake impoundment.

Lubinsky (1973) reported Smirnova (1955) and several other Russian authors found that flooding and subsequent dilution of fish stocks caused a reduction in abundance of parasitic protozoa, monogenetic trematodes and parasitic copepods as the chance of contact with the appropriate host declined. This was followed by a period of rapid increase and these parasites may exceed original levels. Smirnova (1955) and other authors report pathogenic effects on fish as a result. They found that parasites such as digenetic trematodes and cestodes which have invertebrate hosts increase in abundance as their invertebrate host do and are often slow to return to original levels.

Hecky *et al*. (1974) predicted a reduction in primary productivity in the north end of the S.I.L. in response to reduced Churchill River flow through that area. In contrast, productivity of the south-eastern area (Area 6, Fig. 1) is expected to increase with the influx of diverted Churchill River water.

Patalas and Salki (1974) expect zooplankton productivity to decrease in the central and northern part of the lake (Areas 3, 4; Fig. 1). It is expected overall benthic production will be reduced 15-30%, post diversion (Hamilton 1974). While northern areas might decrease 25-50% in productivity the extreme south of the lake should improve.

Ayles and Koshinsky (1974) expect whitefish and cisco populations to increase initially, but over the long term their population sizes will be decreased. They expect pike to increase in size, condition and number with impoundment.

In summary, patterns of primary and zooplankton production will change, benthic production will decrease and pike will become more abundant. With such drastic changes occurring in the lake, including changes in the abundance of intermediate and definite hosts, changes in the parasite fauna is expected. One of these *T. crassus*, is of potential economic importance. Whitefish are an important commercial fish in this lake. Diet has been shown to consist of plankton in younger fish which changes to benthos in older fish. The former consists of *Cyclops* and other copepods which vector the cestodes *Proteocephalus* and *Triaenophorus* and the later *Gammarus* and *Pontoporeia* which vector *M. salmonis*, *C. truncatus* and *Cy. farionis*, common salmonid parasites in other studies. If as predicted by Hamilton (1974) benthic (amphipod) populations decrease then a similar situation to that studied by Petersson (1971a) will develop. He found that with decreased amphipod populations coregonids with variable gill raker numbers (whitefish and cisco) were forced to feed to a greater extent on cestode vectoring copepods. Cestodes such as *T. crassus* and *Proteocephalus* increased in abundance while amphipod vectored parasites like *M. salmonis*, *C. truncatus* and *Cy. farionis* declined sharply (Petersson 1971a). The same result is predictable at S.I.L. This alone would be expected to increase the number of plerocercoids of *T. crassus* in whitefish. With increased consumption of cestode carrying copepods, the number of *T. crassus* plerocercoids in whitefish could no longer be independent of age but as work by Miller (1952) predicts will begin as with cisco (which have a higher intake rate of infected copepods than whitefish), to accumulate with age. This process will result in a substantially increased number of plerocercoids by the time the fish is of marketable size and age. Until now S.I.L. has been below the rejection level of 40 plerocercoids per 100 pounds of dressed fish but an increase in infection level may cause rejection of whitefish. This would result in a loss of income to fisherman in the area who will already have to cope with other flooding effects such as submerged trees.

In summary:

1) Parasitofauna of whitefish, cisco and pike are evaluated; the species are listed with their intensities, prevalences, abundances, dominances, diversities and similarities.

2) Parasite abundance is modified by five factors: (a) host age (b) season (c) food habits (d) geographical location.

3) Adequate sample size to represent the parasitofauna of these host species was found to be approximately 15 fish of varying ages per month per station, if stations do notdiffer significantly in parasitofauna.

4) Although samples taken were probably representative of the whole lake for *T. crassus* they may not be for other species and erroneous extrapolations must be avoided.

5) Distribution of *T. crassus* and *Diphyllobothrium sp.* plerocercoids within the musculature of their hosts was non random and could not be explained by muscle mass or stomach position in all cases.

6) *T. crassus* plerocercoids significantly reduced host condition in some age groups and not in others suggesting that host immunity and diet are involved.

7) With lake diversion and impoundment cestodes vectored by copepods (*T. crassus* and *Proteocephalus*) will increase in abundance while those vectored by amphipods (*M. salmonis*, *C. truncatus* and *Cy. farionis*) will be reduced as decreased intermediate host availability changes host diet and behavior.

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* reference not seen

Appendix I. Parasite Surveys of the Salmonidae and Esocidae

Author and Date	Location	Codes of species comparable to present study
Petersson 1971b	Sweden	1, 8, 10, 11
Bauer 1970	U.S.S.R.	1, 8, 10, 11 and other European spp.
Rumyantsev 1973	U.S.S.R.	1
Bauer and Nikol'skaya 1957	U.S.S.R. L. Ladoga	8
Hoffman 1967	North America	*all except European spp.
Lawler 1970	North America	*all non European coregonids but 14
Miller 1941	Canada	28, 33*
Smedly 1933	Canada	*4, 24, 33*
Price and Arai 1967	Canada (Review)	*3, 5, 15, 16, 29, 33*, 34
Cooper 1921	Canadian Arctic	*4, 27, 29, 30
Van Cleave 1921	Canadian Arctic	29, 30
Wardle 1933	Sask. to Que., and N.W.T.	*3, *4, 31, 32, 33*, 39
Fantham and Porter 1948	Que. and N.S.	28, 33*, 35
Bangham and Adams 1954	Mainland B.C.	16, 27, 28, 30, 31, 33*, 35
Arai and Chien 1973	Alberta	33*
Lubinsky 1976	Manitoba	3*, 4*, 30, 33*, 34
Wardle 1932	Area of Straits of Georgia, B.C.	19, 20, 21

*species included in this study

Appendix I. Continued

Author and Date		Location	Codes of species comparable to present study
Lyster	1939	Ottawa, St. Lawrence Rivers, L. St. Louis	33*, 34
Sandeman and Pippy	1967	Insular, Nfld.	4*, 24, 25, 26, 28
Threlfall and Hanek	1970a	Labrador	33*
Hicks and Threlfall	1973	Coastal Labrador	4*, 15, 25, 26, 28, 30
Choquette	1951	St. Lawrence Watershed	34
Bangham	1940	Algonquin Park	3*, 4*, 15, 28
MacLulich	1943	Algonquin Park	26, 28
Hare and Burt	1975	Miramichi River, N.B.	25
Threlfall and Hanek	1970b	Avalon Peninsula, Nfld.	4*, 25, 26, 28
Hunter III and Rankin Jr.	1939	Connecticut Lake	32, 33*, 35
Lyster	1940	Lake Commandant, Que.	28, 30
Richardson	1942	Lake Wakonicki, Que.	4*, 28, 33*
Hanek and Molnar	1974	Matemek River, Que.	25, 27, 28
Bangham and Hunter III	1939	Lake Eire	3*, 4*, 32, 33*
Bangham	1955	Lake Huron, Manitoulin Is.	2, 3*, 4*, 15, 24, 28, 30, 33*, 34

*species included in this study

Appendix I. Continued

Author and Date		Location	Codes of species comparable to present study
Hanek and Fernando	1972	Bay of Quinte, Ontario	33*
Leong	1975	Cold Lake, Alta.	3*, 4*, 19, 24, 30, 31, 33*
Dechtiar	1972	Lake of the Woods, Ontario	3*, 4*, 30, 33*, 34
Lawler	1954	Heming Lake, Man.	3*, 4*, 33*
MacTavish	1952	Southern Indian Lake	3*, 4*, 33*

Sub Family Coregoninae (Whitefishes, Ciscoes, and Round Whitefish)

1.	☒ *Coregonus*	*albula*	Linnaeus	cisco
2.	*C.*	*alpenae*	(Koelz)	longjaw cisco
3.	*C.*	* *artedii*	Lesueur	cisco
4.	*C.*	* *clupeaformis*	(Mitchill)	lake whitefish
5.	*C.*	*hoyi*	(Gill)	bloater cisco
6.	*C.*	*johannae*	(Wagner)	deepwater cisco
7.	*C.*	*kiyi*	(Koelz)	kiyi cisco
8.	☒ *C.*	*lavaretus*	Linnaeus	whitefish
9.	*C.*	*nelsoni*	Bean	humpback whitefish
10.	☒ *C.*	*peled*	Gmelin	cisco
11.	☒ *C.*	*pidschian*	Gmelin	whitefish
12.	*C.*	*reighardi*	(Koelz)	shortnose cisco
13.	*C.*	*zenithicus*	(Jordan and Svermann)	shortjaw cisco
14.	*C.*	*nasus*	(Pallas)	broad whitefish
15.	*Prosopium*	*cylindraceum*	(Pallas)	round whitefish
16.	*P.*	*williamsoni*	(Girard)	mountain whitefish

Appendix I. Continued

Sub Family Salmoninae (Salmons, Trouts and Chars)

17.	*Oncorhynchus*	*gorbuscha*	(Walbaum)	pink salmon
18.	*O.*	*keta*	(Walbaum)	chum salmon
19.	*O.*	*kisutch*	(Walbaum)	coho salmon
20.	*O.*	*nerka*	(Walbaum)	sockeye salmon
21.	*O.*	*tshawytscha*	(Walbaum)	chinook salmon
22.	*Salmo*	*aquabonita*	Jordan	golden trout
23.	*S.*	*clarki*	Richardson	cuthroad trout
24.	*S.*	*gairdneri*	Richardson	rainbow trout
25.	*S.*	*salar*	Linnaeus	Atlantic salmon
26.	*S.*	*trutta*	Linnaeus	brown trout
27.	*Salvelinus*	*alpinus*	(Linnaeus)	arctic char
28.	*S.*	*fontinalis*	(Mitchill)	brook trout
29.	*S.*	*malma*	(Walbaum)	Dolly Varden
30.	*S.*	*namaycush*	(Walbaum)	lake trout

Sub Family Thymallinae (Grayling)

31.	*Thymallus*	*arcticus*	(Pallas)	arctic grayling

Family Esocidae (Pikes and Pickerels)

32.	*Esox*	*americanus*	Gmelin	redfin pickerel
33.	*E.*	**lucius*	Linnaeus	northern pike
34.	*E.*	*masquinongy*	Mitchill	muskellunge
35.	*E.*	*niger*	Lesueur	chain pickerel

☒ non North American species

* species of present study

Taxonomy after Scott and Crossman (1973)

Appendix II. Species of fishes in Southern Indian Lake, Manitoba. (after Scott and Crossman 1973)

Fish Species		Common Name
Salmonidae		
Coregonus clupeaformis	(Mitchill)	Lake whitefish
C. artedii	LeSueur	Cisco
Esocidae		
Esox lucius	Linnaeus	Northern pike
Percidae		
Etheostoma nigrum	Rafinesque	Johnny darter
Perca flavescens	(Mitchill)	Yellow perch
Stizostedion vitreum	(Mitchill)	Walleye
S. canadense	(Smith)	Sauger
Catostomidae		
Catostomus commersoni	(Lacepede)	Whitesucker
C. catostomus	(Forester)	Longnose sucker
Percopsidae		
Percopsis omiscomaycus	(Walbaum)	Trout-perch
Gadidae		
Lota lota	(LeSueur)	Burbot
Cottidae		
Cottus cognatus	Richardson	Slimy sculpin
Gasteroteidae		
Pungitius pungitius	(Linnaeus)	Ninespined stickleback
Culaea inconstans	(Kirtland)	

Appendix II. Continued

Fish Species		Common Name
Hiodontidae		
Hiodon alosoides	(Rafinesque)	Goldeye
Cyprinidae		
Notropis hudsonius	(Clinton)	Spottail shiner
N. atherinoides	Rafinesque	Emerald shiner

Appendix III. Calculation of diversity measures (after Leong 1975)

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1. The number (S) of parasites recovered.
2. The total number of individuals of all species of parasites (N) in the sample.
3. The Shannon-Weaver index of diversity (H') (Shannon and Weaver 1949) calculated as:

$$H' = -\sum_{i=1}^{S} Pi \; \ln Pi$$

where Pi = the proportional abundance of parasite i and $\ln$ = natural logarithm

4. The reciprocal of Simpson's index (SI) (Simpson 1949) calculated as:

$$SI = \frac{1}{\sum_{i=1}^{S} (Pi)^2}$$

5. An index of evenness (E) (Hurlburt, 1971) calculated as:

$$E = \frac{H' - H' \text{ min}}{H'_{max} - H'_{min}}$$

where $H'_{min} = \ln N - \frac{N-S+1}{n} \ln(N-S+1)$

and $H'_{max} = \ln S$

Appendix IV. Abundance of major whitefish parasites with host age

	A G E (YRS)									
	0	1	2	3	4	5	6	7	8	9+
Number Examined	27	47	12	25	52	53	64	78	65	63
T. intermedia	(.04)	(.04)	0.55 (.50) [0.87]	1.74 (.80) [4.55]	2.69 (.81) [11.86]	2.86 (.81) [14.19]	3.34 (.83) [23.48]	3.57 (.96) [34.24]	3.27 (.92) [24.31]	3.50(.95) [31.59]
D. spathaceum	(.04)	(.00)	(.08)	1.54 (.52) [2.42]	1.90 (.50) [3.41]	2.25 (.55) [5.20]	2.23 (.48) [4.49]	1.79 (.55) [3.31]	2.00 (.49) [3.64]	2.52(.51) [6.32]
M. salmonis	(.00)	0.65 (.15) [0.29]	1.31 (.42) [1.54]	0.88 (.56) [1.36]	1.14 (.36) [1.14]	1.34 (.51) [1.94]	1.67 (.39) [2.07]	1.20 (.49) [1.62]	1.61 (.48) [2.38]	1.63(.46) [2.34]
C. truncatus	(.00)	(.00)	(.17)	1.90 (.24) [1.60]	2.23 (.15) [1.43]	1.97 (.23) [1.62]	1.91 (.22) [1.48]	1.67 (.31) [1.64]	1.68 (.37) [1.98]	2.14(.37) [3.10]
Cy. farionis	(.04)	(.02)	(.08)	(.20)	0.82 (.23) [0.53]	1.23 (.36) [1.23]	1.48 (.47) [2.07]	1.44 (.36) [1.52]	1.41 (.43) [1.76]	1.94(.49) [2.33]
P. exiguus	1.30 (.82) [3.00]	1.99 (.83) [6.09]	1.62 (.83) [4.23]	2.95 (.84) [16.05]	2.46 (.75) [8.79]	2.37 (.68) [7.24]	2.42 (.75) [8.46]	2.50 (.70) [8.63]	2.54 (.69) [8.77]	2.78(.62) [9.97]
T. crassus	0.38 (.31) [0.45]	0.61 (.31) [0.58]	0.51 (.54) [0.90]	0.45 (.56) [0.89]	0.54 (.53) [0.91	0.66 (.53) [1.01]	0.63 (.48) [0.90]	0.57 (.45) [0.79]	0.45 (.48) [0.75]	0.56(.50) [0.88]
Raphidascaris sp.	(.04)	(.04)	(.08)	0.41 (.28) [0.42]	0.60 (.27) [0.49]	0.95 (.19) [0.49]	0.89 (.33) [0.80]	0.65 (.23) [0.44]	1.48 (.20) [0.88]	0.77 (.33) [0.72]
D. sagittata	(.00)	(.02)	(.08)	0.80 (.48) [1.06]	0.49 (.21) [0.35]	0.37 (.34) [0.49]	0.38 (.33) [0.48]	0.57 (.41) [0.72]	0.70 (.25) [0.49]	0.66 (.43) [0.83]
Cr. farionis	(.00)	(.04)	(.00)	(.00)	(.04)	(.17)	(.16)	(.14)	(.20)	(.19)
S. extumescens	(.00)	(.00)	(.00)	(.00)	(.15)	(.15)	(.14)	(.24)	(.26)	(.13)
E. nerkae	(.15)	(.27)	(.08)	(.18)	(.15)	(.04)	(.08)	(.04)	(.02)	(.00)

I(P) I = Log Intensity P, Prevalence A, Abundance
(A)

Appendix V. Abundance of major cisco parasites with host age

	A G E (YRS)							
	0	1	2	3	4	5	6	7+
Number Examined	33	69	24	60	65	63	49	40
T. intermedia	(.00)	(.01)	(.04)	0.45 (.18) [0.29]	0.74 (.32) [0.68]	1.13 (.40) [1.23]	1.54 (.55) [2.58]	1.45 (.68) [2.88]
D. spathaceum	(.00)	(.01)	(.08)	0.81 (.10) [0.22]	1.19 (.17) [0.56]	1.42 (.35) [1.44]	2.00 (.43) [3.18]	2.00 (.42) [3.15]
T. crassus	0.17 (.40) [0.47]	0.31 (.46) [0.62]	0.51 (.70) [1.17]	0.58 (.77) [1.38]	0.54 (.71) [1.22]	0.70 (.74) [1.49]	0.69 (.72) [1.44]	1.08 (.74) [2.16]
P. filicollis exiguus	3.24 (.94) [23.93]	2.33 (.94) [9.71]	2.43 (.92) [10.37]	3.01 (.93) [18.85]	3.21 (.86) [21.40]	3.25 (.75) [19.18]	3.01 (.69) [14.12]	3.26 (.75) [19.64]
D. sagittata	(.00)	(.00)	(.00)	(.08)	0.24 (.22) [0.27]	0.36 (.24) [0.34]	0.58 (.18) [0.33]	0.50 (.12) [0.20]
Raphidascaris sp.	(.00)	1.05 (.60) [1.71]	1.04 (.57) [1.61]	1.63 (.47) [2.41]	1.27 (.46) [1.63]	1.58 (.58) [2.80]	1.52 (.48) [2.18]	2.00 (.50) [3.68]
E. nerkae	0.31 (.24) [0.33]	0.86 (.17) [0.41]	1.03 (.29) [0.82]	1.29 (.33) [1.20]	1.65 (.22) [1.12]	0.93 (.21) [0.52]	(.08)	(.05)

Same key as Appendix IV

Appendix VI. Abundance of major pike parasites with host age

	A G E (YRS)							
	0	1	2	3	4	5	6	7+
Number Examined	2	10	21	55	74	78	46	68
Diphyllobothrium sp.II	(.00)	(.00)	(.14)	0.50 (.35) [0.57]	0.65 (.49) [0.93]	1.13 (.64) [1.98]	1.13 (.61) [1.88]	1.11 (.66) [2.00]
Proteocephalus pinguis	(1.00)	3.62 (1.00) [37.41]	3.24 (1.00) [25.48]	3.22 (.93) [23.08]	3.30 (.96) [26.03]	3.55 (.99) [34.29]	3.56 (.96) [33.48]	3.82 (.96) [32.38]
Raphidascaris sp.	(.00)	3.62 (.60) [1.71]	1.04 (.57) [1.61]	1.63 (.47) [1.41]	1.27 (.46) [1.63]	1.58 (.58) [2.80]	1.52 (.48) [2.18]	2.00 (.50) [3.68]
Centrovarium lobotes	(.00)	(.10)	1.33 (.29) [1.08]	2.20 (.13) [1.15]	1.81 (.12) [0.75]	2.12 (.17) [1.40]	1.46 (.20) [0.84]	2.10 (.25) [2.04]
Triaenophorus nodulosus	(.00)	0.82 (.50) [1.13]	1.60 (.29) [1.42]	1.05 (.27) [1.12]	1.05 (.28) [0.81]	1.33 (.26) [0.97]	1.69 (.15) [0.82]	1.33 (.24) [0.92]
Triaenophorus crassus	(.00)	1.10 (.60) [1.80]	1.02 (.62) [1.72]	2.22 (.76) [7.07]	2.00 (.78) [5.79]	2.40 (.82) [9.07]	2.30 (.83) [8.20]	2.17 (.84) [7.37]
Tetraonchus monenteron	(.00)	3.60 (.50) [18.24]	3.85 (.67) [31.25]	4.13 (.71) [44.22]	4.26 (.73) [51.95]	4.63 (.63) [64.38]	4.82 (.67) [83.89]	4.85 (.60) [76.72]

Same Key as Appendix IV.

Appendix VII. Abundance of major whitefish parasites with season

	JAN.	MARCH	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	DEC.
Number Examined	7	4	41	147	118	135	87	7	23
T. intermedia	3.13 (1.00) [22.83]	3.60 (1.00) [36.64]	3.46 (.85) [27.05]	3.04 (.83) [17.32]	3.20 (.60) [14.67]	3.25 (.71) [18.34]	3.38 (.77) [22.44]	(1.00)	(1.00)
D. spathaceum		(1.00)	1.73 (.35) [1.99]	2.12 (.80) [6.69]	2.20 (.45) [4.09]	1.98 (.53) [3.84]	1.95 (.51) [3.56]	(.29)	(.96)
P. exiguus	(.86)	(.50)	2.70 (.88) [13.01]	2.56 (.73) [9.41]	2.44 (.76) [8.71]	2.28 (.85) [8.35]	2.16 (.78) [6.79]	(.29)	(.09)
T. crassus	0.32 (.54) [0.75]	(.50)	0.58 (.57) [1.02]	0.63 (.49) [0.92]	0.60 (.48) [0.88]	0.59 (.52) [0.94]	0.31 (.45) [0.61]	(.43)	(.26)
D. sagittata	(1.00)	(1.00)	0.40 (.58) [0.87]	0.35 (.82) [1.16]	0.76 (.75) [1.59]	0.63 (.61) [1.14]	0.44 (.71) [1.10]		0.61 (.48)
Raphidascaris sp.	(.14)		(.05)	0.51 (.18) [0.30]	0.84 (.30) [0.70]	0.74 (.22) [0.45]	1.06 (.38) [1.09]	(.43)	

	WINTER	SPRING	SUMMER	FALL
Number Examined	11	189	340	30
Cr. farionis	0.35 (.18) [0.26]	2.14 (.26) [2.17]	0.86 (.09) [0.22]	
M. salmonis	2.53 (.64) [8.02]	1.50 (.36) [1.63]	1.24 (.33) [1.13]	3.41 (.93) [28.12]
C. truncatus	3.34 (.73) [20.56]	2.09 (.38) [3.05]	0.98 (.05) [0.14]	3.91 (.93) [45.04]
Cy. farionis	2.18 (.54) [4.84]	1.35 (.46) [1.76]	1.28 (.24) [0.88]	1.40 (.47) [1.90]

Same Key as Appendix IV.

Appendix VIII. Abundance of major cisco parasites with season

	JAN.	MARCH	MAY	JUNE	JULY	AUGUST	SEPT.
Number Examined	4	12	21	122	112	115	60
Tetracotyle intermedia	(.75)	2.19 (.91) [8.16]	1.31 (.47) [1.75]	0.87 (.38) [0.90]	1.06 (.13) [0.39]	1.32 (.29) [1.07]	1.30 (.23) [0.86]
Diplostomulum spathaceum		1.41 (.54) [2.34]	1.56 (.43) [1.76]	1.89 (.36) [2.41]	1.23 (.09) [0.32]	1.33 (.24) [0.90]	1.64 (.32) [1.66]
Proteocephalus filicollis exiguus	2.35 (.50) [5.24]	2.86 (.67) [11.64]	3.08 (1.00) [21.78]	3.38 (.75) [22.23]	2.72 (.93) [14.10]	2.66 (.85) [12.23]	2.97 (.93) [18.15]
Triaenophorus crassus	Young 0-4yrs. 0.50 (.50) [0.82]		0.44 (.60) [0.92]	0.53 (.70) [1.19]	0.49 (.53) [0.86]	0.54 (.70) [1.21]	0.40 (.65) [0.97]
	Old 5+ yrs. 0.58 (.87)	(.54)	0.76 (.74) [1.57]	0.95 (.75) [1.95]	1.07 (.80) [2.32]	0.58 (.70) [1.26]	(.50)
Ergasilus nerkae				0.55 (0.2) [0.03]	1.62 (.19) [0.95]	1.27 (.19) [1.33]	0.72 (.45) [0.92]

	WINTER	SPRING	SUMMER
Number Examined	16	143	287
Discocotyle sagittata	(0.6)	0.28 (0.9) [0.12]	0.49 (.14) [0.22]
Raphidascans sp.	0.83 (.56) [1.29]	0.73 (.13) [0.26]	0.45 (.13) [0.20]

Same Key as Appendix IV.

Appendix IX. Abundance of major pike parasites with season

	JAN.	MARCH	MAY	JUNE	JULY	AUGUST	SEPT.
Number Examined	5	11	74	117	85	107	45
Tetraonchus monenteron			4.47 (.86) [75.56]	4.47 (.68) [59.75]	4.71 (.74) [82.29]	4.36 (.67) [52.82]	3.73 (.73) [30.52]
Diphyllobothrium sp. II		0.96 (.64) [1.66]	0.62 (.53) [0.98]	1.00 (.43) [1.16]	1.01 (.52) [1.42]	0.88 (.59) [1.41]	0.88 (.58) [1.40]
Proteocephalus pinguis	4.52 (1.00) [92.02]	4.32 (1.00) [75.56]	4.26 (.97) [68.69]	3.89 (.98) [48.13]	3.30 (.94) [25.56]	2.94 (.94) [17.63]	3.22 (.98) [24.52]
Triaenophorus nodulosus		1.85 (.46) [2.90]	2.92 (.74) [13.80]	1.50 (.20) [0.92]	0.94 (.13) [0.33]	0.67 (.24) [0.48]	1.44 (.56) [2.35]
Raphidascans sp.	(.40)	1.88 (.73) [4.77]	1.54 (.32) [1.50]	2.17 (.43) [3.74]	1.82 (.67) [4.13]	0.82 (.46) [1.04]	0.56 (.36) [0.62]
Triaenophorus crassus	3.16 (1.00) [23.45]	2.47 (.82) [9.71]	2.35 (.40) [4.25]	2.35 (.77) [8.06]	2.04 (.74) [5.73]	2.25 (.84) [7.97	1.70 (.78) [4.27]
	SPRING	SUMMER					
Number Examined	191	237					
Centrovarium lobotes	2.07 (.24) [1.92]	1.39 (.11) [0.46]					

Same Key as Appendix IV.

Appendix X. Abundance of whitefish food items with age

Whitefish Food	Food Age Groups		
	0 - 4	5 - 7	8^+
Empty	5.00(14)	2.57(10)	1.78(5)
Digest (unid)	25.00(70)	13.11(51)	12.50(35)
Insecta (unid)	* 0.36(1)	1.54(6)	1.07(3)
Coleoptera	(0)	(0)	0.71(2)
Ephemeroptera	5.00(14)	5.66(22)	7.86(22)
Hemiptera (Corixidae)	0.36(1)	1.80(7)	2.14(6)
Trichoptera (*Hexagenia*)	3.21(9)	9.25(36)	5.71(16)
Plecoptera	(0)	0.26(1)	(0)
Odonata	(0)	0.26(1)	(0)
Neuroptera	0.71(2)	0.26(1)	1.07(3)
Diptera (unid)	(0)	1.03(4)	1.07(3)
Chironomid adult	0.71(2)	(0)	(0)
Chironomid larvae	13.93(39)	10.02(39)	12.86(36)
Insect egg	0.36(1)	1.03(4)	0.71(2)
Phytoplankton	0.36(1)	0.26(1)	(0)
Zooplankton (unid)	1.43(4)	0.51(2)	1.07(3)
Cyclops sp.	2.86(8)	(0)	(0)
Other sp.	6.07(17)	0.26(1)	1.43(4)
Vegetation (macroaquatics)	0.36(1)	2.83(11)	1.78(5)
Hirudinae	0.36(1)	(0)	0.71(2)
Mollusca (unid)	0.71(2)	0.26(1)	(0)
Pelecopoda	9.64(27)	16.97(66)	16.78(47)
Gastropoda	10.36(29)	15.17(59)	12.86(36)

Appendix X. Continued

Whitefish Food	Food Age Groups 0 - 4	5 - 7	8$^+$
Amphipoda (unid)	2.14(6)	4.37(17)	5.36(15)
Hyallela	(0)	1.54(6)	1.43(4)
Gammarus	(0)	0.77(3)	1.78(5)
Pontoporeia	1.07(3)	3.08(12)	6.78(19)
Hydrachellidae	9.64(27)	5.40(21)	2.14(6)
Ostracoda	(0)	0.26(1)	(0)
Nematomorpha	(0)	0.26(1)	(0)
Fish (unid)	0.36(1)	(0)	0.36(1)
Walleye	(0)	0.51(2)	(0)
Fish egg	(0)	0.77(3)	(0)

a(b)
a, percentage with food item
b, number with food item

Appendix XI. Abundance of cisco food items with age

Cisco Food	Food Age Groups 0 - 4 yr.	5$^+$
Empty	45.64(246)	44.71(148)
Digest (unid)	16.70(90)	13.90(46)
Insecta (unid)	0.37(2)	2.42(8)
Coleoptera	0.18(1)	(0)
Ephemeroptera	3.15(17)	10.27(34)
Hemiptera (Corixidae)	0.37(2)	(0)
Trichoptera (*Hexagenia*)	3.34(18)	8.16(27)
Plecoptera	(0)	0.30(1)
Odonata	(0)	0.30(1)
Neuroptera	0.37(2)	0.30(1)
Diptera (unid)	0.74(4)	1.51(5)
Chironomid adult	(0)	0.30(1)
Chironomid larvae	2.97(16)	1.21(4)
Insect egg	0.56(3)	0.30(1)
Phytoplankton	0.37(2)	0.60(2)
Zooplankton	3.52(19)	1.81(6)
Cyclops sp.	6.68(36)	2.11(7)
Other sp.	12.99(70)	5.14(14)
Vegetation (macroaquatics)	(0)	0.30(1)
Pelecopoda	(0)	0.30(1)
Gastropoda	(0)	0.30(1)
Amphipoda (unid)	0.56(3)	0.60(2)
Hyallela	(0)	0.60(2)
Hydrachnellidae	0.18(1)	0.91(3)

Appendix XI. Continued

Cisco Food	Food Age Groups 0 - 4 yr.	 5$^+$
Fish (egg)	(0)	0.60(2)
Fish (unid)	(0)	1.81(6)
Percidae (unid)	0.37(2)	(0)
Walleye	0.18(1)	0.91(3)
Stickleback	0.74(4)	(0)
Shiner	(0)	0.91(3)
Other fish	(0)	0.30(1)

Key as Appendix X

Appendix XII. Abundance of pike food items with age

Pike Food	Food Age Groups	N/S
	0 - 4 yrs.	5^+
Empty	47.46(159)	43.75(182)
Digest	21.49(72)	18.75(78)
Insect (unid)	(0)	0.48(2)
Coleoptera	(0)	0.24(1)
Ephemeroptera	0.90(3)	4.33(18)
Trichoptera (*Hexagenia*)	3.58(12)	2.88(12)
Odonata	2.09(7)	1.68(7)
Diptera (Chironomid larvae)	(0)	0.24(1)
Zooplankton	0.30(1)	(0)
Hirudinae	0.60(2)	1.92(8)
Gastropoda	0.60(2)	0.24(1)
Amphipoda (unid)	0.90(3)	1.20(5)
Gammarus	0.60(2)	0.96(4)
Decapoda (*Oconecthes*)	0.90(3)	1.92(8)
Fish (unid)	10.15(34)	10.10(42)
Percidae (unid)	2.09(7)	3.60(15)
Perch	(0)	0.96(4)
Walleye	0.90(3)	(0)
Sauger	0.60(2)	(0)
Stickleback	1.49(5)	(0)
Troutperch	1.79(6)	1.44(6)
Shiner	1.19(4)	1.44(6)

Appendix XII. Continued

Pike Food	Food Age Groups	N/S
	0 - 4 yrs.	5^+
Coregonid (unid)	0.90(3)	0.96(4)
Whitefish	0.30(1)	0.24(1)
Cisco	0.30(1)	2.16(9)
Other fish	0.90(3)	0.48(2)

Key as Appendix X .

Appendix XIII. Abundance of major whitefish parasites of sampling sites

Parasites	SITES A	B	C	D
Tetracotyle intermedia	3.17(.65)	3.32(.59)	3.12(.63)	3.24(.81)
	[15.5] 1	[16.4] 1	[14.3] 1	[20.6] 1
Diplostomulum spathaceum	2.40(.56)	2.08(.53)	1.96(.58)	1.89(.54)
	[6.2] 3	[4.2] 3	[4.1] 3	[3.6] 3
Raphidascaris sp.	0.58(.38)	0.81(.19)	0.80(.31)	0.78(.19)
	[0.7] 8	[0.4] 9.5	[0.7] 8	[0.4] 10
Proteocephalus exiguus	2.24(.80)	1.80(.82)	2.43(.92)	2.86(.88)
	[7.5] 2	[4.9] 2	[10.4] 2	[15.4] 2
Cyathocephalus truncatus	1.15(.06)	1.71(.12)	2.15(.11)	1.89(.13)
	[0.2] 11	[0.6] 8	[1.0] 5	[0.8] 7.5
Metechinorhynchus salmonis	1.12(.21)	1.33(.43)	0.55(.21)	1.25(.16)
	[0.6] 9	[1.6] 4	[0.4] 10.5	[0.5] 9
Cystidicola farionis	1.46(.22)	1.36(.30)	1.17(.26)	1.09(.32)
	[0.9] 7	[1.2] 6	[0.8] 7	[1.0] 5
Salmincola extumescens	0.30(.11)	0.25(.12)	0.08(.14)	0.05(.18)
	[0.1] 12	[0.2] 12	[0.2] 12	[0.2] 12
Ergasilus nerkae	1.61(.26)	0.86(.17)	1.61(.26)	0.93(.14)
	[1.3] 4	[0.4] 9.5	[1.3] 4	[0.3] 11
Discocotyle sagittata	0.15(.23)	0.41(.23)	0.60(.35)	0.65(.40)
	[0.3] 10	[0.3] 11	[0.6] 9	[0.8] 7.5
Crepidostomum farionis	1.49(.23)	2.11(.16)	0.95(.15)	2.12(.16)
	[1.0] 6	[1.3] 5	[0.4] 10.5	[1.4] 4
Triaenophorus crassus	0.67(.56)	0.58(.49)	0.58(.49)	0.49(.54)
	[1.1] 5	[0.9] 7	[0.9] 6	[0.9] 6

Appendix XIII. Continued

	AREA 4 and 5	
Tetracotyle intermedia	3.73	(.94)
	[39.2]	(34)
Triaenophorus crassus	0.62	(.50)
	[0.9]	(198)

a(b) a, log intensity; b, prevalence

[c]d c, abundance; d, rank

Appendix XIV. Abundance of major cisco parasites at sampling sites

Parasites	SITES A	 B	 C	 D
Tetracotyle intermedia	0.68(.15)	1.28(.38)	1.21(.33)	1.33(.28)
	[0.3] 5	[1.4] 3	[1.1] 2	[1.1] 4
Diplostomulum spathaceum	1.29(.13)	1.79(.31)	0.56(.30)	1.43(.28)
	[0.5] 4	[1.8] 2	[0.5] 5	[1.2] 3
Raphidascaris sp.	0.36(.10)	0.55(.23)	0.57(.16)	0.48(.12)
	[0.1] 6	[0.4] 5	[0.3] 6	[0.2] 6
Proteocephalus filicollis	2.34(.90)	3.34(.96)	3.22(.95)	2.97(.81)
	[9.4] 1	[27.1] 1	[23.7] 1	[13.0] 1
Ergasilus nerkae	1.52(.32)	1.34(.23)	0.86(.28)	0.96(.18)
	[1.5] 2	[0.9] 6	[0.7] 4	[0.5] 5
Discocotyle sagittata	0.22(0.7)	0.52(.17)	0.30(.16)	0.49(.10)
	[0.1] 7	[0.3] 7	[0.2] 7	[0.2] 7
Triaenophorus crassus	0.54(.41)	0.61(.70)	0.48(.64)	0.52(.69)
	[0.7] 3	[1.3] 4	[1.0] 3	[1.2] 2

	AREA 4 and 5	
Tetracotyle intermedia	1.54	(.16)
	[0.7)	(22)
Triaenophorus crassus	0.50	(.64)
	[1.0]	(19)

Key as Appendix XIII.

Appendix XV. Abundance of major pike parasites of sampling sites

	SITES			
Parasites	A	B	C	D
Tetraonchus monenteron	4.28(.95)	4.46(.99)	4.45(.95)	4.43(.93)
	[68.4] 1	[85.3] 1	[81.0] 1	[77.9] 1
Diphyllobothrium sp.	0.60(.43)	0.84(.56)	1.01(.64)	0.94(.66)
	[0.8] 6	[1.3] 5	[1.8] 6	[1.7] 5
Raphidascaris sp.	1.75(.59)	2.01(.55)	1.22(.60)	1.43(.39)
	[3.4] 4	[4.1] 4	[2.0] 5	[1.6] 6
Triaenophorus crassus	1.87(.64)	2.35(.90)	1.80(.69)	2.39(.70)
	[4.1] 3	[9.5] 3	[4.0] 3	[7.7] 3
Proteocephalus pinguis	3.69(.95)	3.26(.97)	3.54(.96)	3.74(.98)
	[38.1] 2	[25.3] 2	[33.1] 2	[41.1] 2
Triaenophorus nodulosus	1.00(.25)	1.21(.26)	1.12(.45)	2.70(.40)
	[0.7] 7	[0.9] 7	[1.4] 7	[5.9] 4
Centrovarium lobotes	1.94(.18)	1.68(.23)	2.31(.21)	1.70(.13)
	[1.2] 5	[1.2] 6	[2.1] 4	[0.7] 7

Key as Appendix XIII