

THE UNIVERSITY OF MANITOBA

INDICATORS (PARASITES AND STABLE ISOTOPES) OF TROPHIC STATUS OF
YELLOW PERCH (*PERCA FLAVESCENS* MITCHILL) IN NUTRIENT POOR
CANADIAN SHIELD LAKES.

BY

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**INDICATORS (PARASITES AND STABLE ISOTOPES) OF TROPHIC STATUS OF YELLOW
PERCH (*PERCA FLAVESCENS* MITCHELL) IN NUTRIENT POOR CANADIAN SHIELD
LAKES**

BY

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A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of

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MASTER OF SCIENCE

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ABSTRACT

The fish parasite communities of four Canadian Shield lakes (L239, L240, L377 and Triangle Lake) in the Experimental Lakes Area (ELA), Ontario were surveyed over three seasons in 1997 and 1998 and one season in 1999. Thirteen of fifteen fish species sampled from the study lakes harboured parasites; northern pike (*Esox lucius*), lake cisco (*Coregonus artedii*), pearl dace (*Margariscus margarita*), blacknose shiner (*Notropis heterolepis*), spottail shiner (*Notropis hudsonius*), fathead minnow (*Pimephales promelas*), longnose dace (*Rhinichthys cataractae*), white sucker (*Catostomus commersoni*), burbot (*Lota lota*), brook stickleback (*Culea inconstans*), slimy sculpin (*Cottus cognatus*), Iowa darter (*Etheostoma exile*) and yellow perch (*Perca flavescens*). A total of 112,188 parasites were detected, with 87% (n = 1926) of the necropsied fish having at least one parasite. Forty-one species of parasites representing 32 genera and 26 families were found; 35 species used fish as definitive hosts and six species used birds as the definitive hosts. The most omnivorous fish species (perch, white sucker and pearl dace) had the most diverse parasite infracommunities while the most specialized consumers had the least diverse parasite infracommunities (the piscivores, pike and burbot and the zooplanktivorous cisco) or lacked parasites entirely (the algavorous northern redbelly dace, *Phoxinus eos*, and finescale dace, *P. neogaeus*). The parasite communities of the four ELA lakes were less speciose than those reported from larger lacustrine systems in Ontario and Manitoba. The parasite community composition of yellow perch was typical of perch in other systems, however, there were new host and locality records for several parasite species infecting other fish species. For example, the pearl dace was infected with five parasites not previously reported from this host in North

America and two not previously reported from this host in Canada. There were distinct seasonal and age-related trends in the parasite communities of yellow perch populations that correlated with seasonal and ontogenetic dietary shifts, respectively.

Understanding parasite community structure can improve understanding of host population ecology and clarify many aspects of ecosystem biotic and abiotic interactions. Detailed analysis as performed in this study is a useful tool for describing the factors affecting parasite community composition. A restricted invertebrate and fish fauna in these nutrient poor lakes can be important in controlling the parasite fauna infecting yellow perch, which could be more predictable than that observed in large, productive lakes.

Allogenic parasites are most common in Triangle Lake and enterics in L239. Parasite species richness is highest in L239 and diversity is highest in L240. *Glugea* sp. is the most dominant and abundant parasite species in all but Triangle Lake. Triangle Lake and L377 perch have the fastest growth rates and reach the greatest total length and age of all sampled perch. Yellow perch length and age are both highly correlated with parasite richness, intensity and abundance. Female perch usually had significantly greater species richness than males but intensity and abundance were significantly higher than males in only two lakes each. L239 and Triangle Lake had parasite assemblages that were significantly non-random largely due to subpopulations of parasite species transmitted through macrobenthos. Perch parasite communities in all four lakes showed significantly more nestedness than expected by chance.

Parasite-induced pathology of yellow perch was also examined in these shield lakes. *Glugea* sp. xenomas in cells of the intestinal wall and in visceral fat and

Apophallus brevis metacercariae infecting the musculature reduced the growth of perch resulting in mortality in younger and smaller fish. High numbers of *Raphidascaris acus*, encysted in the liver of yellow perch, correlated significantly with a reduction in visceral fat weight in 1+ females and 0+ and 1+ males. A significant correlation in these subsamples indicates that host sex, size, trophic status and relative weight of the liver are linked to *R. acus* density. The data suggests that interactions among parasitic infections and age, size and sex of the fish host can affect growth and survival of the host, especially during periods of low energy inputs and reproductive stress.

Stable isotopes (C and N) have proven to be important tools for obtaining information on the trophic relationships within food webs. Combining parasite community studies with stable isotopes could improve the effectiveness of detailed food web analyses. Parasite communities are particularly useful since they can identify both prey and non-prey components of the host's community. Triangle Lake perch had distinct isotope ratios that separated them from the other three populations. Stable C isotope ratios for all perch ranged from $\sim -34^{0}/_{00}$ to $-19^{0}/_{00}$ while stable N isotope ratios ranged from $\sim 4.5^{0}/_{00}$ to $12.5^{0}/_{00}$. These ranges are larger than those observed in many other fish species. Perch diet was the most significant predictor of stable C isotope ratio. Perch parasite fauna was the most significant predictor of stable N ratios. In particular, parasite fauna indicative of zooplanktivorous or piscivorous perch were most accurate for predicting fish trophic position and thus stable isotope ratio. Fish length and age showed no significant relationship with isotope ratios .

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STUDY AREA

Perch were captured from three lakes in the Experimental Lakes Area (ELA) approximately 370 km east of Winnipeg, Manitoba and 80 km east-southeast of Kenora, Ontario in the Canadian Shield and from one additional shield lake north of this region (Fig. S.1). All waters in the region lie in the Winnipeg River drainage, some entering the Winnipeg River via the English River and some via Lake of the Woods. These are nutrient-poor lakes typical of the Canadian Shield. Three ELA lakes (L239, L240 and L377) and Triangle Lake located 15 km east of Pine Road, accessible from the Trans-Canada Highway were sampled for all fish species present.

INDIVIDUAL LAKE CHARACTERISTICS

The physical characteristics of L239, L240 and L377 (area, depth, etc.) and the invertebrate biota of L239 and L240 were described in a special publication of the Journal of the Fisheries Research Board of Canada (**28**:121-304). Other data for these lakes were obtained from alternate sources (described below) or were examined during this study.

L239

This lake is one of two in this study located adjacent to the ELA field station (49°39'48"N, 93°43'15"W) (Fig. S.2). It is the largest of the study lakes at 1000 m long and 575 m wide (the south end of the lake has an additional bay and is 1000 m wide at this point) with a surface area of 56.1 ha. It has a mean depth of 10.5 m and a maximum depth of 30.4 m. Secchi disc visibility (SDV) is 4.8 m, total dissolved solids (TDS) are 20 mg/l and conductivity (C) is 25 μ S/cm. 70-80% of the littoral zone (to 4 m depth) is composed of broken rock shelf, large boulders and coarse gravel, about 15% is sand and the rest is

Figure S.1. Map showing the location of the three Experimental Lakes Area study lakes (shaded). Triangle Lake is located 15 km east of where the camp road intersects with Highway 17 and is adjacent to the highway.

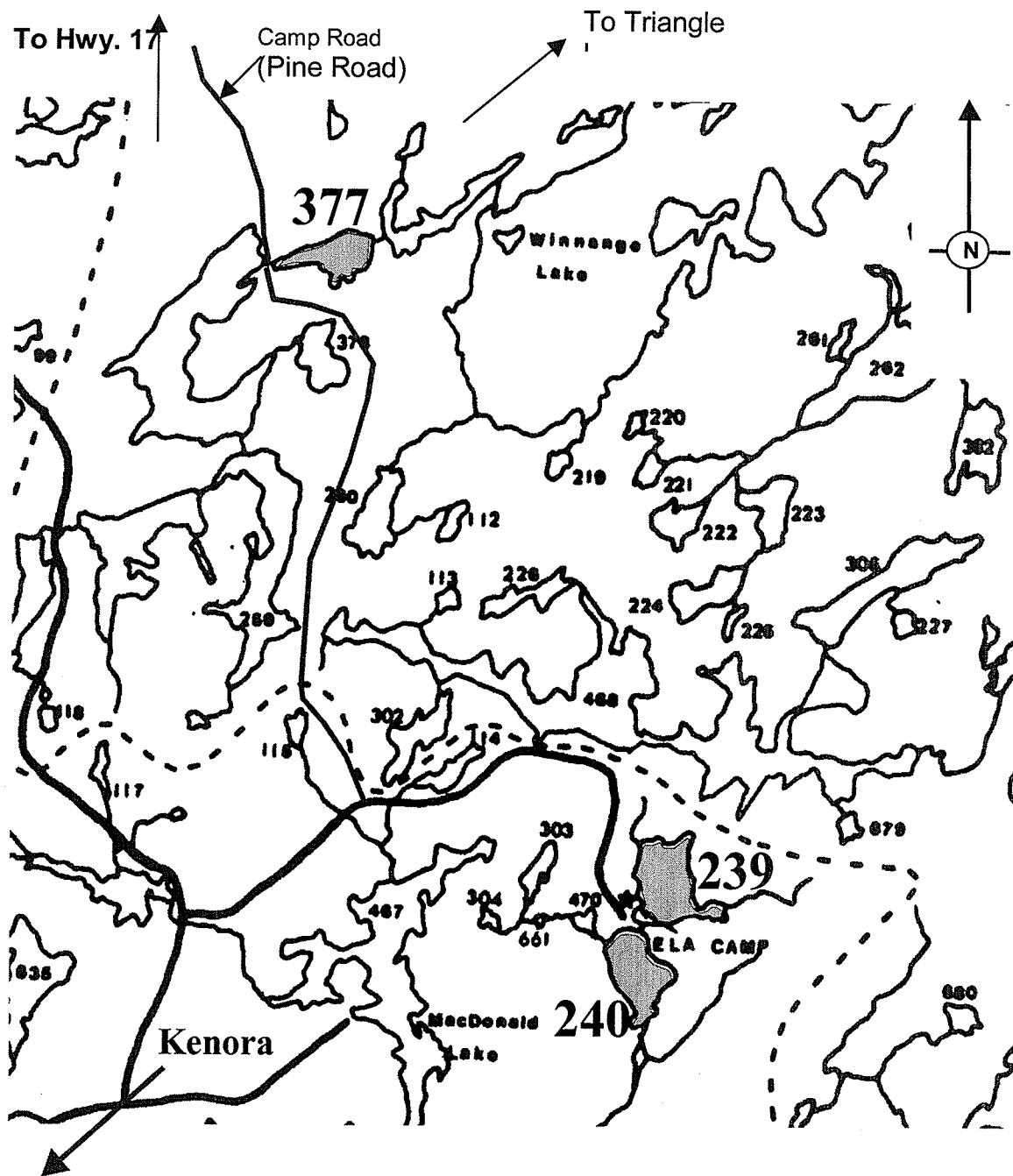






Figure S.2. L239 bathymetry map and sampling site locations. All scale and depth measurements are in meters.

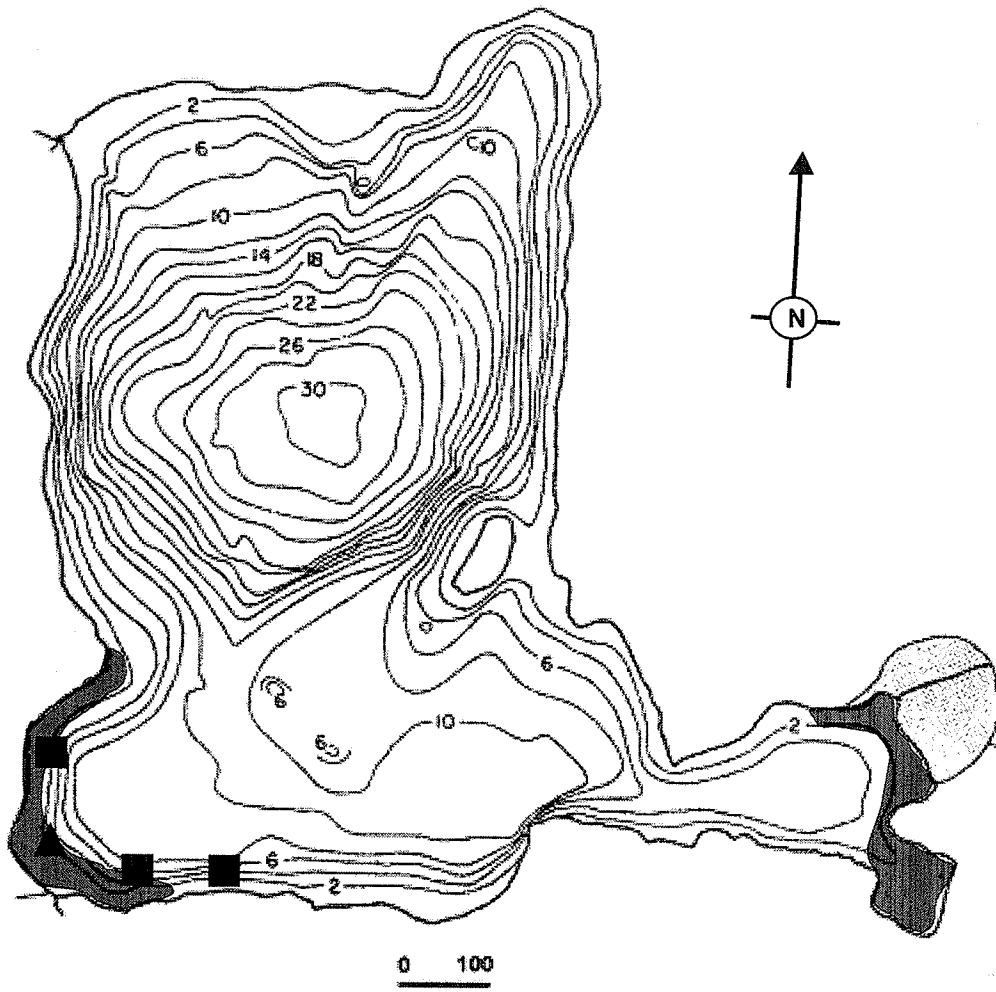
For Figures 2-5:

 Electroshocking

 Trap net set

 Minnow trap set

 Gill net set



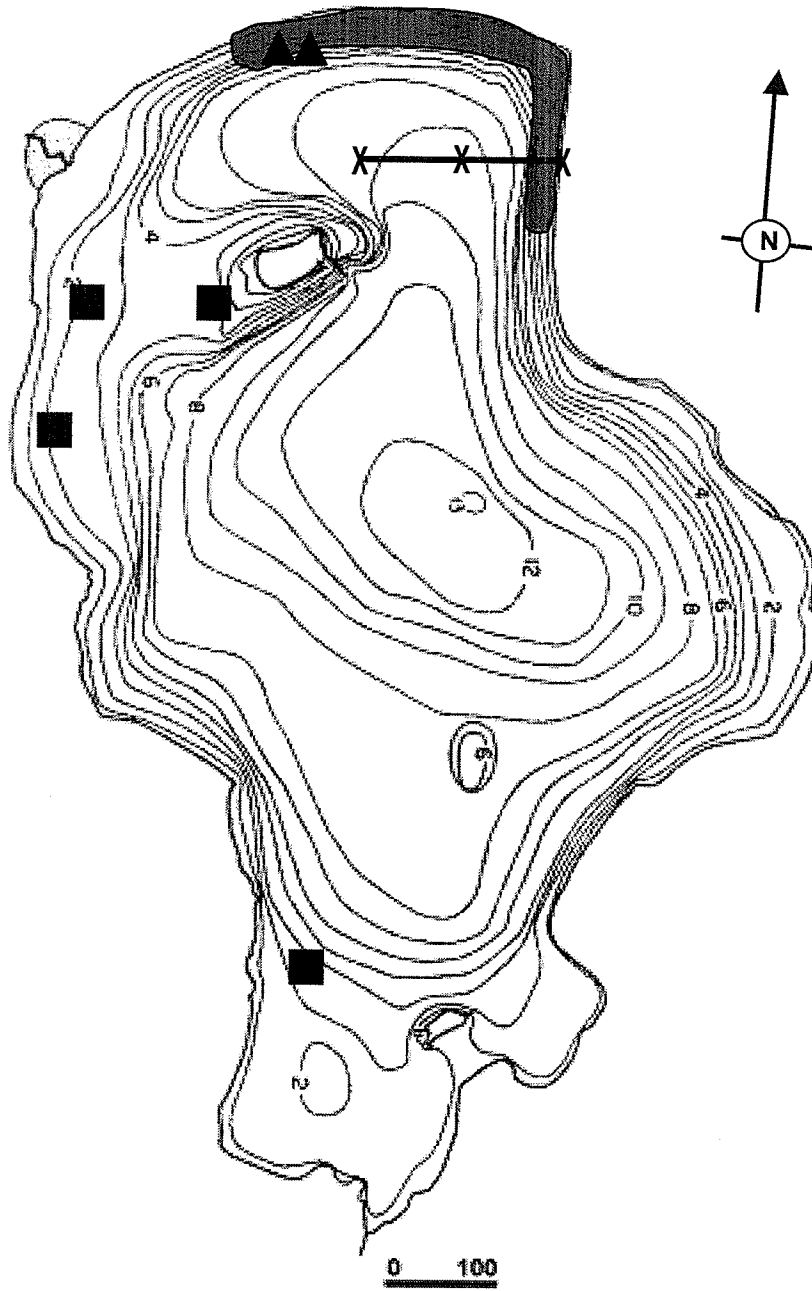
organic sediment (silt and clay). The lake bottom consists of bedrock with a thin layer of sediment. There is a small shallow bay in the southeast with abundant macrophytes (submerged and emerged). Average chlorophyll a (chl a) levels and phytoplankton biomass in this lake are low (1.8 mg/m^3 and 700 mg/m^3 respectively) relative to other lakes in the area. It has one outlet that drains into L240 and two inlets from other lakes.

Like most shield lakes it has a poor invertebrate fauna. There are nine species of zooplankton including the copepod *Cyclops bicuspidatus* and the cladocerans *Bosmina*, *Eubosmina*, *Holopedium* and *Daphnia* spp. The most common benthos (as observed in this study) include chironomids, Ephemeroptera (primarily *Hexagenia* sp.), Trichoptera and Amphipoda (largely *Gammarus*). There are additional deepwater specialized invertebrates such as Mysid shrimp. Seven species of fish had been previously identified from this lake (Beamish *et al.* 1976) and one additional species was sampled in this study (northern redbelly dace, *Phoxinus eos*). Three species (white sucker, *Catostomus commersoni*, yellow perch, *Perca flavescens*, and slimy sculpins, *Cottus cognatus*) are considered to be moderately abundant or abundant (Beamish *et al.* 1976). This is the only lake in this study that currently has a population of lake trout (*Salvelinus namaycush*). Pike (*Esox lucius*), white sucker, yellow perch and northern redbelly dace were sampled in this study. Local avian fauna includes loons, herons and gulls. Sample sites and sampling methods at each site are indicated in Figure S.2.

L240

L240 is also adjacent to the ELA field station ($49^{\circ}39'15''\text{N}$, $93^{\circ}43'35''\text{W}$). It is 1050 m long and 550 m wide and has a surface area of 44.1 ha. Mean depth is 6.1 m and maximum is 13.1 m (Fig. S.3). SDV, TDS and C were all similar to L239 values (4.2 m,

Figure S.3. L240 bathymetry map and sampling site locations. All scale and depth measurements are in meters. Symbols as per Figure S.2.



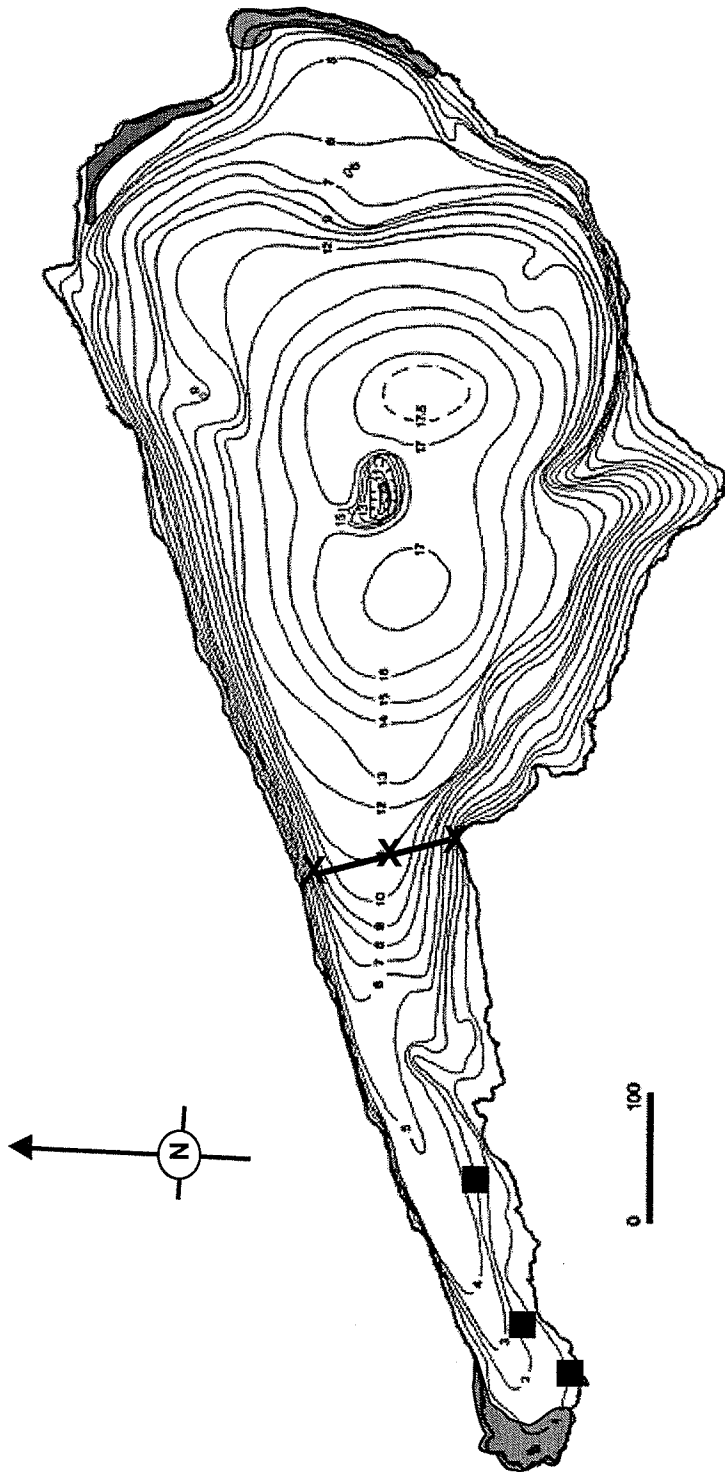
20 mg/l and 22 $\mu\text{S}/\text{cm}$ respectively). Lake bottom and littoral zone substrates are also similar to L239 except that there are fewer areas with macrophyte growth. Chl a and phytoplankton biomass levels are also comparable to L239 (2.0 mg/m^3 and 600 mg/m^3 respectively). There are two inlets (one from L239) and one outlet.

The same zooplankton (8 spp.) and benthos dominate this lake although it lacks some of the deepwater fauna found in L239. Six species of fish were previously reported from this lake (Beamish *et al.* 1976). Two additional species were recovered in this study (Iowa darter, *Etheostoma nigrum*, and northern redbelly dace, *Phoxinus eos*). White sucker and yellow perch are the most abundant species. Northern pike is the only major piscivore in L240. Loons, herons and gulls are also present in this system. Sample sites and sampling methods at each site are indicated in Figure S.3.

L377

L377 (49⁰43'15"N, 93⁰46'30"W) is a small, sheltered lake that is 1150m long and varies from 100 to 400 m width (Fig. S.4). The surface area is 27.2 ha, mean depth is 9.2 m and maximum depth is 17.8 m. SDV and C are similar to L239 and L240 at 4.5 m and 23 $\mu\text{S}/\text{cm}$ respectively but TDS are lower (10 mg/l). The majority of the littoral zone (about 90%) is composed of large boulders and broken shelf and the rest is sand and gravel. There are a few macrophytes at the east end of the lake and a small riffle zone at the west inlet. Chl a and phytoplankton levels are unknown but likely similar to the two previous lakes. There are two inlets and one outlet.

Figure S.4. L377 bathymetry map and sampling site locations (After Salki 1993). All scale and depth measurements are in meters. Symbols as per Figure S.2.



Deep lakes commonly have low zooplankton diversity, however, L377 zooplankton abundances are higher than those in many nearby shallow lakes (>70 individuals/cm²) (Salki 1993, 1995). *Bosmina* sp. and *Cyclops* sp. are the dominant zooplankton species. The same benthic species are present as in L239 and L240 but the abundances of most are lower as evidenced from benthic grabs and stomach contents. There are more sphaerid clams than in any other study lake. This lake had the richest fish fauna of all study lakes. There are 12 species in the lake and although trout perch (*Percopsis omiscomaycus*) have been reported from the lake, they were not recovered despite the use of three different fish sampling methods. The most abundant fish are yellow perch, white sucker and pearl dace (*Margariscus margarita*). There are presently no large piscivores in this lake. Lake trout were extirpated approximately a decade ago due to sport fishing pressure (K. Mills pers. comm.). Larger perch are the only current piscivores. Personal observations reveal few birds in the vicinity of this lake. Sample sites and sampling methods at each site are indicated in Figure S.4.

Triangle Lake

Triangle Lake (44°50'33"N, 93°34'28"W) is located about 70 km northeast of L377 outside the ELA (Fig. S.5). It is a small lake with a surface area of only 13.44 ha. Maximum depth is approximately 13 m. SDV is unknown but TDS and C are both higher than the ELA lakes (approximately 80 mg/l and 130 μ S/cm). The lake bottom is bedrock covered by silt and organic material and 80% of the littoral zone is organic material and the other 20% consists of large boulders. Large concentrations of macrophytes populate four shallow bays in the lake. Chl a levels are similar to the other sampled lakes at approximately 2 mg/l. There is no defined inflow and little to no

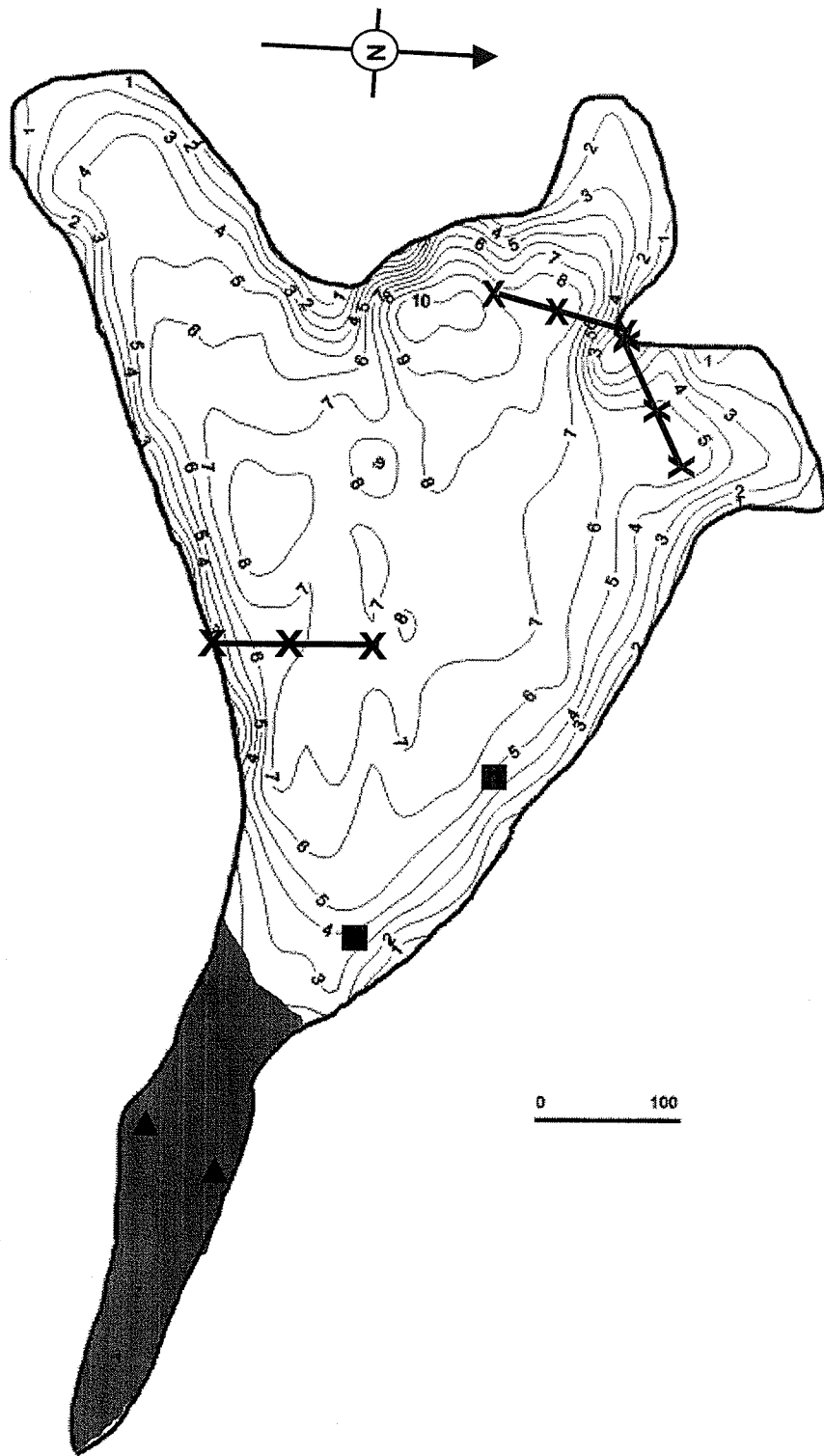
outflow from this lake. This lake has been used in the Ontario bait fishery, has undergone perch population control in the early 1980's and was fertilized with carbon in the winter of 1984-85 (Ken Mills unpubl. data).

Cladoceran richness and abundances are comparable with L239 and L240 but copepod numbers are reduced. Aquatic insects, both larvae and adults, and mollusca are more abundant in Triangle Lake than in the other three. Eight species of fish were captured during this study, five of which are cyprinids. The most abundant fish are yellow perch, pearl dace and blacknose shiner. Sample sites and sampling methods at each site are indicated in Figure S.5.

Triangle Lake bathymetry analysis

Triangle Lake bathymetry (Fig. S.5) was analysed in July 1998. The lake was divided into twenty-six transects with a rope. Depth soundings were recorded at two meter intervals along each transect and GPS coordinates were obtained every 25 meters. The computer software program Surfer for Windows (Golden Software, Inc.) was used to create contour lines on a Triangle Lake map outline with these depth data. This map was then exported to Corel Photopaint (Version 10) where a scale bar and compass arrow were added.

Figure S.5. Triangle Lake bathymetry map and sampling site locations. All scale and depth measurements are in meters. Symbols as per Figure S.2.



CHAPTER 1: Historical Introduction

FISH PARASITES

The parasite fauna of a fish can reveal much about the biology of the host and of the host's aquatic ecosystem (Williams et al. 1992, Carney & Dick 1999, 2000a). However, there have been few surveys of the parasite communities in lakes of the Canadian Shield (Dechtiar 1972) and none from the Experiment Lakes Area, Ontario, Canada. A relatively poor invertebrate community in small shield lakes would likely result in a poor parasite community but one that would still be an important component of the ecosystem. Of the fish species recovered from the study lakes, only northern pike, white sucker, burbot and yellow perch have extensive parasite lists (McDonald & Margolis 1995, Hoffman 1999). Few parasite surveys have focussed on cyprinids and other small fish thus omitting an important part of the parasite transmission cycle within an aquatic system. The emphasis of this research was on yellow perch and their interactions with their parasite fauna but no sampled fish species were neglected and few fish species known to occur in these lakes were absent from the samples. The parasite communities were used to determine the relative position of each fish species within the food web.

Yellow perch are one of the best studied fish species (Scott & Crossman 1973) and have one of the most extensive parasite lists of any potential host (Craig 1987, McDonald & Margolis 1995, Hoffman 1999). Ciliophora, Myxozoa and Microsporidea species are poorly represented in yellow perch and other fish in North America (McDonald & Margolis 1995, Hoffman 1999) because they are largely ignored in most surveys. Surveys that recorded these parasite species found them at relatively low prevalence and mean intensity (Bangham 1972, Dechtiar *et al.* 1989). The most

commonly recovered genera are *Ichthyophthirius*, *Trichodina*, *Henneguya*, and *Myxobolus* (Hunter 1942, Fischthal 1947, Fantham & Porter 1948, Bangham 1972, Dechtiar *et al.* 1989, McDonald & Margolis 1995).

Monogeneans

Monogeneans are another group of parasites that are often ignored in large scale surveys despite the fact they can exhibit a high degree of host specificity (Cone & Burt 1982). *Gyrodactylus* is a common parasite of North American cyprinids but can be found at low levels in some populations of yellow perch (*G. freemani* in 2% of yellow perch in Algonquin Park) (Dechtiar *et al.* 1989). The only common monogenean of yellow perch is *Urocleidus adspetus* (Tedla & Fernando 1969b, Noble 1970, Cone 1978, Cone & Burt 1982). It can occur at high levels in some populations (41% of Oneida Lake perch, Noble 1970). Cone & Burt (1982) demonstrated the host specificity of *U. adspetus* by exposing onchomiracidia to several species of live fish and also detached scales of these fish.

Digeneans

The most common adult digeneans in yellow perch are *Crepidostomum cooperi* (Lyster 1939, Bangham & Venard 1946, Fischthal 1947, Fantham & Porter 1948, Tedla & Fernando 1969b, Noble 1970, Bangham 1972, Cannon 1972, Cannon 1973, Muzzall 1983, Forstie & Holloway 1984, Carney 1999, 2000a), *Bunodera sacculata* (Hunninen 1935, Hunter 1942, Bangham & Venard 1946, Fischthal 1947, Sindermann 1953, Anthony 1963, Tedla & Fernando 1969b, Noble 1970, Cannon 1971, Cannon 1972, Cannon 1973, Carney 1999, 2000a) and *Bunodera luciopercae* (Pearse 1924, Fischthal 1947, Tedla & Fernando 1969b, Cannon 1971, Cannon 1972, Muzzall 1983, Carney

1999, 2000a). These parasites can occur at high prevalences. *C. cooperi* and *B. sacculata* were found in 74% and 31%, respectively, of the perch of Oneida Lake (Noble 1970) while Bangham (1972) found *C. cooperi* in 65.5% of Lake Erie yellow perch. It is unusual to find a population of European perch (*P. fluviatilis*) without a *B. luciopercae* infection (Wisniewski 1958, Kozička 1959, Chubb 1963, Chubb 1970, Halvorsen 1971, Wierzbicki 1971, Wootten 1973, Kennedy 1974, Rokicki 1975, Ravckis 1977, Andersen 1978, Andrews 1979, Priemer 1979, Pojmanska *et al.* 1980, Scholz 1986, Tarmachanov 1987, Ozcelik & Deufel 1989). *Bunodera luciopercae* can be found in 100% of a European perch population (e.g. in summer in Poland, Ravckis 1977) and at intensities as high as 100 parasites/fish (Wierzbicki 1971).

The most common digeneans on both continents belong to the papillose Family Allocreadiidae (Carney 1999). *Bunodera luciopercae*, although common to both perch species, shows considerable morphological variability between the Nearctic and Palearctic populations (Cannon 1971). North American *B. luciopercae* undergo metacercarial development primarily in amphipods (*Hyallela azteca*) and insects (*Siphonurus quebecensis*) and do not have a glandular ventral sucker at this stage (Cannon 1971). The European morphotype is found as a metacercaria primarily in Cladocerans and does possess a glandular ventral sucker, similar to the entirely North American *B. sacculata* (Cannon 1971). Despite these differences, Cannon (1971) states that this morphological variability is no greater than what should be expected from populations at either end of a species' distribution.

Cestodes

Six genera and four species are shared between the two perch species. Yellow perch have two unique genera and seven unique species. The most common adult cestodes of all perch are *Proteocephalus* spp. There are two common species of *Proteocephalus* found in yellow perch; *P. ambloplitis* and *P. pearsei* (Pearse 1924, Hunninen 1935, Bangham & Venard 1946, Fischthal 1947, Meyer 1954, Larson 1966, Tedla & Fernando 1969b, Noble 1970, Bangham 1972, Forstie & Holloway 1984). *Proteocephalus ambloplitis* is most frequently found as a plerocercoid in yellow perch (Centrarchids are the typical definitive hosts) (Noble 1970). *Proteocephalus pearsei* adults can be found in the intestine, although levels are usually low when compared with adult *P. percae* in European perch (Bangham 1972). These two adult *Proteocephalus* species differ in timing of infections. *Proteocephalus pearsei* peaks in intensity and prevalence in the summer and (Tedla & Fernando 1969b) and *P. percae* is highest (at much higher levels than *P. pearsei*) in the spring and lowest in the summer (Andersen 1978).

Nematodes

The most common and one of the most biologically important nematode species in perch is *Raphidascaaris acus*. It is larval in perch and must mature in pike. It is more frequently encountered in Europe (Kennedy 1974, Tarmachanov 1987) than it is in North America (Poole & Dick 1986). *Dichelyne cotylophora* (Pearse 1924, Hunninen 1935, Bangham & Venard 1946, Fischthal 1947, Meyer 1954, Larson 1966, Tedla & Fernando 1969b, Noble 1970, Bangham 1972, Amin 1977, Muzzall 1983, Baker 1984), *Spinitectus gracilis* (Hunninen 1935, Bangham & Venard 1946, Fischthal 1947, Muzzall 1983,

Forstie & Holloway 1984) and *Camallanus oxycephalus* (Fischthal 1947, Zischke & Vaughn 1962, Anthony 1963, Bangham 1972, Muzzall 1983) are also common in North America. The prevalence of *D. cotylophora* ranges from 3.6% (Algonquin Park, Bangham & Venard 1946) to 31.2% (Lake Erie, Bangham 1972) while the prevalence of *C. lacustris* in European perch ranges from about 60% to about 95% (Lee 1977, Kennedy & Burroughs 1978) with typical intensities of 1-30 worms/fish (Lee 1977, Andersen 1978).

Acanthocephalans

Echinorhynchus salmonis and *Neoechinorhynchus rutili* are more commonly found in Salmonids but can infect most freshwater fish including yellow perch (McDonald & Margolis 1995). *Leptorhynchoides thecatus* is a common parasite of yellow perch (Hunninen 1935, Hunter 1942, Fischthal 1947, Larson 1966, Noble 1970, Bangham 1972, Muzzall 1983). Prevalence ranges from $\leq 5\%$ (Noble 1970, Muzzall 1983) to 44% (Lawler 1969). *Pomphorhynchus bulbocolli*, the next most frequently encountered acanthocephalan of yellow perch is rarely found at prevalences exceeding 5% (Fischthal 1947, Bangham 1972, Forstie & Holloway 1984). *Neoechinorhynchus cylindratus*, though not recovered in as many surveys as *P. bulbocolli*, can occur at locally high levels (Noble 1970, found 39% of Oneida Lake perch with this parasite).

Crustaceans

Ergasilus is the only common crustacean parasite genus of yellow perch. Two species have been commonly reported, *E. caeruleus* and *E. confusus*, and like their European congeners they can attain high prevalence (91.5%, 3.2/fish, Tedla & Fernando 1969a) in their hosts. Tedla & Fernando (1969a) hypothesized that each species of

Ergasilus has a preferred host and that *E. confusus* is the one that prefers yellow perch. They also suggest that many of the previously identified *E. caeruleus* from yellow perch (Bangham 1972) are actually *E. confusus* because *E. caeruleus* parasitizes pumpkinseed (*Lepomis gibbosus*) and bluegill (*Lepomis macrochirus*).

PARASITE COMMUNITIES

Parasite community structure patterns and processes are useful tools not only for describing interactions between a host and its fauna but also for understanding the ecology of the host population. A host population's interactions with its biotic and abiotic environments can affect the composition of its parasite fauna. The parasite community can in turn alter or enhance those host-ecosystem interactions. Certain parasites have been shown to affect fish host growth and development (Szalai & Dick 1991, Szalai & Dick 1992). This can affect host trophic status and thus its relationship with the environment by delaying host ontogenetic changes in feeding strategies or by reducing reproductive potential of the host population.

There are obvious advantages an understanding of parasite community structure can have towards a more thorough understanding of the ecology of the host. However, as with much that can be learned from host-parasite interactions, very little focus has been applied to this topic except by parasitologists (Dogiel 1958, Poulin 1995). Many models of parasite community structure have been developed from the study of freshwater fish populations (Dogiel 1958, Wisniewski 1958, Esch *et al.* 1990, Kennedy 1990). It is typically thought that these parasite communities in fish are random assemblages of non-interacting species guided by stochastic processes (Kennedy 1990) but recent studies have shown that the helminth infra- and component communities of yellow perch have an

additional predictable component both at the continental (Carney & Dick 1999) and local scale (Carney & Dick 2000a). The yellow perch is an ideal fish host when considering studies of this nature. The biology of perch is a well researched and understood topic (Scott & Crossman 1973, Craig 1987). It is found in most types of aquatic environments from riverine to lacustrine, large eutrophic lakes to tiny Canadian Shield lakes poor in nutrients and biodiversity. It also has one of the most extensive parasite species lists found in freshwater fish (Hoffman 1999, McDonald & Margolis 1995, Craig 1987). Yellow perch have few unique species (Cone & Burt 1982), which prevents host specificity from affecting components of community structure. In addition, there are relatively few natural populations of yellow perch that lack a parasite fauna or have a fauna consisting of only a few species (Bangham 1944, Fischthal 1950, Dechtiar 1972, Dechtiar *et al.* 1989, Szalai & Dick 1991), which ensures a large and diverse community of parasites from which data can be acquired.

Both biotic and abiotic factors have been used to explain richness and diversity of various parasite assemblages in freshwater fish. Kennedy *et al.* (1986) suggested that feeding rates, vagility and physiology of the host could explain richness values of its parasite fauna. These same three factors have also been used to describe a model of the parasite communities in cyprinids and salmonids (Chubb 1970). Carney & Dick (2000a) suggested that predictable patterns at the local level and increased richness of the parasite assemblage were the direct result of a rich invertebrate prey community upon which the yellow perch could feed. This was indirectly affected by lake trophic status, which determined what potential prey/intermediate hosts would be available to the perch. Host morphometric characteristics, age, sex and phylogeny can also explain faunal richness

(Aho & Bush 1993). Choudhury & Dick (1998) found that the parasite fauna of lake sturgeon (*Acipenser fulvescens*) was affected by host specificity and feeding habits of the host as described by host phylogeny. The presence of piscivorous hosts can also explain the parasite richness seen in fish populations (Esch 1971, Esch *et al.* 1988). The colonization abilities of parasites that mature in piscivorous birds and mammals is better than those observed for other parasite species in that they can infect many different host species (Esch *et al.* 1988). Esch *et al.* (1988) determined that this increased colonization ability leads to an increase in the numbers of these parasites in eutrophic systems where the fish-eating hosts are abundant. On the other hand, oligotrophic systems with fewer bird and mammal hosts and increased intermediate host prey for fish are dominated by parasite assemblages that mature in fish. While Wisniewski (1958), Esch (1971) and Esch *et al.* (1988) suggest a more direct role for lake trophic status on parasite community structure, Carney & Dick (2000a) found no evidence of this direct role on yellow perch fauna in lake systems of Manitoba and Wisconsin.

Other abiotic factors which have been suggested to affect fish parasite assemblages include lake size (Dogiel 1958, Kennedy 1978), host geographic range (Wisniewski 1958, Price & Clancy 1983) and elapsed time after colonization (Guegan & Kennedy 1993). Although Kennedy (1978) found that brown trout (*Salmo salmo*) in larger lakes had a richer parasite fauna there was no effect of lake size on the richness of yellow perch assemblages (Carney & Dick 2000a). Host fish with larger geographical distribution are believed to possess richer parasite communities (Wisniewski 1958, Price & Clancy 1983). Perch in Europe and yellow perch in North America both have broad geographical distributions and also have among the richest of parasite faunas found in

freshwater fish (Craig 1987). Therefore, with a better understanding of host parasite assemblages and the processes that produce those assemblages it is possible to predict certain characteristics of a host species' individual, population and community biology. Future whole-lake ecosystem studies need to incorporate knowledge of parasite communities or a great deal of information could be missed or misinterpreted.

YELLOW PERCH GROWTH AND THE INFLUENCE OF PARASITES

The growth of yellow perch has been well studied in the past (Craig 1987). They show extreme plasticity in growth rates and maximum sizes they can attain. These variations are caused by the influences of both abiotic and biotic factors and are observable between different populations, between year classes in one population and between individuals in a single year class (Craig 1987). Sexual dimorphic growth is often seen in natural (Craig 1987) and laboratory raised (Schott *et al.* 1978, Dick unpubl. data) perch populations where females grow faster and reach a greater ultimate size than males. Somatic growth can also differ in timing and extent among age-sex groups with the fastest growth rates in the youngest perch (Tanasichuk & Mackay 1989). Age-at-maturity plays an important role in somatic growth as some energy must be directed to the development of the gonads each fall for spring spawning (Craig 1987). Energy stored in somatic tissue (usually protein and lipid tissue) is transferred to gonadal tissue resulting in loss of growth (Craig 1987). It was also found that the amount of stored energy decreased as perch aged indicating that the drain of surplus energy to the gonads resulted in decreased growth and possibly senescence.

Temperature is perhaps the most important factor influencing yellow perch growth with a physiological optimum of about 25⁰C (Craig 1987). Perch in the northern

hemisphere grow slower at greater latitudes, which is a reflection of a decrease in mean annual temperatures (Craig 1987). LeCren (1958) found that two-thirds of the variation in European perch growth in Lake Windermere could be explained by temperature. Yellow perch kept under simulated winter conditions in the laboratory lost weight and suffered higher mortality (Post & Evans 1989b, Johnson & Evans 1991). Temperature can thus influence recruitment through effects on body size and growth. Correlations between body size and overwinter survival suggest cohorts of fish with larger mean body size suffer less overwinter mortality. LeCren (1992) determined that warm summer temperatures were partially responsible for the exceptionally large European perch (463mm total length max.) observed in Lake Windermere, England prior to 1967.

Prey type and size can also contribute to extreme variability in growth rates among populations (Boisclair & Leggett 1989b, Parrish & Margraf 1991, Schael *et al.* 1991, Byström *et al.* 1998, Cobb & Watzin 1998). Boisclair & Leggett (1989b) found that the percent contribution of four prey taxonomic groups and six prey size-classes, alone or combined with food consumption estimates, explained between 41 and 95% of among-population variability in growth rates or growth efficiency. When different sizes of *Daphnia pulex* were fed to experimental yellow perch it was found that the intermediate-sized prey were preferentially selected and that prey size contributed significantly to specific growth rates (Mills *et al.* 1989). The majority of prey consumed by experimental yellow perch are smaller taxa and perch growth rates were reduced when forced to switch to an alternate prey type (Mills & Forney 1981, Arts & Sprules 1989, Parrish & Margraf 1991). Schael *et al.* (1991) observed that despite the maximum size prey (*D. pulex*) that can be consumed with a certain yellow perch gape size, all perch age-

size classes preferentially selected smaller prey species (copepods). Mills *et al.* (1986) determined that larger prey are not digested as efficiently as smaller prey. Mean prey weight cannot explain variability in growth rates and/or efficiency because it doesn't adequately account for prey abundance or availability (Boisclair & Leggett 1989b). This also explains why the quantity of food consumed cannot explain the variability seen in growth rates in different systems (Boisclair & Leggett 1989a).

The absence or abundance of groups or trophic levels of prey items can also have an impact on perch growth and survival (LeCren 1992, Heath & Roff 1996). Perch typically show three ontogenetic stages in feeding behaviour (Scott & Crossman 1973). They begin life as zooplanktivores then switch to benthos, the timing of which can be age or size-specific (usually by age 2+), followed by piscivory in the largest and oldest fish. Heath & Roff (1996) used a computer simulation to limit the availability of each of the three prey trophic levels to growing perch and found that only the reduced benthic ration simulated stunted growth observed in a natural population of perch in Lac Hertel, Quebec. The only non-stunted benthivore in this lake (white sucker) was believed to be a more efficient benthic feeder and outcompeted yellow perch for this prey resource (Heath & Roff 1996). European perch are one of three stunted benthivores in the Thames River, England, which also suggests that benthos is an important component in *Perca* spp. diets (Williams 1967). Perch can achieve faster growth from a diet of fish than from invertebrates (Craig 1980, LeCren 1992). If, however, a trophic level that is consumed at an earlier life cycle stage is reduced, perch may not reach an adequate size to become piscivorous. This cascade effect of prey type and abundance can seriously affect the ultimate survival of perch as they are recruited into each age class and any one of these

may explain the possible stunting of perch growth and maximum age in several North American systems.

There are several other factors that affect perch growth either directly or indirectly. Eutrophication of a system appears to decrease growth rate, particularly of older fish (Hartman *et al.* 1980, Hayward & Margraf 1987). The absence of certain benthic prey types in eutrophic lakes is believed to be the cause for reduced growth (Hayward & Margraf 1987). Abbey & Mackay (1991) predicted perch growth from measures of whole lake productivity. It was found that the interaction of total phosphorus and chlorophyll a levels could explain 61% and 57% of the variance in total length and wet weight respectively of age 0 perch sampled at the end of August. The ability to predict first year fish growth from lake productivity is strongest at low levels of productivity (total phosphorus <35 ug/l) since high productivity implies more complex communities with more complex community interactions. Zooplankton may be the limiting factor in these systems as total phosphorus has been shown to be positively correlated with zooplankton biomass (Hanson & Leggett 1982).

Competition with other fish species can also play an important role in the growth of yellow perch (Persson 1990, Hayes *et al.* 1992, Bergman & Greenberg 1994, Hayes & Taylor 1994, Mason & Brandt 1996, Byström *et al.* 1998). The removal of 80% of the white sucker population from a yellow perch lake resulted in an increase in the benthic invertebrate population, a shift of perch diet from predominantly zooplankton to predominantly benthos, increased feeding rate and increased growth (especially female gonad growth) of yellow perch (Hayes *et al.* 1992, Hayes & Taylor 1994). Alewife (*Alosa pseudoharengus*) predation has been shown to affect larval perch recruitment in

Lake Ontario (Mason & Brandt 1996). The highest mortality rates in North Pond coincided with the highest alewife abundance during three years of observation in Lake Ontario. Persson (1990) found that European perch age at maturity and gonad size in pond experiments are affected by the presence of roach (*Rutilus rutilus*). As the productivity of lakes increased the abundance of European perch initially increased but then decreased as the abundances of roach and ruffe increased (Bergman & Greenberg 1994). It is suggested that roach outcompete perch during the planktonic dietary stage and ruffe outcompete perch when they shift to benthos.

Other animals can also affect the growth of perch (Thayer *et al.* 1997). It was found that the presence of zebra mussels (*Dreissena polymorpha*) in experimental ponds significantly increased growth rates of yellow perch. The effect was indirect as the mussels alter the prey composition available to the perch. When mussels are present there is an increase in the quantity of macrobenthic crustaceans and oligochaetes and a reduction in zooplankton due to their effective filtration of the water.

Predation, parasitism, reproductive demands, and senescence are the major contributors to mortality in fishes according to Ricker (1975). Growth rates of young-of-the-year (YOY) are important for survival of yellow perch. It has been hypothesized that within a cohort, smaller YOY yellow perch have a greater risk of mortality owing to size selective predation by older yellow perch (Post & Evans 1989a). Post & Evans (1989b) also found that smaller juvenile yellow perch had significantly higher over-winter mortality than larger individuals of the same cohort. Undoubtedly the ability of perch to survive their first winter is critical but interactions among their energy reserves, gonad maturation and survival, largely unexplored, are important as some male perch reach

sexual maturity in their first year. If one adds to these variables the impact of parasitism then survival and fecundity could be further compromised.

Indirect evidence has been used to suggest that parasitism increases mortality in fish (Anderson & Gordon 1982, Gordon & Rau 1982, Kennedy 1984, Szalai & Dick 1991, Szalai *et al.* 1992). Several studies have evaluated the effects of various parasites on fish growth (Lemly & Esch 1984, Singhal *et al.* 1990, Lowe-Jinde & Zimmerman 1991, Szalai & Dick 1991, Szalai *et al.* 1992, Birkeland 1996, Marks *et al.* 1996, Tierney *et al.* 1996). Few, however, have examined the effects of parasites on specific organs and tissues, reproduction and health of fish and the effects on total body weight or length of fish from natural populations. The potential trophic feeding changes of subpopulations of fish with high infection levels of parasites that affect growth but not mortality and the effect these slower growing individuals may have on the entire population structure are not well understood. Crustaceans (Singhal *et al.* 1990, Urawa 1992, Urawa 1995, Birkeland 1996, Marks *et al.* 1996), protozoans (Lowe-Jinde & Zimmerman 1991) and cestodes (Bristow & Berland 1991, Tierney *et al.* 1996) have all been implicated in reduced growth in the form of length and/or body weight in several cultured and natural populations of fish. Reproductive status is also negatively affected by parasitism, particularly by larval cestodes in the body cavity of small fish (Szalai *et al.* 1989, Tierney *et al.* 1996). Yellow perch are good freshwater fish models in which to study these interactions since much is known about their biology and, as previously described, they have one of the most extensive lists of parasites reported for a freshwater fish species (Craig 1987, Hoffman 1999, McDonald & Margolis 1995). Yellow perch in Dauphin Lake, Manitoba with high density infections (>50 cysts/g of liver) of the nematode

Raphidascaris acus in the liver showed lower condition factors and weight-at-age curves with reduced slopes (Szalai & Dick 1991). These parasites also accounted for much of the mortality not explained by predation or abiotic environmental factors. Males with heavy infections often did not mature and those that did were smaller. Females either matured at a later age or died shortly after vitellogenesis (Szalai & Dick 1991).

The factor(s) controlling growth of perch in any system are all important in determining the ultimate survival of perch (particularly juveniles). Both predation mortality (Post & Evans 1989a) and winter survival (Post & Evans 1989b) have been shown to be highly dependent on size. Smaller cohorts of perch always suffer the highest rates of mortality. Those that survive are likely to be permanently stunted and will be more prone to mortality at all age classes than larger-sized populations and will likely also experience reduced fecundity (the proportion of gonads is likely to remain the same in most circumstances). Understanding the growth of perch in a variety of situations is vital to a better understanding of perch populations as a whole and more studies would enhance current knowledge. Of particular importance (especially to fisheries) is a better understanding of stunted perch populations such as those observed in nutrient and biota poor Canadian Shield lakes.

STABLE ISOTOPES

Over the last decade, stable isotope analysis has become an increasingly important tool for solving biogeochemical problems in ecosystem studies and will likely become more useful as more experimenters are exposed to the possible applications of this technique. The popularity of stable isotopes owes to the fact that they can contribute both source-sink and process information. Plant ecologists have used naturally occurring

stable isotope ratios of carbon (C^{13}/C^{12}), nitrogen (N^{15}/N^{14}) and hydrogen (H^1/H^2) for decades to determine a plant's photosynthetic mode (C_4 versus C_3 plants) (Ehleringer & Monson 1993), to trace the source of a plant's nitrogen (Handley & Raven 1992), and to measure water balance and relations (Farquhar *et al.* 1989, Smith *et al.* 1998, Jackson *et al.* 1999). Other recent studies have examined the importance of nitrogen fixation to burned forest ecosystems (Hendricks & Boring 1999), fog water use by plants in the California redwood forest (Dawson 1998), and the identification of mycorrhizal and saprophytic fungi (Hogberg *et al.* 1999) and their roles in the carbon and nitrogen cycles (Hobbie *et al.* 1999). Animal ecologists have also seen potential applications for these analyses and stable isotope ratios in animal tissues have recently been used to reconstruct diets of both extant and extinct animals (Boutton *et al.* 1980, Boutton *et al.* 1983, Ambrose & DeNiro 1986, Bunn *et al.* 1989, Sullivan & Moncreiff 1990, Monteiro *et al.* 1991, Sholto-Douglas *et al.* 1991, Hamilton *et al.* 1992, Hobson & Clark 1992, Forsberg *et al.* 1993, Thomas & Cahoon 1993, Angerbjorn *et al.* 1994, Hobson & Welch 1995, Koch *et al.* 1995, Bootsma *et al.* 1996, France & Steedman 1996, Gu *et al.* 1996), to trace movements (Fry 1983, Hesslein *et al.* 1991, Koch *et al.* 1995), biomagnification of toxins (Kiriluk *et al.* 1995), the effects of introduced species on a native ecosystem (Mitchell *et al.* 1996), long-term changes in a system's food web (Ambrose & DeNiro 1986, Wainright *et al.* 1993), the importance of nitrogen and carbon from decaying semelparous salmon to the trophic system of their spawning stream (Bilby *et al.* 1996), to assess physiological condition (Hobson *et al.* 1993) and to determine where assimilated nutrients accumulate in an animal and how long it takes for those nutrients to be assimilated (Tieszen *et al.* 1983, Hesslein *et al.* 1993, Tieszen & Fagre 1993). Some of

these applications will be discussed in greater detail later. Gannes *et al.* (1997) foresee an explosive increase in the application of these methods as it is becoming easier and less expensive to measure isotopes in animal tissues (Handley *et al.* 1991) and technological improvements are making it more accessible to animal ecologists. Several elements including sulfur, oxygen, hydrogen, nitrogen and carbon are used in stable isotope analyses with the latter two being the focus of the research discussed here.

Fractionation Process

As described earlier, stable isotopes record information about the origins of samples (source information) and the reaction conditions under which fractionation of stable isotopes occurs (process information). This fractionation can shift an isotopic baseline set by a source. Peterson & Fry (1987) used the well-studied example of fractionation in photosynthesis. They used a 1974 study that showed that terrestrial C₃ plants have an average $\delta^{13}\text{C}$ value of -27.8‰ (Troughton *et al.* 1974 in Peterson & Fry 1987). In 1974 the carbon source for plants, CO₂ in air, had an average value of -7.4‰ (Keeling *et al.* 1979). The plant value reflects both the source (-7.4‰) and fractionation (-20.4‰) information: $-27.8_{\text{PLANT}} = -7.4_{\text{SOURCE}} - 20.4_{\text{FRACTIONATION}}$ (Peterson & Fry 1987). In most biochemical reactions, isotopic fractionation arises when similar molecules of slightly different mass (C¹³ and C¹² for example) react at different rates. These chemical and biochemical reactions are divided into a series of individual steps that, when combined in kinetic models, result in the appropriate fractionation for the overall reaction (Peterson & Fry 1987). These models are only just beginning to be applied at an ecosystem level to understand the fluxes of materials.

Stable Isotopes in Animals

Several experiments have shown that diet is clearly the primary determinant of the isotopic ratio of an animal where the C in animal tissue is isotopically similar to the diet (C may be about 1⁰/₀₀ heavier than the diet in some cases) and N averages 3-5⁰/₀₀ heavier than the diet (Minigawa & Wada 1984). For example, broad whitefish that were switched from a 11.4⁰/₀₀ S, -21.4⁰/₀₀ C, 7.8⁰/₀₀ N diet to a -6.3⁰/₀₀ S, -26.3⁰/₀₀ C, 9.7⁰/₀₀ N diet had an isotopic composition that approached that of the second diet with the caveat that the fish were somewhat enriched in ¹⁵N (3.8⁰/₀₀) (Hesslein *et al.* 1993). Animals are enriched in ¹⁵N relative to the diet because of the isotopically light nitrogen in urine (Checkley & Entzeroth 1985, Checkley & Miller 1986, Steele & Daniel 1978). For example, Steele & Daniel (1978) found that cow urine is about -1 to -4⁰/₀₀ relative to the diet while faeces and blood were enriched by +2 and +4⁰/₀₀ respectively. Deamination in the production of urine is believed to be the fractioning reaction. The enrichment in animal tissues preserves the mass balance that must be maintained by counteracting the ¹⁵N depleted urine. The small (<1⁰/₀₀) increases in carbon isotopic composition of an animal over its diet observed on occasion are possibly the result of carbon isotopic fractionation during many formation and breakdown reactions including assimilation and respiration (DeNiro & Epstein 1978).

When C, N, and S are used to analyze food webs, the differences between animal processing of the isotopes are easily observed. Nitrogen isotopic values can be used as indicators of trophic position assuming that at each trophic level the ¹⁵N/¹⁴N ratio increases by about 3-5⁰/₀₀ (Minigawa & Wada 1984). Carbon and sulfur isotopes which show little or no change at each trophic level can be used as indicators of which plant or

bacterial food sources are most important to a particular food web (Fry & Sherr 1984, Peterson *et al.* 1986). Sulfur can also help to identify anadromous organisms as freshwater and marine habitats have different sulfur isotopic ratios (Fry 1983, Hesslein *et al.* 1991).

Although diet is the major contributing factor to the isotopic composition of an animal, there still exists variation between different tissues and metabolites within an individual. For example, bone collagen is $2-6^{0}/_{00}$ enriched in ^{13}C over the diet while fat reserves are depleted by $2-8^{0}/_{00}$ (Parker 1964). The differences arise from the many internal enzymatic steps that fractionate stable isotopes after uptake from the diet (Abelson & Hoering 1961). The tissues that are analyzed for stable isotopes chosen in each situation bear a fixed isotopic enrichment or depletion versus the diet. Whole animals may be used (and in fact becomes necessary when the animals being examined are very small) but samples of muscle or protein will function as adequately as indicators of diet. Stable isotopes can be used to complement other methods of studying diet (stomach content analysis and parasite community composition) in that the stable isotope compositions of tissues are a measure of the assimilated (not just ingested) diet. Both long-term and short-term diets can be identified depending on the turnover rate of the tissues being examined. Slow turnover rates occur in bone collagen and fast turnover rates in the epithelial lining of the gut wall and liver. This method is ideal for learning the diets of extinct animals and those for which it is difficult to make direct observations of feeding behaviour such as for aquatic animals.

The following are several of the diverse possible uses for stable isotopes. Carbon isotope analyses of termite nests in East African grasslands demonstrates that they

acquire their carbon by consuming both C₃ and C₄ plants (Boutton *et al.* 1983). There was also a hierarchy (worker-soldier-queen) within the termite colony as revealed by enrichment of ¹³C by 1⁰/₀₀ at each step. Hendrix *et al.* (1999) were able to distinguish between soil organic matter and surface residues from C₃ plants as potential food sources of two species of earthworms in Florida. Thorp *et al.* (1998) used stable C and N isotopes to conclude that the influential flood pulse concept, which stresses the importance of organic matter, especially terrestrial matter, originating from the floodplain to the riverine food web, is not an adequate explanation of food web structure in the constricted and floodplain regions of the Ohio River. It was concluded that the less popular riverine productivity model, which emphasizes the primary role of autotrophic production in large rivers, is more appropriate in the constricted region. Vander Zanden *et al.* (1999b) found that food chain length as measured by stable isotope ratios was most closely related to the number of fish species present and the size of 14 Ontario and Quebec lakes. Pike, which are often considered to be specialist piscivores, were found to consume a large proportion of invertebrates by stable isotope analysis in five Alberta lakes (Beaudoin *et al.* 1999). Water velocity shows a strong negative relationship with the carbon ratio of herbivores in three productive northern California streams which explains wide variations in published river biota ¹³C levels (Finlay *et al.* 1999). Stable isotope studies conducted in the Amazon River (Forsberg *et al.* 1993) and the Orinoco River floodplain (Hamilton *et al.* 1992) revealed that the most abundant primary producers in the system were not the most important to the riverine food chain as previously assumed. Herbaceous vegetation accounts for approximately 52% of total primary production in the Amazon study area but accounted on average for only 2.5-

17.6% of the carbon in fish (Forsberg *et al.* 1993). C_3 plants accounted for the remainder (82.4-97.5%) of fish carbon. Phytoplankton, which constitutes only 8% of primary production, accounted for a minimum of 36.6% of the carbon in fish. Forsberg *et al.* (1993) hypothesize that selective herbivory may be occurring as algae is by far the best protein source and is readily assimilated by most animals. Algae also appears to be the primary food source in North American east coast estuarine food webs (Sullivan & Moncrieff 1990) but vascular plants (*Spartina* spp.) are more important on the west coast (Kwak & Zedler 1997). The west coast study also demonstrated that there is an ecological link between the salt marsh and tidal channel thus suggesting that any conservation efforts for the marsh must also consider the channel in order to properly manage the various biotic elements of this ecosystem (Kwak & Zedler 1997). Orem *et al.* (1999) used stable isotopes to identify historical changes in the Florida Bay ecosystem and understand changes necessary to restore the bay to its natural (non-human influenced) condition. Preconceived concepts of marine food webs have also changed in light of stable isotope data. For example, Monteiro *et al.* (1991) used $d^{13}C$ values to confirm earlier suspicions that anchovies in the Southern Benguela ecosystem are largely zooplanktivorous and not phytoplanktivores as was the long-held hypothesis.

Cyanobacteria, not seagrasses are the most important food sources for heterotrophs at Dravuni Island, Fiji (Yamamuro 1999). Stapp *et al.* (1999) found that ocean-derived nutrients, especially from seabirds, drive the dynamics of terrestrial food webs on small islands and that this effect is particularly prominent in wet El Nino Southern Oscillation years.

The diets of extinct animals have also been analyzed using stable isotope ratios. Stable carbon isotope ratios of bone collagen of East African mammals discriminate between (1) grazers (C_4 plants) and browsers (C_3 plants) in savannah grasslands, (2) forest floor and savannah herbivores and (3) forest floor (low $d^{13}C$ values) and canopy (high $d^{13}C$ values) species (Ambrose & DeNiro 1986). Nitrogen isotope ratios discriminate between (1) carnivores and herbivores (and the exact trophic level of each carnivore), (2) forest and grassland herbivores and (3) drought tolerant and drought intolerant herbivores. Nitrogen fixation in soils that results in nitrogen depleted in ^{15}N is inhibited by high temperatures and soil dryness (Bate 1981). This means that a drought resistant animal (extinct or extant) will show the high heavy isotope values common in dry soil and the plants which utilize this nitrogen (Ambrose & DeNiro 1986). Thus, the habitats of extinct animals can be indirectly analysed. The diets of brown and black bear populations in several western North America ecosystems are relatively unchanged from historical diets (Jacoby *et al.* 1999). The diets of bottlenose dolphins are also unchanged from the 1880s to the 1980s as revealed by isotopes (Walker *et al.* 1999). Wainright *et al.* (1993) used C and N stable isotopic compositions of fish scales from several species from the Georges Bank. They analyzed fish from 1929 to 1987 and found that, in the case of haddock (*Melanogrammus aeglefinus*), there was a trend toward feeding at two thirds of one trophic level (2.45‰ in $d^{15}N$) lower in 1987 than in 1929. Values of $d^{13}C$ decreased by 1.5‰ from 1929 to 1960 and then increased again toward the present which indicates that there have been some changes occurring at the level of primary production. These isotopic trends were significantly correlated with several environmental and population factors (Greenland Pressure Anomaly, North Atlantic Oscillation, weight-at-

age-2, stock size and fishing mortality). Stable isotope analyses also suggest that several of the fish that were studied may undergo considerable year-to-year and geographic variation (Wainright *et al.* 1993).

Stable isotopes have also been used to determine ancient human diets (van der Merwe & Vogel 1978). Isotope analysis of human bone collagen revealed that $\delta^{13}\text{C}$ values of North American Indians averaged -21 to -22‰ from 3000BC to 500AD but rapidly increased to ~ -11 ‰ by 1300AD. This increase results from the advent and spread of maize cultivation so that about 60% of the diet was derived from corn by 1300AD. Previous archaeological data suggested that widespread maize cultivation began much earlier. In addition to ancient diets, stable isotopes can identify ancient habitats. Isotopic evidence was used to help identify nonmarine coelacanths and pycnodontiform fishes from the Early Cretaceous (Poyato-Ariza *et al.* 1998). These two fish groups were previously uncontested as solely marine taxa.

Several other studies have used stable isotopes to further clarify food web structure and individual and population diets in many different kinds of freshwater (Bunn *et al.* 1989, Hobson & Welch 1995, Bootsma *et al.* 1996, France & Steedman 1996, Gu *et al.* 1996, Keough *et al.* 1996, Kline *et al.* 1998, Vander Zanden *et al.* 1999c, Fry *et al.* 1999, Yoshii *et al.* 1999), marine (Sholto-Douglas *et al.* 1991, Thomas & Cahoon 1993, Pauly *et al.* 1998) and terrestrial (Boutton *et al.* 1980, Angerbjorn *et al.* 1994) environments. Keough *et al.* (1996) found that both coastal and offshore Lake Superior food webs were based upon carbon fixed by phytoplankton but had distinct carbon signatures suggesting different types of phytoplankton were involved. It was also observed that the nitrogen isotope ratio of YOY yellow perch indicated a planktivorous

diet. As the perch grew the isotope ratio increased thus supporting observed dietary shifts from plankton to benthos and finally to fish.

Stable isotopes can also be used as indicators of migratory patterns. Sulfur isotope analysis of whitefish muscle in the Mackenzie Delta region showed that Travaillant Lake broad whitefish and Kukjuktuk Creek lake whitefish were migrant populations which had grown primarily on sources outside the local food base (Hesslein *et al.* 1991). It was determined, due to the relatively high levels of heavy sulfur isotope, that a marine origin was likely for these lake whitefish. Natural stable carbon isotopes were used to distinguish exclusively freshwater, freshwater-marine migrants, and entirely marine fish from one another in Prudhoe Bay, Alaska (Kline *et al.* 1998). Anadromous and non-anadromous populations of brook trout (*Salvelinus fontinalis*) and the maternal origins of age 0 progeny were identified in the Tabusintac River, New Brunswick (Doucett *et al.* 1999a). Stable isotopes were used as evidence for anadromy in a southern relict population of Arctic charr (*Salvelinus alpinus*) in Quebec that is associated with niche shift (Doucett *et al.* 1999b). Others have also used isotopes to identify animal migratory movements for which it is difficult to make direct observations (Fry 1983, Schell *et al.* 1989, Fleming *et al.* 1993, Koch *et al.* 1995).

Stock and population identification in fish communities can also benefit from stable isotope techniques. The stable oxygen and carbon isotope ratio analyses in sagittal otoliths of sockeye salmon (*Onchorhynchus nerka*) can be used as a chemical tracer in population identification and in the study of ocean environmental changes (Gao & Beamish, 1999). Analysis of stable isotopes in pink snapper (*Pagrus auratus*) and bluefish (*Pomatomus saltratrix*) otoliths showed location specific stocks (one in

hypersaline Shark Bay and another north of this bay) of pink snapper but not bluefish (migrated between the two areas) (Edmonds *et al.* 1999). Lake Biwa catfish (*Silurus biwaensis*) are separated into two local populations (north and south) which rarely mix as revealed by isotope analysis (Takai & Sakamoto 1999).

Biomagnification of toxins in higher tiers of a food web can also be identified with stable isotopes. Cabana & Rasmussen (1994) found a significant correlation between $d^{15}N$ and mercury levels in shield lakes. Kidd *et al.* (1995) interpreted significant correlations between organochlorine concentrations and $d^{15}N$ in the biota from Lake Laberge and concluded that organochlorine levels could be predicted on the basis of $d^{15}N$ values. Kiriluk *et al.* (1995) described a significant correlation between $d^{15}N$ enrichment (trophic status of an organism) and biomagnification of lipophilic contaminants.

Invasive species and their impact on local ecosystems can be analyzed with stable isotopes. Zebra mussel infestation may have a marked effect on the food web of a recently invaded lake (Mitchell *et al.* 1996). The mussels filter planktonic algae at high rates and deposit any unwanted material in the form of pseudofaeces onto sediments and the typically high densities of zebra mussels can have a serious impact on phytoplankton biomass and on the coupling of benthic and pelagic food pathways. Mitchell *et al.* (1996) found that the isotopic ratios of C for zebra mussels more closely resembled those of the seston than did the values for *Daphnia* spp. (another phytoplankton feeder). Therefore, the zebra mussels have a greater reliance on that food source than *Daphnia* spp. Northern pike addition to two experimental lakes (ELA) resulted in a shift of fathead minnow diet in one lake from zooplankton to zoobenthos as evidenced by stable C and N isotope

ratios but did not affect pollutant accumulation (Kidd *et al.* 1999). Vander Zanden *et al.* (1999a) found that lakes invaded by smallmouth bass and rock bass showed a decline in littoral prey fish abundance and shift in trophic position of resident lake trout from a fish diet to a zooplankton diet.

Stable isotopes have also been used extensively to interpret the importance of nitrogen and carbon from spawning salmon and other anadromous fish to the trophic structure of small streams and their riparian zones. Bilby *et al.* (1996, 1998) determined the importance of semelparous coho salmon to their spawning streams using stable isotopes. They found that epilithic organic matter, all aquatic macroinvertebrates except shredders, and fish were significantly enriched with ^{15}N and ^{13}C where post-spawning coho salmon carcasses were present. Shredders and riparian vegetation were only enriched in the heavy nitrogen isotope. The growth rate of young coho salmon in carcass-enriched streams doubled over that of fish in non-spawning streams. The amount of dead fish nitrogen that was incorporated varied among trophic levels from 17% in collector-gatherers to >30% in young fish. Hilderbrand *et al.* (1999) found that salmon-eating bears in Alaska vector salmon nitrogen (ie. marine nitrogen) through excretion and carcass dispersal into riparian ecosystems. Distance from the stream is inversely proportional to the amount of salmon nitrogen in riparian plants (Ben *et al.* 1998, Hilderbrand *et al.* 1999). Anadromous clupeid (*Alosa* spp.) fishes on the Atlantic coast of North America also contribute significantly to the biomass accumulation in piscivores in migratory streams during clupeid spawning runs (Garman & Macko 1998).

Stable isotopes can be used to determine tissue turnover rates. The turnover rates for various organ tissues in gerbils (Tieszen *et al.* 1983), birds (Hobson & Clarke 1992),

shrimp (Parker *et al.* 1988) and fish (Hesslein *et al.* 1993) have all been analyzed. Broad whitefish (*Coregonus nasus*) muscle and liver were analyzed for S, C and N isotopic ratios following an experimental shift to a new diet which was isotopically different from the original diet (Hesslein *et al.* 1993). Despite the depleted S and C values (-4.4 and -4.1‰ respectively) in liver relative to the muscle, the actual turnover rates were similar. In gerbils (Tieszen *et al.* 1983) and birds (Hobson & Clarke 1992), faster growing liver tissue had a much faster turnover rate (eg. quail liver turnover 0.27/d and muscle 0.056/d). Hesslein *et al.* (1993) hypothesized that in slow-growing populations of fish the response to a change in food could take years whereas in fast-growing populations the rate of change would directly reflect the growth rate.

Because of the potential for explosive use of this technique it is important that it be done properly. There are several assumptions and caveats of which a researcher must be aware before attempting to use stable isotopes. In determination of an animal's diet using stable isotopes it must be assumed that the isotopic composition of an animal's tissues equals the weighted average of the isotopic composition of the components of its diet (Gannes *et al.* 1997). For example, a herbivore eating C₃ and C₄ plants,

$$\delta^{13}\text{C} (\text{animal tissue}) = p \cdot \delta^{13}\text{C}_{\text{C}_4} + (1-p) \cdot \delta^{13}\text{C}_{\text{C}_3},$$

where p equals the proportion of C₄ grasses in the diet. There are three reasons why this assumption is often invalid: (1) dietary components are assimilated with varying efficiencies, (2) dietary isotopes are fractionated by animal tissues (changing the isotopic ratios) and (3) nutrients are allocated differently to specific tissues. For example, as lipids are synthesized from dietary carbohydrates they become enriched in the lighter isotope (DeNiro & Epstein 1977) whereas bone collagen, because it contains 33%

glycine, becomes enriched with the heavy isotope relative to other tissues (Hare *et al.* 1991). This fractionation can be compensated for if proper laboratory experiments are performed to provide comparative data on the fractionation values for different tissues and tissue components (Gannes *et al.* 1997). However, there is currently comparatively little laboratory data and because different species may fractionate at different rates it is important to increase experimental work on a larger assemblage of species.

Another problem is the phenomenon termed “isotopic routing” where isotopes contained in the diet are routed differentially to specific tissues (Tieszen & Fagre 1993, Gannes *et al.* 1997). Consequently, the isotopic composition of the nutrient component of the diet from which the tissue was synthesized and not that of the bulk diet is reflected in the tissues. This has led many researchers to shift from bone collagen to the carbonates within bone apatite (Tieszen & Fagre 1993). Bone collagen is mostly protein and therefore may reflect the isotopic composition only of the dietary protein and not the bulk diet that may include carbohydrates and protein each from different sources only one of which will get recognized. Carbonates, however, are synthesized from circulating bicarbonates and probably reflect isotopic composition of the components of the diet that are catabolized (Ambrose & Norr 1993). Foregut fermentation (e.g. ruminants) solves this problem by complete mixing of the nitrogen in all dietary components (Macrae & Reeds 1980). Hindgut fermenters (e.g. horses, rabbits, rodents) and omnivores with modest fermenting abilities may or may not mix the dietary nitrogen sufficiently before assimilation so the degree of mixing must be measured before any isotopic data can be examined (Gannes *et al.* 1997). Urea recycling and protein balance can also affect the isotopic composition (Gannes *et al.* 1997). It is important that we gather as much

comparative data as possible from laboratory experiments in order to further validate field observations.

Using stable isotopes to determine the trophic level of an animal can also be misleading. The tissues of starving animals become progressively more enriched in ^{15}N as lean body mass decreases (Hobson *et al.* 1993). This may have the effect of making the animal appear to be at a higher trophic level than it actually is. Measuring the nitrogen isotope ratios in urine, hair and blood may be good indicators of lean-tissue losses under these circumstances (Hobson *et al.* 1993).

Gannes *et al.* (1997) suggest that stable isotopic analysis is a useful tool for ecosystem studies. However, more laboratory experiments involving all aspects of stable isotopes must be performed before the processes involved can be better understood. This would allow an animal ecologist to acquire more complete, accurate data for each field study.

CHAPTER 2: Parasitological and dietary survey of some Experimental Lakes Area fishes with an emphasis on yellow perch parasite assemblages.

INTRODUCTION

The parasites of freshwater fishes of Canada have been well documented (McDonald & Margolis 1995). In particular, the Manitoba fish parasite fauna has been studied by Poole (1985), Watson & Dick (1979, 1980), Choudhury & Dick (1993), Szalai *et al.* (1992), and Carney & Dick (2000a), Lake of the Woods by Dechtiar (1972) and Manitoba and Lake of the Woods reviewed by Lubinsky & Loch (1979). With the exception of Poole's studies most fish communities were from large lakes with complex biota. The small nutrient poor shield lakes from the Experimental Lakes Area (ELA) in Ontario were of interest since much is known about this system and the biota, including the fish community, is much less complex than other systems studied to date. The goal of the overall study was to determine the parasite community composition in fish from four of these lakes, especially yellow perch (*Perca flavescens*), to compare the results with the communities found in other systems and to determine if the parasite communities had predictable components, even though they contained less complex communities. Seasonal and age-related parasite community trends and food habits for yellow perch are presented.

METHODS AND MATERIALS

Sample collection and examination

Fish were caught with minnow traps (baited with bread or dog food), trap nets, gill nets and backpack electroshocking. A total of 2304 fish of 15 species were captured from 1997 to 1999 of which 2216 were completely examined for all parasites. Only yellow perch (*P. flavescens*, N=1841) and white sucker (*Catostomus commersoni*, N=57) were found in all four lakes (Table 2.1). All other fish species were found in only one or two study lakes. Samples were collected in June, July and October of 1997, May, July, September and October of 1998 and September of 1999. Water temperatures ranged from 5°C during October sampling to 20°C during July sampling.

All fish were examined with the aid of a dissecting microscope for external parasites and external lesions and tumors. Total length, fork length, and round weight were measured for all fish. Several additional morphometric and meristic characteristics were measured for all fish species and these data are summarized in Appendix I. Liver weight was recorded for all but the June 1997 sample, for which the liver weights were estimated using a regression equation of the proportion of known liver weights to overall body weight. A fillet from one side of each fish was removed and weighed to determine the density of parasites found in the muscle tissue. Perch sex and maturity was determined by inspection of the gonads using criteria established by Craig (1987). Sex and maturity of all other fish were examined. Gonad weight was recorded for each fish. Visceral fat was removed, weighed (yellow perch only and for all but the June 1997 sample) and

Table 2.1. The sample sizes of each species of fish sampled from four study lakes in the Canadian Shield.

Fish species	LAKE			
	L239	L240	L377	Triangle L.
Northern pike (<i>Esox lucius</i>)	1	15	NP	NP
Cisco (<i>Coregonus artedii</i>)	NC	NC	13	NP
Pearl dace (<i>Margariscus margarita</i>)	NP	NC	70	69
Blacknose shiner (<i>Notropis heterolepis</i>)	NP	NP	10	103
Spottail shiner (<i>Notropis hudsonius</i>)	NP	NP	29	NP
Northern redbelly dace (<i>Phoxinus eos</i>)	1	2	NP	5
Finescale dace (<i>Phoxinus neogaeus</i>)	NP	1	NP	3
Fathead minnow (<i>Pimephales promelas</i>)	NP	NP	1	5
Longnose dace (<i>Rhynchichthys cataractae</i>)	NP	NP	17	NP
White sucker (<i>Catostomus commersoni</i>)	9	4	37	7
Burbot (<i>Lota lota</i>)	NP	NP	1	NP
Brook stickleback (<i>Culea inconstans</i>)	NP	NP	10	16
Slimy sculpin (<i>Cottus cognatus</i>)	NC	5	21	NP
Iowa darter (<i>Etheostoma exile</i>)	NP	8	NP	NP
Yellow perch (<i>Perca flavescens</i>)	564	504	371	402

Note: NP = not present, this species is not known to occur in this lake.

NC = not captured, this species has been reported from the lake but was not recovered in this study.

examined for parasites. All weights were recorded to the nearest 0.001g and gonad and visceral fat weights were then converted to percent of total body weight (perch only). Weights of gonads and visceral fat were compared to obtain a ratio for each fish (perch only). Complete necropsies were performed on fresh fish when possible (~140 fish) and if not they were frozen (-20° C) and examined later. Live parasites were examined in physiological saline, killed in 90 °C tap water, fixed in AFA (Humason 1978) and stored in 70% ethanol. Frozen specimens were examined in tap water, fixed in AFA and stored in 70% ethanol. Numbers and species of internal parasites found in the gills, eyes, musculature, heart, swim bladder and viscera were obtained. All tissues were examined with a dissecting microscope. Intramuscular parasites were observed by making a series of vertical slices through one fillet (from the left side of the fish) approximately 1cm wide and then carefully examining the exposed surfaces of the muscle with a dissecting microscope. All tissues except the liver were isolated, slit open longitudinally and the contents were scraped into a petri dish. Frozen specimens of parasites were examined in tap water and fresh specimens in physiological saline. Livers were compressed between two glass plates and numbers and life cycle stage of encysted parasites were recorded according to Szalai & Dick (1991). Invasive and noninvasive parasites were categorized based on whether they resided in host tissue or in the lumen of an organ. Several keys were used to assist with parasite species identifications (Beverly-Burton 1984, Schell 1985, Kabata 1988, Hoffman 1999). The methods for calculating parasite infrapopulation statistics used in this chapter follow Margolis *et al.* (1982). Stomach contents were removed and identified with aquatic invertebrate keys when the degree of

decomposition permitted (Fitzpatrick 1983; Merritt & Cummins 1984). Abundance and prevalence of dietary items were recorded.

Aging structures removed from each fish included scales, opercula and otoliths. Yellow perch opercula were aged according to the methods of LeCren (1947) (i.e., age 0 fish had no annuli, age 1 fish have one annulus, etc). Perch otoliths were cleaned in hot water, placed in canola oil and observed with a dissecting microscope using reflected light. The annuli were counted as per the opercula. Scales of 50 perch were also aged by a method similar to the opercula. The annuli of scales and opercula were difficult to distinguish in older perch (> 2+). Annuli in the otoliths were clearly distinguishable at all ages and therefore the ages recorded from these structures were used in all further calculations. The weights of perch otoliths (to the nearest 0.001g) were measured and correlated with perch size (Appendix II). Age classes of yellow perch were further subdivided according to time of year caught. June was designated as the beginning of each year as perch typically hatch at this time of year (Scott & Crossman 1973, Craig 1987) and was given a post-decimal value of 0. One-twelfth (0.083333) was added to each following month and then rounded to two decimal places. For example, one year old perch caught in June were labeled as 1.00, July 1.08, September 1.25, October 1.33 and May 1.92. The predicted June hatching time for perch in ELA was supported by sampled females that had not yet spawned by May 23. The June 1997 sample was small (25 perch from only L240) and those data were included with the July 1997 sample for much of the analysis.

RESULTS

Fish morphometrics

Mean total lengths (TL) and weights of each sampled fish species are presented in Table 2.2. Mean age of yellow perch in each lake is also given in Table 2.2. Pike were the largest of the sampled fish. L240 pike were larger but the L239 sample consisted of only one specimen. Cisco were also among the larger sampled fish at over 200mm mean TL and over 80g weight. The cyprinids range from approximately 50mm to 100mm and from approximately 1g to 11g mean total length and mean weight respectively. The cyprinid species that are found in more than one lake show no difference in mean size between lakes. L239 white suckers are much smaller than the other sucker samples. One large L240 white sucker (512mm, 2000g) in a sample of four fish resulted in a large mean intensity with a large standard deviation. L377 and Triangle Lake have white sucker populations with similar mean TL and weight. One large burbot was recovered from L377. Brook sticklebacks in L377 are larger than those removed from Triangle Lake (average 15mm, 0.75g larger). Slimy sculpins from L240 average approximately 20mm and 2g larger than those obtained from L377. Iowa darters were the smallest fish (TL and weight) sampled from the study lakes.

Yellow perch from L239 are the smallest and youngest of the four perch populations (Table 2.2). L240 perch have slightly higher mean TL and age and a mean weight almost twice that of L239 perch. The mean age of L377 yellow perch is the same as L240 but the mean TL and weight are higher by approximately 20mm and 6g respectively. Triangle Lake yellow perch are the largest and oldest of all the populations. They average about one year older, 20mm longer and 10g heavier than the perch from

Table 2.2. Mean total length [TL(mm)] and mean weight [Wt(g)] of 15 species of fish, with the inclusion of mean age of yellow perch, recovered from four study lakes in the Canadian Shield. Results are presented as means + SD with the range in parentheses.

Fish species		LAKE			
		L239	L240	L377	Triangle L.
Northern pike (<i>Esox lucius</i>)	TL	391 (391)	605.8 ± 211.4 (136-802)	NP	NP
	Wt.	356.4 (356.4)	1796 ± 925.8 (12.0-2550)		
Cisco (<i>Coregonus artedii</i>)	TL	NC	NC	213.2 ± 43.1 (142-259)	NP
	Wt.			82.4 ± 40.5 (24.3-136.0)	
Pearl dace (<i>Margariscus margarita</i>)	TL	NP	NC	100.7 ± 11.6 (68-124)	103.3 ± 20.6 (41-137)
	Wt.			9.02 ± 3.05 (2.7-16.5)	11.2 ± 6.24 (0.5-26.3)
Blacknose shiner (<i>Notropis heterolepis</i>)	TL	NP	NP	54.3 ± 11.3 (32-67)	57.2 ± 6.15 (28-67)
	Wt.			1.22 ± 0.65 (0.2-2.15)	1.50 ± 0.44 (0.11-3.16)
Spottail shiner (<i>Notropis hudsonius</i>)	TL	NP	NP	93.2 ± 6.86 (83-109)	NP
	Wt.			6.93 ± 2.00 (4.44-12.6)	
Northern redbelly dace (<i>Phoxinus eos</i>)	TL	63 (63)	56.5 ± 0.71 (56-57)	NP	54.2 ± 4.49 (48-60)
	Wt.	1.58 (1.58)	1.61 ± 0.02 (1.59-1.62)		1.53 ± 0.31 (1.13-1.85)

Table 2.2. Continued.

Fish species		LAKE			
		L239	L240	L377	Triangle L.
Finescale dace (<i>Phoxinus neogaeus</i>)	TL		77 (77)		68.0 ± 4.00 (64-72)
	Wt.	NP	4.02 (4.02)	NP	3.03 ± 0.13 (2.88-3.14)
Fathead minnow (<i>Pimephales promelas</i>)	TL			82 (82)	89.2 ± 14.7 (63-97)
	Wt.	NP	NP	5.63 (5.63)	7.64 ± 3.47 (2.05-10.5)
Longnose dace (<i>Rhynchithys cataractae</i>)	TL			53.8 ± 13.7 (38-87)	
	Wt.	NP	NP	1.46 ± 1.35 (0.47-5.10)	NP
White sucker (<i>Catostomus commersoni</i>)	TL	138.6 ± 51.1 (63-224)	263.5 ± 177.2 (114-512)	201.1 ± 86.6 (61-410)	201.7 ± 93.7 (46-298)
	Wt.	32.6 ± 31.2 (2.27-103.0)	561.1 ± 962.3 (10.5-2000)	129.1 ± 179 (2.16-730.6)	129.6 ± 122 (0.77-281)
Burbot (<i>Lota lota</i>)	TL			413 (413)	
	Wt.	NP	NP	484.2 (484.2)	NP
Brook stickleback (<i>Culea inconstans</i>)	TL			57.6 ± 6.45 (49-71)	42.1 ± 7.01 (31-54)
	Wt.	NP	NP	1.39 ± 0.56 (0.77-2.80)	0.66 ± 0.35 (0.17-1.33)

Table 2.2. Continued.

Fish species		LAKE			
		L239	L240	L377	Triangle L.
Slimy sculpin (<i>Cottus cognatus</i>)	TL		74.8 ± 17.6 (52-93)	56.0 ± 14.6 (34-83)	
		NC			NP
	Wt.		4.03 ± 2.80 (1.08-8.28)	1.99 ± 1.83 (0.20-6.33)	
Iowa darter (<i>Etheostoma exile</i>)	TL		42.0 ± 4.44 (36-49)		
		NP		NP	NP
	Wt.		0.56 ± 0.16 (0.37-0.72)		
Yellow perch (<i>Perca flavescens</i>)	TL	71.1 ± 17.2 (39-156)	79.6 ± 25.9 (35-177)	92.2 ± 33.6 (31-270)	116.0 ± 46.0 (35-270)
	Wt.	3.72 ± 4.09 (0.45-44.2)	6.10 ± 6.83 (0.37-52.0)	10.7 ± 14.9 (0.19-208.5)	22.2 ± 25.8 (0.44-219.7)
	Age	1.10 ± 0.76 (0.08-6.08)	1.50 ± 1.02 (0.08-7.25)	1.47 ± 1.29 (0.08-8.08)	2.43 ± 1.69 (0.08-8.33)

Note: NP = not present, this species is not known to occur in this lake.
 NC = not captured, this species has been reported from the lake (Beamish et al. 1976) but was not recovered in this study.

L377. All four lake samples have 0+ to 4+ year-old perch. The oldest perch samples from L239 were 6+ but there were no males older than 3+ in this lake. The L240 sample had more perch from 2+ to 4+ than L239 fish but had only one old fish, a 7+ male. There were one 8+ and two 7+ fish and no 6+ females L377 perch. Triangle Lake had several fish older than 4+.

YOY perch from Triangle Lake had greater mean total lengths than perch from the other three systems (Table 2.3). At age 1+ L377 and Triangle perch had mean lengths approximately 2cm longer than L239 and L240 perch. Triangle Lake perch continued to grow at a faster rate and were the largest fish at each subsequent age class. L377 perch were next largest at each age class. At age 3+, L240 perch started to grow at a faster rate than L239 hosts. In yellow perch younger than 2+, females were significantly larger than males only in L239 samples (Table 2.3). 2+ to 4+ females were significantly larger than males in all classes where males were present. There were no significant differences in samples older than 4+ due to small sample sizes and few classes with both sexes present.

Fish stomach contents

Of the four smallest cyprinid species sampled from these lakes, blacknose shiner consumed the widest variety of food items (7 types) (Fig. 2.1). Cladocerans were found in about 40% and 30% of L377 and Triangle Lake shiner stomachs respectively. All other food items were found in less than 10% of fish stomachs. Cladocerans were the only prey type of fathead minnows (Fig. 2.1). Both *Phoxinus* minnows fed exclusively on filamentous algae. Lake cisco and spottail shiners, which are often pelagic offshore fish, had only three prey types each; the dominant types were zooplankton (Cladocera

Table 2.3. Within age-class comparison of total length (TL) of female and male yellow perch collected from four Canadian Shield lakes in the ELA and surrounding region. A sequential Bonferroni was applied to the *t*-test *P* values. Significant *P* values (≤ 0.05) are displayed and NS denotes no significant difference between means.

AGE (yrs)	T-test statistics	L239		L240		L377		Triangle	
		F	M	F	M	F	M	F	M
0+	N	162	127	78	78	41	48	54	49
	Mean TL (mm)	59.7	58.6	53.2	53.1	52.0	52.1	61.2	62.6
	SE	5.1	5.5	7.1	8.6	13.2	16.5	10.2	8.1
	Significance	NS		NS		NS		NS	
1+	N	140	72	98	112	71	60	66	31
	Mean	77.6	75.7	79.1	77.7	97.3	97.7	99.1	96.1
	SE	8.9	8.3	10.3	7.7	8.1	5.9	12.5	9.7
	Significance	NS		NS		NS		NS	
2+	N	37	12	42	30	34	8	61	18
	Mean	103.6	96.1	105.3	97.4	121.4	112.3	132.8	114.8
	SE	13.3	7.9	9.0	8.5	15.7	4.9	18.2	13.7
	Significance	NS		0.0002		NS		0.00003	

Table 2.3. Continued.

AGE (yrs)	T-test statistics	L239		L240		L377		Triangle	
		F	M	F	M	F	M	F	M
3+	N	4	3	40	10	32	2	40	12
	Mean	114.0	100.0	126.3	118.3	138.5	120.5	161.5	133.3
	SE	15.5	2.6	13.8	13.6	18.3	2.1	25.6	13.2
	Significance	NS		NS		0.00004		0.000006	
4+	N	3	0	8	3	11	1	28	5
	Mean	124	0	138.9	114.3	144.6	123.0	176.3	153.0
	SE	17.1	n/a	11.4	8.4	11.4	n/a	26.6	18.3
	Significance	NS		NS		NS		NS	
5+	N	2	0			4	0	13	2
	Mean	142	0			157.5	0	169.8	161.5
	SE	5.7	n/a			38.0	n/a	37.6	12.0
	Significance	NS				NS		NS	
6+	N	2	0					9	1
	Mean	146.5	0					181	205
	SE	13.4	n/a					21.2	n/a
	Significance	NS						NS	

Table 2.3. Continued.

AGE (yrs)	T-test statistics	L239		L240		L377		Triangle	
		F	M	F	M	F	M	F	M
7+	N			0	1	1	1	8	0
	Mean			0	177	127	138	195.9	0
	SE			n/a	n/a	n/a	n/a	7.5	n/a
	Significance			NS		NS		NS	
8+	N					1	0	4	0
	Mean					270.0	0	219.8	0
	SE					n/a	n/a	1.9	n/a
	Significance					NS		NS	

Figure 2.1. Prey types and prevalences in the stomachs of four small species of Cyprinidae sampled from four Canadian Shield lakes, Ontario, Canada in spring, summer and fall of 1997 and 1998. Sample sizes are indicated by n for each lake.

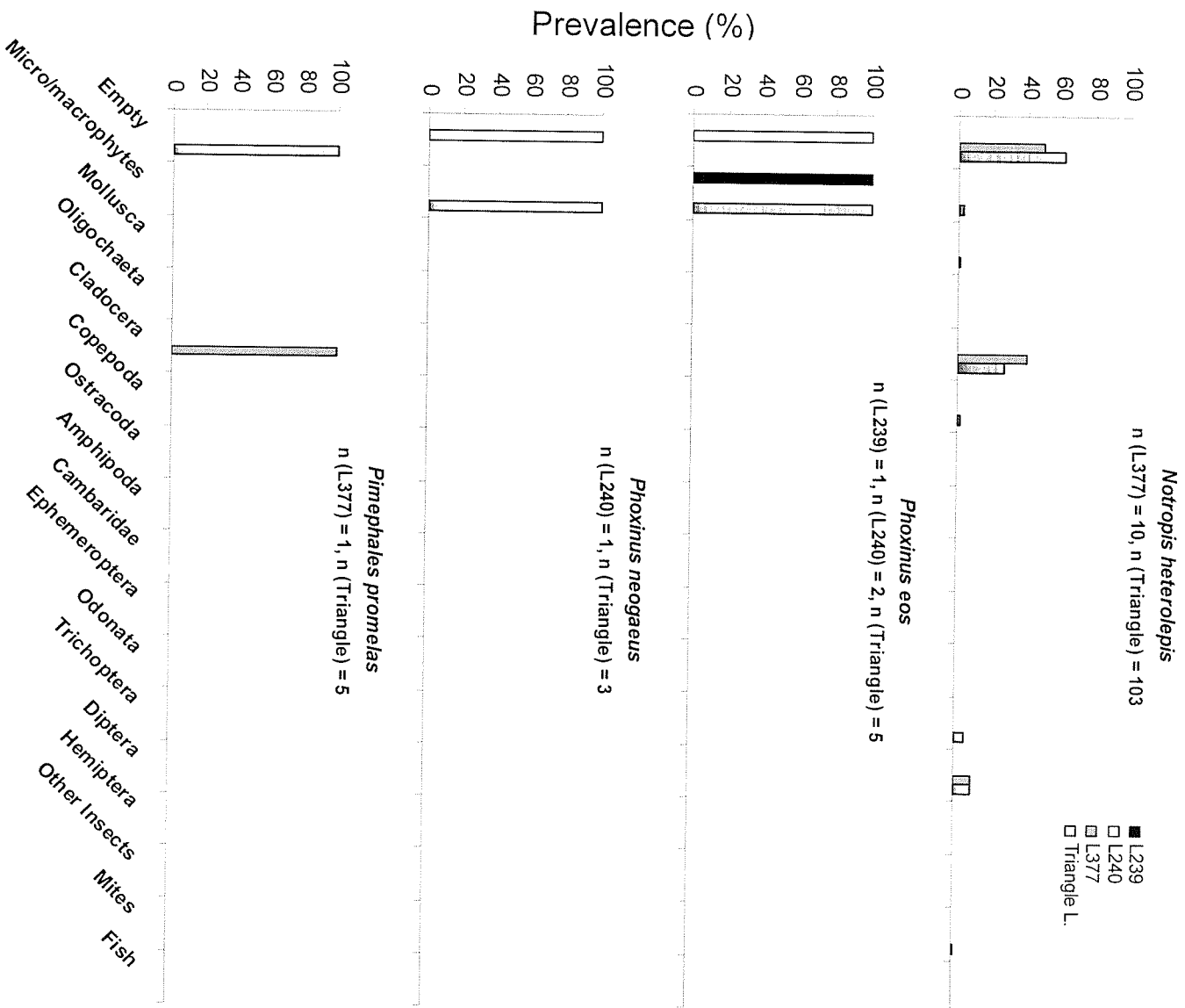
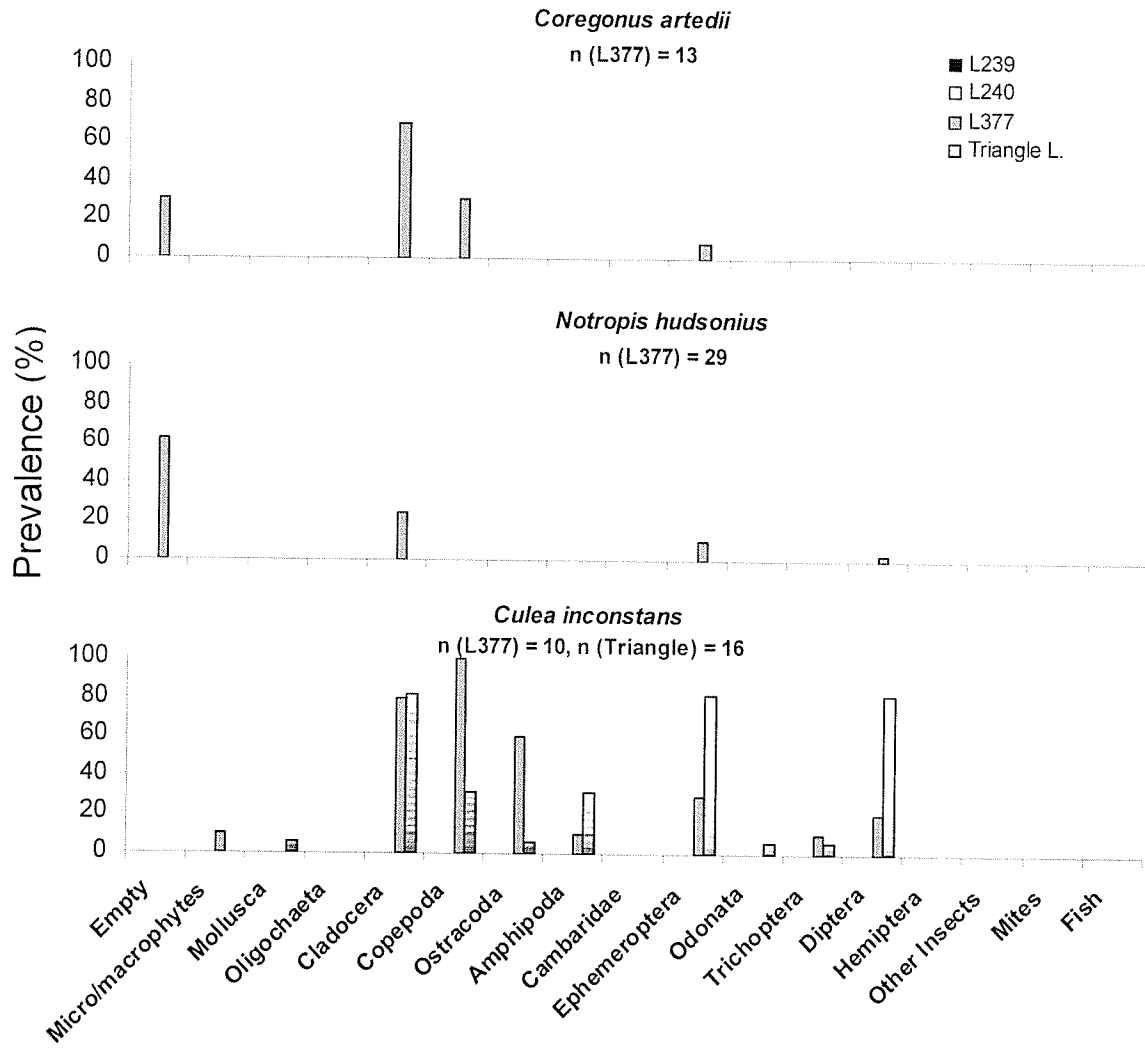


Figure 2.2. Prey types and prevalences in the stomachs of three primarily planktivorous fish species (lake cisco, spottail shiner and brook stickleback) sampled from L377 and Triangle Lake, Ontario in spring, summer and fall 1997 and 1998. Sample sizes are indicated by n for each lake.



and Copepoda) (Fig. 2.2). Small gape size forces sticklebacks to be primarily zooplanktivorous. L377 sticklebacks had 8 different prey types in their stomachs but cladocerans, copepods and ostracods were most prevalent (Fig. 2.2). Triangle Lake sticklebacks preyed upon nine food types and the most prevalent items were cladocerans, small Ephemeroptera nymphs and Diptera, which was a less zooplanktivorous diet for this species than it was in L377 (Fig. 2.2). In four benthic fish species (*R. cataractae*, *C. commersoni*, *C. cognatus* and *E. exile*), dominant prey types included Amphipoda, Ephemeroptera, Trichoptera, Diptera and Mollusca with few pelagic prey items (Fig. 2.3). White suckers showed the greatest variety of prey types (11) of all benthivores sampled. The two primarily piscivorous fish species sampled each had three prey types in the stomach (Fig. 2.4). Fish were the dominant prey item in pike. Ephemeroptera and Odonata nymphs and fish were most prevalent in burbot.

Pearl dace consumed eleven prey types and perch 13 prey types (Fig. 2.5). L377 pearl dace had consumed largely cladocerans and dipterans. Perch from L239 and L240 had nearly identical prevalences of each prey type in their diets (Fig. 2.5). Perch from L377 show increased prevalences of zooplankton and reduced prevalences of benthos in their diet. Perch in L377 and Triangle Lake preyed more frequently upon fish than did perch in the other two lakes (Fig. 2.5).

Seasonal dietary trends

Benthic prey items were most prevalent in the summer or fall perch stomachs although chironomids also showed high prevalence in spring diets (Fig. 2.6). Chaoborids, hemipterans and mysid shrimp were absent or rare in perch stomachs except during the fall. Zooplankton were most prevalent in spring or summer diets in all but

Figure 2.3. Prey types and prevalences in the stomachs of four benthic fish species recovered from four Canadian Shield lakes, Ontario, Canada in spring, summer and fall 1997 and 1998. Sample sizes are indicated by n for each lake.

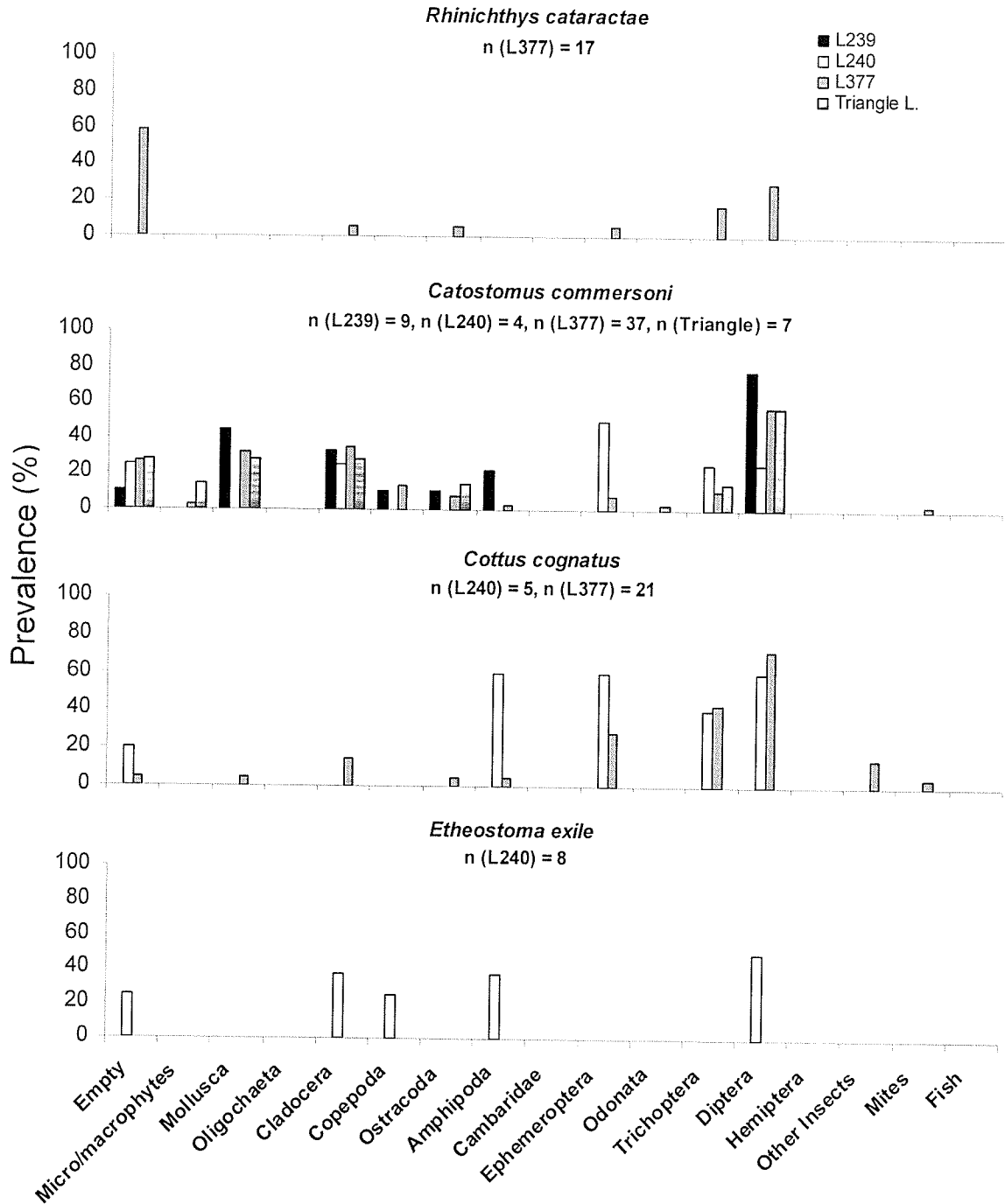


Figure 2.4. Prey types and prevalences in the stomachs of two primarily piscivorous fish species (pike and burbot) sampled from three Canadian Shield lakes in Ontario in spring, summer and fall 1997 and 1998. Sample sizes are indicated by n for each lake.

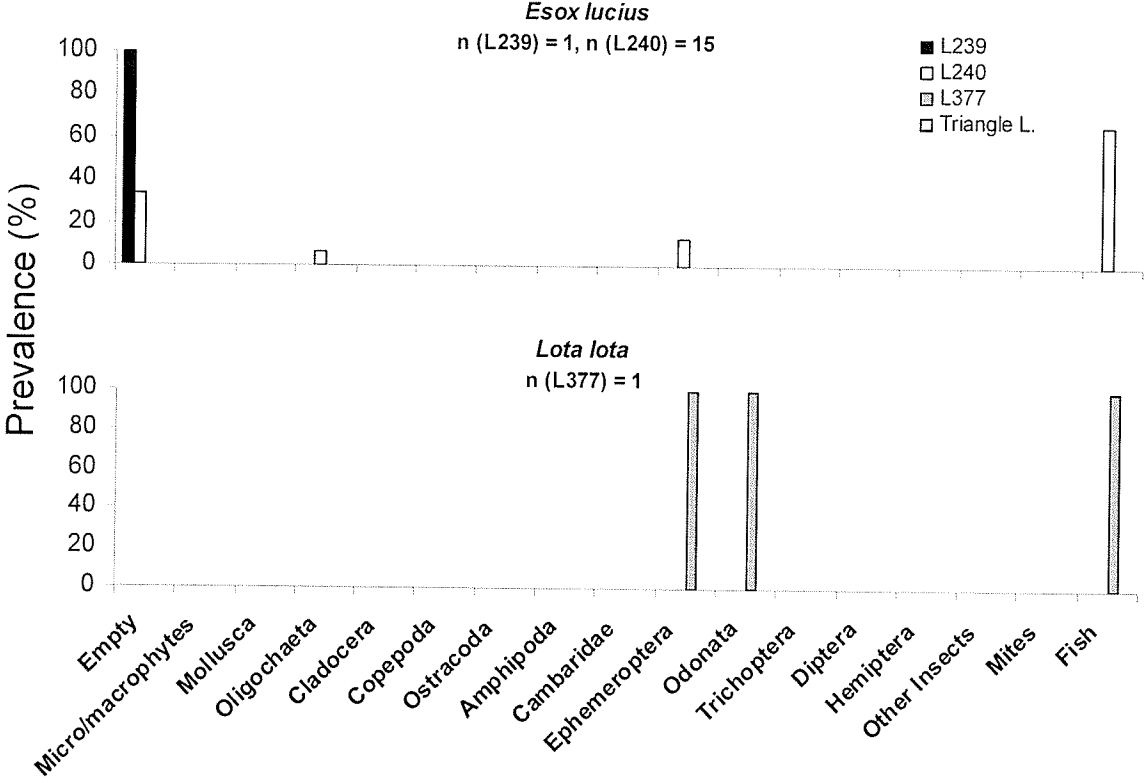


Figure 2.5. Prey types and prevalences in the stomachs of two generalist fish species (pearl dace and yellow perch) recovered from four Canadian Shield lakes, Ontario, Canada in spring, summer and fall 1997 and 1998. Sample sizes are indicated by n for each lake.

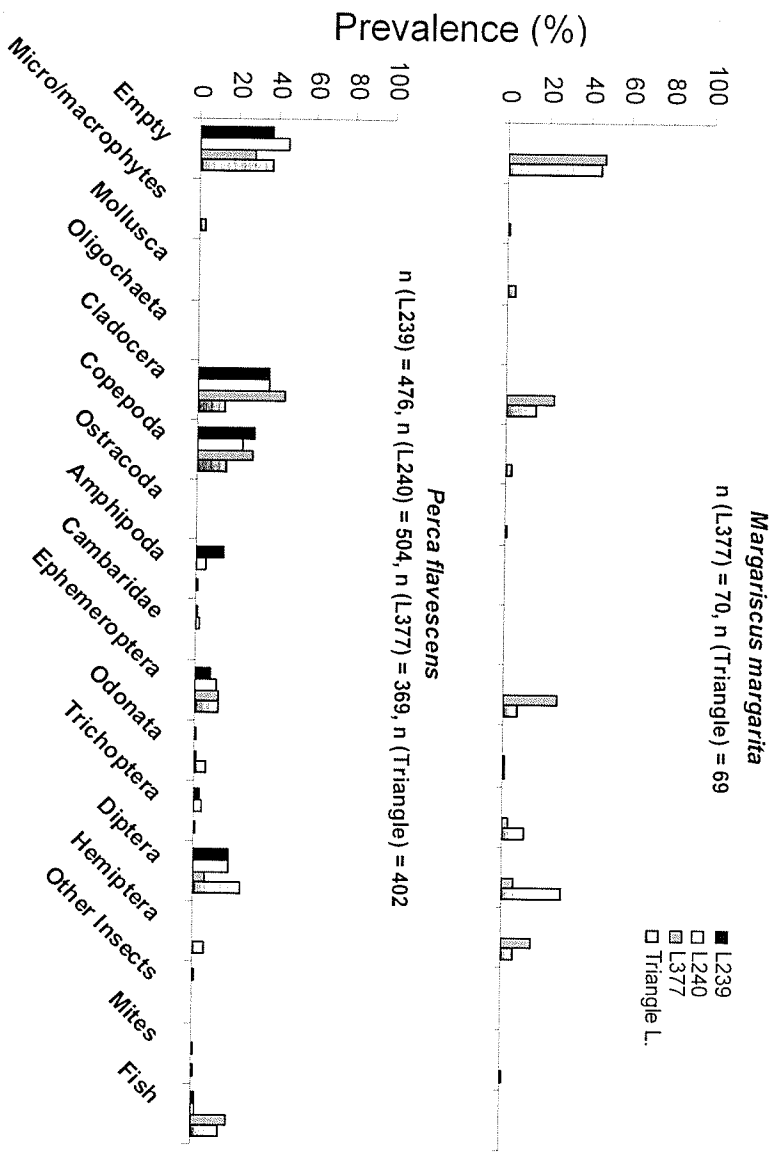
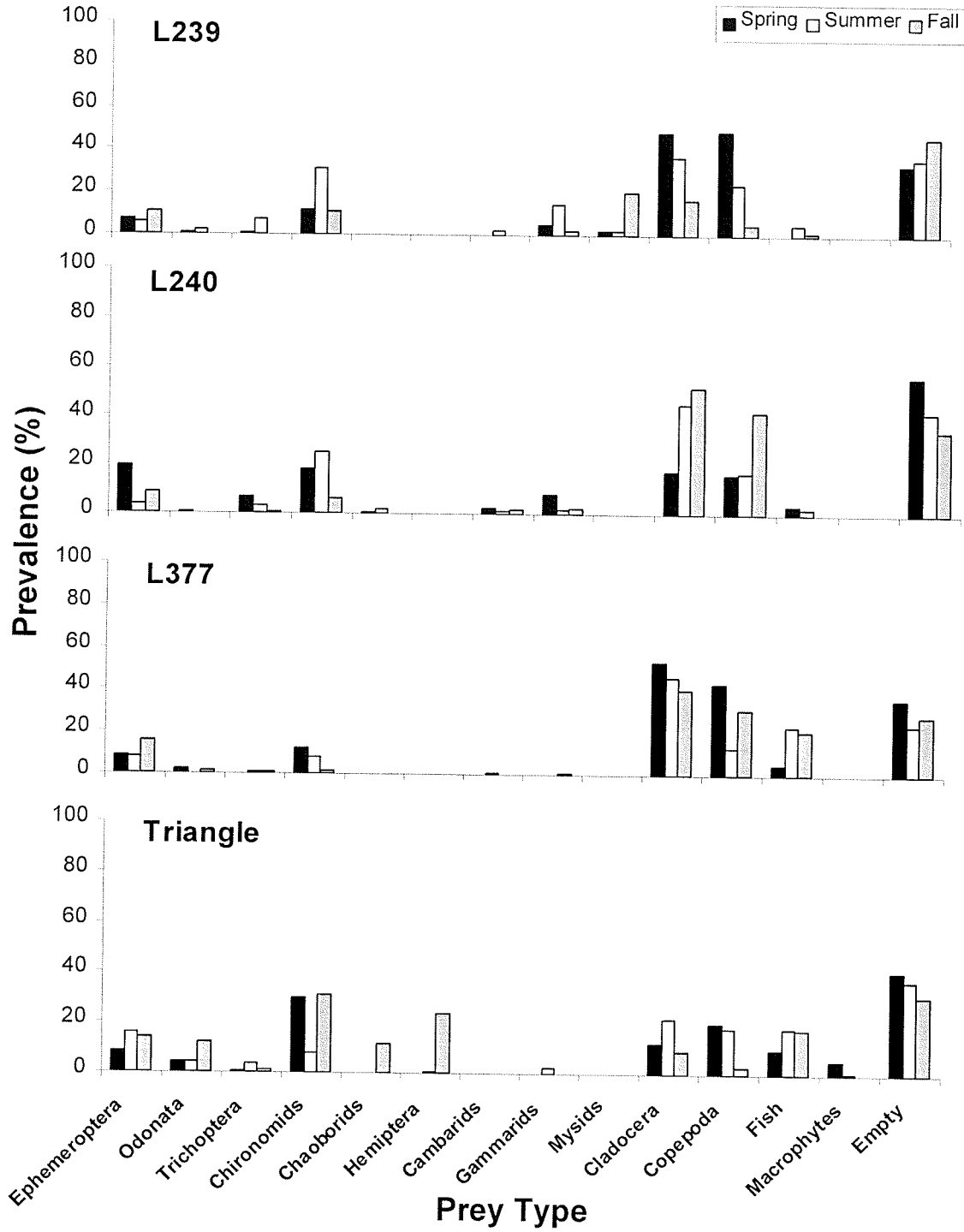


Figure 2.6. Seasonal trends in the prevalence of fourteen prey items sampled from yellow perch (*Perca flavescens*) stomachs in four Canadian Shield lakes, Ontario, Canada. Prey types that were rare in all sampled lakes were omitted.



L240 where prevalence peaked in the fall (Fig. 2.6). Fish were typically more prevalent prey items in the fall (Fig. 2.6). Empty stomachs were most prevalent in the spring in all lakes except L239 where empty stomachs peaked in the fall. Mean intensity trends were similar for benthic and fish prey but the highest mean intensities of zooplankton in the diet were observed primarily in the summer and fall (Fig. 2.7). Zooplankton were the most prevalent and intense of all prey types regardless of season or lake.

Age-related dietary trends

Benthic prey items were most prevalent in 1+ and 2+ L239 females but showed the highest mean intensity in >2+ females (Fig. 2.8). Males >1+ had the highest prevalence and mean intensity of benthos in the diet (Fig. 2.8). Zooplankton was most prevalent in L239 YOY perch of both sexes and rare in the oldest fish. Fish were only common in the diets of the oldest females while few males were piscivorous. Empty stomachs were most prevalent during the benthic feeding stage in 1+ fish of both sexes (Fig. 2.8). Larger benthic prey items (Ephemeroptera, Trichoptera, Odonata, Amphipoda etc.) were usually most prevalent and intense in the oldest L240 males and females (Fig. 2.9). Smaller zoobenthos (chironomids) showed similar prevalence in the diet in most male and female age classes but was most intense in 0+ and 1+. Zooplankton prevalence and mean intensity in L240 perch diets decreased with age. Fish in the diet were common only in the oldest L240 females (Fig. 2.9) but prevalences were not as high as in L239 (Fig. 2.8). Empty stomachs were relatively equally prevalent in all age classes in L240 (Fig. 2.9).

Benthos was rare in the stomachs of L377 perch but the trends were similar to L239 and L240 (Fig. 2.10). Larger benthos was prevalent in the older perch and small

Figure 2.7. Seasonal trends in the mean intensity of fourteen prey items sampled from yellow perch (*Perca flavescens*) stomachs in four Canadian Shield lakes, Ontario, Canada. Prey types that were rare in all lakes were omitted. The higher mean intensities of zooplankton are indicated above their respective bars.

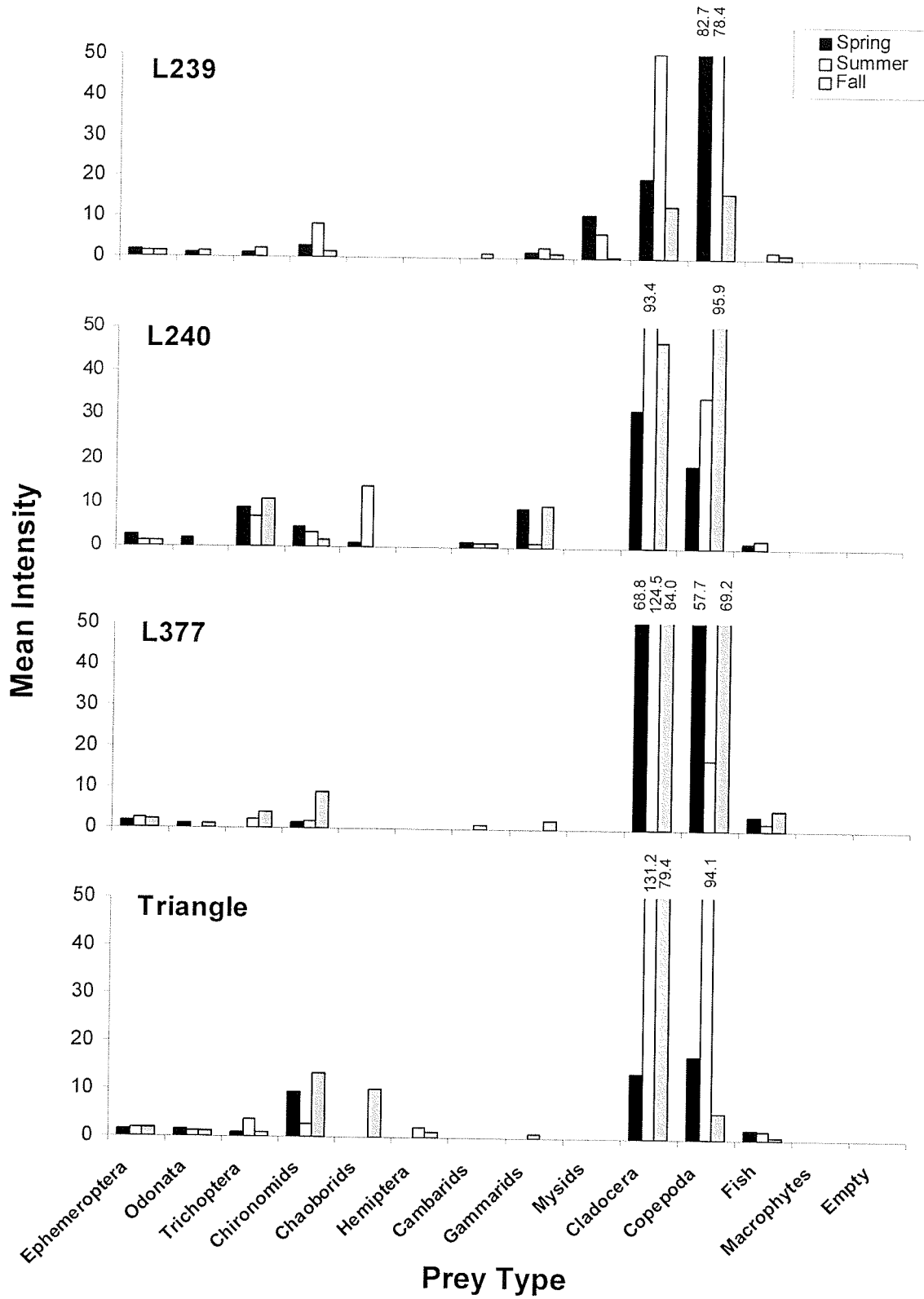


Figure 2.8. Age-related trends in the prevalence of fourteen prey items sampled from L239 yellow perch (*Perca flavescens*) stomachs. The numbers above each bar represent the corresponding mean intensities of each prey type for comparison.

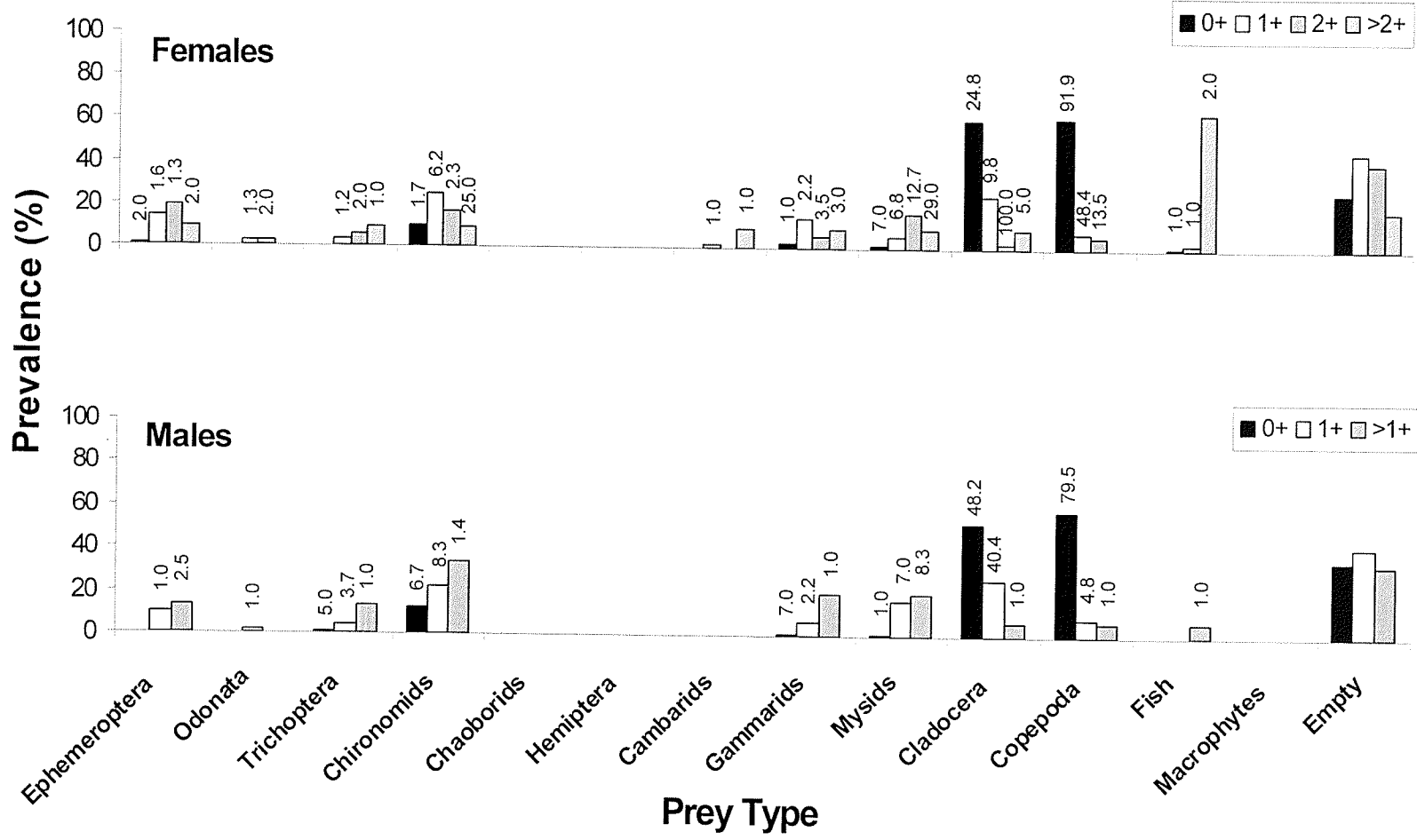


Figure 2.9. Age-related trends in the prevalence of fourteen prey items sampled from L240 yellow perch (*Perca flavescens*) stomachs. The numbers above each bar represent the corresponding mean intensities of each prey type for comparison.

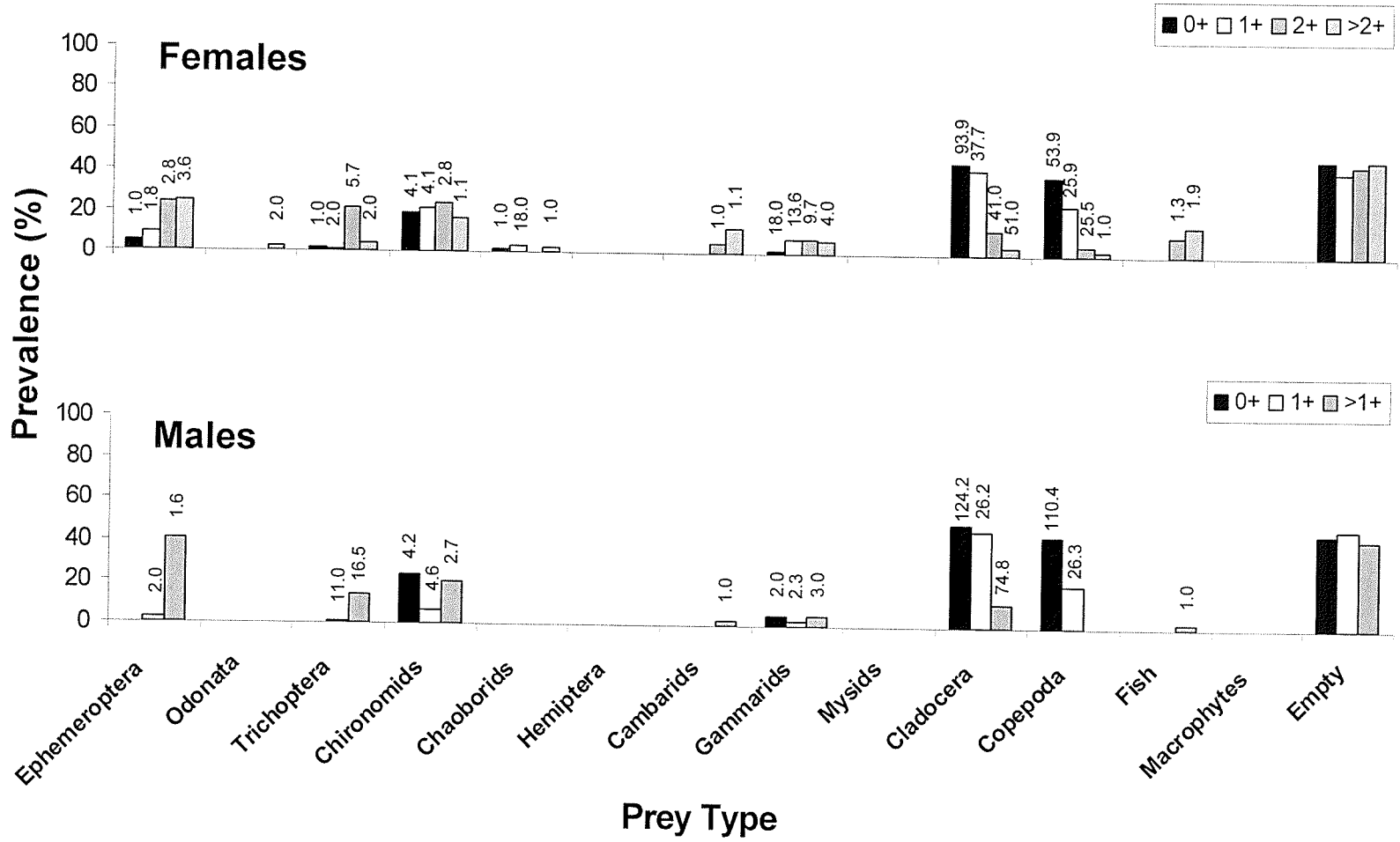
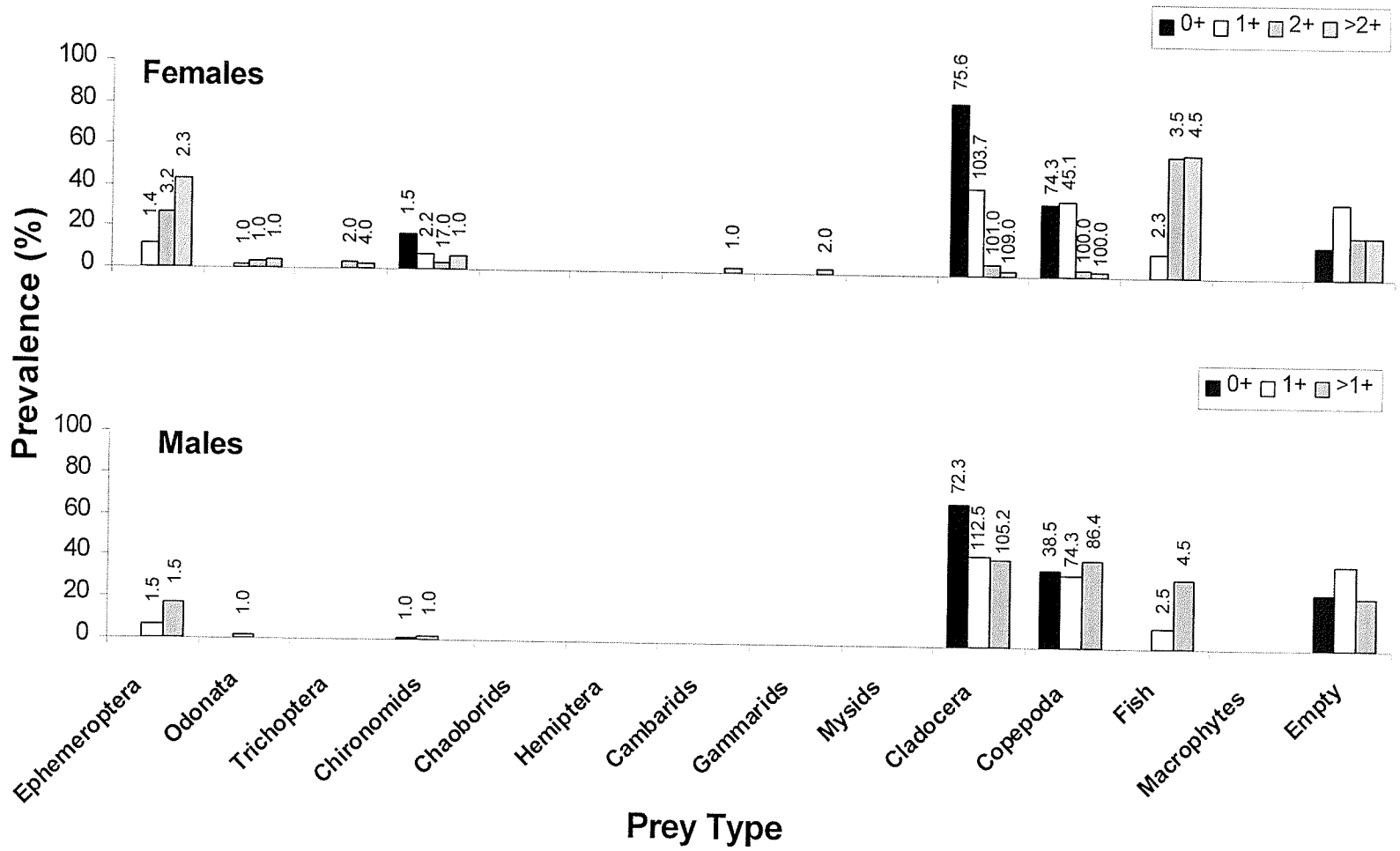


Figure 2.10. Age-related trends in the prevalence of fourteen prey items sampled from L377 yellow perch (*Perca flavescens*) stomachs. The numbers above each bar represent the corresponding mean intensities of each prey type for comparison.



benthos in the younger perch. Zooplankton in L377 perch did not show a large decrease in prevalence with increased age especially in males and mean intensity was often as high or higher in the oldest perch. Fish were highly prevalent in older perch of both sexes in L377 (Fig. 2.10). Empty stomachs were most common in 1+ L377 perch. Prevalences of most benthic prey items were highest in Triangle Lake perch older than 1+ (Fig. 2.11) and were generally higher than in the other three lakes. Zooplankton prevalence decreased and fish prevalence increased with age but only female perch were frequently piscivorous. Empty stomachs and macrophytes were most common in the intermediate age classes (1+ and 2+) (Fig. 2.11).

Parasite fauna

Fifteen species of fish were collected of which thirteen harboured parasites. In total, 112,188 parasites were found and 87% (n = 1926) of the necropsied fish had at least one parasite. Forty-one species of parasites spanning 32 genera and 26 families were found (Table 2.4). Eight of these species use birds as the definitive hosts and the remainder use fish. Eleven of the 33 fish definitive host parasites (33%) are directly transmitted and the rest are obtained in the diet (Table 2.4). Metacercariae of the genera *Diplostomum* and *Apophallus brevis* were the most prevalent of all recovered species and *Ichthyophthirius multifiliis* and *Glugea* sp. were the most intense in their hosts (Table 2.4).

Seven species of parasites were recovered from northern pike (n = 16) in two lakes (Table 2.5). There was one ectoparasite, one larval parasite (*A. brevis*), which was likely acquired from consuming a yellow perch and will not become established, and five adult internal parasites. The gill monogenean, *Tetraonchus*

Figure 2.11. Age-related trends in the prevalence of fourteen prey items sampled from Triangle Lake yellow perch (*Perca flavescens*) stomachs. The numbers above each bar represent the corresponding mean intensities of each prey type for comparison.

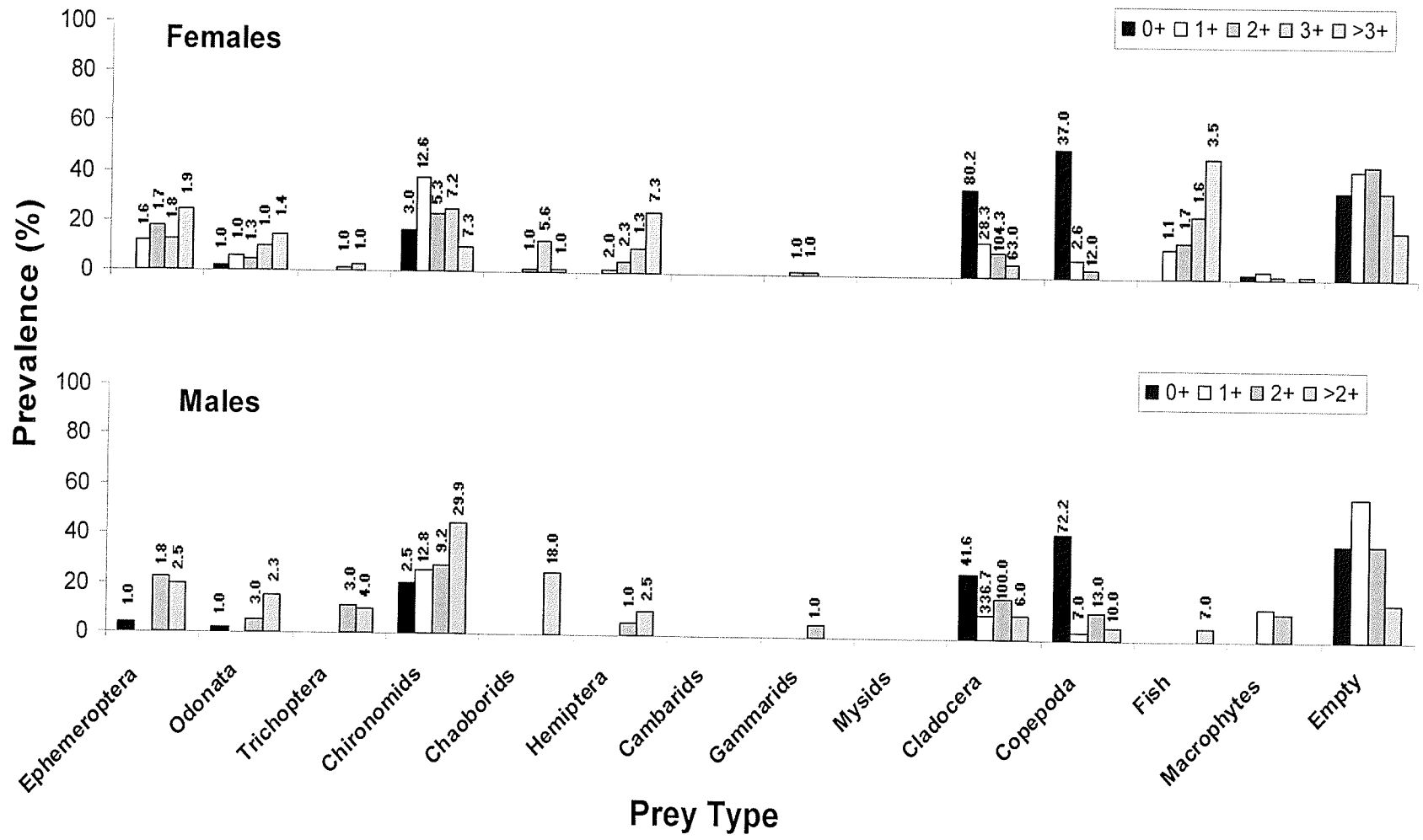


Table 2.4. Life cycle (LC), mean intensity \pm standard deviation (MI), range (R), and prevalence (P%) of parasite species recovered from 2216 fish from four ELA lakes.

Family Species	LC	MI	R	P%
Hymenostomata ^a				
<i>Ichthyophthirius multifiliis</i>	direct	643.0 \pm 727.6	(1000-2000)	0.3
Myxobolidae				
<i>Myxobolus</i> sp. ^b	direct	11.0 \pm 5.7	(7-15)	0.1
Pleistophoridae				
<i>Glugea</i> sp.	direct	229.1 \pm 479.9	(1-5000)	8.3
Gyrodactylidae				
<i>Gyrodactylus</i> sp.	direct	1.4 \pm 0.9	(1-3)	0.2
Ancyrocephalidae				
<i>Urocleidus adspectus</i>	direct	3.8 \pm 5.9	(1-63)	32.3
<i>Urocleidus</i> sp.	direct	1.0	(1-1)	0.05
Tetraonchidae				
<i>Tetraonchus monenteron</i>	direct	50.1 \pm 56.3	(1-192)	0.6
Discocotylidae				
<i>Octomacrum lanceatum</i>	direct	2.7 \pm 2.1	(1-5)	0.1
<i>O. semotili</i>	direct	1.8 \pm 1.0	(1-4)	0.8
Allocreadiidae				
<i>Allocreadium lobatum</i>	clam-amphipod- fish	1.4 \pm 0.8	(1-4)	0.9
<i>Bunodera eucaliae</i>	clam-copepod- fish	4.0 \pm 2.9	(1-6)	0.5
<i>B. sacculata</i>	clam-copepod- fish	8.1 \pm 14.1	(1-148)	20.9
<i>Crepidostomum cooperi</i>	clam-mayfly nymph-fish	17.8 \pm 35.3	(1-427)	13.3
Lissorchiidae				
<i>Lissorchis attenuatum</i>	snail- oligochaete-fish	3.0 \pm 4.1	(1-13)	0.4
Diplostomatidae				
<i>Diplostomum</i> sp. ^c	snail-fish-bird	14.3 \pm 15.6	(1-101)	49.6
<i>Neascus</i> sp.	snail-fish-bird	22.9 \pm 10.0	(8-34)	0.4

Table 2.4. Continued.

Family Species	LC	MI	R	P%
<i>Posthodiplostomum minimum</i>	<i>Physa</i> -fish-bird	14.0 \pm 25.0	(1-317)	16.6
Clinostomidae				
<i>Clinostomum complanatum</i>	snail-fish-bird	1.2 \pm 0.6	(1-4)	1.7
Heterophyidae				
<i>Apophallus brevis</i> ^d	snail-fish-bird	16.1 \pm 19.4	(1-145)	52.5
Caryophyllaeidae				
<i>Isoglaridacris bulbocirrus</i>	snail- oligochaete-fish	7.8 \pm 11.8	(1-44)	0.2
Bothriocephalidae				
<i>Bothriocephalus cuspidatus</i>	<i>Cyclops</i> -fish ^e	4.4 \pm 6.8	(1-32)	2.8
<i>B. formosus</i>	copepod-fish	1.0	(1-1)	0.09
Diphyllobothriidae				
<i>Ligula intestinalis</i>	copepod-fish- bird	1.1 \pm 0.4	(1-3)	1.6
<i>Schistocephalus solidus</i>	copepod-fish- bird	1.8 \pm 1.0	(1-3)	0.2
Traienophoridae				
<i>Triaenophorus crassus</i>	<i>Cyclops</i> -fish-fish	37.5 \pm 28.6	(2-92)	0.5
Proteocephalidae				
<i>Proteocephalus</i> sp.	copepod-fish	3.0 \pm 2.8	(1-5)	0.09
<i>Proteocephalus</i> sp2	copepod-fish	2.2 \pm 2.3	(1-8)	0.9
<i>P. exiguus</i>	copepod-fish	9.4 \pm 6.4	(2-21)	0.5
<i>P. pearsei</i>	copepod-fish ^f	5.8 \pm 10.1	(1-159)	26.4
<i>P. pinguis</i>	copepod-fish	38.9 \pm 45.7	(1-132)	0.5
Unidentified Cestoda	unknown	34.0	(34-34)	0.05
Diactophymatoidea ^g				
<i>Eustrongylides</i> sp.	snail-fish-bird	3.4 \pm 3.9	(1-18)	3.5
Anisakidae				
<i>Raphidascaris acus</i>	<i>Cyclops</i> -fish- fish ^h	7.0 \pm 10.1	(1-119)	19.7
Cystidicolidae				
<i>Spinitectus gracilis</i>	mayfly nymph- fish	7.4 \pm 11.4	(1-95)	16.6
Rhabdochonidae				
<i>Rhabdochona cascadilla</i>	mayfly nymph- fish	3.6 \pm 3.3	(1-13)	2.2

Table 4. Continued.

Family Species	LC	MI	R	P%
Neoechinorhynchidae				
<i>Neoechinorhynchus cristatus</i>	amphipod-fish	18.0 ± 20.2	(1-90)	2.0
<i>N. tumidus</i>	amphipod-fish	8.7 ± 8.1	(3-18)	0.1
Echinorhynchidae				
<i>Echinorhynchus salmonis</i>	amphipod-fish	4.4 ± 22.6	(1-269)	6.4
Pomphorhynchidae				
<i>Pomphorhynchus bulbocolli</i>	amphipod-fish	7.3 ± 9.7	(1-52)	2.5
Piscicolidae				
<i>Piscicola punctata</i>	direct	1.2 ± 0.5	(1-4)	2.9
Ergasilidae				
<i>Ergasilus centrarchidum</i>	direct	1.0	(1-1)	0.09
<i>E. cyprinaceus</i>	direct	1.8 ± 1.7	(1-8)	0.7
<i>E. nerkae</i>	direct	5.3 ± 8.8	(1-25)	0.3

^a Hymenostomata is a Subclass

^b *Myxobolus* sp. is likely *M. poecilichthidis* due to site of infection (intestinal wall) and host (*Etheostoma exile*) and this species has been observed in Ontario and Quebec (Hoffman 1999).

^c *Diplostomum* sp. is likely *D. scheuringi* based on site of infection (vitreous chamber of eye), distribution and small hindbody size (Hoffman 1999).

^d *Apophallus* is likely *A. brevis* based on extensive surveys in this region of North America and species confirmation by experimental infections from other systems.

^e small fish can also act as reservoir hosts for this parasite and can transmit it to larger piscivorous fish.

^f this parasite may also be transmitted laterally from young perch to cannibalistic adults.

^g Dioctophymatoidea is a Superfamily.

^h *R. acus* larvae may also be transmitted laterally in perch from cannibalism.

Table 2.5. Infection statistics of seven parasite species of northern pike (*Esox lucius*) recovered from two Canadian Shield lakes, Ontario, Canada. For Tables 2-14 inclusive prevalence (%) for each parasite species in each lake is given followed by mean intensity \pm standard deviation, range in parentheses and then relative abundance (%). The number of fish necropsied from each lake is indicated by n and MF is the mean number of parasite species recovered per fish \pm standard deviation. Species not recovered from the same host in other systems are indicated by * from Lake of the Woods (Dechtiar 1972), by ** from Canada (McDonald & Margolis 1995), and by *** from North America (Hoffman 1999).

Parasite	Stage ^a	Site of infection	Lake	
			L239 n = 1 MF = 1.0	L240 n = 15 MF = 3.9 \pm 1.3
<i>Tetraonchus monenteron</i>	A	gills	100.0 192.0 (192) 100.0	86.7 39.2 \pm 40.3 (1-145) 35.1
<i>Apophallus brevis</i> ^b	M	stomach and intestine	0	13.3 2.0 \pm 1.4 (1-3) 0.3
<i>Proteocephalus pinguis</i>	A	intestine	0	66.7 38.9 \pm 45.7 (1-132) 26.8

Table 2.5. Continued.

Parasite	Stage ^a	Site of infection	Lake	
			L239 n = 1 MF = 1.0	L240 n = 15 MF = 3.9 ± 1.3
<i>Triaenophorus crassus</i>	A	intestine	0	73.3 37.5 ± 28.7 (2-92) 28.4
<i>Raphidascaris acus</i> *	A	intestine	0	73.3 5.4 ± 5.0 (1-14) 4.1
<i>Spinitectus gracilis</i> *	A	stomach	0	20.0 5.0 ± 4.6 (1-10) 1.0
<i>Echinorhynchus salmonis</i>	A	intestine	0	60.0 6.9 ± 4.3 (1-13) 0.2

^a A, adults; M, metacercariae

^b Metacercariae of *A. brevis*. probably represent encysted worms liberated from digested yellow perch.

monenteron, was the only parasite species recovered from a single L239 pike and was the most relatively abundant parasite in L240 pike (Table 2.5). There were no uninfected pike and only two of the recovered parasite species (*A. brevis* and *Spinitectus gracilis*) were found in less than 60% of the sampled fish. Mean intensities of the two cestodes (*Traienophorus crassus* and *Proteocephalus pinguis*) and *T. monenteron* were all >30 individuals/fish (Table 2.5). Two intestinal parasite species (*Proteocephalus sp.* and *Neoechinorhynchus tumidus*) were recovered from L377 cisco (n = 13), *Coregonus artedii* (Table 2.6). The cestode, *Proteocephalus sp.* had the highest prevalence, mean intensity of infection and relative abundance (Table 2.6).

Pearl dace had more parasite species than any other cyprinid and only white sucker and yellow perch were infected with more species (Table 2.7). Ten species were recovered from L377 and Triangle Lake fish (n = 139). Three ectoparasite species, three larval species and four adult intestinal parasites were recovered from L377 pearl dace (n = 70) and one ectoparasite, two larval parasites and one adult intestinal parasite were recovered from Triangle Lake dace (n = 69) (Table 2.7). Four parasites, *Octomacrum semotili* (gill monogenean), *Diplostomum sp.* and *Posthodiplostomum minimum* (trematode metacercariae), and *Proteocephalus sp.*, (a cestode) were found in both lakes (Table 2.7). There were no uninfected L377 pearl dace. *Posthodiplostomum minimum* was recovered from all L377 pearl dace with a mean intensity over 40 parasites/fish and the highest relative abundance of all pearl dace parasites (Table 2.7). The same parasite in Triangle Lake was rare, found in approximately 6% of the sample, while *Proteocephalus* had the highest relative abundance. The two pearl dace populations also differed with respect to the most prevalent and intense species (Table 2.7). Four species

Table 2.6. Infection statistics of two parasite species of lake cisco (*Coregonus artedii*) recovered from one Canadian Shield lake, Ontario, Canada.

Parasite	Stage ^a	Site of infection	Lake
			L377 n = 13 MF = 1.2 ± 0.4
<i>Proteocephalus exiguus</i>	A	intestine and cecae	76.9 9.4 ± 6.4 (2-21) 78.3
<i>Neoechinorhynchus tumidus</i>	A	intestine	23.1 8.7 ± 8.1 (3-18) 21.7

^a A, adults

Table 2.7. Infection statistics of ten parasite species of pearl dace (*Margariscus margarita*) recovered from two Canadian Shield lakes, Ontario, Canada.

Parasite	Stage ^a	Site of infection	Lake	
			L377 n = 70 MF = 2.0 ± 1.0	Triangle L. n = 69 MF = 1.2 ± 0.4
Monogenea	A	gills	1.4 1.0 (1) 0.03	0
<i>Octomacrum semotili</i>	A	gills	10.0 2.1 ± 1.2 (1-4) 0.5	14.5 1.5 ± 0.7 (1-3) 26.8
<i>Ergasilus cyprinaceus</i> ***	A	gills	17.1 1.3 ± 0.5 (1-2) 0.5	0
<i>Diplostomum</i> sp.	M	eyes	1.4 1.0 (1) 0.03	1.4 1.0 (1) 1.8

Table 2.7. Continued.

Parasite	Stage ^a	Site of infection	Lake	
			L377 n = 70 MF = 2.0 ± 1.0	Triangle L. n = 69 MF = 1.2 ± 0.4
<i>Posthodiplostomum minimum</i> **	M	mesenteries and intestine	100.0 44.4 ± 43.9 (1-317) 95.2	5.8 2.0 ± 2.0 (1-5) 14.3
<i>Ligula intestinalis</i> ***	P	body cavity	1.4 1.0 (1) 0.03	0
<i>Allocreadium lobatum</i> ***	A	stomach and intestine	28.6 1.4 ± 0.8 (1-4) 0.9	0
<i>Proteocephalus</i> sp.***	A	intestine	2.9 4.5 ± 4.9 (1-8) 0.3	24.6 1.9 ± 1.9 (1-8) 57.1

Table 2.7. Continued.

Parasite	Stage ^a	Site of infection	Lake	
			L377 n = 70 MF = 2.0 ± 1.0	Triangle L. n = 69 MF = 1.2 ± 0.4
<i>Rhabdochona cascadilla</i> **	A	intestine	37.1 3.3 ± 2.8 (1-10) 2.6	0
<i>Pomphorhynchus bulbocolli</i> ***	A	intestine	2.9 1.0 (1) 0.06	0

^a A, adults; M, metacercariae; P, plerocercoid

Table 2.8. Infection statistics of four parasite species of blacknose shiner (*Notropis heterolepis*) recovered from two Canadian Shield lakes, Ontario, Canada.

Parasite	Stage ^a	Site of infection	Lake	
			L377 n = 10 MF = 1.3 ± 0.6	Triangle L. n = 103 MF = 1.1 ± 0.4
<i>Diplostomum</i> sp.	M	eyes	0	2.9 1.3 ± 0.6 (1-2) 8.9
<i>Posthodiplostomum minimum</i>	M	mesenteries and intestine	10.0 1.0 (1) 6.3	1.9 1.5 ± 0.7 (1-2) 6.7
<i>Ligula intestinalis</i> *	P	body cavity	0	34.0 1.1 ± 0.4 (1-3) 84.4
<i>Rhabdochona cascadilla</i> ***	A	intestine	30.0 5.0 ± 6.1 (1-12) 93.8	0

^a A, adults; M, metacercariae; P, plerocercoid

of parasites were removed from blacknose shiners ($n = 113$) in L377 and Triangle Lake (Table 2.8). L377 shiners ($n = 10$) had one larval parasite and one gut parasite and Triangle Lake shiners ($n = 103$) had three larval parasites. Only *P. minimum* occurred in both lakes. Thirty percent of the sampled L377 shiners were infected with the nematode *Rhabdochona cascadilla* and this species had the highest mean intensity and relative abundance of all L377 shiner parasite species (Table 2.8). The plerocercoid stage of the cestode, *Ligula intestinalis*, was the most prevalent and abundant parasite in Triangle Lake shiners, but it had a mean intensity similar to the other species present (Table 2.8). Three species of parasites including one larval and two adult species were recovered from 29 L377 spottail shiners (Table 2.9). The most prevalent, intense and abundant parasite was *P. minimum*. No parasites were recovered from eight northern redbelly dace in three lakes (L239, L240 and Triangle L.) and none were found in four finescale dace in L240 and Triangle L. Therefore, these two fish species were not considered in any further analyses. Two parasite species were found in six fathead minnows (*Pimephales promelas*) from L377 and Triangle L. (Table 2.10). A single larval species was found in five Triangle fish and two larval species were identified from one L377 fish. Only *P. minimum* was shared between the two host populations and, as in most sampled cyprinids, it showed the highest prevalence, mean intensity and relative abundance of all species present. One ectoparasite, two larval parasites and three adult intestinal parasites were found in L377 longnose dace, *R. cataractae* ($n = 17$) (Table 2.11). Both acanthocephalans (*Pomphorhynchus bulbocolli* and an unidentified species) and *Diplostomum* sp. were found in a single host each. The remaining three parasites infected

Table 2.9. Infection statistics of three parasite species of spottail shiner (*Notropis hudsonius*) recovered from one Canadian Shield lake, Ontario, Canada.

Parasite	Stage ^a	Site of infection	Lake
			L377 n = 29 MF = 1.4 ± 0.5
<i>Posthodiplostomum minimum</i>	M	mesenteries and intestine	69.0 13.3 ± 9.0 (1-33) 89.0
<i>Allocreadium lobatum</i> *	A	stomach and intestine	3.4 1.0 (1) 0.3
<i>Rhabdochona cascadilla</i>	A	intestine	44.8 2.5 ± 2.6 (1-10) 10.7

^a A, adults; M, metacercariae

Table 2.10. Infection statistics of two parasite species of fathead minnow (*Pimephales promelas*) recovered from two Canadian Shield lakes, Ontario, Canada.

Parasite	Stage ^a	Site of infection	Lake	
			L377 n = 1 MF = 1.0	Triangle L. n = 5 MF = 1.0
<i>Diplostomum</i> sp.	M	eyes	0	20.0 13.0 (13) 86.7
<i>Posthodiplostomum minimum</i>	M	mesenteries and intestine	100.0 24.0 (24) 100.0	20.0 2.0 (2) 13.3

^a M, metacercariae

Table 2.11. Infection statistics of six parasite species of longnose dace (*Rhinichthys cataractae*) recovered from one Canadian Shield lake, Ontario, Canada.

Parasite	Stage ^a	Site of infection	Lake
			L377 n = 17 MF = 1.8 ± 1.2
<i>Ergasilus cyprinaceus</i> ***	A	gills	23.5 3.3 ± 3.2 (1-8) 5.9
<i>Diplostomum</i> sp.	M	eyes	5.9 1.0 (1) 0.5
<i>Posthodiplostomum minimum</i>	M	mesenteries and intestine	52.9 17.6 ± 29.2 (1-85) 72.1
<i>Rhabdochona cascadilla</i> **	A	intestine	41.2 6.4 ± 4.4 (2-13) 20.5

Table 2.11. Continued.

Parasite	Stage ^a	Site of infection	Lake
			L377 n = 17 MF = 1.8 ± 1.2
<i>Pomphorhynchus bulbocolli</i> *	A	intestine	5.9 1.0 (1) 0.5
Acanthocephala	A	intestine	5.9 1.0 (1) 0.5

^a A, adults; M, metacercariae

Table 2.12. Infection statistics of eleven parasite species of white sucker (*Catostomus commersoni*) recovered from four Canadian Shield lakes, Ontario, Canada.

Parasite	Stage ^a	Site of infection	Lake			
			L239 n = 9 MF = 2.7 ± 0.7	L240 n = 4 MF = 2.3 ± 1.0	L377 n = 37 MF = 2.3 ± 0.9	Triangle L. n = 7 MF = 1.8 ± 1.0
<i>Octomacrum lanceatum</i>	A	gills	0	0	8.1 2.7 ± 2.1 (1-5) 0.9	0
<i>Ergasilus centrarchidum</i> **	A	gills	0	0	5.4 1.0 (1) 0.2	0
<i>Diplostomum</i> sp.	M	eyes	0	0	0	14.3 7.0 (7) 4.3
<i>Raphidascaris acus</i> *	L	stomach	0	25.0 1.0 (1) 0.7	0	0

Table 2.12. Continued.

Parasite	Stage ^a	Site of infection	Lake			
			L239 n = 9 MF = 2.7 ± 0.7	L240 n = 4 MF = 2.3 ± 1.0	L377 n = 37 MF = 2.3 ± 0.9	Triangle L. n = 7 MF = 1.8 ± 1.0
<i>Lissorchis attenuatum</i> *	A	intestine	33.3 2.7 ± 2.9 (1-6) 3.9	0	13.5 3.6 ± 5.3 (1-13) 2.1	14.3 1.0 (1) 0.6
<i>Isoglaridacris bulbocirrus</i> *	A	intestine	22.2 1.5 ± 0.7 (1-2) 1.4	25.0 20.0 (20) 13.2	29.7 8.5 ± 13.4 (1-44) 10.9	28.6 4.0 ± 4.2 (1-7) 5.0
<i>Proteocephalus</i> sp.**	A	intestine	22.2 3.0 ± 2.8 (1-5) 2.9	0	0	0
Nematoda	L	intestine	0	25.0 1.0 (1) 0.7	5.4 2.0 ± 1.4 (1-3) 0.5	0

Table 2.12. Continued.

Parasite	Stage ^a	Site of infection	Lake			
			L239 n = 9 MF = 2.7 ± 0.7	L240 n = 4 MF = 2.3 ± 1.0	L377 n = 37 MF = 2.3 ± 0.9	Triangle L. n = 7 MF = 1.8 ± 1.0
<i>Echinorhynchus</i> sp.*	A	intestine	0	0	0	14.3 2.0 (2) 1.2
<i>Neoechinorhynchus cristatus</i>	A	intestine	77.8 9.7 ± 7.3 (4-23) 32.9	75.0 32.3 ± 24.8 (10-59) 64.2	89.2 15.2 ± 16.4 (1-75) 58.2	28.6 71.5 ± 26.2 (53-90) 88.8
<i>Pomphorhynchus bulbocolli</i>	A	intestine	100.0 13.4 ± 16.5 (1-52) 58.5	75.0 10.7 ± 9.8 (5-22) 21.2	78.4 8.1 ± 8.1 (1-35) 27.2	0

^a A, adults; L, larvae; M, metacercariae

at least 20% of the host population and again *P. minimum* was most intense, prevalent and abundant (Table 2.11).

Eleven parasite species were identified from 57 white suckers from all four lakes (Table 2.12). Five species were found in L239 white suckers (n = 9). One larval nematode and four adult species were found in L240 fish (n = 4). Two ectoparasites and five endoparasites were recovered from L377 hosts (n = 37). One larval and four adult species were observed in Triangle Lake white suckers (n = 7). Triangle Lake white sucker parasite fauna showed the lowest overall prevalence and mean intensity of all samples. Both the cestode *Isoglaridacris* sp. and the acanthocephalan *Neoechinorhynchus cylindratus* were found in fish from all four lakes (Table 2.12). The trematode *Lissorchis attenuatum* and the acanthocephalan *Pomphorhynchus bulbocolli* were each found in three lakes. The most prevalent, intense and relatively abundant parasite species in all four lakes were the acanthocephalans (*N. cylindratus* and *P. bulbocolli*) and they infected at least 75% of all sampled white suckers except in Triangle Lake (Table 2.12). Two adult parasite species were found in one L377 burbot, *Lota lota* (Table 2.13). The unidentified cestode was the most abundant species. Four parasite species were recovered from brook sticklebacks, *Culea inconstans*, (n = 26) from L377 and Triangle Lake (Table 2.14). L377 fish (n = 10) had one larval and two adult parasite species and Triangle Lake hosts (n = 16) had one larval and one adult species. Only *Bunodera eucaliae* was found in samples from both lakes and was approximately equal in mean intensity and prevalence in both lakes. *Neascus* sp., a larval trematode in the flesh, was the most prevalent and intense parasite species in sticklebacks (Table 2.14). Nine

Table 2.13. Infection statistics of two parasite species of burbot (*Lota lota*) recovered from one Canadian Shield lake, Ontario, Canada.

Parasite	Stage ^a	Site of infection	Lake
			L377 n = 1 MF = 2.0
Cestoda	A	intestine and caecae	100.0 34.0 (34) 97.1
<i>Spinitectus gracilis</i>	A	stomach	100.0 1.0 (1) 2.9

^a A, adults

Table 2.14. Infection statistics of four parasite species of brook stickleback (*Culea inconstans*) recovered from two Canadian Shield lakes, Ontario, Canada.

Parasite	Stage ^a	Site of infection	Lake	
			L377 n = 10 MF = 1.7 ± 0.4	Triangle L. n = 16 MF = 1.1 ± 0.4
<i>Diplostomum</i> sp.	M	eyes	0	6.3 2.0 (2) 6.7
<i>Neascus</i> sp.	M	flesh and skin	80.0 22.9 ± 10.0 (8-34) 89.3	0
<i>Bunoderina eucaliae</i>	A	intestine	40.0 4.0 ± 4.1 (2-10) 7.8	43.8 4.0 ± 2.4 (1-8) 93.3
<i>Pomphorhynchus bulbocolli</i> **	A	intestine	30.0 2.0 ± 1.0 (1-3) 2.9	0

^a A, adults; M, metacercariae

Table 2.15. Infection statistics of nine parasite species of slimy sculpin (*Cottus cognatus*) recovered from two Canadian Shield lakes, Ontario, Canada.

Parasite	Stage ^a	Site of infection	Lake	
			L240 n = 5 MF = 2.0 ± 1.4	L377 n = 21 MF = 2.1 ± 1.1
<i>Gyrodactylus</i> sp.	A	gills	0	19.0 1.5 ± 1.0 (1-3) 4.9
<i>Ergasilus nerkae</i> ***	A	gills	0	33.3 5.3 ± 8.8 (1-25) 30.1
<i>Diplostomum</i> sp.	M	eyes	40.0 20.5 ± 27.6 (1-40) 41.4	0
<i>Posthodiplostomum minimum</i> ***	M	mesenteries and intestine	60.0 4.0 ± 2.6 (2-7) 12.1	14.3 1.3 ± 0.6 (1-2) 3.3

Table 2.15. Continued.

Parasite	Stage ^a	Site of infection	Lake	
			L240 n = 5 MF = 2.0 ± 1.4	L377 n = 21 MF = 2.1 ± 1.1
<i>Pomphorhynchus bulbocolli</i> **	A	intestine	0	28.6 1.2 ± 0.4 (1-2) 5.7

^a A, adults; L, larvae; M, metacercariae; P, plerocercoid

parasite species were identified from slimy sculpins ($n = 26$) from two lakes (Table 2.15). Two ectoparasite species, three larval and two adult endoparasite species were in L240 fish ($n = 5$) and two larval and three adult endoparasite species were found in L377 hosts ($n = 21$). *Posthodiplostomum minimum*, *Spinitectus gracilis*, and *Echinorhynchus salmonis* were identified in L240 and L377 (Table 2.15). For slimy sculpin, the parasite with the highest mean intensity and relative abundance in L240 and L377 respectively were *Diplostomum* sp. and the nematode *S. gracilis*. *Posthodiplostomum minimum* and *Ergasilus nerkae* showed the highest prevalence in L240 and L377 respectively (Table 2.15). Six species of parasites were recovered from L240 Iowa darters ($n = 8$) including one ectoparasite, three larval, one adult endoparasite and *Myxobolus* sp. (Table 2.16). All parasite species had prevalences 25% or less with *Myxobolus* sp. being the most intense and abundant.

A total of 17 parasite species were identified from yellow perch ($n = 1741$) from all four lakes (Table 2.17). Yellow perch from L239 ($n = 476$) had the most parasite species, 16, which included two ectoparasites, six larval species, six adult endoparasite species and *Glugea* sp. and *I. multifiliis*. Perch from L240 ($n = 504$) harboured 13 species of parasites including two ectoparasites, five larval, five adult endoparasites and *Glugea* sp. Two ectoparasites, five larval, six adult endoparasites and *Glugea* sp. were identified from L377 yellow perch ($n = 369$). Triangle Lake perch ($n = 402$) had one ectoparasite, five larval, four adult endoparasites and *Glugea* sp., which was the fewest of any system (11 species). The species consistently found in yellow perch from all four lakes included the gill monogenean, *Urocleidus*

Table 2.16. Infection statistics of six parasite species of Iowa darter (*Etheostoma exile*) recovered from one Canadian Shield lake, Ontario, Canada.

Parasite	Stage ^a	Site of infection	Lake
			L240 n = 8 MF = 2.3 ± 1.5
<i>Urocleidus</i> sp.**	A	gills	12.5 1.0 (1) 2.0
<i>Posthodiplostomum minimum</i> **	M	mesenteries and intestine	12.5 3.0 (3) 5.9
<i>Eustrongylides</i> sp.***	L	intestinal wall	25.0 8.5 ± 3.5 (6-11) 33.3
<i>Raphidascaris acus</i> *	L	liver	12.5 6.0 (6) 11.8

Table 2.16. Continued.

Parasite	Stage ^a	Site of infection	Lake
			L240 n = 8 MF = 2.3 ± 1.5
<i>Bothriocephalus formosus</i>	A	intestine	25.0 1.0 (1) 3.9
<i>Myxobolus</i> sp.	C	intestinal wall	25.0 11.0 ± 5.7 (7-15) 43.1

^a A, adults; C, cysts; L, larvae; M, metacercariae

Table 2.17. Infection statistics of seventeen parasite species of yellow perch (*Perca flavescens*) recovered from four Canadian Shield lakes, Ontario, Canada.

Parasite	Stage ^a	Site of infection	Lake			
			L239 n = 476 MF = 3.1 ± 1.8	L240 n = 504 MF = 4.3 ± 1.4	L377 n = 369 MF = 2.3 ± 1.2	Triangle L. n = 402 MF = 4.4 ± 1.4
<i>Urocleidus adspectus</i>	A	gills	34.7 2.7 ± 3.2 (1-26) 1.8	44.8 2.8 ± 3.8 (1-42) 2.0	20.3 4.0 ± 5.5 (1-31) 2.4	61.9 5.3 ± 5.0 (1-63) 3.7
<i>Piscicola punctata</i> *	A	fins and skin	9.9 1.3 ± 0.6 (1-4) 0.2	2.6 1.0 (1) 0.04	1.1 1.0 (1) 0.03	0
<i>Apophallus brevis</i>	M	flesh and fins	33.4 2.4 ± 2.2 (1-15) 1.5	88.9 8.9 ± 10.9 (1-127) 12.7	41.5 3.3 ± 4.7 (1-45) 3.9	100.0 34.5 ± 20.3 (2-145) 38.6
<i>Clinostomum complanatum</i>	M	flesh	0.2 1.0 (1) 0.004	0	0.3 1.0 (1) 0.01	8.7 1.2 ± 0.6 (1-4) 0.1

Table 2.17. Continued.

Parasite	Stage ^a	Site of infection	Lake			
			L239 n = 476 MF = 3.1 ± 1.8	L240 n = 504 MF = 4.3 ± 1.4	L377 n = 369 MF = 2.3 ± 1.2	Triangle L. n = 402 MF = 4.4 ± 1.4
<i>Diplostomum</i> sp.	M	eyes	32.8	89.1	23.3	99.0
			2.2 ± 2.3 (1-20)	13.7 ± 14.9 (1-101)	3.0 ± 5.9 (1-46)	22.5 ± 15.9 (1-94)
			1.4	19.6	2.0	24.9
<i>Posthodiplostomum minimum</i> *	M	mesenteric	0.2	1.2	1.9	59.5
			8.0 (8)	6.8 ± 6.1 (1-14)	2.0 ± 1.4 (1-4)	6.2 ± 7.5 (1-50)
			0.03	0.1	0.1	4.1
<i>Eustrongylides</i> sp.	L	intestinal wall	1.9	3.6	10.8	1.5
			1.8 ± 2.0 (1-7)	4.6 ± 5.2 (1-18)	3.4 ± 3.6 (1-12)	1.3 ± 0.4 (1-3)
			0.07	0.3	1.1	0.02
<i>Raphidascaris acus</i> *	L	liver	8.2	76.2	0	0
			1.2 ± 0.5 (1-3)	7.7 ± 10.6 (1-119)		
			0.2	9.4		

Table 2.17. Continued.

Parasite	Stage ^a	Site of infection	Lake			
			L239 n = 476 MF = 3.1 ± 1.8	L240 n = 504 MF = 4.3 ± 1.4	L377 n = 369 MF = 2.3 ± 1.2	Triangle L. n = 402 MF = 4.4 ± 1.4
<i>Bunoderina sacculata</i>	A	intestine	37.2 10.7 ± 16.2 (1-148) 7.7	23.4 4.2 ± 5.0 (1-30) 1.6	19.8 1.9 ± 2.1 (1-14) 1.1	23.6 12.9 ± 19.7 (1-134) 3.4
<i>Crepidostomum cooperi</i> *	A	intestine	20.4 7.0 ± 8.5 (1-49) 2.8	4.7 4.4 ± 4.8 (1-23) 0.3	5.1 2.6 ± 2.8 (1-12) 0.4	38.1 28.7 ± 45.7 (1-427) 12.2
<i>Bothriocephalus cuspidatus</i> (immature only)	J	intestine	0	0	17.1 4.4 ± 6.7 (1-32) 2.2	0
<i>Proteocephalus pearsei</i>	A	intestine	45.6 6.4 ± 7.4 (1-45) 5.7	47.6 5.9 ± 12.4 (1-159) 4.5	17.9 2.2 ± 1.7 (1-9) 1.1	15.7 6.8 ± 13.1 (1-79) 1.2

Table 2.17. Continued.

Parasite	Stage ^a	Site of infection	Lake			
			L239 n = 476 MF = 3.1 ± 1.8	L240 n = 504 MF = 4.3 ± 1.4	L377 n = 369 MF = 2.3 ± 1.2	Triangle L. n = 402 MF = 4.4 ± 1.4
<i>Spinitectus gracilis</i>	A	stomach	15.1	24.8	13.3	27.4
			7.7 ± 13.9	9.9 ± 13.4	4.1 ± 4.3	5.6 ± 7.6
			(1-95)	(1-67)	(1-21)	(1-52)
			2.3	4.0	1.6	1.7
<i>Echinorhynchus salmonis</i> *	A	intestine	24.6	1.6	0.5	0
			4.6 ± 24.0	1.6 ± 0.5	1.0	
			(1-269)	(1-2)	1.0	
			2.2	0.04	0.02	
<i>Pomphorhynchus bulbocolli</i> *	A	intestine	0.6	0	0	0
			1.0			
			(1)			
			0.01			
<i>Glugea</i> sp.***	C	intestinal wall and fat bodies	8.2	11.1	16.0	7.5
			350.1 ± 886.9	254.0 ± 333.8	181.2 ± 243.0	119.8 ± 214.6
			(3-5000)	(1-1000)	(1-1000)	(4-1000)
			55.7	45.3	84.0	10.0

Table 2.17. Continued.

Parasite	Stage ^a	Site of infection	Lake			
			L239 n = 476 MF = 3.1 ± 1.8	L240 n = 504 MF = 4.3 ± 1.4	L377 n = 369 MF = 2.3 ± 1.2	Triangle L. n = 402 MF = 4.4 ± 1.4
<i>Ichthyophthirius multifiliis</i>	C	fins	1.5 643.0 ± 727.6 (1000-2000) 18.4	0	0	0

^a A, adults; C, cysts; J, juvenile; L, larvae; M, metacercariae

adspectus; the allogenic flukes, *A. brevis*, *Diplostomum* sp., and *P. minimum*; the allogenic nematode *Eustrongylides* sp.; the enteric trematodes *Bunodera sacculata* and *Crepidostomum cooperi*; the cestode *Proteocephalus pearsei*; the nematode *S. gracilis*; and the microsporidean *Glugea* sp. (Table 2.17).

When the entire parasite community was considered, Triangle Lake perch had the highest mean species richness, prevalence, intensity and abundance of parasites of all four lakes. L377 had the lowest values in all categories except in number of parasite species present. Adult endoparasites showed their highest prevalence in L239 perch but their highest mean intensity and relative abundance were in Triangle Lake, primarily due to the large numbers of *C. cooperi* (Table 2.17). L377 perch had the poorest adult endoparasite fauna. All four lakes shared an almost identical set of larval parasites but L239 and L377 had very low infection characteristics. Larval parasites in these two populations made up less than 10% of all parasites recovered. Larval prevalence in both L240 and Triangle L. was very high and all the other infection statistics were much higher than the other two lakes. Triangle L. had a larval parasite community that was more prevalent and abundant than all other Triangle L. parasite communities. This lake also had higher ectoparasite infection statistics than all other lakes. The other three lakes had widely varying prevalences of ectoparasites (from 21% to 46%) but had similar richness, abundance and intensity values (Table 2.17). Seasonal changes and age-related trends in the mean intensity and prevalence of parasites in ELA yellow perch were examined for the above species that were common to all or most of the systems or which had a high prevalence and intensity in one particular system (e.g. *E. salmonis* in L239). These data are presented in the following section.

Seasonal trends in yellow perch infection statistics

Prevalence of *Glugea* sp. was higher in the spring and fall in all four lakes than in the summer but the changes were small (Fig. 2.12). The mean intensities of *Glugea* sp. differed much more among spring, summer and fall samples (Fig. 2.13). Prevalence of *U. adspetus* always peaked in the summer. Prevalences of both *A. brevis* and *Diplostomum* sp. varied among lakes but were usually high in all fall samples and lowest in the summer (Fig. 2.12). *Posthodiplostomum minimum* showed similar trends in Triangle Lake but was too uncommon in the other three lakes to analyze. Prevalences of *B. sacculata*, *C. cooperi* and *P. pearsei* all peaked in the summer or fall in each lake. *Raphidascaris acus* prevalence showed no consistent changes with season but in L240 where it was more common it was higher in the spring and fall (Fig. 2.12). Prevalences of *S. gracilis* and *E. salmonis* were highest in the spring and fall and lowest in the summer. *Bothriocephalus cuspidatus* prevalence was highest in the spring (Fig. 2.12). Mean intensity seasonal trends were similar for all parasite species in all lakes (Fig. 2.13).

Age and sex related trends in yellow perch infection statistics

Age and sex related trends in prevalence and mean intensity are summarized for each lake in Figures 2.14-2.17. *Glugea* sp. prevalence and intensity decreased with increasing age of male and female perch in all four lakes. *Urocleidus adspetus* prevalence and mean intensity increased with perch age in L239 and Triangle Lake (Figs. 2.14 and 2.17) and peaked around age 2+ in the other lakes (Figs. 2.15 and 2.16). The prevalence of all three metacercariae always increased with host age and the mean intensity increased rapidly after age 1+ except in Triangle Lake where prevalence and

Figure 2.12. Seasonal trends in the prevalence of twelve species of parasites infecting yellow perch (*Perca flavescens*) in four Canadian Shield lakes, Ontario, Canada. Species that were absent or rare were omitted for each lake.

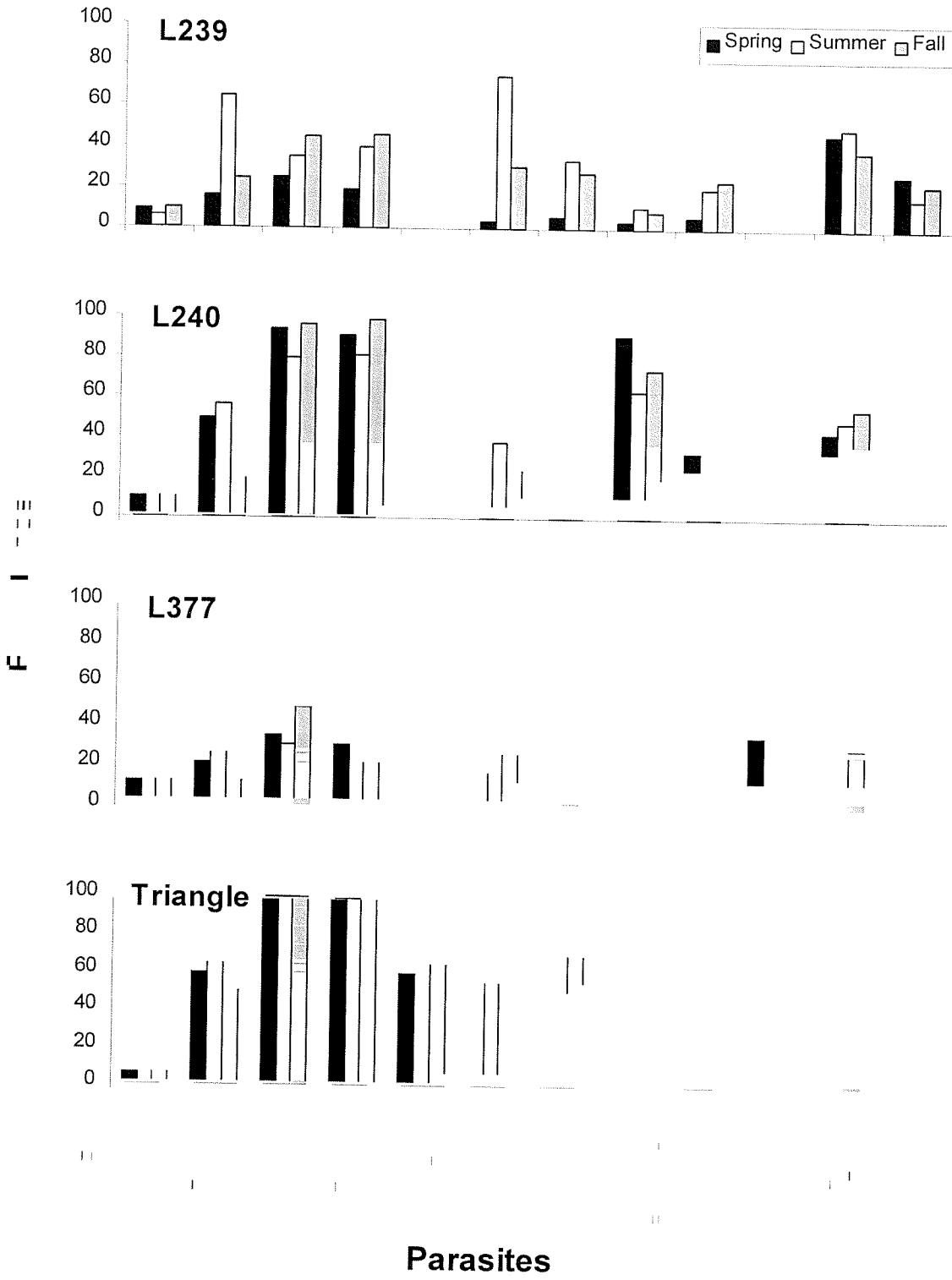


Figure 2.12. Seasonal trends in the prevalence of twelve species of parasites infecting yellow perch (*Perca flavescens*) in four Canadian Shield lakes, Ontario, Canada. Species that were absent or rare were omitted for each lake.

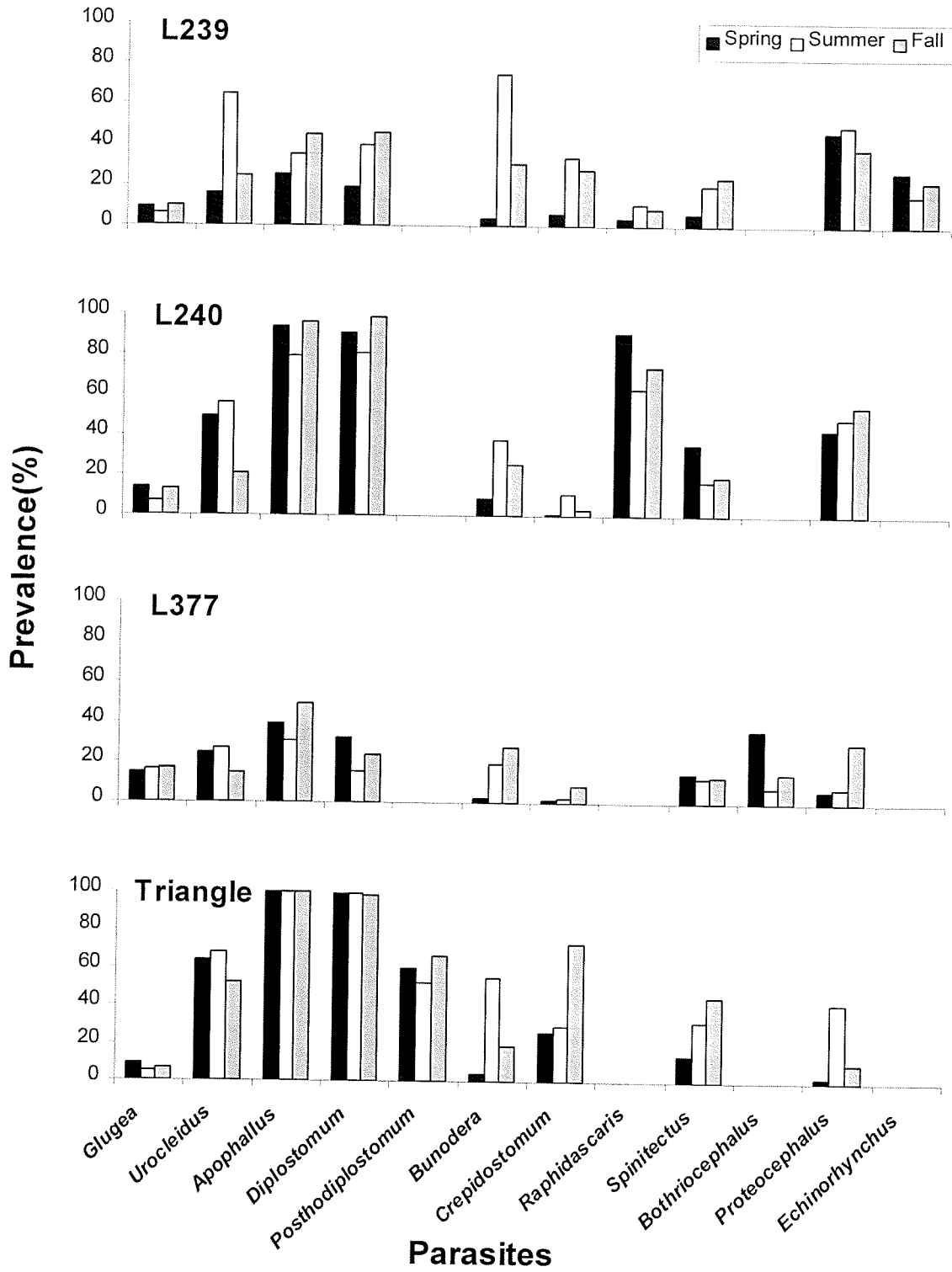


Figure 2.13. Seasonal trends in the mean intensity of twelve species of parasites infecting yellow perch (*Perca flavescens*) in four Canadian Shield lakes, Ontario, Canada. Species that were absent or rare were omitted for each lake. The very high mean intensities of *Glugea* sp. xenomas are indicated above their respective bars.

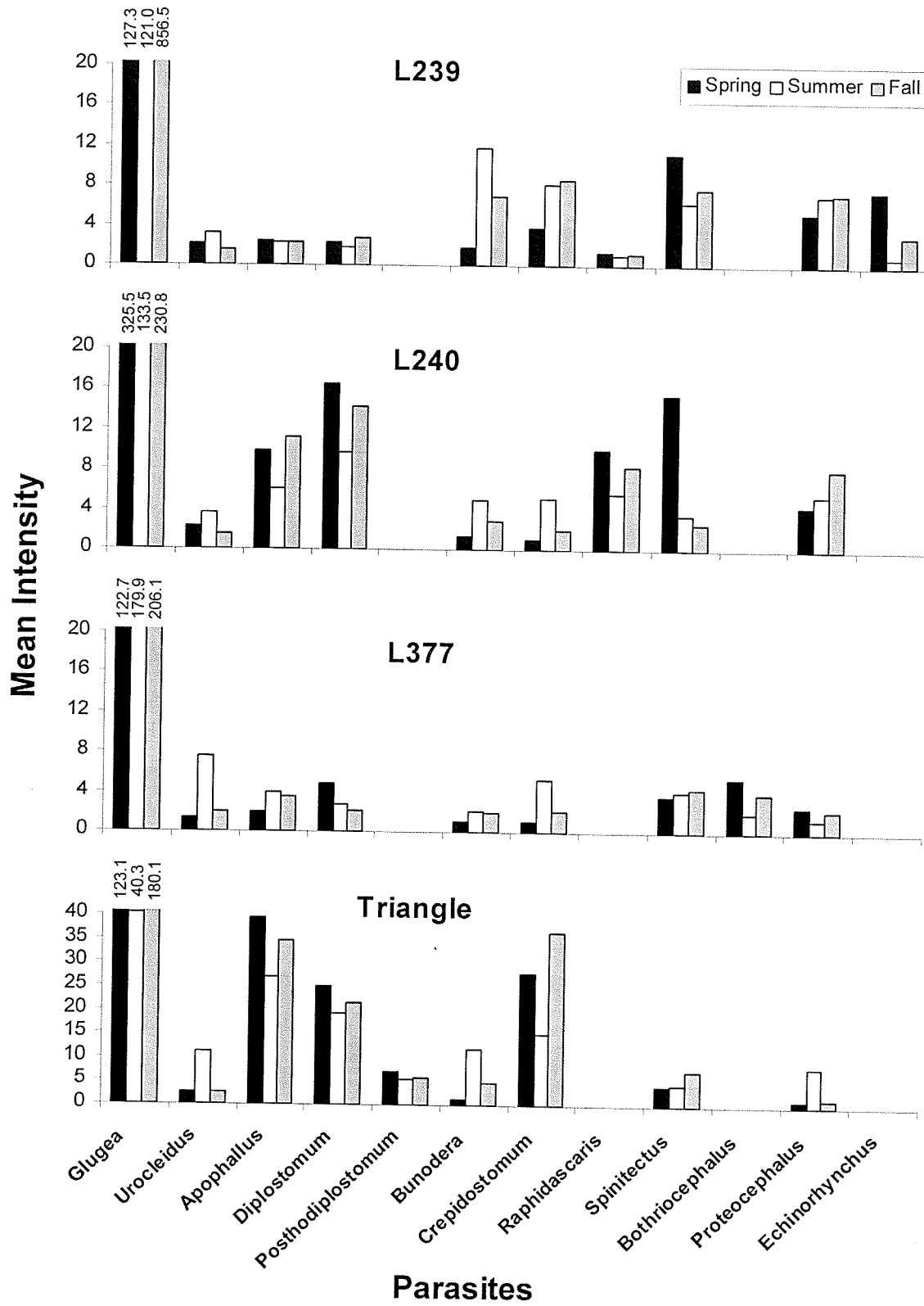


Figure 2.14. Age-related trends in parasite species prevalence in female and male yellow perch (*Perca flavescens*) from L239. The numbers above each bar represent the corresponding mean intensities of each parasite species in each yellow perch age class for comparison.

Prevalence (%)

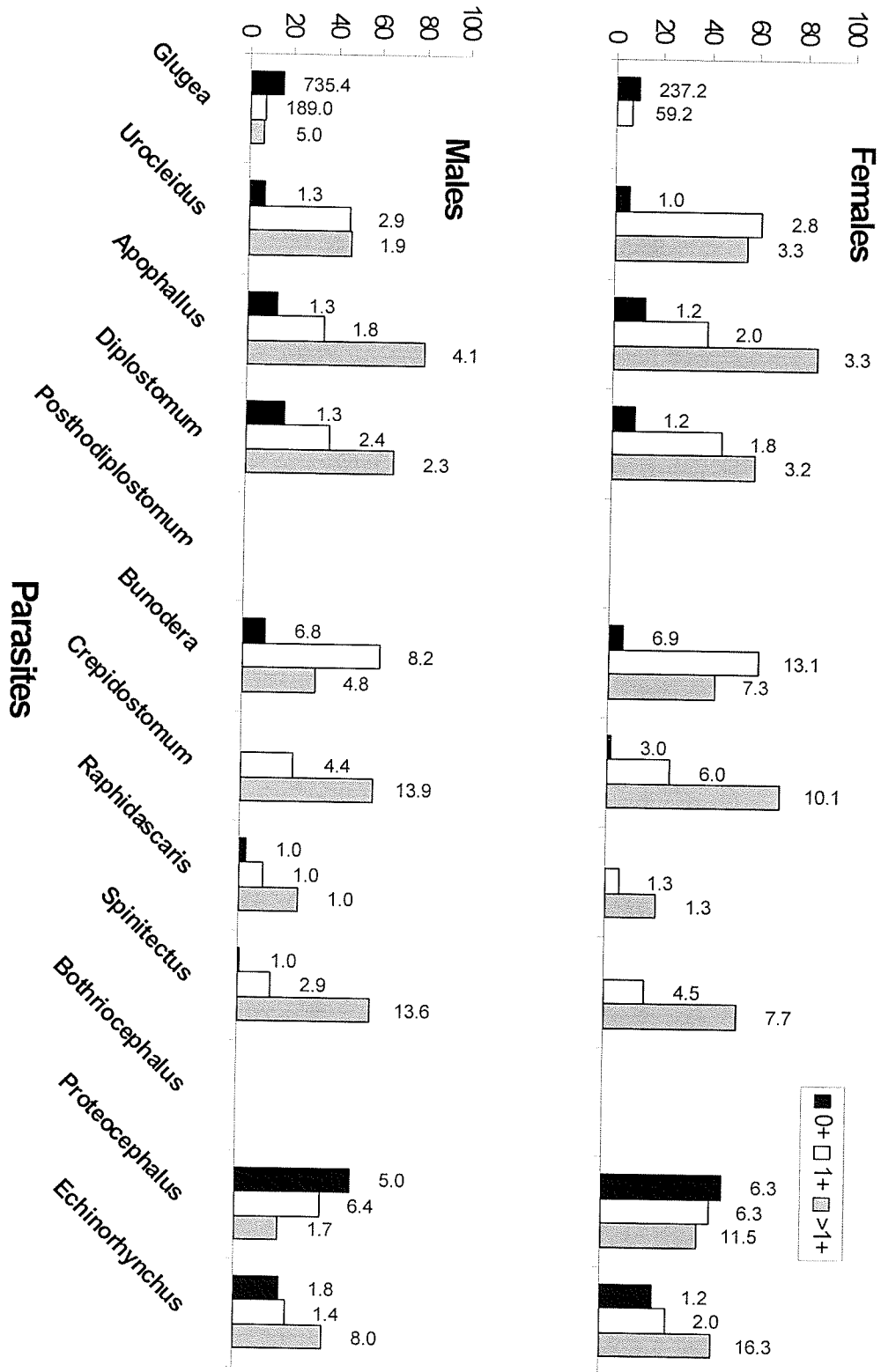


Figure 2.15. Age-related trends in parasite species prevalence in female and male yellow perch (*Perca flavescens*) from L240. The numbers above each bar represent the corresponding mean intensities of each parasite species in each yellow perch age class for comparison.

Prevalence (%)

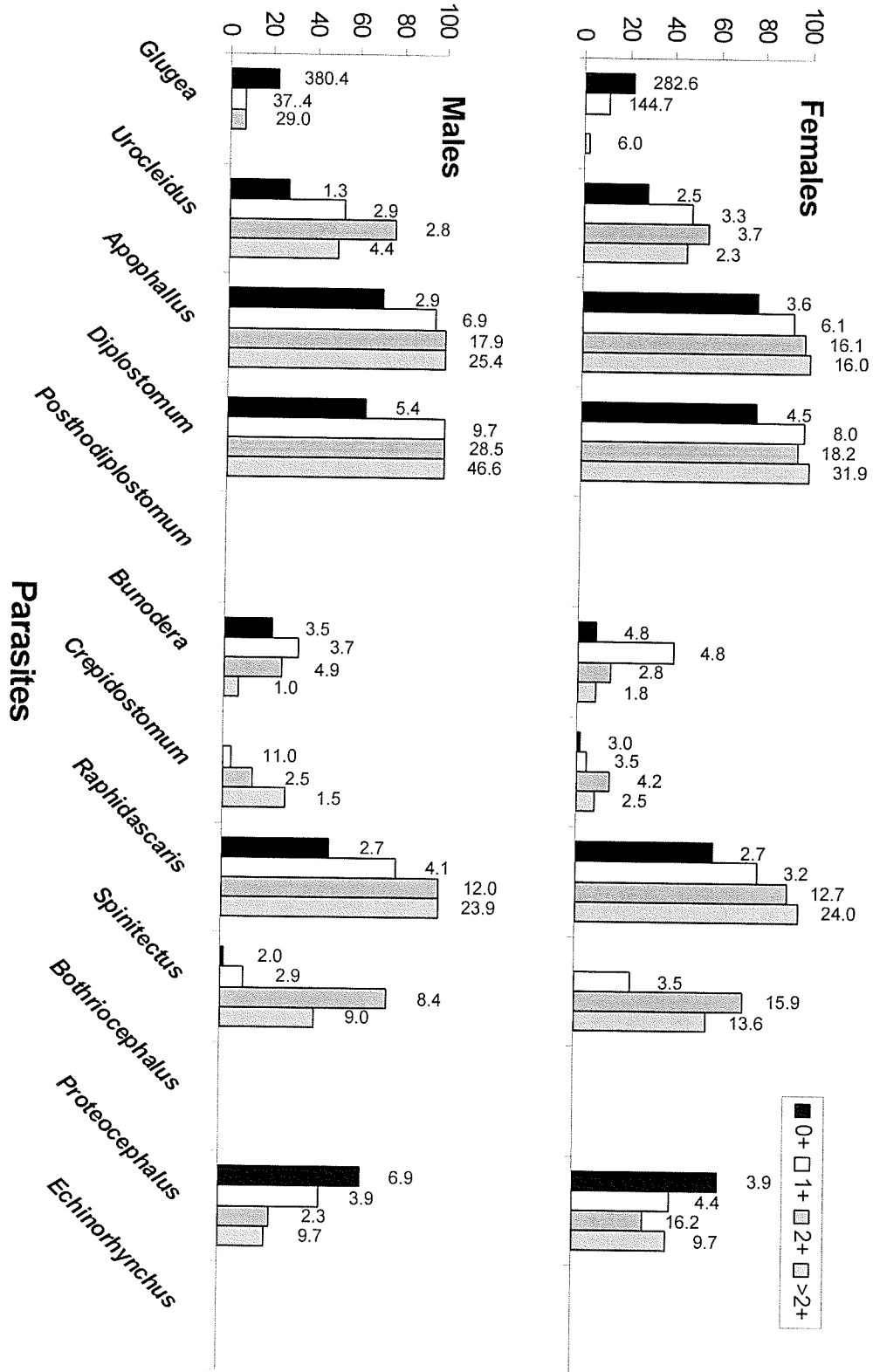


Figure 2.16. Age-related trends in parasite species prevalence in female and male yellow perch (*Perca flavescens*) from L377. The numbers above each bar represent the corresponding mean intensities of each parasite species in each yellow perch age class for comparison.

Prevalence (%)

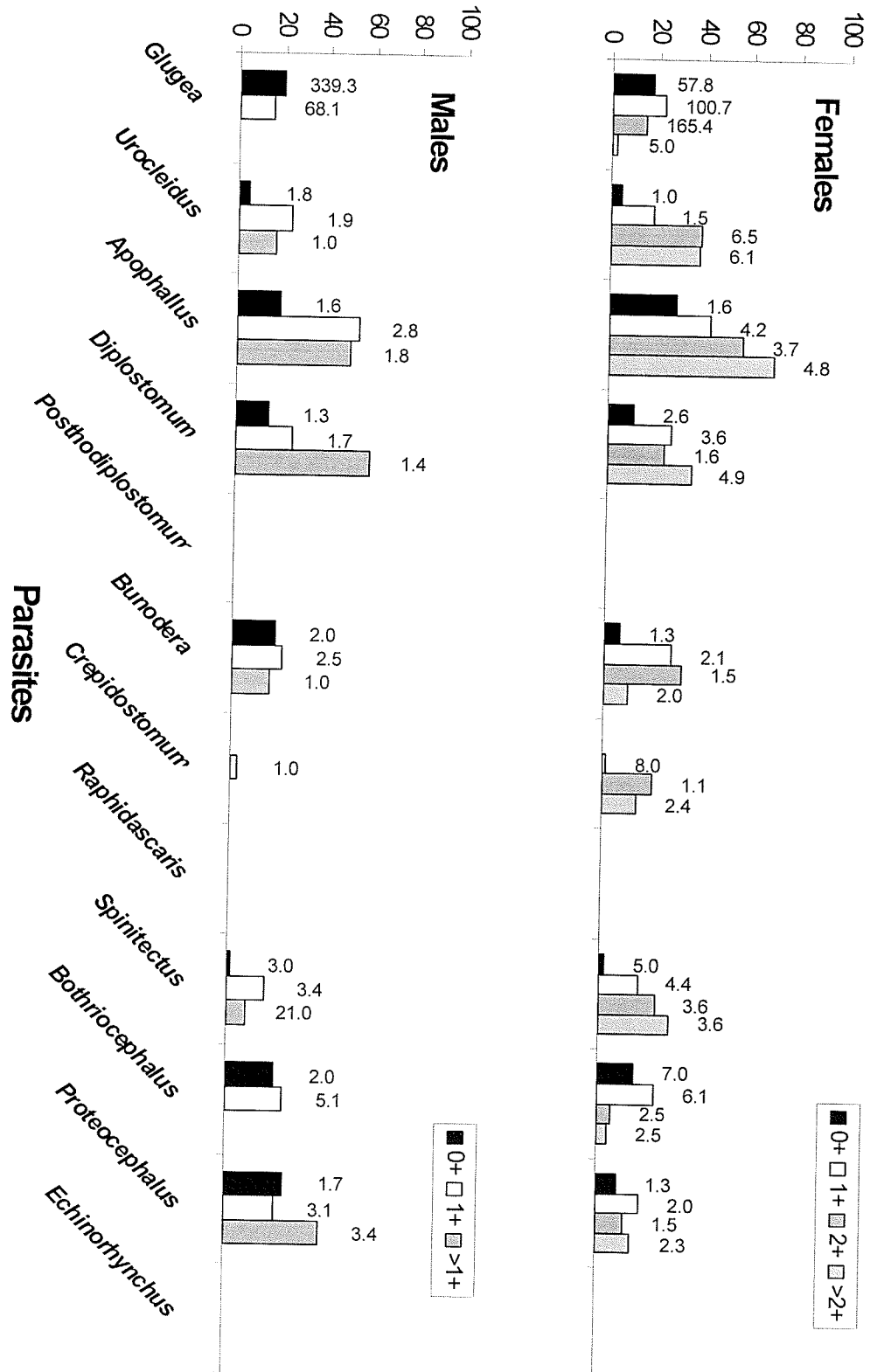
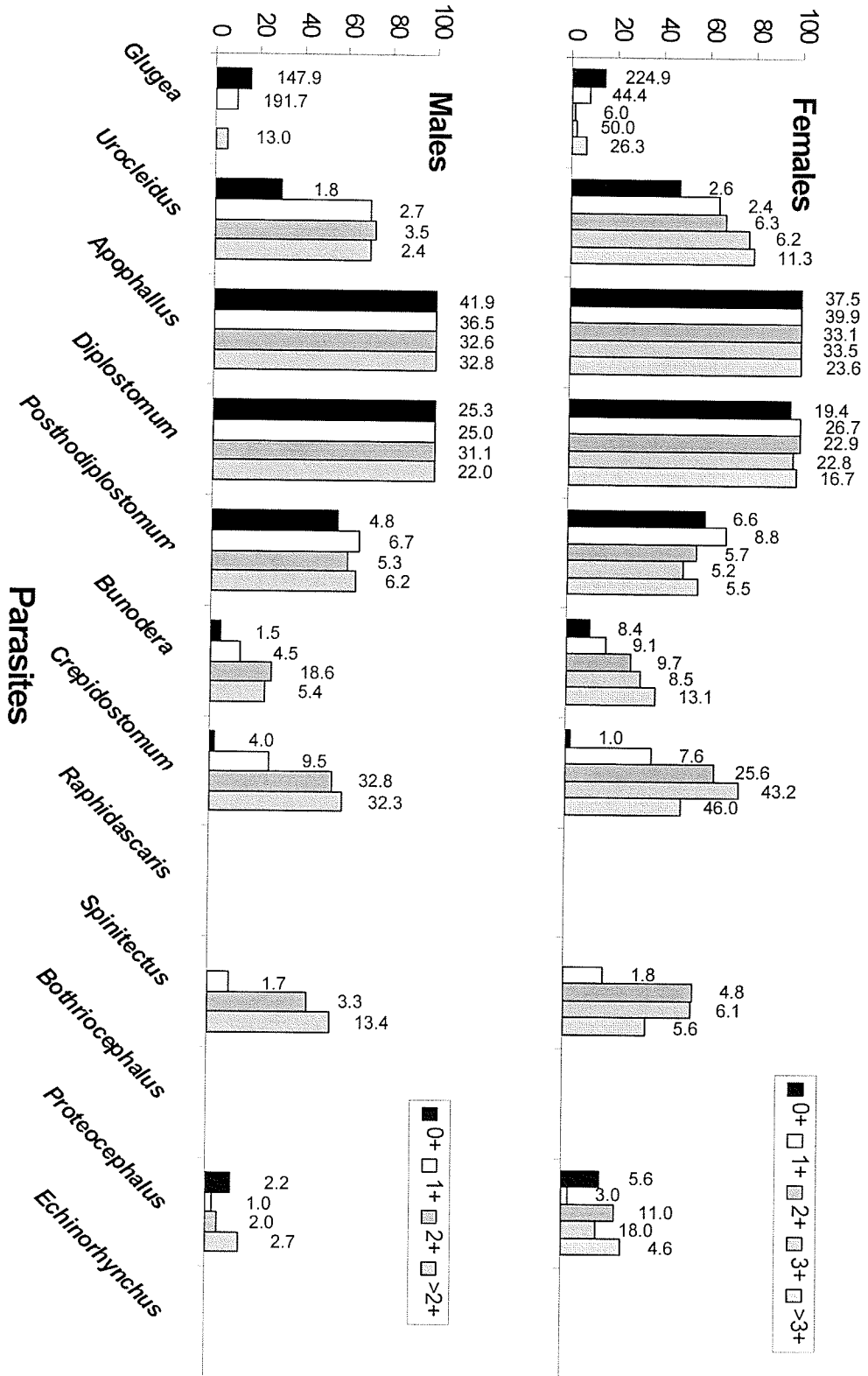


Figure 2.17. Age-related trends in parasite species prevalence in female and male yellow perch (*Perca flavescens*) from Triangle Lake. The numbers above each bar represent the corresponding mean intensities of each parasite species in each yellow perch age class for comparison.

Prevalence (%)



intensity were always high. *Bunodera sacculata* levels usually peaked in male and female age 1+ perch in all lakes. *Crepidostomum cooperi*, *R. acus* (where present) and *S. gracilis* prevalences and mean intensities were higher in the older, larger perch and were rare or absent in young-of-the-year (YOY). *Proteocephalus pearsei* prevalence initially decreased with age but showed an additional increase in the oldest perch especially in mean intensities. *Bothriocephalus cuspidatus* peaked in 1+ yellow perch in L377 (Fig. 2.16) and *E. salmonis* increased with perch age in L239 (Fig. 2.14).

DISCUSSION

Parasite fauna

The parasite community of yellow perch in North America has been well documented (Tedla & Fernando 1969b, Noble 1970, Bangham 1972, Craig 1987, Poole 1985, Szalai et al. 1992, McDonald & Margolis 1995, Hoffman 1999, Carney & Dick 2000a) as have the communities of other freshwater fish species (McDonald & Margolis 1995, Hoffman 1999). Yellow perch commonly have large, speciose parasite infracommunities (McDonald & Margolis 1995, Hoffman 1999), which is a reflection of their generalist diet (Craig 1987), the lack of coevolution between the host and its parasites (Carney & Dick 2000b), and the importance of ecological associations and shared feeding patterns with sympatric hosts (Carney & Dick 2000c). Kennedy *et al.* (1986) also predicted that omnivorous fish and host vagility were essential for diverse parasitofauna in fish. While host movements were not quantified in this study and cannot be related to parasite communities, those fish that had more generalist/omnivorous diets (perch, suckers and pearl dace) also had the highest parasite species richness. Fish with more restricted diets such as the piscivores and smaller cyprinids had less diverse parasite

faunas. The small (2 species) parasite community of cisco, the only salmonid in L377, supports the hypothesis of Wisniewski (1958) that the numerically dominant fish hosts (Cypriniformes and perch) control parasite community structure. Additionally the restricted diet of cisco (planktivores) will further reduce the number of potential infections. Despite the presence of parasite species not previously recorded in certain hosts in Canada or even North America (for example, the pearl dace), the parasite fauna of these shield lake systems is less diverse than the infracommunities of many other North American freshwater communities. For example, the yellow perch community in our study lakes had 11 to 16 species of parasites compared to up to 30 reported from some systems (Tedla & Fernando 1969b, Bangham 1972, Amin 1977, Poole 1985, Dechtiar *et al.* 1989, Szalai *et al.* 1992, Carney & Dick 2000a). The fish parasite species from ELA were typical of yellow perch (McDonald & Margolis 1995, Hoffman 1999, Carney & Dick 2000a). One hundred species of parasites belonging to 68 genera and 51 families were reported from fourteen fish species surveyed in the Lake of the Woods (Dechtiar 1972). Of these fish ($n = 297$) 97% were infected with at least one parasite (Dechtiar 1972). Dechtiar (1972) did not sample *Phoxinus eos* and *Cottus cognatus*. When similar fish species, excluding northern redbelly dace, were considered from the ELA, Lake of the Woods fish had higher parasite species richness than the ELA fish, despite a smaller sample size. Moreover, a bootstrap (see Chapter 3) of the parasite assemblage of ELA yellow perch revealed that no parasite species were missed. This may explain why several species of different, but relatively rare parasites, were recovered from the ELA perch samples and not from fish in the Lake of the Woods survey. This

further illustrates that the smaller parasite community in the ELA is likely a reflection of smaller lake size and fewer species of fish and invertebrates.

Parasite faunal composition (Noble 1970, Amin 1977, Zelmer & Arai 1998, Carney & Dick 2000a) and diet (Craig 1987, Wahl *et al.* 1994) are both influenced by ontogenetic changes yet parasite surveys rarely attempt to reveal any age-related trends. Poole & Dick (1985) found that stocked young-of-the-year (YOY) walleye in Heming Lake were infected with more parasite species in the first summer than resident fish. They attributed this to feeding location and a more diverse diet of zooplankton, chironomids and mayflies. Parasite species composition would change as walleye switch over to piscivory and parasites such as *R. acus* (a potential cause of mortality) would accumulate. The use of parasites to determine age-specific feeding patterns could enhance data gathered from stomach contents. Since parasites transmitted through food are a long-term reflection of what was consumed, fewer samples are required to obtain the same information as that obtained from stomach content analyses.

Although the changes were small, there was a trend towards higher intensities and prevalences of digenean metacercariae in the late summer and fall months in three of the four sampled lakes. Hoglund & Thulin (1990) observed an earlier increase in prevalence of *Diplostomum baeri* in perch (*Perca fluviatilis*) from 93% in May to 100% by June and hypothesized that water temperature was the factor that determined recruitment of eye flukes. Hoglund & Thulin (1990) found that the perch sampled from the warm water effluent of a nuclear power station had an increased rate of accumulation but identical end levels of *D. baeri* to a cooler water perch population. The identical end levels suggest that too much heat in the summer and fall effluent water may also increase

mortality of the parasite (Hoglund & Thulin 1990). Perhaps higher water temperatures in the study lakes in the summer and fall contributed to increased prevalences. Faulkner *et al.* (1989) found that the highest worm burden of *Cotylurus variegatus* metacercariae in perch was from May to June. They suggest that higher spring levels of metacercariae correspond to perch breeding season when spawners (especially females) have a thinner body wall, which allows easier penetration by these parasites. All three common metacercariae species from Triangle Lake had peaks in the spring and it is possible that spawning condition was at least partially responsible. Recruitment of diplostomatid eye flukes in forage fish and young-of-the-year (YOY) of several other species in the St. Lawrence River was highest in the spring and early summer (Marcogliese & Compagna 1999). Marcogliese & Compagna (1999) suggest that YOY and other small fish in close association with gastropods in the spring showed increased metacercariae accumulation. Small Triangle Lake yellow perch, in particular, concentrated in areas with dense macrophyte growth in the spring where the first intermediate gastropod hosts are most abundant. Since many of the heavily infected fish were $\leq 1+$ years old when most females are not yet mature than host behaviour (ie. schooling in high-risk areas) is another factor that can explain seasonal changes. Ultimately, all of these factors may be contributing to seasonal differences in metacercarial infection levels in ELA perch and require further study for precise conclusions.

There was often an initial increase in metacercarial numbers with host age, up to two years, followed by a plateau or a decline. This observation contradicts the prediction of Zelmer and Arai (1998) where directly transmitted, long-lived parasites (allogenic metacercariae) accumulate with host age. The lack of any age-related trends in

metacercariae infections has also been observed in perch in Europe (Faulkner *et al.* 1989) and in yellow perch populations in Manitoba and Wisconsin (Carney & Dick 2000a). In these shield lake systems factors such as host behaviour and spawning condition and water temperature are likely more important determinants of metacercarial infections in yellow perch than host physical attributes, such as age and size.

Fish diet and parasite infection trends

Crepidostomum cooperi requires *Hexagenia limbata* (Ephemeroptera) and *Hyalella azteca* (Amphipoda) as second intermediate hosts (Esch *et al.* 1986). *Spinitectus gracilis* is also utilizes Ephemeroptera as intermediate hosts (Hoffman 1999). Yellow perch consumption of these insects is reduced (abundance and prevalence) in the fall and is non-existent in YOY, which explains the observed seasonal and age-related trends for these parasites. Perch consuming this prey type would likely have a parasite infracommunity that included at least these two parasites.

The increased piscivory by older, larger male and female yellow perch in L377 and Triangle Lake with a concomitant decrease in Ephemeroptera predation resulted in lower *C. cooperi* and *S. gracilis* infections in older perch. The same trend was observed in *C. cooperi* infections of blue catfish (Hoffnagle *et al.* 1990). As blue catfish grew they became more piscivorous and *Crepidostomum cooperi* abundances decreased. Zelmer & Arai (1998) suggest that *C. cooperi* recruitment increases with yellow perch size. A continuous increase in parasite abundance with perch size was observed in ELA only as long as the perch remained non-piscivorous (most males and most L239 fish). The primary influencing factor is, therefore, the availability and consumption rate of the

intermediate Ephemeroptera. Abiotic factors such as water depth and lake nutrient levels may be indirectly affecting the availability of this intermediate host.

There are three parasites in this study which perch acquire through zooplankton ingestion: *Bunodera sacculata*, which utilizes cladocerans or copepods as intermediates and *Proteocephalus pearsei* and *Bothriocephalus cuspidatus* (the latter found only in L377), which utilize copepods. In addition, the horizontal transmission of both juvenile and mature *Proteocephalus* sp. by fish predation or cannibalism has been demonstrated experimentally (Priemer 1980, 1987) and observed in natural fish populations (Moravec 1979, Chubb 1982, Chubb *et al.* 1987, Sholz & Hanzelová 1998). Cladoceran and copepod abundance peaked in perch stomachs and in the epilimnion of L377 (Salki 1993, 1995) in the summer and summer to early fall respectively. This was reflected in the parasite trends as *B. sacculata* numbers were higher in the summer and the two cestodes higher in the fall. Piscivory also peaked in the fall (when most other food sources were reduced in abundance) in most of the lakes and, thus, lateral transmission could have contributed to the fall peak of *P. pearsei*. Post-winter zooplankton densities in the lakes are low, so the prevalences of zooplankton and their transmitted parasites in spring samples of yellow perch are also low. The cladocerans likely reach maximum density first so opportunistic yellow perch use this abundant food source but they switch to copepods when levels of that prey reach maximum later in the year. Valtonen & Rintamaki (1989) observed that *P. percae* and *P. cernuae* infecting perch and ruff respectively in northern Finland were least abundant in the late summer and fall. They also observed a decrease in mean intensity of *P. percae* in perch over winter, which was related to reduced feeding activity of perch. Perhaps, reduced rate of zooplankton

consumption, particularly cladocerans, and increased piscivory in the fall resulted in decreased numbers of *B. sacculata* but not of the cestodes. Seasonal cycles of prevalence have been reported for many species of *Proteocephalus* (Connor 1953, Hopkins 1959, Kennedy & Hine 1969) with maximum levels occurring earlier in the summer than those observed in this study. The lack of a decrease in *B. sacculata* prevalence with increasing age of the host suggests that large cladocerans are still an important food source in older ELA perch. Because of the reduced abundance of benthos in these systems, the yellow perch do not complete the ontogenetic shift from zooplankton to benthos and even the oldest, largest piscivorous perch still consume some cladocerans. Therefore, cladoceran derived parasites should still be part of the infracommunity in larger perch. The smaller copepods, although an energetically efficient food source, disappear at a much faster rate from the diet as yellow perch age. *Bothriocephalus cuspidatus* levels decreased with age but *P. pearsei* levels did not. In fact, *P. pearsei* numbers were often at maximum in both the youngest and oldest fish. This suggests that lateral transfer through cannibalism by older perch was possibly reintroducing *P. pearsei* populations into the parasite infracommunity. Zelmer & Arai (1998), however, found that *Bothriocephalus* accumulation increased with age of yellow perch. This difference from the current study was likely a reflection of differences in perch dietary choices or perhaps a different intermediate host for *B. cuspidatus*.

Raphidascaris acus can be transmitted to yellow perch through chironomid larvae (Smith 1984). Chironomid larvae consumption in L239 and L240 peaked in the summer. Corresponding seasonal peaks for *R. acus* were observed in L240 but not in L239. Lack of seasonality in L239 was likely a result of the scarcity of pike (the definitive host).

Small populations of the definitive host would result in smaller populations of the parasite being transmitted to the intermediate hosts. Chironomid consumption increased with age in L239 as did *R. acus* prevalence. However, despite decreased chironomid ingestion with yellow perch age in L240 there was a continued increase in prevalence and intensity of *R. acus* in perch livers. There are two possible explanations. Either chironomids are still important to older fish and are not found in the short-term stomach contents or, more likely, larvae are laterally transferred through cannibalism. L240 is the only lake where piscivory actually peaks in the summer and not the fall, which coincides with the summer peak of *R. acus*. The lateral transfer of *R. acus* larvae has been previously suggested (Dick 1998).

Amphipods were absent or rare in the diets of perch in all but L239. Amphipod transmitted parasites (especially acanthocephalans) were similarly rare or absent. The prevalence of *Gammarus* in L239 perch diets was low all year but peaked in the summer while *Mysis* intensity and prevalence were highest in the fall and spring. *Mysis* abundance also increased and *Gammarus* abundance decreased in the diets of ELA perch with increased fish age. *Echinorhynchus salmonis* was most intense in the fall and spring and increased with perch age, which suggests that Mysid shrimp are the most important intermediate hosts of this parasite. Numbers of *E. salmonis* have also been observed to increase with age in salmonids (Muzzall 1993).

The gill monogenean, *Urocleidus adspectus*, is a directly transmitted parasite that is specific to yellow perch (Cone & Burt 1982). Its mean intensity and prevalence were highest in the summer and lowest in the fall. Water temperature is likely the influencing factor. The parasite requires certain water temperatures to survive and to mature and

reproduce the next generation. The increased recruitment of this parasite with host age, especially in the faster growing females, is a direct result of increased gill surface area for attachment.

The directly transmitted microsporidean, *Glugea* sp., is most intense in the fall. Shul'man (1989) found that some myxosporideans of fish in Russia cannot infect fish in water warmer than 13°C. *Glugea* sp. infections also appear to be temperature dependent although the critical temperature is unknown. Dense schooling of perch such as in YOY populations increases the rate of transmission of *Glugea* sp. (Dykova 1995). Immature immune systems in YOY may also be contributing to increased *Glugea* sp. infections in young yellow perch. The schooling behaviour in YOY perch combined with low overwinter temperatures would increase the intensity of *Glugea* infections and, thus, increase the mortality rate of infected perch during the winter in ELA (see Chapter 4).

In summary, these findings suggest that parasite transmission in lakes of the Experimental Lakes Area of northwestern Ontario is largely influenced by water temperature, host behaviour and physiology. The availability of particular intermediate host prey seems to be the factor influencing seasonal and age-related trends of dietary parasite fauna in ELA yellow perch. The continuing dependence upon zooplankton by older fish and the switch to piscivory at an earlier age (as young as 1+ to 2+ in L377) likely resulted in a corresponding decrease in the numbers of benthos derived parasites especially acanthocephalans. Furthermore, this dependence also resulted in increased presence of zooplankton acquired parasites in older fish, and the generally lower numbers of parasite species in older perch as there are few fish-to-fish transferred parasites in these lakes.

CHAPTER 3: Yellow perch parasite community patterns and predictability

INTRODUCTION

Parasite community structure patterns and processes are useful tools not only for describing interactions between host and its fauna but also for understanding the overall ecology of the host population. A host population's interactions with its biotic and abiotic environments can affect the composition of its parasite fauna. The parasite community can in turn alter or enhance those host-ecosystem interactions. Certain parasites have been shown to affect fish host growth and development (Szalai & Dick 1991, Szalai *et al.* 1992, Chapter 4). This can affect host trophic status and thus its relationship with the environment by delaying host ontogenetic changes in feeding strategies or by reducing reproductive potential of the host population.

There are obvious advantages an understanding of parasite community structure can have towards a more thorough understanding of the ecology of the host. However, as with much that can be learned from host-parasite interactions, very little focus has been applied to this topic except by parasitologists (Dogiel 1958, Poulin 1995). Many models of parasite community structure have been developed from the study of freshwater fish populations (Dogiel 1958, Wisniewski 1958, Esch *et al.* 1990, Kennedy 1990). It is typically thought that these parasite communities in fish are random assemblages of non-interacting species guided by stochastic processes (Kennedy 1990) but recent studies have shown that the helminth infra- and component communities of yellow perch (*Perca flavescens*, Mitchill) have a predictable component both at the continental (Carney & Dick 1999) and local scale (Carney & Dick 2000a). The yellow perch is an ideal fish host when considering studies of this nature as its biology is well researched (Scott & Crossman 1973, Craig 1987). It is found in most types of aquatic environments from

riverine to lacustrine, large eutrophic lakes to tiny nutrient and biodiversity poor Canadian Shield lakes. It also has one of the most extensive parasite species lists found in freshwater fish (Craig 1987, McDonald & Margolis 1995, Hoffman 1999) with only one strict host specific species (see definition by Carney & Dick 2000c), the gill monogenean *Urocleidus adspectus* (Cone & Burt 1982). Consequently, host specificity is not major factor shaping the component parasite community. In addition, there are relatively few natural populations of yellow perch that lack a parasite fauna or have a fauna consisting of only a few species (Bangham 1944, Fischthal 1950, Dechtiar 1972, Dechtiar *et al.* 1989, Szalai & Dick 1991, Carney & Dick 1999, Carney & Dick 2000a) thereby ensuring a large and diverse community of parasites from which data can be acquired.

Both biotic and abiotic factors have been used to explain richness and diversity of various parasite assemblages in freshwater fish. Kennedy *et al.* (1986) suggested that feeding rates, vagility and physiology of the host could explain richness values of its parasite fauna. These same three factors have also been used to describe a model of the parasite communities in cyprinids and salmonids (Chubb 1970). Carney & Dick (2000a) suggested that predictable patterns at the local level and increased richness of the parasite assemblage were the direct result of a rich invertebrate prey community upon which the yellow perch could feed. This was indirectly affected by lake trophic status, which determined what potential prey/intermediate hosts, would be available to the perch. Host morphometric characteristics, age, sex and phylogeny have also been suggested to explain faunal richness (Aho & Bush 1993). Choudhury & Dick (1998) found that the parasite fauna of the lake sturgeon (*Acipenser fulvescens*) was affected by host specificity

and feeding habits of the host as described by host phylogeny. The presence of piscivorous hosts in the aquatic system can also explain the parasite richness seen in fish populations (Esch 1971, Esch *et al.* 1988). Esch *et al.* (1988) determined that increased colonization abilities of parasites that mature in piscivorous birds and mammals lead to an increase in the numbers of these parasites in eutrophic systems where the fish-eating hosts are abundant. On the other hand, oligotrophic systems with fewer bird and mammal hosts and increased intermediate host prey for fish are dominated by parasite assemblages that mature in fish. While Wisniewski (1958), Esch (1971) and Esch *et al.* (1988) suggest a more direct role for lake trophic status on parasite community structure (Carney & Dick 2000a) found no evidence of this direct role on yellow perch fauna in lake systems of Manitoba and Wisconsin.

Other abiotic factors that have been suggested to affect fish parasite assemblages include lake size (Dogiel 1958, Kennedy 1978), host geographic range (Wisniewski 1958, Price & Clancy 1983) and elapsed time after colonization (Guegan & Kennedy 1993). Although Kennedy (1978) found that brown trout (*Salmo salmo*) in larger lakes had a richer parasite fauna there was no effect of lake size on the richness of yellow perch assemblages (Carney & Dick 2000a). Host fish with larger geographical distribution are believed to possess richer parasite communities (Wisniewski 1958, Price & Clancy 1983). Perch in Europe and yellow perch in North America both have broad geographical distributions and also have one of the richer parasite faunas found in freshwater fish (Craig 1987).

Despite all these varied explanations of the occurrence of particular assemblages Carney and Dick (2000a) suggest that more emphasis need be placed upon the host's

interactions with the intermediate hosts. Since the majority of parasites inhabiting the visceral organs and in particular the intestine are acquired through the diet then the particular infracommunity in a host is a reflection of its diet and vice versa. The availability of prey items to the host would therefore influence the parasite community, especially the endohelminths, of an aquatic ecosystem. Other biotic and abiotic factors may simply be indirectly affecting parasite assemblages by affecting availability of the intermediate hosts.

Carney & Dick (1999, 2000a) provided important insights into perch-parasite interactions but did not include information on young-of-the-year YOY or early second year perch. This is the period when perch grow fastest, when sexual maturation begins and where feeding patterns are most likely to change. Furthermore, the studies of Carney & Dick were done on lakes with high productivity and, while localized to North America, were from latitudinally different drainage systems. These lakes, with the exception of one were large, all were commercially or sport fished and all had some anthropogenic influences including shoreline modifications, inputs from intensive agriculture, fish stockings and intensive commercial and/or sport fishing in the past or currently. The lakes for this study are from an isolated region of the Canadian Shield, from the same drainage, are small, have similar trophic status and invertebrate communities, have low productivity (low nutrient and dissolved solids), have similar abiotic components (with the exception of depth) and diversity and there was background information for these lakes. Furthermore these smaller lakes ensure that a sample of fish is representative of the entire lake, especially when several fishing gear types are used. The lakes were chosen for their different fish species composition. With the exception of L377 where

lake trout were extirpated due to an intensive sports fishery i.e. the removal of the key piscivore, and the occasional use of Triangle Lake for a bait fishery in the past the ELA lakes used in this study are unperturbed.

The goal of this chapter was to assess the richness, structure and species associations of the parasite fauna of yellow perch in four small shield lakes to determine if these assemblages are stochastic or predictable, if there is parasite interaction and to compare the results to aquatic systems more nutrient rich and diverse but perturbed. The emphasis of these analyses was placed upon yellow perch in these systems however, 14 other species of fish were also examined including seven cyprinids, white sucker, slimy sculpin, brook stickleback, burbot, lake cisco, pike and Iowa darter (see Appendix III for these additional analyses).

MATERIALS AND METHODS

Terminology

Only biotic factors such as host sex, length and age class, diet and the presence of potential predators or competitors are evaluated. Prevalence, mean intensity and abundance values were calculated as defined by Margolis *et al.* (1982). Proportional abundance, as used here, refers to the abundance of a parasite or group of parasites as a proportion of the total parasite population. Species richness refers to the total number of parasite species in a sample of fish and mean species richness is the mean number of parasite species per host. The term infracommunity as described by Bush & Holmes (1986) and Bush *et al.* (1997) refers to the parasite community within an individual host. Component community as described by Holmes & Price (1986) and Bush *et al.* (1997) refers to the parasite community within all hosts of a particular sample or lake. A sample

as used here can represent all the fish recovered from a single lake, all fish of a particular age class in a single lake or all fish captured from a particular season in a single lake. A host-specific parasite is one that reproduces in only one host species. Predictability refers to an association that occurs at greater than 50% frequency. Allogenic parasites are those species that mature in piscivorous birds (Esch *et al.* 1988), enteric parasites are those which are mature in the viscera of the fish host and ectoparasites are those found on the gills, mouth or body surface of the fish. All parasite species that do not match the previous categorical descriptions are called other parasites

Statistical analyses

The Berger-Parker index of dominance was used to identify dominant parasite species within each sample. Jackknife estimates of species richness were calculated using a formula described by Krebs (1989) and bootstrap estimates were calculated using the program Species Diversity and Richness 2.1 (Pisces 1998). Species diversity was calculated using both Shannon-Weiner and Simpson's diversity indices. Similarity between the component communities of each lake was calculated using both the Jaccard index of similarity and Renkonen's percent similarity. Spearman's rank correlation coefficients were calculated to determine if host size or age had an effect on the richness, intensity and abundance of the parasite fauna. A Mann-Whitney *U* statistic was used to test for an effect of sex on the composition of parasite communities.

Chi-squared tests were performed to determine if food-transmitted parasites were randomly associated with individual hosts in a sample. The prevalence and anti-prevalence (1-prevalence) were used to calculate the expected values and these were then compared with the observed values. Numbers of uninfected fish, fish with single species

infections, fish with two species infections and fish with three or more species infections. Fish were pooled in richer infections because the expected values for each of these multispecies infections did not exceed one.

Nestedness of the parasite infracommunities in each lake sample was calculated using the nestedness calculator described by Atmar & Patterson (1993, 1995). A presence-absence matrix was calculated for each sample where one represented the presence of a parasite species and zero represented its absence in each individual host in the sample. Each matrix was then reordered or packed so that species presence is maximized in the upper left-hand corner. These packed matrices are compared with an optimally nested matrix with the same proportion of species so that unexpected presences or absences in the generated matrix can be identified. For each of these matrices a T value is calculated where 0 represents a perfectly nested matrix and 100 represents a completely random matrix. The significance of this T value is calculated by comparing the T value of the observed matrix with the distribution of T values of 500 randomly generated matrices.

Unless otherwise noted, all statistics were analyzed using Microsoft Excel 1997 and SPSS version 10.0. Results were considered significant when P values were ≤ 0.05 . These data were discussed with reference to the morphometric, dietary and parasite data of yellow perch described in chapter 2.

RESULTS

Parasite fauna dominance, richness and diversity

When total parasites are considered, Triangle Lake perch had the highest prevalence, mean species richness, intensity and abundance of parasites but had the

smallest number of parasite species of all four populations (Table 3.1). L377 had the lowest values for total parasites in all categories except number of parasite species present. Enteric parasites showed the highest prevalence, proportional abundance and mean richness in L239 perch, but the highest mean intensity and abundance were in Triangle Lake primarily due to large numbers of *C. cooperi* (Table 3.1). Enteric parasites in L239 had a higher proportional abundance than either allogenic or ectoparasites. L377 perch had the poorest enteric parasite fauna, although proportional abundance of this fauna (0.07) was the highest of all three parasite groups in this lake. All four lakes shared an almost identical set of allogenic parasite species. Allogenic parasites in L239 and L377 included less than 10% of all parasites recovered (Table 3.1). Allogenic infection statistics in both L240 and Triangle L. were much higher than those in the other two lakes with the largest, most diverse community of these parasites being observed in Triangle Lake perch (Table 3.1). In addition, allogenic proportional abundance was higher than for the other two parasite types in L240 and Triangle Lake. Triangle Lake also had higher ectoparasite infection statistics than all other lakes. Ectoparasite faunal prevalence varied among perch populations in the other three lakes (from 21% to 46%) but richness, abundance and intensity values were similar.

The dominant parasite in all but Triangle Lake was *Glugea* sp., which was not a member of the three previously described parasite categories (Table 3.2). *Apophallus brevis* was dominant in Triangle Lake. The dominant enteric species differed in each lake. The trematodes *B. sacculata* and *C. cooperi* were dominant in L239 and Triangle, respectively, and the cestodes *P. pearsei* and *Bothriocephalus cuspidatus* were dominant in Triangle Lake.

Table 3.1. Parasite infrapopulation infection statistics of yellow perch total, enteric, allogenic and ectoparasite communities collected from four Canadian Shield lakes.

	L239 (N = 476)	L240 (N = 504)	L377 (N = 369)	Triangle L. (N = 402)	
All Parasites	# infected hosts (prevalence %)	420 (88.2)	499 (99.0)	296 (80.2)	402 (100)
	Total # species	16	13	14	11
	Mean species richness (range)	3.1 ± 1.8 (1-9)	4.3 ± 1.4 (1-8)	2.3 ± 1.2 (1-6)	4.4 ± 1.4 (2-9)
	Mean intensity (range)	58.4 ± 308.8 (1-5008)	62.9 ± 137.7 (1-1029)	41.6 ± 134.9 (1-1002)	89.4 ± 78.7 (12-1053)
	Mean abundance	51.5 ± 290.7	62.3 ± 137.2	34.5 ± 123.5	89.4 ± 78.7
	# infected hosts (prevalence %)	372 (78.2)	378 (75.0)	208 (56.4)	257 (63.9)
	Total # species	6	5	6	4
Enteric Parasites	Proportional Abundance	0.19	0.10	0.06	0.18
	Mean species richness (range)	1.8 ± 0.9 (1-5)	1.4 ± 0.6 (1-4)	1.3 ± 0.5 (1-3)	1.6 ± 0.8 (1-4)
	Mean intensity (range)	13.6 ± 24.1 (1-322)	8.7 ± 18.3 (1-160)	3.9 ± 5.0 (1-35)	25.9 ± 41.6 (1-448)
	Mean abundance	10.6 ± 22.1	6.5 ± 12.0	2.2 ± 4.2	16.6 ± 35.5
	# infected hosts (prevalence %)	239 (50.2)	477 (94.6)	203 (55.0)	402 (100)
Allogenic parasites	Total # species	5	4	5	5
	Proportional Abundance	0.03	0.32	0.07	0.68
	Mean species richness (range)	1.4 ± 0.5 (1-3)	1.9 ± 0.4 (1-3)	1.4 ± 0.6 (1-3)	2.7 ± 0.6 (1-5)
	Mean intensity (range)	3.1 ± 3.6 (1-37)	21.5 ± 23.0 (1-189)	4.5 ± 7.0 (1-67)	60.6 ± 29.2 (8-161)
	Mean abundance	1.6 ± 3.0	20.4 ± 22.9	2.5 ± 5.6	60.6 ± 29.2

Table 3.1. Continued.

	L239 (N = 476)	L240 (N = 504)	L377 (N = 369)	Triangle L. (N = 402)
# infected hosts (prevalence %)	184 (38.7)	231 (45.8)	78 (21.1)	249 (61.9)
Total # species	2	2	2	1
Ectoparasites				
Proportional Abundance	0.02	0.02	0.02	0.04
Mean species richness (range)	1.2 \pm 0.4 (1-2)	1.0 \pm 0.18 (1-2)	1.0 \pm 0.11 (1-2)	1.0 \pm 0.0 (1-1)
Mean intensity (range)	2.8 \pm 3.3 (1-27)	2.8 \pm 3.7 (1-42)	3.9 \pm 5.4 (1-31)	5.3 \pm 8.3 (1-63)
Mean abundance	1.1 \pm 2.5	1.3 \pm 2.9	0.8 \pm 3.0	3.3 \pm 7.0

Table 3.2. The dominant enteric, allogenic, and ectoparasite and the overall dominant parasite of yellow perch in four Canadian Shield lakes. The Berger-Parker index of dominance was used to obtain proportions.

Lake	Dominant Parasite (proportion)			
	Enteric	Allogenic	Ectoparasite	Other
L239	<i>Bunodera sacculata</i> (0.06)	<i>Apophallus brevis</i> (0.01)	<i>Urocleidus adspectus</i> (0.02)	<i>Glugea</i> sp.* (0.57)
L240	<i>Proteocephalus pearsei</i> (0.04)	<i>Diplostomum sp.</i> (0.19)	<i>Urocleidus adspectus</i> (0.02)	<i>Glugea</i> sp.* (0.45)
L377	<i>Bothriocephalus cuspidatus</i> (0.02)	<i>Apophallus brevis</i> (0.04)	<i>Urocleidus adspectus</i> (0.02)	<i>Glugea</i> sp.* (0.84)
Triangle Lake	<i>Crepidostomum cooperi</i> (0.12)	<i>Apophallus</i> * <i>brevis</i> (0.39)	<i>Urocleidus adspectus</i> (0.04)	<i>Glugea</i> sp. (0.10)

* Refers to the most dominant parasite in each lake.

Apophallus brevis was the dominant allogenic parasite in all but L240 where *Diplostomum* sp. dominated. *Urocleidus adspetus* was always the dominant ectoparasite (Table 3.2).

Total parasite percent similarity was highest between L239 and L377 and lowest between L239 and Triangle Lake and L377 and Triangle (Table 3.3). Although the differences were not as great, L240 was still more similar to L239 and L377 than to Triangle Lake. L240 shared approximately 60% of its enteric parasites with both L377 and L239 while L240 and L377 each shared less than 40% of their enteric parasite fauna with Triangle Lake. Allogenic parasite similarities were higher than 69% for all lake comparisons. The highest similarity was between L239 and Triangle Lake and the lowest between L240 and L377. Ectoparasite similarities were all approximately 90% or higher with the lower values all involving comparisons with L239.

The estimated richness values were higher than the observed values only for L239 and L377 (Table 3.4). L239 perch had two unique parasite species among the four perch populations (*Ichthyophthirius multifiliis* and *P. bulbocollis*) and L377 perch had one unique parasite species (*B. cuspidatus*). L240 perch had the most diverse fauna, L377 the least and in all lakes female perch had more diverse assemblages than males (Table 3.5). Table 3.6 shows that as perch in these lakes age their parasite faunas become more diverse until they reach a plateau usually around age 2+. Within each age class there are seasonal trends apparent as well with diversity at its lowest usually in the fall of each year in all lakes. In only one sample (L377 0+ perch) was fall diversity higher than both spring and summer.

Table 3.3. The Jaccard index of similarity (J) and Renkonen's percent similarity (%) of yellow perch parasite fauna in four Canadian Shield lakes.

Lake Comparisons *	SIMILARITY							
	Total Parasites		Enteric Parasites		Allogenic Parasites		Ectoparasites	
	J	%	J	%	J	%	J	%
1 and 2	0.81	0.58	0.83	0.59	0.80	0.86	1.00	0.91
1 and 3	0.67	0.66	0.71	0.51	1.00	0.82	1.00	0.90
1 and 4	0.69	0.24	0.67	0.48	1.00	0.89	0.50	0.89
2 and 3	0.69	0.58	0.83	0.61	0.80	0.69	1.00	0.99
2 and 4	0.71	0.49	0.80	0.34	0.80	0.76	0.50	0.98
3 and 4	0.79	0.23	0.67	0.39	1.00	0.85	0.50	0.99
All four lakes	0.23	0.19	0.57	0.34	0.80	0.68	0.33	0.90

* 1 = L239, 2 = L240, 3 = L377, 4 = Triangle Lake

Table 3.4. Observed total parasite species richness in ELA yellow perch and estimates of total richness using jackknife procedures written by Krebs (1989) and bootstrap procedures written by Pisces Conservation Ltd. (1998).

	L239 n = 476	L240 n = 499	L377 n = 358	Triangle L. n = 390
Observed richness	16	13	14	11
Jackknife (\pm SD)	17.0 \pm 2.64	13.0 \pm 0.00	15.0 \pm 7.93	11.0 \pm 0.00
Bootstrap	15.6	13.0	13.6	11.1

Table 3.5. Female, male and total yellow perch parasite diversity in four Canadian Shield lakes. Diversity was calculated with Simpson's (Si) and Shannon-Weiner (S/W) diversity indices. Sample size (N) is given for each lake and sex.

Lake Parasite Diversity										
	L239		L240		L377		Triangle L.		All Lakes	
	Si	S/W	Si	S/W	Si	S/W	Si	S/W	Si	S/W
	(N)		(N)		(N)		(N)		(N)	
Female diversity	1.78	-0.91	2.82	-0.47	1.52	-0.21	2.61	-0.43	2.20	-0.53
	(301)		(266)		(200)		(276)		(1043)	
Male diversity	1.62	-0.75	2.66	-0.45	1.27	-0.14	2.34	-0.41	2.00	-0.46
	(175)		(233)		(158)		(114)		(680)	
Total diversity	1.72	-0.85	2.75	-0.47	1.41	-0.18	2.53	-0.45	2.14	-0.51
	(476)		(499)		(358)		(390)		(1723)	

Table 3.6. Age and seasonal trends of yellow perch parasite diversity in four Canadian Shield lakes. Diversity was calculated with Simpson's (Si) and Shannon-Weiner (S/W) diversity indices. Sample size (N) is given for each lake and sex.

		Lake Parasite Diversity							
Age	Season*	L239		L240		L377		Triangle L.	
		Si (N)	S/W (N)	Si (N)	S/W (N)	Si (N)	S/W (N)	Si (N)	S/W (N)
	Su	1.36 (7)	-0.49	1.53 (38)	-0.18	0.49 (57)	-0.01	2.28 (18)	-0.39
0+	Fa	0.95 (35)	-0.26	1.82 (26)	-0.30	1.33 (47)	-0.14	1.87 (3)	-0.33
	Sp	1.00 (159)	-0.31	2.64 (91)	-0.42	0.98 (28)	-0.06	2.05 (74)	-0.36
	Su	1.98 (126)	-1.11	3.04 (108)	-0.52	1.69 (12)	-0.23	2.55 (14)	-0.45
1+	Fa	2.02 (59)	-1.00	2.60 (65)	-0.46	1.60 (77)	-0.21	2.16 (7)	-0.41
	Sp	2.93 (27)	-1.62	3.09 (37)	-0.53	1.43 (42)	-0.19	2.30 (73)	-0.41
	Su	2.70 (18)	-1.60	3.16 (33)	-0.54	1.38 (11)	-0.17	3.28 (27)	-0.58
2+	Fa	2.60 (25)	-1.57	2.39 (8)	-0.45	1.73 (25)	-0.24	2.72 (29)	-0.48
	Sp	2.30 (6)	-1.37	3.43 (31)	-0.59	1.90 (6)	-0.28	2.35 (23)	-0.43
>2+		3.11 (14)	-1.83	2.97 (62)	-0.53	2.14 (53)	-0.35	2.87 (122)	-0.51

*Su = summer (x.08 yrs), Fa = fall (x.25 and x.33 yrs), Sp = spring (x.92 yrs).

Yellow perch age and length vs. infection

Yellow perch age was significantly positively correlated with total species richness and all four lakes (Table 3.7). Total species intensity and abundance was significantly correlated with age in all but the Triangle Lake sample. Enteric species richness, intensity and abundance were all significantly correlated with perch age in all four lakes. Allogenic species richness was significantly correlated with age in all lakes. Only Triangle Lake perch showed no significant correlation between age and allogenic parasite species intensity and abundance. Ectoparasite species richness, intensity and abundance were significantly correlated with perch age in all lakes.

Spearman rank correlations of yellow perch total length with parasite richness, intensity and abundance show patterns identical to the age versus infection correlations (Table 3.8). Only total species intensity and abundance and allogenic species intensity and abundance of Triangle Lake perch are not significantly correlated with perch length.

Fish sex versus infection

Female yellow perch had significantly higher total species richness than males in all but the L240 sample (Table 3.9). Total species intensity was higher in L377 and Triangle Lake females and abundance was higher in L240 and L377 females. L239 and Triangle Lake females had significantly higher enteric species richness. Enteric species intensity and abundance were significantly higher in females in all but the L377 sample. Allogenic species richness was higher in L240 and L377 females and allogenic species intensity and abundance were higher in L377 and Triangle Lake female perch. Ectoparasite species richness, intensity and abundance were significantly higher in all but L240 females (Table 3.9).

Table 3.7. Spearman rank correlations of yellow perch age versus species richness, intensity and abundance of total, enteric, allogenic and ectoparasites from four Canadian Shield lakes from the ELA and surrounding region. Spearman correlation value (r_s), t value and P value are given when significant (≤ 0.05), NS indicates no significance. N is the sample size used for Spearman rank correlation calculations.

	L239 N = 476	L240 N = 499	L377 N = 358	Triangle L. N = 390
Total species richness	$r_s = 0.64$ $t = 17.94$ $p < 0.0001$	$r_s = 0.46$ $t = 11.70$ $p < 0.0001$	$r_s = 0.48$ $t = 10.38$ $p < 0.0001$	$r_s = 0.51$ $t = 11.62$ $p < 0.0001$
Total species intensity	$r_s = 0.26$ $t = 5.89$ $p < 0.0001$	$r_s = 0.57$ $t = 15.54$ $p < 0.0001$	$r_s = 0.33$ $t = 6.56$ $p < 0.0001$	NS
Total species abundance	$r_s = 0.42$ $t = 9.97$ $p < 0.0001$	$r_s = 0.61$ $t = 17.23$ $p < 0.0001$	$r_s = 0.37$ $t = 7.51$ $p < 0.0001$	NS
Enteric species richness	$r_s = 0.48$ $t = 11.91$ $p < 0.0001$	$r_s = 0.25$ $t = 5.75$ $p < 0.0001$	$r_s = 0.24$ $t = 4.74$ $p < 0.0001$	$r_s = 0.53$ $t = 12.22$ $p < 0.0001$
Enteric species intensity	$r_s = 0.27$ $t = 6.13$ $p < 0.0001$	$r_s = 0.26$ $t = 5.91$ $p < 0.0001$	$r_s = 0.25$ $t = 4.81$ $p < 0.0001$	$r_s = 0.52$ $t = 12.04$ $p < 0.0001$
Enteric species abundance	$r_s = 0.36$ $t = 8.47$ $p < 0.0001$	$r_s = 0.22$ $t = 5.11$ $p < 0.0001$	$r_s = 0.24$ $t = 4.71$ $p < 0.0001$	$r_s = 0.54$ $t = 12.61$ $p < 0.0001$
Allogenic species richness	$r_s = 0.60$ $t = 16.36$ $p < 0.0001$	$r_s = 0.62$ $t = 17.79$ $p < 0.0001$	$r_s = 0.48$ $t = 10.42$ $p < 0.0001$	$r_s = 0.20$ $t = 4.09$ $p < 0.0001$
Allogenic species intensity	$r_s = 0.63$ $t = 17.54$ $p < 0.0001$	$r_s = 0.82$ $t = 31.65$ $p < 0.0001$	$r_s = 0.45$ $t = 9.58$ $p < 0.0001$	NS
Allogenic species abundance	$r_s = 0.64$ $t = 18.01$ $p < 0.0001$	$r_s = 0.83$ $t = 33.17$ $p < 0.0001$	$r_s = 0.47$ $t = 10.15$ $p < 0.0001$	NS

Table 3.7. Continued.

Ectoparasite	$r_s = 0.48$	$r_s = 0.31$	$r_s = 0.51$	$r_s = 0.39$
species	$t = 12.07$	$t = 7.28$	$t = 11.31$	$t = 8.45$
richness	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
Ectoparasite	$r_s = 0.47$	$r_s = 0.28$	$r_s = 0.52$	$r_s = 0.38$
species	$t = 11.71$	$t = 6.46$	$t = 11.97$	$t = 8.12$
intensity	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
Ectoparasite	$r_s = 0.48$	$r_s = 0.28$	$r_s = 0.52$	$r_s = 0.38$
species	$t = 11.81$	$t = 6.56$	$t = 11.49$	$t = 8.12$
abundance	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$

Table 3.8. Spearman rank correlations of yellow perch total length versus species richness, intensity and abundance of total, enteric, allogenic and ectoparasites from four Canadian Shield lakes from the ELA and surrounding region. Spearman correlation value (r_s), t value and P value are given when significant (≤ 0.05), NS indicates no significance. N is the sample size used for Spearman rank correlation calculations.

	L239 N = 476	L240 N = 499	L377 N = 358	Triangle L. N = 390
Total species richness	$r_s = 0.61$ $t = 16.71$ $p < 0.0001$	$r_s = 0.45$ $t = 11.10$ $p < 0.0001$	$r_s = 0.49$ $t = 10.61$ $p < 0.0001$	$r_s = 0.48$ $t = 10.75$ $p < 0.0001$
Total species intensity	$r_s = 0.23$ $t = 5.20$ $p < 0.0001$	$r_s = 0.53$ $t = 14.05$ $p < 0.0001$	$r_s = 0.33$ $t = 6.51$ $p < 0.0001$	NS
Total species abundance	$r_s = 0.40$ $t = 9.55$ $p < 0.0001$	$r_s = 0.57$ $t = 15.59$ $p < 0.0001$	$r_s = 0.37$ $t = 7.48$ $p < 0.0001$	NS
Enteric species richness	$r_s = 0.45$ $t = 10.85$ $p < 0.0001$	$r_s = 0.26$ $t = 6.17$ $p < 0.0001$	$r_s = 0.26$ $t = 5.05$ $p < 0.0001$	$r_s = 0.53$ $t = 12.31$ $p < 0.0001$
Enteric species intensity	$r_s = 0.26$ $t = 5.97$ $p < 0.0001$	$r_s = 0.22$ $t = 5.01$ $p < 0.0001$	$r_s = 0.25$ $t = 4.83$ $p < 0.0001$	$r_s = 0.52$ $t = 12.02$ $p < 0.0001$
Enteric species abundance	$r_s = 0.36$ $t = 8.27$ $p < 0.0001$	$r_s = 0.26$ $t = 5.89$ $p < 0.0001$	$r_s = 0.25$ $t = 4.81$ $p < 0.0001$	$r_s = 0.54$ $t = 12.62$ $p < 0.0001$
Allogenic species richness	$r_s = 0.61$ $t = 16.59$ $p < 0.0001$	$r_s = 0.62$ $t = 17.63$ $p < 0.0001$	$r_s = 0.51$ $t = 11.14$ $p < 0.0001$	$r_s = 0.18$ $t = 3.69$ $p = 0.0003$
Allogenic species intensity	$r_s = 0.62$ $t = 17.41$ $p < 0.0001$	$r_s = 0.80$ $t = 29.46$ $p < 0.0001$	$r_s = 0.48$ $t = 10.29$ $p < 0.0001$	NS
Allogenic species abundance	$r_s = 0.64$ $t = 17.90$ $p < 0.0001$	$r_s = 0.81$ $t = 30.90$ $p < 0.0001$	$r_s = 0.50$ $t = 10.94$ $p < 0.0001$	NS

Table 3.8. Continued.

Ectoparasite species richness	$r_s = 0.44$ $t = 10.66$ $p < 0.0001$	$r_s = 0.29$ $t = 6.77$ $p < 0.0001$	$r_s = 0.48$ $t = 10.44$ $p < 0.0001$	$r_s = 0.34$ $t = 7.09$ $p < 0.0001$
Ectoparasite species intensity	$r_s = 0.43$ $t = 10.38$ $p < 0.0001$	$r_s = 0.26$ $t = 5.95$ $p < 0.0001$	$r_s = 0.50$ $t = 10.60$ $p < 0.0001$	$r_s = 0.30$ $t = 6.29$ $p < 0.0001$
Ectoparasite species abundance	$r_s = 0.43$ $t = 10.43$ $p < 0.0001$	$r_s = 0.26$ $t = 6.04$ $p < 0.0001$	$r_s = 0.49$ $t = 10.62$ $p < 0.0001$	$r_s = 0.30$ $t = 6.29$ $p < 0.0001$

Table 3.9. Mann-Whitney U test to examine the effect of sex on parasite species richness, intensity and abundance in yellow perch, *Perca flavescens* from four Canadian Shield lakes from the ELA and surrounding region. *P* value is given when significant (≤ 0.05), NS indicates no significance.

	L239 N = 476	L240 N = 499	L377 N = 358	Triangle Lake N = 390
Total species richness	p = 0.0052	NS	p = 0.0011	p = 0.0001
Total species intensity	NS	NS	p = 0.0023	p = 0.0150
Total species abundance	NS	p = 0.0317	p = 0.0019	NS
Enteric species richness	p = 0.0033	NS	NS	p < 0.0001
Enteric species intensity	p = 0.0348	p = 0.0475	NS	p = 0.0009
Enteric species abundance	p = 0.0051	p = 0.0292	NS	p = 0.0003
Allogenic species richness	NS	p = 0.0190	p = 0.0006	NS
Allogenic species intensity	NS	NS	p = 0.0003	p = 0.0223
Allogenic species abundance	NS	NS	p = 0.0002	p = 0.0072
Ectoparasite species richness	p = 0.0021	NS	p = 0.0005	p = 0.0186
Ectoparasite species intensity	p = 0.0037	NS	p = 0.0002	p = 0.0005
Ectoparasite species abundance	p = 0.0032	NS	p = 0.0002	p = 0.0005

Parasite community predictability

The total perch samples from L239 and Triangle Lake were the only ones whose parasite communities showed significant departure from random species associations (Tables 3.10-3.13). More perch with no parasites, with the combination of *S. gracilis*, *C. cooperi*, *Echinorhynchus salmonis* and *Proteocephalus pearsei* and with the combination of *R. acus*, *S. gracilis*, *C. cooperi* and *E. salmonis* than expected and fewer fish with only *R. acus* or only *E. salmonis* present than expected by chance were the major sources of non-randomness in L239 (Table 3.10). Age 0+ to 2+ L239 perch parasite communities showed random species associations. There were a few small derivations from expected in age 0+ perch fauna and the largest was fewer *E. salmonis* than expected. Age 1+ perch had more *S. gracilis* and fewer *P. pearsei* single-species communities than expected. There were more parasite-free age 2+ perch than expected. Perch older than 2+ in L239 had significantly predictable parasite communities. The primary sources of this non-randomness were more perch with no parasites and more with the two combinations of four parasites each (described earlier) than expected (Table 3.10).

There were more *P. pearsei* than expected in L240 perch but the parasite community, as a whole, did not depart from random (Table 3.11). There were no parasites or combinations of parasites that showed large departures from expected values in age 0+ and 2+ L240 perch. There were more *P. pearsei* solo infections than expected in 1+ perch but the entire community at this age was still random. Perch older than 2+ had assemblages that significantly departed from random (Table 3.11). More fish with only *S. gracilis* and only *B. sacculata* and with the combination of *R. acus*, *S. gracilis* and

Table 3.10. Chi-square test of randomness of the parasite fauna of all sampled L239 yellow perch (*Perca flavescens*) and of individual age classes.

Parasite community*	0	1	2	3	4	5	6	7	Any 2 spp.	Any 3 spp.	> 3 spp.	X ² Total	X ² Crit.	P
<u>Total</u>														
Expected (number of perch)	86.40	6.84	11.22	13.71	31.78	25.07	0.64	76.44	113.5	36.81	6.58			
Observed (number of perch)	104	2	11	11	32	15	1	74	101	43	15			
X ²	3.59	3.42	0.00	0.53	0.00	4.05	0.20	0.08	1.38	1.04	10.78	25.08	18.31	0.005
<u>0+ perch</u>														
Expected (number of perch)	68.05	1.06	0.35	0.35	4.86	17.01	0.35	73.12	27.69	2.10	0.05			
Observed (number of perch)	76	0	0	0	5	11	1	65	34	3	0			
X ²	0.93	1.06	0.35	0.35	0.00	2.12	1.20	0.90	1.44	0.38	0.05	8.79	18.31	0.552

Table 3.10. Continued.

Parasite community*	0	1	2	3	4	5	6	7	Any 2 spp.	Any 3 spp.	> 3 spp.	X ² Total	X ² Crit.	P
<u>1+ perch</u>														
Expected (number of perch)	20.97	2.44	4.22	4.58	25.54	4.94	0.25	17.22	59.25	26.80	6.79			
Observed (number of perch)	24	1	9	7	27	4	0	9	57	34	5			
X ²	0.44	0.85	5.40	1.28	0.08	0.18	0.25	3.92	0.09	1.94	0.47	14.89	18.31	0.136
<u>2+ perch</u>														
Expected (number of perch)	1.51	0.42	2.91	2.13	0.08	1.44	0.00	0.70	11.40	9.47	4.06			
Observed (number of perch)	4	1	3	4	0	0	0	0	11	6	6			
X ²	4.12	0.78	0.00	1.65	0.08	1.44	0.00	0.70	0.01	1.27	0.92	10.98	16.92	0.277

Table 3.10. Continued.

Parasite community*	0	1	2	3	4	5	6	7	Any 2 spp.	Any 3 spp.	> 3 spp.	X ² Total	X ² Crit.	P	
>2+ perch															
Expected (number of perch)	0.33	0.16	0.41	0.26	0.00	0.66	0.00	0.16	3.09	2.67	1.24				
Observed (number of perch)	2	0	0	1	0	0	0	0	2	0	4				
X ²	8.48	0.16	0.41	2.06	0.00	0.66	0.00	0.16	0.39	2.67	6.12	21.11	15.51	0.007	

* 0, Empty; 1, *Raphidascaris acus*; 2, *Spinitectus gracilis*; 3, *Crepidostomum cooperi*; 4, *Bunodera sacculata*; 5, *Echinorhynchus salmonis*; 6, *Pomphorhynchus bulbocolli*; 7, *Proteocephalus pearsei*.

Table 3.11. Chi-square test of randomness of the parasite fauna of all sampled L240 yellow perch (*Perca flavescens*) and of individual age classes.

Parasite community *	0	1	2	3	4	5	6	Any 2 spp.	Any 3 spp.	> 3 spp.	X ² Total	X ² Crit.	P
<u>Total</u>													
Expected (number of perch)	20.68	95.92	6.76	0.74	6.14	0.42	18.92	168.6	75.01	12.85			
Observed (number of perch)	19	98	3	1	6	0	31	159	73	16			
X ²	0.14	0.05	2.09	0.09	0.00	0.42	7.71	0.54	0.05	0.77	11.87	16.92	0.221
<u>0+ perch</u>													
Expected (number of perch)	10.02	24.38	0.10	0.00	0.96	0.51	15.78	44.74	6.27	0.25			
Observed (number of perch)	10	25	0	0	1	0	16	44	5	1			
X ²	0.00	0.02	0.10	0.00	0.00	0.51	0.00	0.01	0.26	2.30	3.20	15.51	0.921

Table 3.11. Continued.

Parasite community*	0	1	2	3	4	5	6	Any 2 spp.	Any 3 spp.	> 3 spp.	X ² Total	X ² Crit.	p
<u>1+ perch</u>													
Expected (number of perch)	11.44	46.63	2.47	0.23	6.02	0.11	9.48	83.52	37.50	5.59			
Observed (number of perch)	9	52	2	0	5	0	15	76	36	8			
X ²	0.52	0.62	0.09	0.23	0.17	0.11	3.21	0.68	0.06	1.04	6.73	16.92	0.665
<u>2+ perch</u>													
Expected (number of perch)	0.11	5.83	0.38	0.01	0.02	0.00	0.05	25.52	17.90	4.17			
Observed (number of perch)	0	6	1	0	0	0	0	25	18	4			
X ²	0.11	0.01	0.98	0.01	0.02	0.00	0.05	0.01	0.00	0.01	1.21	16.92	0.999

Table 3.11. Continued.

Parasite community*	0	1	2	3	4	5	6	Any 2 spp.	Any 3 spp.	> 3 spp.	X ² Total	X ² Crit.	P
>2+ perch													
Expected (number of perch)	0.23	10.56	0.20	0.03	0.03	0.00	0.20	20.58	11.98	2.19			
Observed (number of perch)	0	15	0	1	0	0	0	12	15	3			
X ²	0.23	1.87	0.20	32.97	0.03	0.00	0.20	3.58	0.76	0.30	40.13	15.51	0.000

* 0, Empty; 1, *Raphidascaris acus*; 2, *Spinitectus gracilis*; 3, *Crepidostomum cooperi*; 4, *Bunodera sacculata*; 5, *Echinorhynchus salmonis*; 6, *Proteocephalus pearsei*.

P. pearsei than expected by chance and fewer combinations of *R. acus* and *P. pearsei* and of *R. acus* and *S. gracilis* than expected resulted in predictability.

YOY L377 yellow perch parasite fauna was significantly non-random (Table 3.12) which was caused by more combinations of *B. sacculata*, *P. pearsei* and *B. cuspidatus* than expected. No other single parasite or combination was different from expected by chance at any age class.

More fish with no parasites and more with the infracommunity of *C. cooperi*, *B. sacculata* and *P. pearsei* and more with *S. gracilis*, *C. cooperi*, *B. sacculata* and *P. pearsei* than expected and fewer with only *S. gracilis* or only *C. cooperi* than expected were the sources that caused non-randomness in Triangle Lake perch (Table 3.13). All individual age classes had random parasite assemblages.

All four yellow perch samples showed significantly more nestedness than expected by chance (Table 3.14). Matrix fill ranged from 16.4% in L377 to 40.4% in Triangle Lake and the T value ranged from 14.64 in Triangle Lake 19.49 in L377 (all highly nested values).

DISCUSSION

Yellow perch (*Perca flavescens*) in North America and European perch (*Perca fluviatilis*) in Eurasia have been shown to possess a predictable component to the parasite community at the broad, continental scale (Carney & Dick 1999). Carney & Dick (2000a) showed that there is predictability of parasite infracommunities and component communities of yellow perch at the local or fine scale. Fine scale analysis allowed Carney & Dick (2000a) to better quantify the factors that affect parasite community structure. Carney & Dick (2000a) suggest that the complexity of the invertebrate host

Table 3.12. Chi-square test of randomness of the parasite fauna of all sampled L377 yellow perch (*Perca flavescens*) and of individual age classes.

Parasite community*	0	1	2	3	4	5	Any 2 spp.	> 2 spp.	X ² Total	X ² Crit.	P
<u>Total</u>											
Expected (number of perch)	128.96	20.26	8.66	28.08	30.65	33.31	43.85	8.23			
Observed (number of perch)	128	23	7	23	31	37	45	8			
X ²	0.01	0.37	0.32	0.92	0.00	0.41	0.03	0.01	2.06	14.07	0.956
<u>0+ perch</u>											
Expected (number of perch)	53.78	0.53	0.00	8.46	12.96	17.24	9.28	0.75			
Observed (number of perch)	58	1	0	6	9	18	7	4			
X ²	0.33	0.42	0.00	0.72	1.21	0.03	0.56	14.16	17.44	12.59	0.008

Table 3.12. Continued.

Parasite community*	0	1	2	3	4	5	Any 2 spp.	> 2 spp.	X ² Total	X ² Crit.	P
<u>1+ perch</u>											
Expected (number of perch)	43.59	8.81	1.13	12.19	12.19	15.35	21.27	4.48			
Observed (number of perch)	41	9	1	11	15	19	22	3			
X ²	0.15	0.00	0.01	0.12	0.65	0.87	0.02	0.49	2.32	14.07	0.940
<u>2+ perch</u>											
Expected (number of perch)	10.82	2.08	3.15	3.15	3.76	0.75	5.89	1.40			
Observed (number of perch)	10	3	2	3	6	0	6	1			
X ²	0.06	0.41	0.42	0.01	1.33	0.75	0.00	0.11	3.09	14.07	0.877

Table 3.12. Continued.

Parasite community *	0	1	2	3	4	5	Any 2 spp.	> 2 spp.	X ² Total	X ² Crit.	p
>2+ perch											
Expected (number of perch)	15.91	8.25	4.47	1.72	1.72	1.26	6.53	1.15			
Observed (number of perch)	15	9	4	2	1	2	8	0			
X ²	0.05	0.07	0.05	0.05	0.30	0.44	0.33	1.15	2.43	14.07	0.932

* 0, Empty; 1, *Spinitectus gracilis*; 2, *Crepidostomum cooperi*; 3, *Bunodera sacculata*; 4, *Proteocephalus pearsei*; 5, *Bothriocephalus cuspidatus*.

Table 3.13. Chi-square test of randomness of the parasite fauna of all sampled Triangle Lake yellow perch (*Perca flavescens*) and of individual age classes.

Parasite community*	0	1	2	3	4	Any 2 spp.	> 2 spp.	X ² Total	X ² Crit.	p
<u>Total</u>										
Expected (number of perch)	93.73	36.88	76.22	12.73	11.15	60.33	9.96			
Observed (number of perch)	126	15	57	8	8	68	19			
X ²	11.11	12.98	4.85	1.76	0.89	0.98	8.22	40.79	12.59	0.000
<u>0+ perch</u>										
Expected (number of perch)	66.23	0.00	0.91	1.84	4.80	0.22	0.00			
Observed (number of perch)	67	0	1	2	4	0	0			
X ²	0.01	0.00	0.01	0.01	0.13	0.22	0.00	0.39	9.49	0.996

Table 3.13. Continued.

Parasite community *	0	1	2	3	4	Any 2 spp.	> 2 spp.	X ² Total	X ² Crit.	P
<u>1+ perch</u>										
Expected (number of perch)	38.67	7.18	23.06	4.13	0.95	8.36	0.65			
Observed (number of perch)	37	7	24	4	2	9	0			
X ²	0.07	0.00	0.04	0.00	1.14	0.05	0.65	1.97	12.59	0.922
<u>2+ perch</u>										
Expected (number of perch)	6.20	6.78	14.58	1.64	1.35	26.60	9.84			
Observed (number of perch)	9	5	14	1	1	27	10			
X ²	1.26	0.47	0.02	0.25	0.09	0.01	0.00	2.10	12.59	0.901

Table 3.13. Continued.

Parasite community *	0	1	2	3	4	Any 2 spp.	> 2 spp.	X ² Total	X ² Crit.	p
>2+ perch										
Expected (number of perch)	6.68	6.51	19.70	1.27	1.40	29.94	9.49			
Observed (number of perch)	11	3	18	1	1	32	9			
X ²	2.79	1.89	0.15	0.06	0.12	0.14	0.03	5.17	12.59	0.648

* 0, Empty; 1, *Spinitectus gracilis*; 2, *Crepidostomum cooperi*; 3, *Bunodera sacculata*; 4, *Proteocephalus pearsei*.

Table 3.14. Nestedness of yellow perch parasite communities in four Canadian Shield lakes with 500 randomly distributed matrices.

	L239	L240	L377	Triangle L.
Observed fill (%)	19.5	32.8	16.4	40.4
Observed T value	17.45	16.32	19.44	14.64
Simulated T value	54.93 ± 1.67	67.33 ± 1.69	46.41 ± 2.17	66.22 ± 1.78
P value	$2.12 \text{ e-}73$	$3.54 \text{ e-}104$	$2.77 \text{ e-}33$	$3.80 \text{ e-}99$

community and the way the fish host utilises the available prey types affect the composition of parasite assemblages. Lake trophic status plays an indirect role by controlling the abundance and richness of the invertebrates.

Parasite communities

All yellow perch samples shared ten parasite species. Of these ten parasites, three (*P. pearsei*, *C. cooperi* and *U. adspectus*.) are members of a suite of four enteric and one ectoparasite which are predictably associated with yellow perch at the broad continental and fine, local scales (Carney & Dick 1999, 2000a). In fact the presence of the strict host specific (Cone & Burt 1982) *U. adspectus* produced intersample similarities higher than 90%. The relative abundance of enteric and allogenic parasites varied widely but resulted in total percent similarities that were higher than most interlake comparisons in the Carney & Dick (2000a) study. The other two members of this group, *Bothriocephalus cuspidatus* and *Dichelyne cotylophora* were found in one and none of the lakes respectively. This evidence further supports the proposal that at least a portion of these species are predictably part of the parasite community of yellow perch. It would appear that as scale becomes finer than taxonomic predictability increases as a result of greater sharing of species richness and abundance between lakes but it may also be related to these unperturbed systems (see discussion below).

Host characteristics

Host specificity, behaviour, feeding habits, physiology and physical characters of the host (size, age, sex) have all been implicated as factors affecting parasite community structure (Dogiel 1958, Chubb 1970, Esch *et al.* 1975, Kennedy *et al.* 1986, Aho & Bush 1993, Choudhury & Dick 1998, Zelmer & Arai 1998, Carney & Dick, 2000a). Such

characteristics have been used to explain the parasite fauna of perch (Zelmer & Arai 1998, Carney & Dick 2000a), sturgeon (Choudhury & Dick 1998), salmonids and cyprinids (Chubb 1970).

Zelmer & Arai (1998) predict that long-lived allogenic parasites increase in abundance with host age and short-lived enteric or ectoparasites will accumulate with host size. ELA yellow perch size increases as they age and while there is great size variation within an age class there is little overlap between age classes until approximately 3+ or 4+ unlike most perch populations (LeCren 1947, Scott & Crossman 1973, Noble 1975, Craig 1987, Boisclair & Leggett 1989a, Mills *et al.* 1989). Sexual size dimorphism is also quite pronounced during the middle years of these perch. There are highly significant correlations between size of the perch and not only the short-lived enteric and ectoparasites but also with the allogenic parasites in all but Triangle where allogenic parasites dominate. Age correlations show an identical pattern and this disagrees with Zelmer & Arai (1998). If allogenic parasites are more likely to accumulate with host age then the lake with the most abundant allogenic parasites and the largest longest-lived perch should show significant correlations with parasite species intensity and abundance. These data do not entirely support the predictions for yellow perch parasites by Zelmer & Arai (1998). It may be that these predictions simply won't work in small nutrient poor yet relatively parasite rich shield lakes.

Sex has rarely been successfully linked to parasite community structure. Lawrence (1970) found small correlations with sex for white sucker parasites and Carney & Dick (2000a) found that male perch in Dauphin Lake, Manitoba had significantly higher intensity and abundance of allogenic and enteric parasites than female perch. No such

correlations could be found in bowfin, *Amia calva* (Aho & Bush 1993), Atlantic croaker (*Micropogonius undulatus*) and spot (*Leiostomus xanthurus*) (Thoney 1993), and lake sturgeon (*Acipenser fulvescens*) (Choudhury & Dick, 1993). Yellow perch parasites particularly enteric and ectoparasites in this study are correlated with host sex. L377 and Triangle Lake show the most host-sex parasite correlations. Only enterics in L377 cannot be significantly correlated with sex and this is likely due to the small enteric fauna present in this lake (proportional abundance is only 0.06). Perch older than 4+ are predominantly large females. The large surface area for attachment to the gills would explain why females have significantly greater ectoparasites than males. However, relative to small perch these few large females actually have a reduced enteric fauna likely due to diet (largely piscivorous) and would not be a factor influencing parasite correlation with sex in Triangle Lake. Age 3+ and 4+ females in this lake are significantly larger than the males and feed on a richer variety and increased quantities of invertebrate fauna thus exposing females to greater numbers of infective intermediate hosts. This could explain the observed sex-linked parasite community differences in Triangle Lake. In L239 and L240 where sexual dimorphism is not as pronounced there are still some strong correlations between sex and in particular enteric parasites. This suggests that factors such as differential susceptibility of males and females or alternate feeding strategies may influence correlation with sex. Male perch may be choosing microhabitat that has a decreased abundance of infective invertebrates.

Predictability

Predictability in freshwater fish parasite communities stems from the consistent presence of a specific group or groups of parasites in all samples. The abundance of

these groups differs from that expected by chance. Kennedy (1990) suggested that freshwater fish parasite communities are stochastic assemblages. Carney & Dick (1999; 2000a), however, found some structure and predictability in parasite infracommunities and component communities of yellow perch. It is suggested that for predictability of the parasite community to be more likely there needs to be increased similarity of host attributes within and among samples (Carney & Dick 2000a).

Yellow perch in this study do show some predictable components to their parasite assemblages. Host attributes between L239 and L240 and between L377 and Triangle Lake are similar and parasite faunal similarities are also relatively high. In fact, what seems to be the driving factor for predictability in these systems is the proportional abundance and mean species richness, intensity and abundance of the enteric parasite fauna. Both L239 and Triangle total yellow perch samples are significantly predictable and both have high enteric proportional abundance (about 20%). L377 has the lowest abundance of enterics and with one exception (0+ perch have more *B. sacculata*, *P. pearsei* and *B. cuspidatus* in combination than expected) all parasites and combinations of parasites show no deviation from the expected values. This agrees with the results observed by Carney & Dick (2000a). The three samples of yellow perch with predictable parasite communities all had high number of enterics and high total species richness (Carney & Dick 2000a). The three lakes with completely random assemblages had a very poor enteric fauna (Carney & Dick 2000a). Age of yellow perch may also be a factor determining parasite predictability. Perch older than 2+ in L239 and L240 show predictable parasite communities and, although older Triangle Lake perch do not have predictable fauna, the trends are still there. Fish with no parasites, a single species

infection in each and a certain combination in each system all in numbers greater or fewer than is expected by chance contribute to predictability. In fact, unlike yellow perch parasites in the Carney & Dick (2000a) study, single species infections and no infections are often not at frequencies that are consistent with predicted values determined by prevalence. Even when the overall community is a random one the least random component is often a single species infection. This suggests that in certain instances different parasite species are acquired alone or with others more often than expected. The particular combinations of parasites that appear more often in perch hosts in L239 and L240 and cause predictability in older perch fauna are largely parasites that are transmitted through benthic invertebrates such as amphipods and mayfly nymphs. Fish are only a small part of the diet of older fish in these two lakes and so the older fish are predominantly benthivores and this is reflected in the predictable parasite infracommunity. The inclusion of a copepod transmitted parasite *P. pearsei* in all these combinations suggests that zooplankton is at least still a minor part of the diet of older and larger perch in these two lakes. The combination causing predictability of 0+ perch from L377 is three parasites which are all transmitted by copepods. At that age perch are almost exclusively zooplanktivores and since zooplankton is more abundant in this lake to begin with the possibility of instant infracommunities being passed on to young perch seems more likely. The predictable infracommunity in Triangle Lake perch comes from a combination of benthos and zooplankton which are not a part of the diet of many perch older than 2+ in this lake. Older perch have switched to piscivory.

Nestedness

Nestedness can be used to search for structure in freshwater fish parasite communities (Guegan & Hugueny 1994, Carney & Dick 2000a). If a parasite community is nested then the potential species present in a host with a poor infection are a subset of those found in a host with a rich assemblage (Atmar & Patterson 1993). The alternative is that the species present in both poor and rich infracommunities are random samples from a pool of available parasites (the component community). If nestedness and thus structure can be established for a parasite community then this can be used to predict and describe other aspects of host and parasite community ecology (Esch *et al.* 1990). Carney & Dick (2000a) showed ubiquitous nestedness in yellow perch samples that had different parasite richness, poorly filled matrices, come from very trophically different systems and show little host specificity. At the even finer scale in ELA, nestedness appears to be even more pronounced. Fill rates are the highest and T values the lowest in the samples with the highest proportion of allogenic species (L240 and Triangle Lake). There are several factors that can lead to nestedness. Carney & Dick (2000a) suggest that differential susceptibility to infection due to age, size or sex of the host may promote nestedness although their data did not strongly support this hypothesis. Perch in this study did show strong correlations with all host attributes and differential susceptibility is therefore one likely cause of nestedness. From a list of other factors causing nestedness (Wright & Reeves 1992, Wright *et al.* 1998) three (passive sampling, sequential colonizing ability, or differential extinction) may also play a role in these systems. Passive sampling arises from the probability that abundant species are found in more hosts than rare ones. Sequential colonizing suggests that parasites will infect the hosts at

different times. While there are parasite taxa which are infective to perch at different times of the year data from these systems show that most of the local component community peak in the summer and only a few peak in the fall (Chapter 2). This implies that sequential colonizing may not be as important a factor in these shield lakes. Differential extinction where some parasites are seasonal, short-lived and some are chronic, long-lived cannot be ruled out as a cause either. The two systems that are the most nested also happen to have the most abundant allogenic, which does imply that differential extinction may be contributing to nestedness. Still, parasite communities can be useful models for observing and explaining nestedness in community ecology.

Diet

The diet of any given host can greatly influence the composition of its parasite fauna (Dogiel 1958, Kennedy *et al.* 1986, Choudhury *et al.* 1996, Choudhury & Dick 1998, Carney & Dick 2000a). Even though stomach contents only represent short term feeding strategies (Persson 1979, 1981) they can still be used to predict parasite assemblages. A study of the food habits, parasite fauna and stable isotopes (which reflect long term feeding patterns) would be very useful for better understanding a host's interactions with its biotic environment.

Yellow perch are highly opportunistic predators (Scott & Crossman 1973, Craig 1987) and show little host specificity and so are susceptible to several species of parasites. Perch in this study had the most diverse sampling of stomach contents of all fish with 13 different types (Chapter 2). Everything from macrophytes to a frog was found in perch stomachs. There were variations among lakes that were also reflected in parasite communities. The greater richness of amphipods available to L239 perch and

their preference of this food type over other benthos in the diet is reflected in the parasite community particularly when comparing with the neighbouring L240 (with a poorer amphipod fauna). *Pomphorhynchus bulbocolli* is found only in L239 perch and *E. salmonis* is about 25 times more prevalent. Most insect transmitted parasites in L239 show reduced prevalence and intensity. The much larger abundance of *R. acus* in L240 fish is more a reflection of a larger population of pike, which can sustain a larger population of adult worms than of dietary difference between the two lakes.

L377 perch have a greater proportion of zooplankton than benthos in the diet but parasites from both sources are reduced. The only time the parasite community of L377 perch was predictable was during the zooplankton feeding stage and it was caused by a combination of three copepod transmitted parasites. Since perch are not specialist feeders they may be getting outcompeted for certain resources by fish that do specialize. The presence of two species of planktivorous fish one of which is abundant (spottail shiner) may limit the availability of zooplankton despite greater abundances in this lake. In particular, available infective copepods may be reduced especially by cisco, which are highly efficient at filtering small zooplankton from the water. L377 perch do show a much greater proportion of cladocerans than copepods in their diet despite much greater copepod abundances in the epilimnion (Salki 1993, 1995). Perch also reach larger maximum sizes in this lake than in L239 and L240 and may quickly switch over to a larger food source. The availability of a reduced benthic fauna may be further compromised in a system with abundant large white suckers. White suckers are more efficient benthivores than perch and may outcompete and in some cases cause stunting of perch populations (Hayes *et al.* 1992). This could also explain why L377 perch as young

as 1+ and 2+ have already begun to prey upon young perch and minnows. Fish may be the only readily available food source (especially with the large minnow populations in this lake) and in these shield lakes the only parasites that can be transmitted to piscivorous perch are laterally transferred *P. pearsei* and *R. acus* (only present in two lakes).

Triangle Lake perch show reduced zooplankton in the diet and increased benthos and fish. This is reflected in the parasite community with greater prevalences of benthic parasites like *C. cooperi* and *S. gracilis* and reduced numbers of copepod derived parasites like *P. pearsei* and *B. sacculata*. However, reduced abundance of amphipods in this lake has similarly reduced the presence of amphipod transmitted parasites in the community. As per the lakes in the Carney & Dick (2000a) study which had poorer invertebrate fauna (like our shield lakes) parasites that are transmitted through the food contribute greater to overall richness than to abundance. It is the directly transmitted parasites in these systems that are contributing to most of the parasite abundance.

Other biotic and abiotic factors

The different mean and maximum depths of these shield lakes may be indirectly influencing parasite community composition. The two deepest lakes (L239 and L377) have the most speciose yellow perch parasite faunas. Lake depth will also influence the composition of other biotic communities in the lake. Non-host specific parasites typical of species of fish and invertebrates that prefer deeper lakes (lake trout, burbot, some amphipods) can therefore be found in perch in these lakes (acanthocephalans especially).

The diversity of the local fish community at the familial level appears to have a greater impact on the parasite community in perch than simply the number of fish species

present. L377 and Triangle Lake contain the greatest number of fish species however Triangle Lake perch have fewer parasite species than any other lake. The fish fauna of Triangle Lake includes only four families and only one of those families (Cyprinidae) is represented by more than one species. The fish fauna of L377 however includes seven families while six are present in the other two lakes. The presence of pike and salmonids in particular seem to influence the parasite species available to infect yellow perch both of which are absent from Triangle Lake. So even within a sample of nutrient and biota poor shield lakes there can be significant parasite community compositional differences caused by the local absence of certain major groups of fish and/or invertebrates.

The analysis of yellow perch communities at a very local or fine scale within abiotically similar shield lakes has helped to further quantify the various factors influencing lacustrine parasite faunas discussed by Carney & Dick (2000a). Additionally it has shown that despite the lower nutrient levels and smaller invertebrate and fish communities in these shield lakes relative to larger prairie lakes there remains a highly predictable component to parasite community structure and that biotic, not abiotic factors are the greatest predictors.

CHAPTER 4: Parasite effects on the survival, growth and reproductive potential of
yellow perch in Canadian Shield lakes.

INTRODUCTION

Few studies have focussed on perch and the effects of their diverse parasitofauna (Poole & Dick 1984, Szalai & Dick 1991, Szalai *et al.* 1992) and the impact of parasitism on perch is relatively unknown. Szalai & Dick (1991) and Szalai *et al.* (1992) reported that the nematode, *R. acus*, significantly increased the mortality and reduced growth (as measured by round weight) of yellow perch in a large productive lake. A preliminary study of yellow perch in small nutrient-poor Canadian shield lakes in northwestern Ontario indicated that three parasite species occurring at high prevalences, intensities, and densities appeared to affect perch growth and gonad weight. The objective of the research in this chapter was to evaluate the effect of these parasite species on growth, reproductive potential and survival of yellow perch. The premise was that if parasites influenced certain aspects of perch growth there must be trade-offs between growth, survival and reproduction and this will be more pronounced during the initial stages of sexual maturation. These interactions would likely be best expressed by changes in weight of soma, gonads and storage fat.

METHODS AND MATERIALS

Parasite identification and distribution

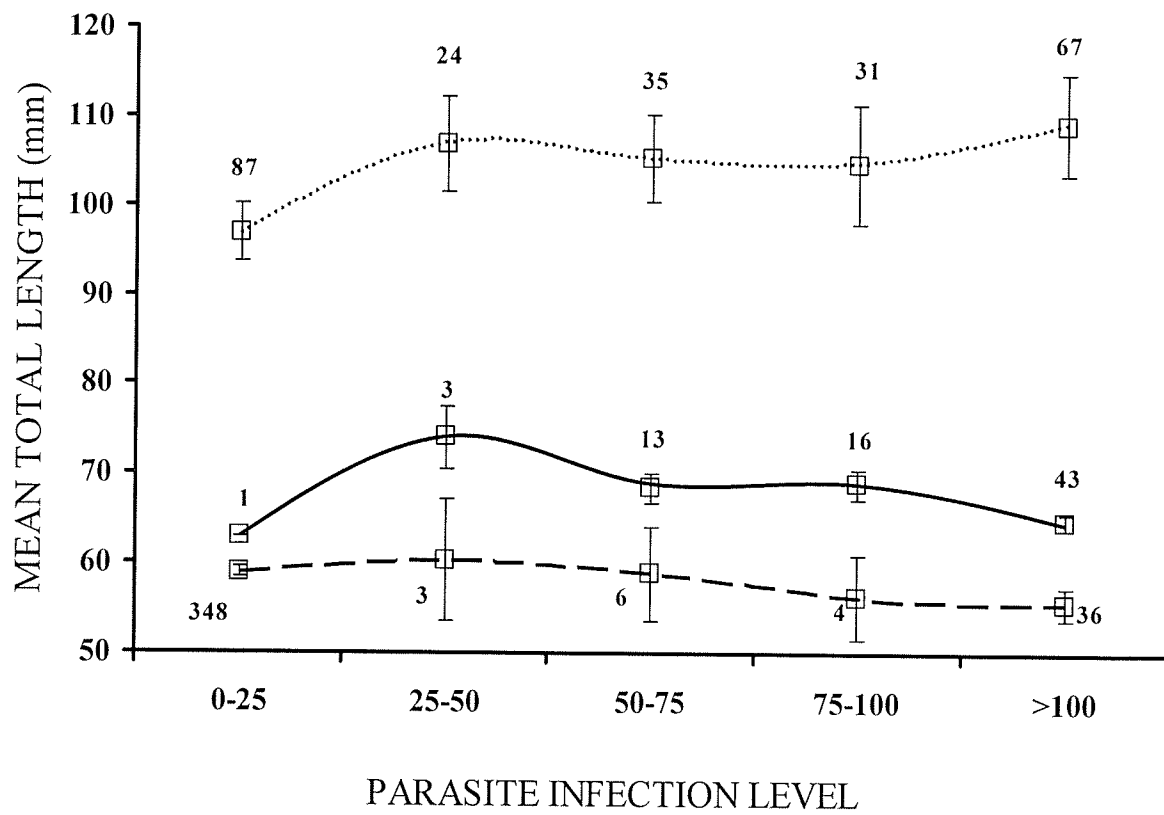
Of the 17 species of parasite reported from yellow perch (Chapter 2) only three species (*Glugea* sp., *A. brevis* and *R. acus*) were considered to have detrimental effects on perch. Identification of the Microsporidea in the genus *Glugea* was based on criteria outlined by Dykova (1995). *Glugea* sp. xenomas were identified from the intestine and visceral fat of perch from all four study lakes but occurred at high prevalence and intensity in fish from L239 and L240. While metacercariae of *A. brevis* were found at

low intensities and densities in perch in all lakes they were found at high intensity/density only in Triangle Lake. *Raphidascaris acus* larvae were located in the liver of perch from L239 and L240 but in high densities only in L240.

Partitioning fish and parasite data for analyses

Since there was no significant sexual size dimorphism in perch age classes < 2+, males and female data from all four lakes for *Glugea* sp. and *A. brevis* infections were pooled for *t*-tests. Figure 4.1 is plot of intensity or density for the three parasite species and perch mean length to determine the point at which length started to decrease. The inflection on graph was the partition point between low and high level infections (for *t*-test analyses). Length of perch infected with *Glugea* sp. and *A. brevis* were similar, but smaller, than perch infected with *R. acus*. Since perch length and *R. acus* densities were correlated decreases in length at different parasite densities were parasite-induced and not artifacts of age-related length trends. The mean length of perch infected with *Glugea* sp. decreased when parasite numbers were >50 xenomas (Fig. 4.1). However, due to small sample sizes for hosts with 50–100 xenomas infections, 100 was chosen as the boundary between high and low intensities. The mean length of perch infected with *A. brevis* decreased when densities >50 cysts/g and again when density was >100 cysts/g (Fig. 4.1). Samples were partitioned into ≤ 100 and > 100 cysts/g groups when numbers of fish were sufficient for statistical analyses but when there were too few fish with > 100 cysts/g groups of ≤ 50 and > 50 cysts/g were used. Since the mean length of perch infected with *R. acus* decreased only between densities of 25-100 larvae/g the midpoint (50 cysts/g) was used as the boundary for comparisons (*t*-tests).

Figure 4.1. Mean total length (\pm 95%C.I.) of yellow perch infected with five different ranges of intensities of *Glugea* sp. xenomas (age 0.25-0.92 perch, dashed line), and densities of *A. brevis*. cysts (age 0.33-0.92 perch, solid line) and *Raphidascaaris acus* cysts (age 1.92-4.25 perch, dotted line). Numbers at each point = sample size.



Statistical analyses

Intensity in this chapter (as per Chapter 2) refers to the number of parasites per infected host (Margolis *et al.* 1982) and density refers to the number of parasites/g infected tissue (Poole & Dick 1984, Szalai & Dick 1991). Ratios and percent values were transformed prior to statistical analyses as described by Sokal & Rohlf (1981). Ratios were square root transformed and percent values were arcsin transformed. Transformed means and confidence intervals (95%C.I.) obtained from statistical analyses were then back transformed for presentation in the results (Sokal & Rohlf 1981). Parasite-induced mortality was suggested when the variance-to-mean ratio (VMR) of parasite intensity or density was highest in the youngest fish and lowest in the oldest fish and when the slope of the regression of log mean vs. log variance (LMLV) was significantly ($P \leq 0.05$) less than 2.0 (Anderson & Gordon 1982, Kennedy 1984). Frequency distributions were plotted for *Glugea* sp. and *A. brevis* infections to determine if the length/weight structure of the host population changed over winter, and if there were changes in parasite intensity/density between the fall and spring. Student's *t*-tests were used for all pairwise comparisons for all three parasite species and $P \leq 0.05$ was considered significant. A sequential Bonferroni technique (Rice 1989) was applied to the *P* values of the *t*-tests, by parasite species to reduce the chance that multiple *t*-tests would produce some falsely significant results.

RESULTS

Glugea sp. infections

The highest mean intensity of *Glugea* sp. xenomas in intestinal walls of perch from L239 and L240 was ~1000 in early autumn of their first year (September, 0.25 year

old samples) (Fig. 4.2a). By the following spring mean intensities had decreased to ~200 xenomas and continued to decrease to <50 xenomas in age 3+ fish. VMRs were, in autumn-collected YOY, ~2500 and decreased to <500 in the oldest fish (Fig. 4.2b). Prevalence of *Glugea* sp. also peaked in autumn collected YOY females (11%) and males (56%). Prevalence of *Glugea* sp. decreased to ~2% in fish >2.92 years. In perch infected with >1000 *Glugea* sp., xenomas fully enveloped the intestine often in two or more layers. Heavily infected perch were typically small, emaciated, had no food in the gut and little or no visceral fat. The slope of the regression of LMLV was significantly <2.0 for females ($\log \text{Var} = 0.82 + 0.28 \log M$, $r^2 = 0.76$, $P = 0.004$) and males ($\log \text{Var} = 0.17 + 0.45 \log M$, $r^2 = 0.95$, $P = 6.43 \cdot 10^{-06}$).

Perch with <50 xenomas decreased significantly in mean size from the fall to spring sample (*t*-test). Total length and somatic weight of fall collected YOY (0.25 and 0.33 yrs) and summer sampled 1+ (1.08 yrs) perch showed that perch with ≥ 100 xenomas were significantly smaller ($P < 0.05$) than fish with ≤ 100 xenomas (Figs. 4.3a, b). Mean percent gonad weight was significantly lower in heavily infected fall collected YOY perch (Fig. 4.4a). Mean percent gonad visceral fat weights of perch with <100 xenomas decreased significantly overwinter (Figs. 4.4a, b). Percent gonad weights were higher and visceral fat weights lower in perch with >100 xenomas following their first winter but these trends were not significant. There were no significant changes in G:F_v ratio.

Figure 4.2. (a) Mean intensity of *Glugea* sp. xenomas infecting female (squares) and male (circles) yellow perch intestines from L239 and L240. (b) Variance:mean ratio (VMR) of *Glugea* sp. xenomas infecting female (squares) and male (circles) yellow perch intestines from L239 and L240. Fish >1.92 years were pooled in both figures due to low prevalence (2% of 197 fish infected).

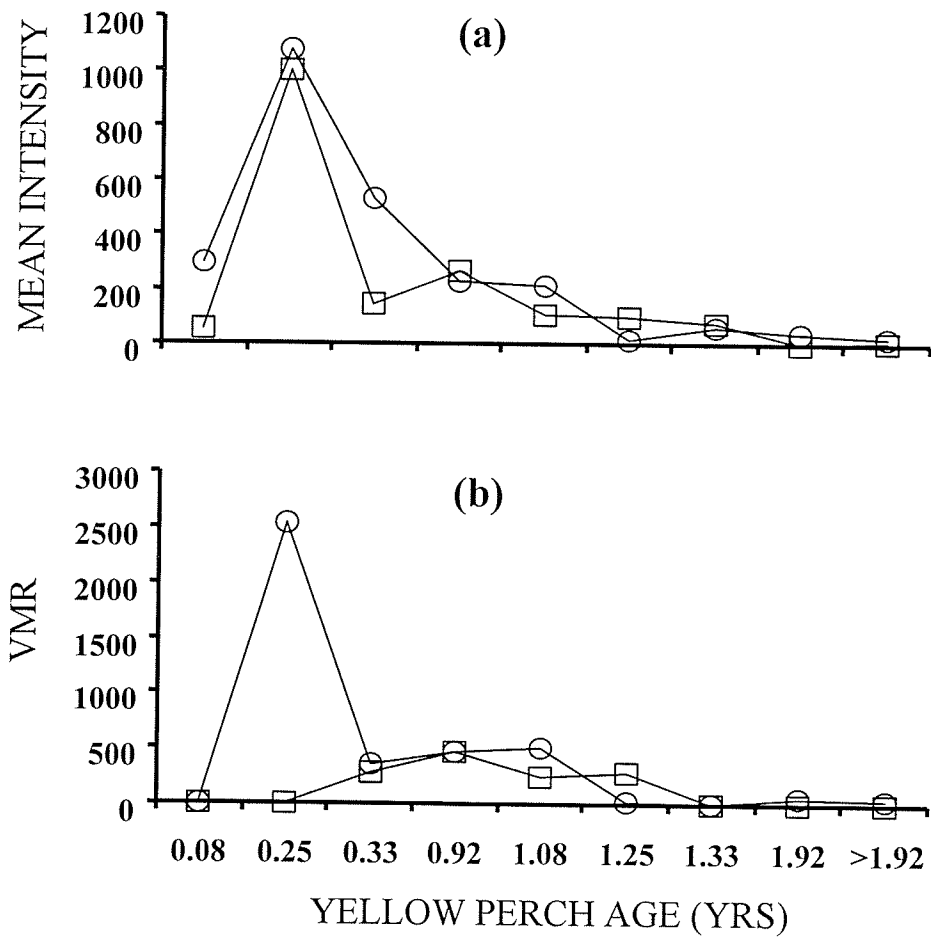
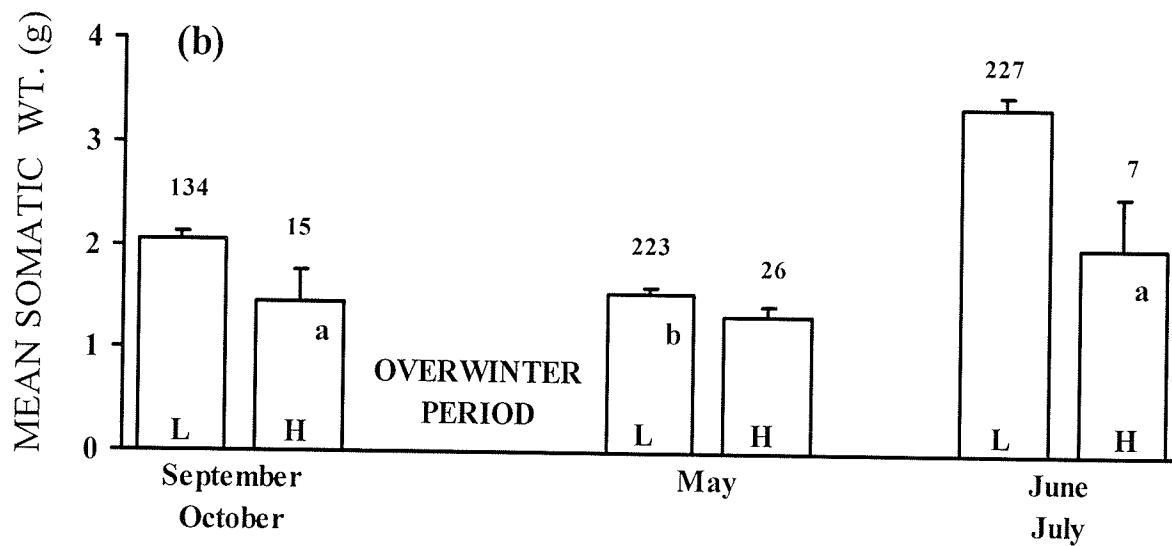
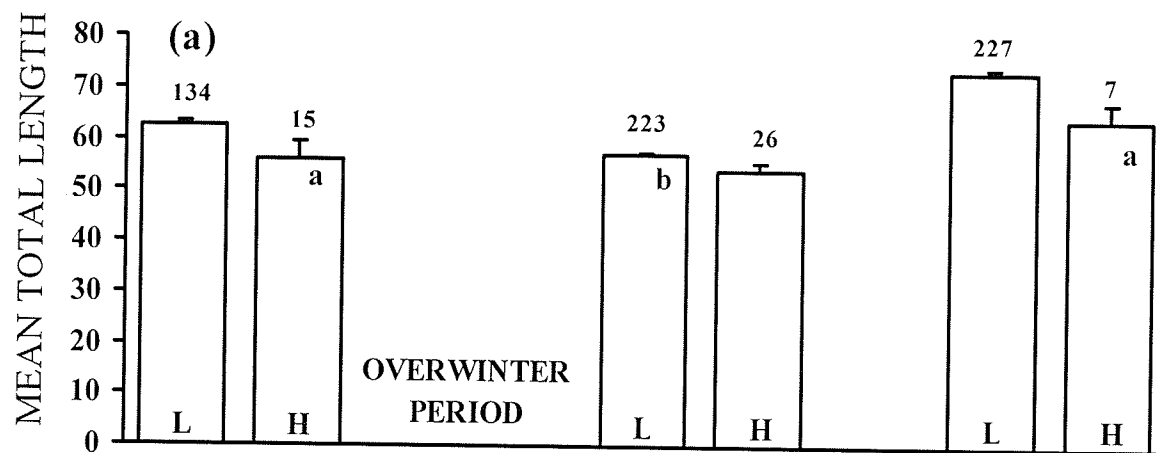
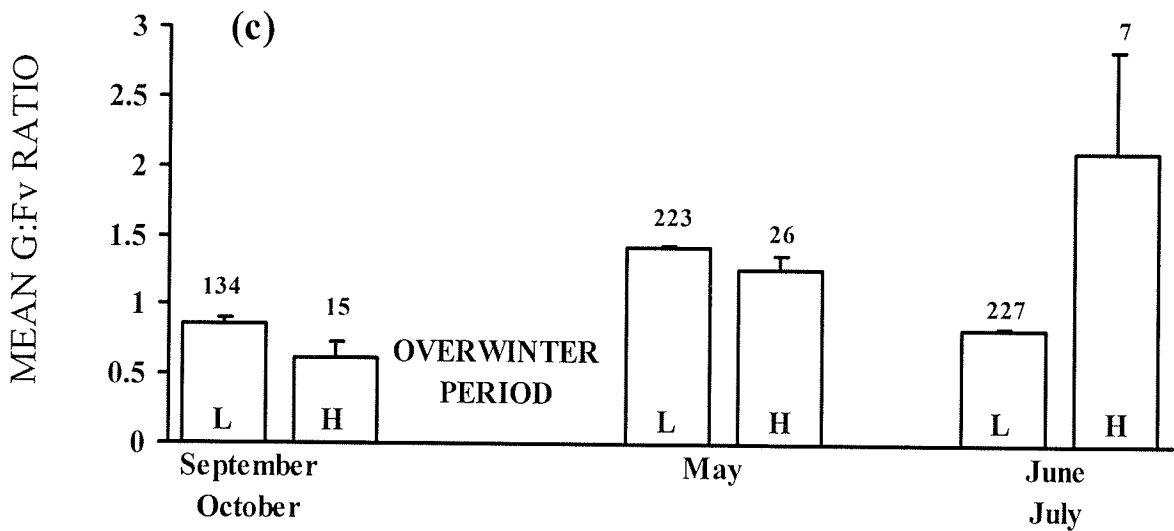
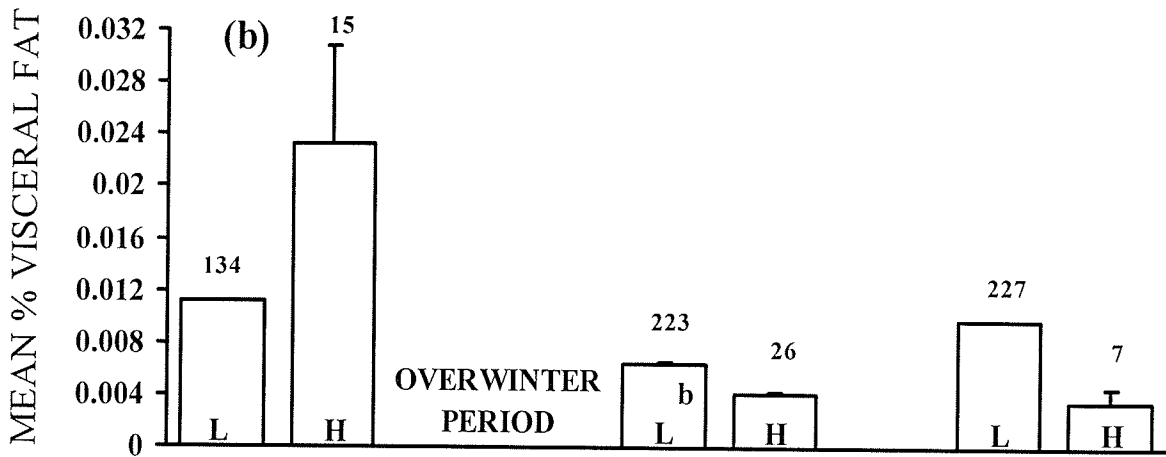
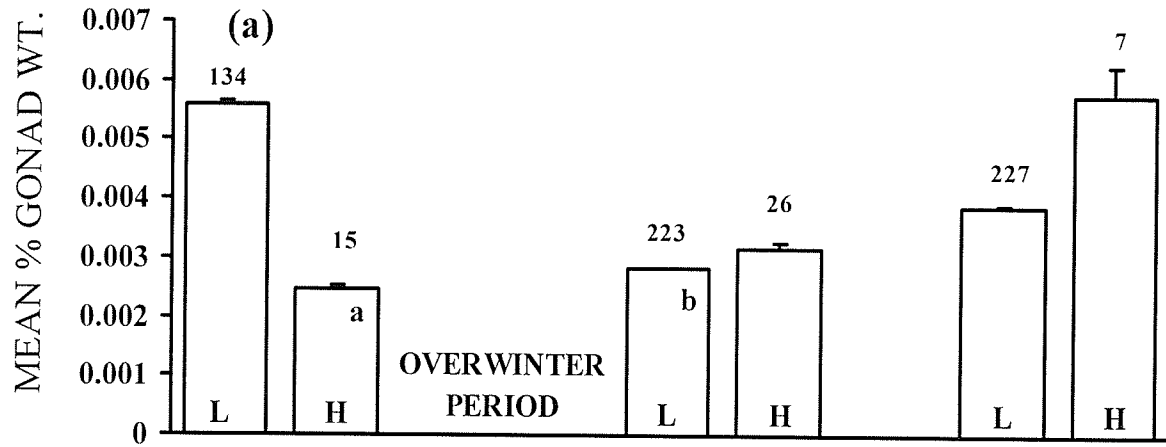


Figure 4.3. Mean total length (a) and somatic weight (b) ($\pm 95\%C.I.$) of 632 young-of-the-year yellow perch from L239 and L240 with low (L) and high (H) intensity *Glugea* sp. infections. Numbers at bar = sample size, a = significant size difference ($P \leq 0.05$) within one sample period b = significant size difference ($P \leq 0.05$) for low levels of parasites (L) following the over-winter period. The ages of fall and spring sampled perch are 0+ and the summer sampled perch are 1+.



YELLOW PERCH SAMPLE SEASON

Figure 4.4. Mean percent gonad weight (a), percent visceral fat (b) and G:F_v ratio (c) (\pm 95%C.I.) of 632 young-of-the-year L239 and L240 yellow perch with low (L) and high (H) intensity *Glugea* sp. infections. Numbers, a, b are as designated for Fig. 4.3.



YELLOW PERCH SAMPLE SEASON

Comparisons of frequency distributions of total length of yellow perch (Fig. 4.5a) revealed that hosts <50mm were essentially absent in the infected population in spring but not the uninfected population (Fig.4.5b).

***Apophallus brevis* infections**

Prevalence of *A. brevis* was 100% in both sexes and all age classes of fish in Triangle Lake. Density in muscle peaked in age 0.92 males (~120 cysts/g) and 0.33 females (~110 cysts/g) and decreased to <10 cysts/g in both sexes >2.92 years (Fig. 4.6a). VMR peaked in age 0.92 males and 0.33 females with V values of ~20 and 43, respectively (Fig. 4.6b). None of age 0.92 perch had <50 cysts/g and few perch >0.92 years old had >50 cysts/g. A plot of *A. brevis* cyst densities and age of perch showed that densities peaked in young, small fish but were lowest in old, large fish (Fig. 4.6b). The regression slope of LMLV was significantly <2.0 for females ($\log V = 0.3 + 0.47\log M$, $r^2 = 0.82$, $P = 5.55 \cdot 10^{-05}$) but not significantly <2.0 for males ($\log V = 0.86 + 0.28\log M$, $r^2 = 0.40$, $P = 0.051$).

Somatic weight and length of perch (ages 0.92 and 1.92) with >100/g and >50/g, respectively, of *A. brevis* were significantly reduced compared with perch with <100/g and <50/g, respectively (Figs. 4.7a and b). Length of age 1.92 perch of both sexes decreased by ~10 mm when *A. brevis* density was >50/g. Percent visceral fat, percent gonad weight, and G:F_v ratio did not vary significantly with increasing parasite level (Figs. 4.8 a, b and c). However, 0+ May perch with heavy *A. brevis* infections showed decreased gonad weight while all other age classes showed increased gonad weight with increased parasite density. *T*-tests revealed that the difference, although not significant after Bonferroni adjustment, was a result of differences in male gonad weights only.

Figure 4.5. Total length frequency distribution of pre-winter and post-winter YOY yellow perch (September, October and May samples). (a) Combined sample of infected and uninfected YOY yellow perch from the sample periods. (b) Uninfected YOY yellow perch from the sample periods.

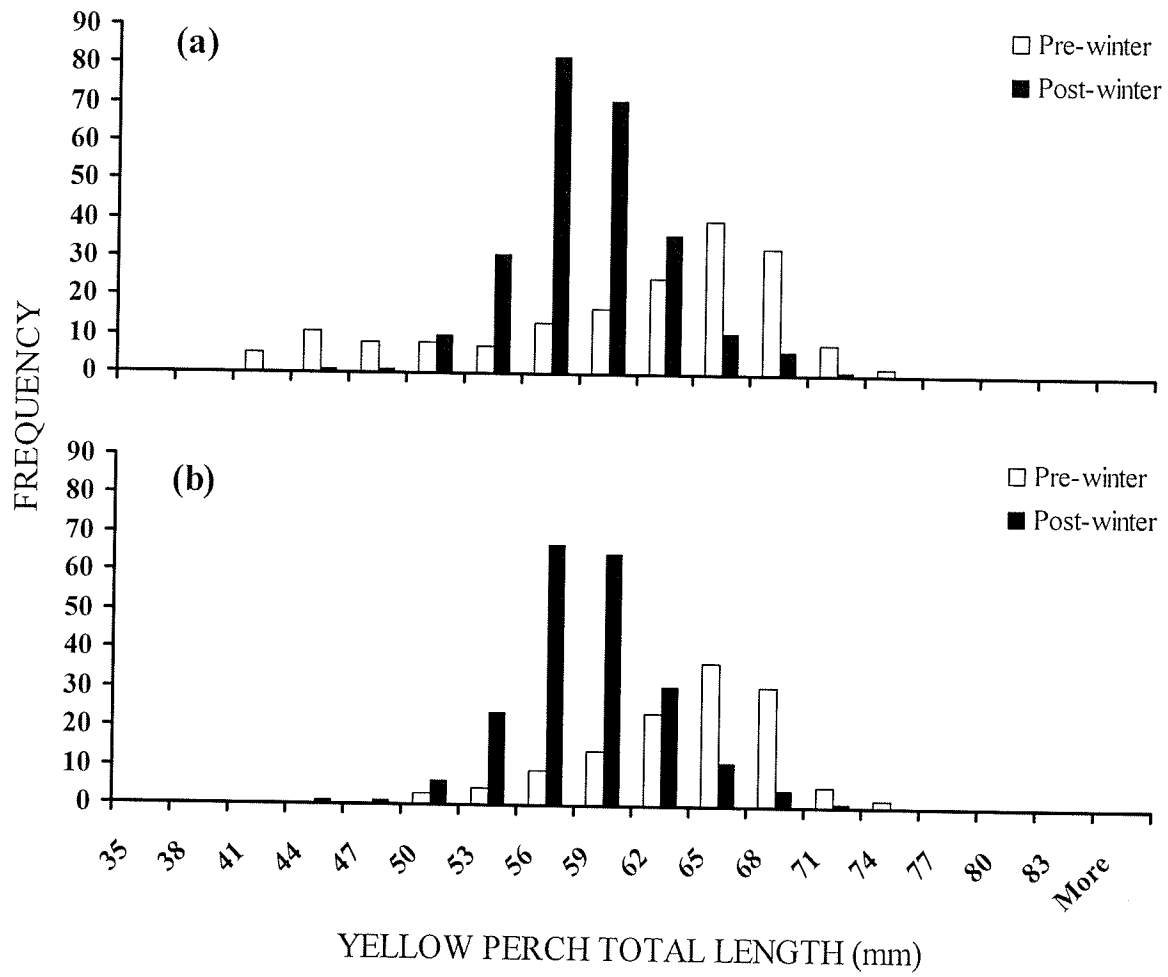
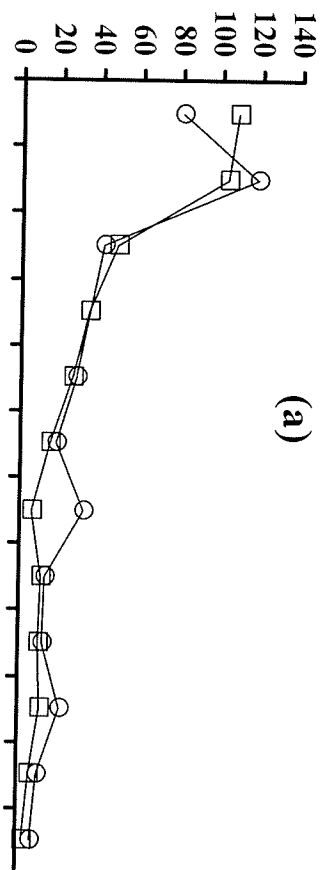


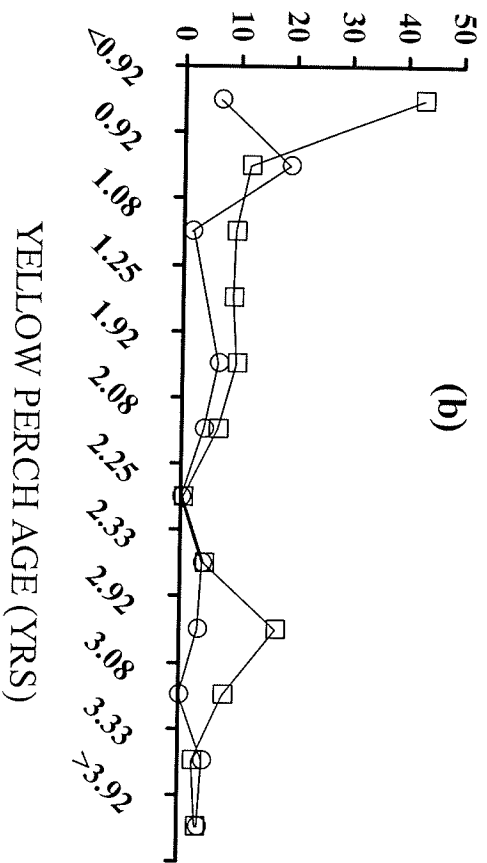
Figure 4.6. (a) Density (cysts/g muscle) of *Apophallus brevis* cysts infecting female (squares) and male (circles) yellow perch from Triangle Lake. (b) Variance:mean ratio (VMR) of *A. brevis* cysts infecting female (squares) and male (circles) yellow perch from Triangle Lake. Fish >3.92 years were pooled in both figures due to small sample sizes and low prevalences at older age classes.

PARASITE DENSITY



(a)

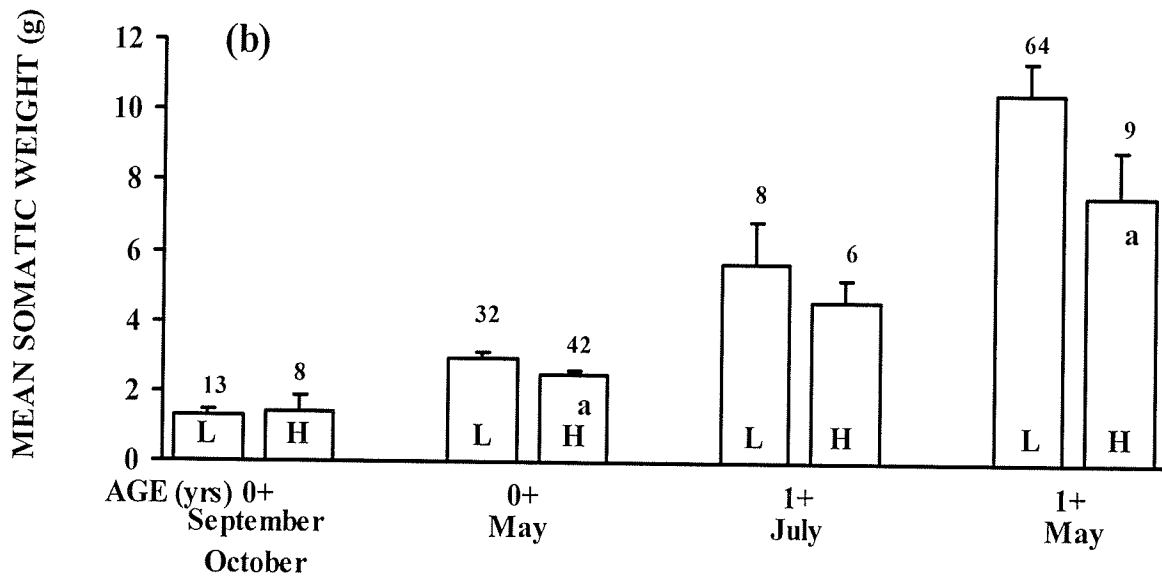
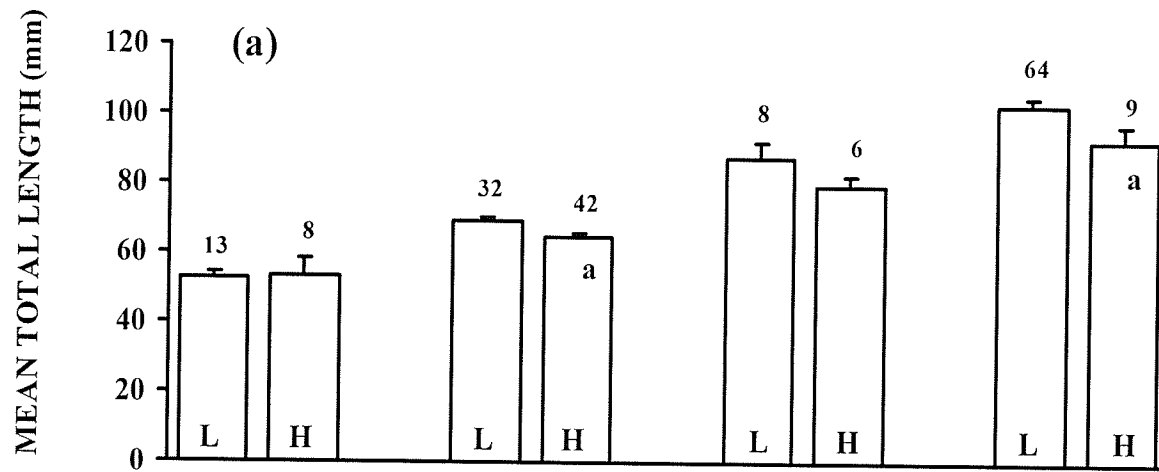
VMR



(b)

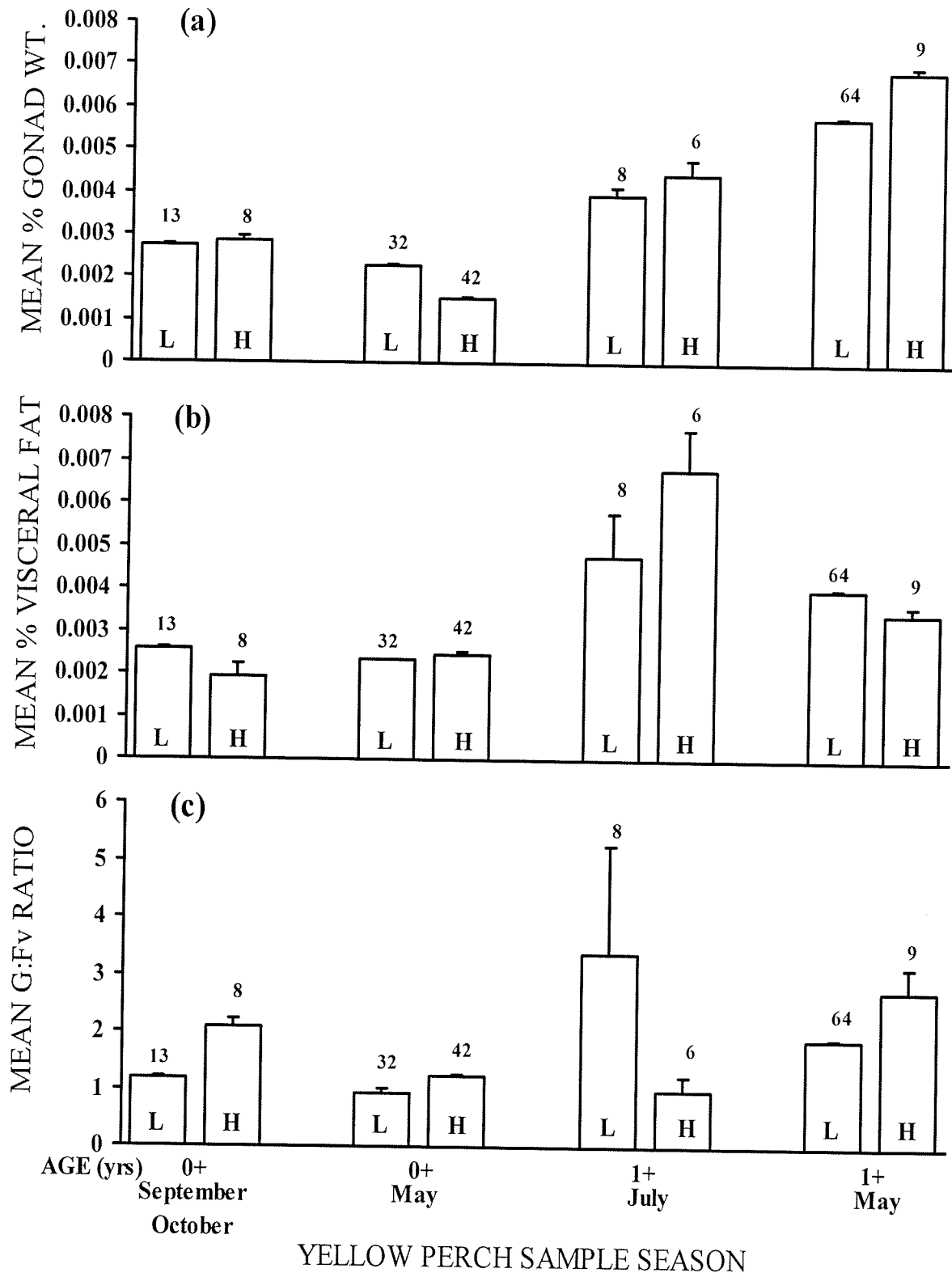
YELLOW PERCH AGE (YRS)

Figure 4.7. Mean total length (a) and somatic weight (b) (\pm 95%C.I.) of 182 Triangle Lake yellow perch with low (L) and high (H) density *Apophallus brevis* infections. Numbers above each bar = sample size, a = significant size difference ($P \leq 0.05$) within an age class.



YELLOW PERCH SAMPLE SEASON

Figure 4.8. Mean gonad weight (a), percent visceral fat (b) and G:F_v ratio (c) (\pm 95%C.I.) of 182 Triangle Lake yellow perch with low (L) and high (H) density *Apophallus brevis* infections. Numbers and a as designated in Fig. 4.7.



***Raphidascaris acus* infections**

Density of *R. acus* cysts in the liver of male and female yellow perch from L240 peaked at age 0.92 (75 cysts/g) and again at age 1.92 (100 cysts/g) (Fig. 4.9a). Density remained between 75 and 100 cysts/g liver in older males and decreased in older females (Fig. 4.9a). The greatest density, 268 cysts/g liver, was found in a 7.25 year-old male. The VMR for both sexes varied with host age and particularly large fluctuations were found in age 2.33 and 3.08 males and age 4.08 females (Fig. 4.9b). Large fluctuations in VMR in older perch were the result of individual fish with >200 cysts/g and small age class sample sizes (Fig. 4.9b). Prevalences increased from 30% at age 0.92 to 100% by age 3.92 for both sexes. The regression equations LMLV for females ($\log V = 1.09 + 0.24\log M$, $r^2 = 0.83$, $P = 5.54 \cdot 10^{-06}$) and males ($\log V = 1.05 + 0.24\log M$, $r^2 = 0.78$, $P = 0.0003$) were significantly <2.0. The mean intensities of *R. acus* cysts in female livers were similar to the intensities in male livers in each age class (Fig. 4.10). The density of cysts was higher in males than in females from ages 1 to 3 and higher in YOY and 4+ females than in males of the same age (Fig. 4.10).

Only the percent visceral fat weight and G:F_v ratio differed significantly between perch with low and high *R. acus* densities (*t*-test) (Fig. 4.11). The shape of the curve of percent visceral fat vs. age in all perch was similar between <50 and >50cysts/g with peaks at age 1+. However, percent weight in perch <2 years old was higher in fish with <50 cysts/g than those with >50cysts/g. The growth rates were similar in age $\geq 2+$ perch with <50 and >50 cysts/g (Fig. 4.11). The G:F_v ratio of female perch increased initially at both <50 and >50 cysts/g but at <50 cysts/g growth plateaued at age 2+ while the G:F_v ratio in perch continued to increase with high densities (>50cysts/g) of *R. acus* (Fig.

Figure 4.9. (a) Density (cysts/g liver) of *Raphidascaris acus* cysts infecting female (squares) and male (circles) yellow perch from L240. (b) Variance:mean ratio (VMR) of *Raphidascaris acus* cysts infecting female (squares) and male (circles) yellow perch from L240.

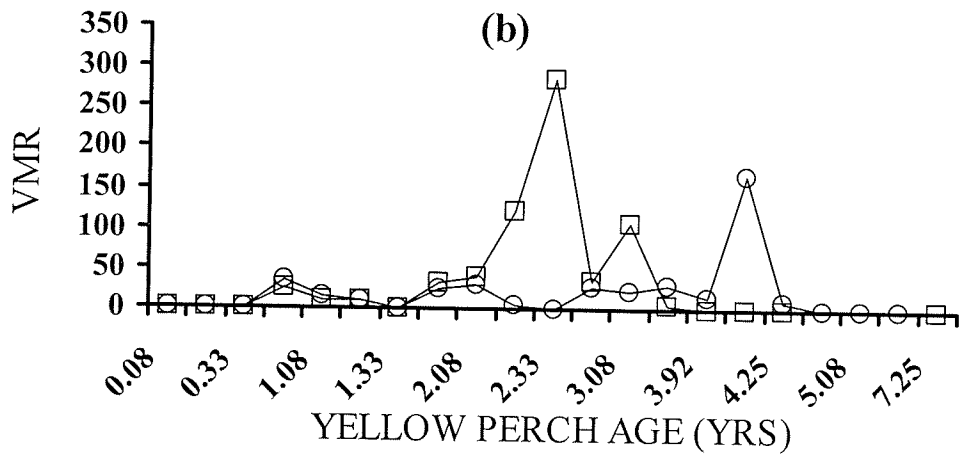
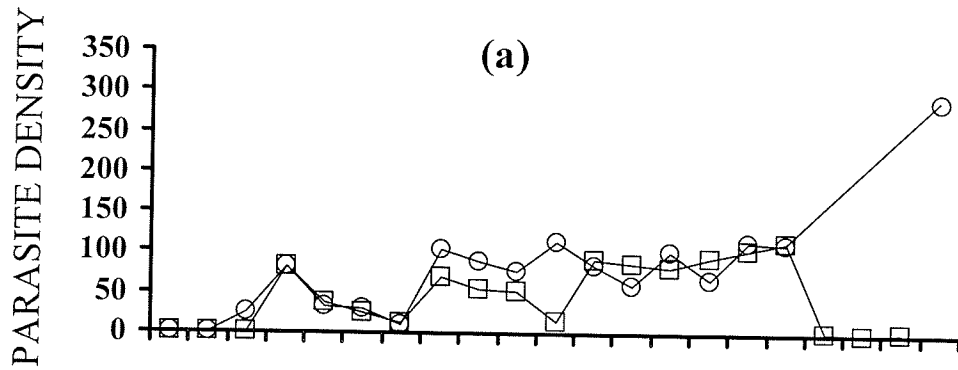


Figure 4.10. Density (squares) and mean intensity (circles) (\pm 95% C.I.) of *Raphidascaris acus* cysts in the livers of different age classes of female (solid line) and male (dashed line) yellow perch from L240. The upper x-axis values = yellow perch age classes, the lower values = male and female sample sizes (n).

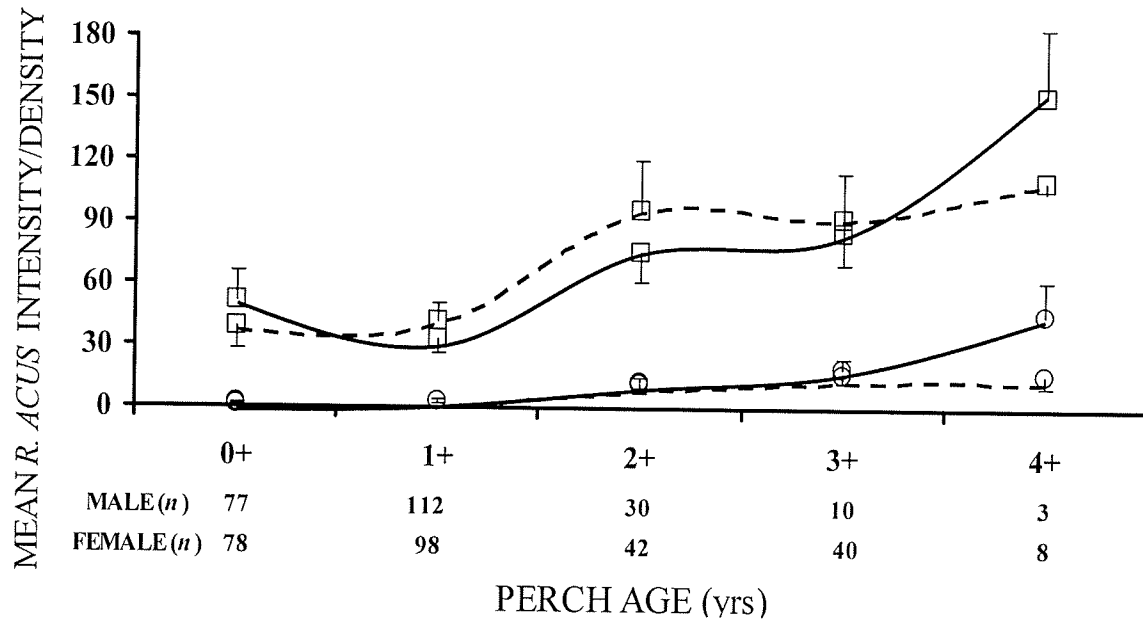
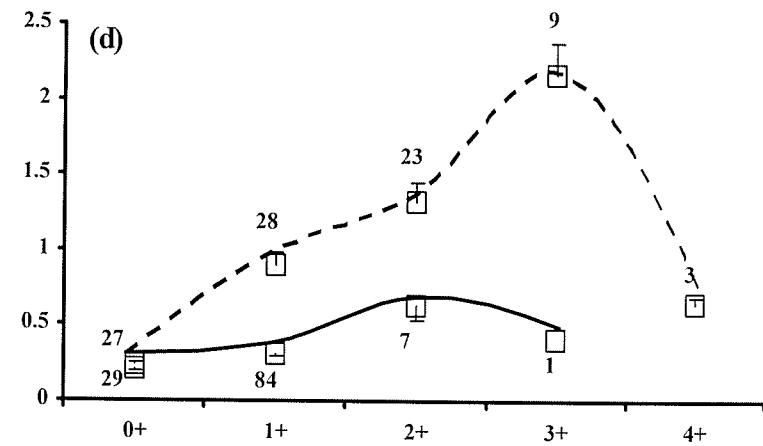
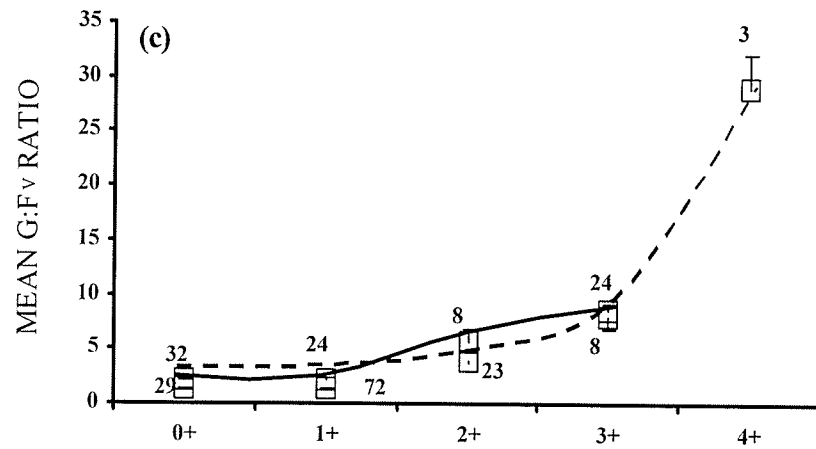
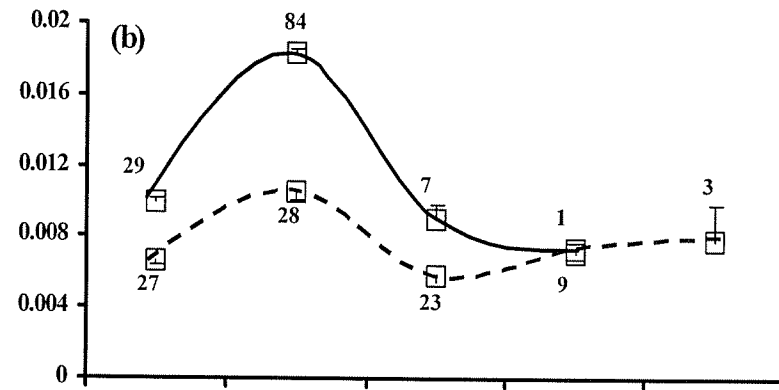
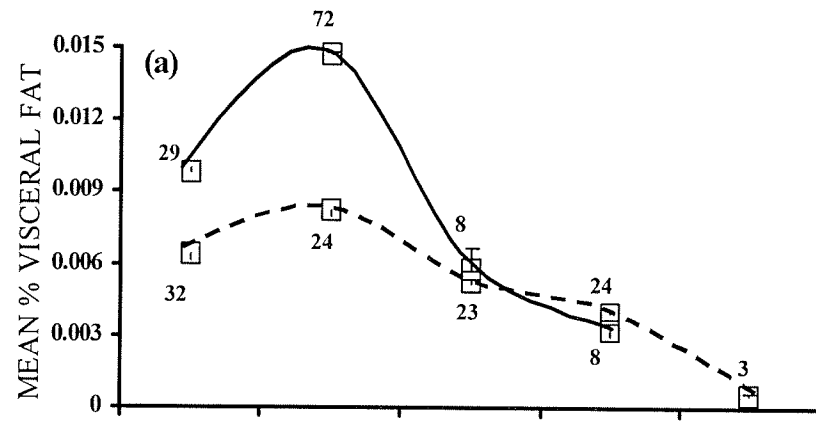


Figure 4.11. Mean visceral fat weight and gonad:visceral fat ratio (\pm 95% C.I.) of 249 female, (a) and (c) respectively, and 211 male L240 yellow perch (b) and (d) respectively, at each age class (0+ to 4+) infected with low (<50 cysts/g, solid line) and high (\geq 50 cysts/g, dashed line) densities of *Raphidascaris acus* cysts in the liver. Numbers at each point = sample size.



YELLOW PERCH AGE

4.11). The G:F_v ratio of male perch was higher in fish with >50 cysts/g for all but the 0+ age class (Fig. 4.11).

Mean length and somatic weight of female and male perch usually increased when *R. acus* infections were >50 cysts/g but never significantly (Table 4.1). Percent female visceral fat decreased with parasite density until age 3+ but a significant decrease occurred only at age 1+. Percent female gonad weight showed no significant changes from low to high infections. The G:F_v ratio was higher in females with >50 cysts/g for all but age 2+ fish, but the difference was never significant. Percent visceral fat in males was insignificantly higher in fish with *R. acus* densities <50 cysts/g (Table 4.1). Gonad weight of males decreased significantly with parasite density only in YOY perch. The G:F_v ratio of males increased significantly with increased parasite densities in age 1+ perch and insignificantly in age 2+ fish.

DISCUSSION

The data show that the survival and growth of yellow perch were affected by three species of parasites in different ways. Overall growth is a complex process, especially in north temperate regions and there are interactions among stored energy, sexual maturation and somatic growth. Furthermore, since each parasite infected different organs of the host their effects on the host differed. Although *Glugea* sp. xenomas and *R. acus* larvae were recovered from L240 yellow perch they are analyzed and discussed separately because of the lack of significant overlap between these parasites in the same system. High *Glugea* sp. intensities were found in YOY but were rare in older perch, while high *R. acus* intensities were not common until age 2+. Perhaps a YOY perch that survived a *Glugea* sp. infection was more susceptible to *R. acus* but this cannot be

Table 4.1. Student's *t*-test values for five growth parameters of female and male yellow perch from L240 infected with *Raphidascaris acus* cysts in the liver. All fish have low and high densities of <50 cysts and \geq 50 cysts respectively. Underlined means are significantly different from other means for the same parameter for that sex at the $P = 0.05$ significance level.

		Mean Total length (mm)		Mean Somatic weight (g)		Mean Visceral fat weight (% total weight)		Mean Gonad weight (% total weight)		Mean G:F _v ratio (+ 95% C.I.)		
		(+ 95% C.I.)		(+ 95% C.I.)		(+ 95% C.I.)		(+ 95% C.I.)				
AGE (yrs)	N ^a	Low	High	Low	High	Low	High	Low	High	Low	High	
FEMALES	0+	29/32	55.7 (2.03)	56.4 (1.38)	1.49 (0.15)	1.52 (0.16)	0.01 (1.5x10 ⁻⁴)	6.4x10 ⁻³ (2.6x10 ⁻⁴)	0.33 (3.0x10 ⁻³)	0.36 (4.0x10 ⁻³)	1.30 (0.01)	2.06 (0.05)
	1+	73/25 ^b	79.7 (2.27)	77.2 (4.43)	4.52 (0.39)	4.12 (0.76)	<u>1.5x10⁻²</u> (1.0x10 ⁻⁴)	<u>8.3x10⁻³</u> (3.3x10 ⁻³)	0.60 (8.6x10 ⁻³)	0.65 (0.02)	1.43 (0.01)	2.19 (0.07)
	2+	13/29 ^c	105 (4.53)	106 (3.42)	10.6 (1.40)	10.9 (1.04)	5.8x10 ⁻³ (8.7x10 ⁻⁴)	5.3x10 ⁻³ (1.2x10 ⁻⁴)	0.80 (0.09)	0.88 (0.03)	5.59 (1.25)	3.84 (0.12)

Table 4.1. Continued.

AGE (yrs)	N ^a	Mean Total length (mm) (± 95% C.I.)		Mean Somatic weight (g) (± 95% C.I.)		Mean Visceral fat weight (% total weight) (± 95% C.I.)		Mean Gonad weight (% total weight) (± 95% C.I.)		Mean G:F _v ratio (± 95% C.I.)		
		Low	High	Low	High	Low	High	Low	High	Low	High	
FEMALES	3+	9/31 ^d	125	127	18.7	19.3	3.2x10 ⁻³	3.9x10 ⁻³	1.00	0.99	8.06	8.62
			(2.79)	(5.49)	(1.55)	(2.87)	(2.4x10 ⁻⁴)	(1.6x10 ⁻⁴)	(0.15)	(0.10)	(1.27)	(0.55)
MALES	0+	29/27	58.4	56.2	1.65	1.52	0.01	6.6x10 ⁻³	<u>1.5x10⁻³</u>	<u>9.2x10⁻⁴</u>	0.21	0.23
			(2.26)	(1.74)	(0.20)	(0.16)	(1.8x10 ⁻⁴)	(1.9x10 ⁻⁴)	(1.7x10 ⁻⁵)	(5.1x10 ⁻⁶)	(0.01)	(0.01)
MALES	1+	84/28	76.7	80.9	3.89	4.59	0.02	0.01	4.4x10 ⁻³	4.8 x10 ⁻³	<u>0.31</u>	<u>0.90</u>
			(1.53)	(3.19)	(0.23)	(0.52)	(1.9x10 ⁻⁴)	(3.9x10 ⁻⁴)	(1.2x10 ⁻⁴)	(1.8x10 ⁻⁴)	(0.01)	(0.08)

Table 4.1. Continued.

AGE (yrs)	N ^a	Mean Total length (mm)		Mean Somatic weight (g)		Mean Visceral fat weight (% total weight)		Mean Gonad weight (% total weight)		Mean G:F _V ratio (± 95% C.I.)		
		Low	High	Low	High	Low	High	Low	High	Low	High	
MALES	2+	7/23 ^e	96.6 (5.56)	97.7 (3.66)	8.35 (1.50)	8.45 (0.92)	9.0x10 ⁻² (8.2x10 ⁻⁴)	5.7 x10 ⁻³ (2.6x10 ⁻⁴)	4.6x10 ⁻² (6.1x10 ⁻⁴)	5.7 x10 ⁻³ (2.7x10 ⁻⁴)	0.63 (0.09)	1.32 (0.13)

^a Total sample size in low/high infections.

^b Sample size for visceral fat and G:F_V ratio t-tests is 72/24.

^c Sample size for visceral fat and G:F_V ratio t-tests is 8/23.

^d Sample size for visceral fat and G:F_V ratio t-tests is 8/24.

^e Sample size for visceral fat and G:F_V ratio t-tests is 7/21.

quantified, as there is no way to identify which older perch have had *Glugea* sp. infections.

Relationship among visceral fat and weight of gonads and soma

The lowest somatic weight and percent visceral fat were found YOY perch infected with high numbers of *Glugea* sp. Declines in somatic tissue weight and percent visceral fat were inversely related to intensity of *Glugea* sp. Perhaps nutrient uptake along the intestine is impaired since the heaviest infections had one or more layers of xenomas completely enveloping the intestinal wall. At intensities >500 xenomas, *Glugea* sp. occupied visceral fat tissue and may have impaired fat deposition and perch with ~1000 xenomas had little or no fat remaining. In contrast, the percent weight of female gonads decreased marginally with increasing *Glugea* sp. numbers. This was not surprising given that most of the fish with high numbers of xenomas were YOY with minimal energy requirements for gonad development. Female perch with high numbers of xenomas had an increased G:F_v ratio, which was probably attributed to a loss of visceral fat without a corresponding loss of gonad tissue. Heavy infection could delay sexual maturation and may cause overwinter mortality (see discussion on mortality). Sample sizes of mature females with high numbers of xenomas were small so percent gonad weights cannot be compared statistically although the percent gonad weights of the few individuals with high infections were smaller. We cannot rule out long lasting effects of parasitism resulting from stunting and late maturation of the over-wintering survivors since male yellow perch mature as early as one year of age in these lakes and the decrease in percent gonad weight is significantly greater than in females. At age 0.33 (October sample) 28% of YOY male perch with low infection intensities and 0% of male

YOY with high infection levels were maturing. The G:F_v fat ratio also decreased in males with high infections suggesting that proportionally more energy is used for fat reserves at the end of the first summer. High numbers of xenomas decreased fecundity and delayed maturation in young males. Fecundity of females was not affected but maturation may have been delayed.

Apophallus brevis had a significant effect on the growth of yellow perch with the difference between total length and weight of uninfected and heavily infected fish being greatest in perch >1.08 years. Slower growth may be due to chronic high-density exposure to this parasite during the first few years of life but the mechanism of growth reduction is more obscure. This parasite induces the formation of a mineralized ossicle or cyst (Taylor *et al.* 1994) and perhaps production of high numbers of cysts are a drain on the perch's calcium reserves and result in reduced bone deposition and growth. This might be an important factor in the waters of Canadian Shield lakes that have calcium concentrations ranging from 0.82-2.15 mg/l (Armstrong & Schindler 1971). The effect of *A. brevis* on older 0+ male gonads is not surprising as these perch are reaching sexual maturity. However, the increased gonad weight observed in older fish (females, in particular) with heavy infections is more difficult to explain. It is possible that calcium metabolism is affected by increased parasite density thus affecting gonad development.

Perch infected with *R. acus* from the ELA system did not show a reduction in overall growth differing from perch in Dauphin Lake, Manitoba studied by Szalai & Dick (1991) and Szalai *et al.* (1992). Reasons for this difference may relate to relative parasite densities and the types of aquatic systems. There were insufficient numbers of perch with >100 cysts/g in the present study to permit detection of stunting similar to that

observed in the Dauphin Lake perch (Szalai & Dick 1991, Szalai *et al.* 1992). However, there was stunting in the few ELA perch with *R. acus* densities >100 cysts/g and especially in those with >200 cysts/g. Habitat may also have an effect as Dauphin Lake is a larger, more productive lake and has larger, faster growing perch than those found in the Canadian Shield lakes.

The G:F_v ratio decreased in 2+ females at a time when most females are maturing and require large amounts of energy for gonad maturation. These females, if they have high densities of *R. acus*, are unable to divert adequate resources from soma growth to meet these needs. Similarly, males showed the same pattern of resource allocation for heavy infections of all three parasites. Reduced gonad growth appears to be most pronounced in YOY males and in the oldest females. Percent weights of gonads, visceral fat and soma were not separated from total weight in the Dauphin Lake study (Szalai & Dick 1991) so it is uncertain if there was a greater effect of parasitism on gonad growth or on somatic tissue, particularly visceral fat deposition. Szalai *et al.* (1989) found that the larval cestode *Ligula intestinalis* caused parasitic castration in spottail shiners (*Notropis hudsonius*) and that there was negative correlation with parasite biomass and fish size. Preliminary results from blacknose shiners infected with *L. intestinalis* in Triangle Lake show a similar effect of this parasite on gonad development (Appendix IV).

Differences in the effects of density of *R. acus* infections on female and male perch showed that host sex and *R. acus* are linked and that parasite numbers and organ weight influence density effects. In contrast, high parasite intensities had no effect on perch growth and provided no linkage with host sex due to variations in liver weight and

the relative weight of other organs, such as gonads, in individual perch. The differences in percent gonad weight of perch with low and high densities of *R. acus* were most pronounced in males with the highest mean densities. Heavily infected male perch from L240 were smaller than females at all age classes >YOY, and invertebrate benthos since only <10% of older males switched to fish and crayfish (Chapter 2). On the other hand, >10% of females are piscivorous by age 2+ and almost 30% by age 4+ (Chapter 2) while most of the remaining females consumed crayfish and large Ephemeroptera. As a consequence exposure of females to potential second intermediate invertebrate hosts was less frequent and of shorter duration than for the smaller males. High densities of *R. acus* in the livers of male perch may have prevented the deposition of visceral fat reducing their ability to survive over winter. In this case, host sex, trophic status and parasite numbers are closely linked.

Mortality

There was statistical evidence for parasite induced mortality of perch that were infected with *Glugea* sp. and *A. brevis* but not for those infected with *R. acus*. This evidence included modified age-density peaks, decreasing VMRs, slopes of <2.0 for LMLV and skewed host length and weight frequency distributions. The results agree, in general, with reports by Anderson and Gordon (1982), Gordon and Rau (1982), and Kennedy (1984) but there are some differences. This study shows that mortality and parasite numbers are correlated and may relate to host behaviour. For example, the much higher prevalences and mean intensities for *Glugea* sp. in YOY may be due to the tendency of young perch to school making transmission among individuals easier (Dykova 1995).

Anderson and Gordon (1982) discussed conditions that imply parasite-induced mortality where none is occurring despite statistical evidence to the contrary. These conditions include age-related differences in infection rates, acquired immunity, parasites with shorter life spans than the host, mortality of a parasite greater than recruitment in older hosts which decreases variability of intensity, increased susceptibility to predation due to infection and different growth rates or susceptibilities of fish with different genotypes within the same system. *Glugea* sp. demonstrated age-related differences in infection rates and, although *A. brevis* density was highest in younger perch, the intensity of this parasite showed less variation. Therefore, age-related differences in infection rates may be implying parasite-induced mortality in perch infected with *Glugea* sp. but not necessarily in those infected with *A. brevis*. Acquired immunity was not likely a factor in *A. brevis* infections as there was no evidence of any necrosed parasite cysts. The potential role of acquired immunity in *Glugea* sp. infections is less clear, however, this parasite was largely absent in older hosts and there was no evidence to suggest that the absence was the result of a successful host immune system reaction. Longevity of *Glugea* sp. and *A. brevis* are not well understood, although *A. brevis* can likely persist encysted in muscle tissue for many years. The possibility of parasite life spans relative to the host perch life span suggesting false parasite-induced mortality cannot be ruled out. In addition, since host genotypes are not known there may be an effect of differential susceptibility to parasites on host mortality. Increased susceptibility to predation as a result of parasite infection is likely an indirect influence on perch mortality in these lakes and will be discussed in detail below.

Direct mortality caused by *Glugea* sp. is likely important as the number of xenomas/fish reported in this chapter are much higher than the 30 xenomas reported to cause mortality in perch, *Perca fluviatilis* L., in Europe (Dykova 1995). Furthermore, perch with high parasite levels were smaller and had little or no visceral fat. The former could make them more susceptible to predation and the latter to over-wintering mortality due to lack of sufficient energy reserves. Predation of YOY by larger perch was observed in L239 and L240 and some of the identifiable prey were infected with *Glugea* sp. Over-winter mortality has been observed in juvenile bluegill (*Lepomis macrochirus*) infected with blackspot (*Uvulifer ambloplitis*) as a result of lipid depletion (Lemly and Esch 1984).

The log-log slope for male yellow perch infected with *A. brevis* in Triangle Lake was not significant but is <2.0 . This non-significance may be the result of a smaller sample of male perch (114 versus 285 females) including several male age classes with few or no fish. Perch in these systems live to a maximum of 9 years, but $<1\%$ of the entire sample was >5 years old. Perhaps older perch in some systems spend less time in habitats with abundant first intermediate hosts (shallow bays with abundant macrophytes) despite being regularly recovered from the same areas as younger fish in Triangle Lake. Increased susceptibility to predation due to infection could influence mortality in this host-parasite system. However, the source of this predation in Triangle Lake was most likely birds since large perch feed almost exclusively on cyprinids (Chapter 2). The importance of *A. brevis* in reducing fish size, therefore increasing perch susceptibility to predation, is less important since gulls are less size selective than fish. Decreased nutritional reserves may be a more important cause of over-wintering mortality in perch.

To summarize, evidence of the importance of *A. brevis* in mortality of perch is equivocal but the effects of the parasite on growth and energy partitioning are clear.

Increased mortality as a result of *R. acus* infections could not be confirmed in perch from L240. Mortality was detected in perch in Dauphin Lake (Szalai & Dick 1991, Szalai *et al.* 1992), but the mean ages of perch were greater and few 0+ and 1+ fish were obtained, and perch had higher densities of *R. acus* in their livers than the perch in this study. Fewer than 10% of all perch caught in the current study had >100 cysts/g of liver and only 1% had >200 cysts/g. Perch with >200 cysts/g were as much as 3cm shorter than uninfected or lightly infected fish of the same age, but the sample size was too small to permit statistical analyses of the effects of such high parasite densities on perch growth and mortality. Densities of *R. acus* were highest in older perch, in contrast with higher intensities of *A. brevis* or *Glugea* sp. in younger perch. Perhaps the higher numbers of *R. acus* in older and larger female perch (Fig. 8) are indicative of lateral transfer of third stage juveniles through piscivory. Interestingly, cannibalism is an important source of mortality in L239 and L240 where >30% of 2+ female perch fed on YOY perch (Chapter 2).

It is apparent that three parasite species influenced the growth, energy partitioning and survival of yellow perch in energy poor Canadian Shield lakes in north temperate regions. It is also evident that the effects of parasitism are expressed at different ages of yellow perch and that this relates to over-wintering energy reserves and the time of sexual maturation. Clearly the host-parasite interaction is complex and studies evaluating trophic feeding patterns of fish should account for the manner in which parasites may alter host size within and among year classes and sexes of fish.

CHAPTER 5: Parasites and Stable Isotopes as Predictors of Yellow Perch Trophic Status.

INTRODUCTION

Several experiments have shown that diet is clearly the primary determinant of the isotopic ratio of an animal where the C in animal tissue is isotopically similar to the diet (C may be about 1‰ heavier than the diet in some cases) and N averages 3-5‰ heavier than the diet (Minigawa & Wada 1984). For example, broad whitefish that were switched from a 11.4‰ S, -21.4‰ C, 7.8‰ N diet to a -6.3‰ S, -26.3‰ C, 9.7‰ N diet had an isotopic composition that approached that of the second diet with the caveat that the fish were somewhat enriched in ¹⁵N (3.8‰) (Hesslein *et al.* 1993). However, ¹⁵N is not very useful for determining the specific preferred prey of an animal only the general trophic level upon which it is feeding. Fish stomach contents are only a snapshot of the previous day or less and may not accurately reflect an animal's true trophic position. Parasites are useful tools for predicting specific prey consumed over longer periods of time (generally for at least one year) (Williams *et al.* 1992). Previous trophic studies have not attempted to link parasite studies with stable isotope analysis in a fish population. Yellow perch (*Perca flavescens*) as a species are highly generalist predators capable of shifting trophic status depending on the complexity of local aquatic community (Craig 1987, Chapter 2). Much is known about perch biology (Craig 1987) and parasite community composition and patterns (McDonald & Margolis 1995, Hoffman 1999, Chapters 2 and 3). Therefore, yellow perch make an ideal model species to compare their trophic status in aquatic systems of differing community composition and to explore a potential link between stable isotopes and parasite fauna an effective indicator of trophic status. The goal of this research was to determine if parasite fauna could be used to more accurately predict stable isotope ratios and thus trophic position of

yellow perch in four small Canadian Shield lakes in Ontario than perch length, age or stomach content analysis.

METHODS AND MATERIALS

Stable Isotope Sample Selection

L239 1997 sample

A total of 19 yellow perch were selected for stable isotope analysis from the 1997 L239 sample (Table 5.1, only the non-transitional perch samples are displayed). Two perch (both males) were selected to represent perch that were infected with few parasites but those parasites present were derived from a zooplanktivorous diet. Three perch (2 females, 1 male) that were in transition from zooplankton to small benthos in the diet and had a supporting parasite assemblage were sampled for isotope ratios. Four female and one male perch were sampled, which should have been largely benthivorous with some residual zooplanktivory and may have also been initiating piscivory. These perch had a parasite fauna that agreed with dietary predictions. Nine large perch (6 females, 3 males) which preyed almost exclusively upon large benthos and some fish and have the related parasites were also selected.

L239 1998 sample

Forty-one yellow perch were analyzed for isotope ratios from the 1998 L239 collection. Twenty-six perch were selected as a sample of exclusively zooplanktivorous fish. The infected individuals in this sample had parasites and/or stomach contents that reflect a zooplanktivorous diet. It is predicted that both the infected and uninfected individuals in this sample should also show a stable isotopic ratio representing a similar diet.

Thirteen (5 males, 8 females) exclusively benthivorous perch were sampled for stable isotopes. They showed infections of parasites that are acquired through zoobenthic

Table 5.1. Sample sizes of the combined yellow perch age and sex classes used in stable isotope analysis. Yellow perch were separated into six trophic categories from each lake based on previously collected parasitological and dietary evidence. All perch that showed parasitological evidence of feeding at two or more trophic levels are not represented in this table.

Lake	Observed Trophic Status		
<u>1997 Sample</u>	Zooplanktivorous	Benthivorous	Piscivorous
L239	2	5	0
L240	10	4	2
L377	5	0	6
Triangle L.	8	6	3
<u>1998 Sample</u>			
L239	26	13	2
L240	10	17	2
L377	25	3	6
Triangle L.	9	15	6

feeding strategies even though benthic invertebrates were not always present in the stomach contents. It was predicted that the isotope results should show some correlation with parasite data.

Yellow perch piscivory was not common in L239 and thus only two exclusively piscivorous fish were sampled (both females). The presence of potential laterally transmitted *Proteocephalus pearsei* (normally acquired from copepod ingestion) can indicate piscivory when the stomach is empty. The absence of all other parasites can also indicate that other modes of feeding do not predominate in these fish. Stable isotopes were used to confirm piscivory.

L240 1997 sample

A subsample of 16 yellow perch was selected from the 1997 L240 sample for stable isotope analysis (Table 5.1). Ten were selected as zooplanktivores for isotope analysis. Many also consume chironomids as evidenced by parasites and stomach contents. Stable isotopes were used to confirm zooplanktivory. Additionally four perch were selected as benthivores and two as piscivores for isotope analysis. The parasites and/or stomach of these individuals indicate diet and isotopes should confirm the source.

L240 1998 sample

Twenty-nine perch were sampled for stable isotopes from the 1998 sample (Table 5.1). Ten of these perch, as indicated by parasites and diet, are zooplanktivores, 17 are benthivores and two are piscivores (again because perch piscivory is not common in this lake). There are also subsamples from this year that represent perch with low and high *Glugea* sp and *Raphidascaris acus* loads.

L377 1997 sample

Nineteen yellow perch sampled in 1997 were selected for stable isotope ratio analysis (Table 5.1, only the non-transitional perch samples are displayed). Five perch were considered to be zooplanktivorous fish and six as piscivorous based on fish in the stomach and no parasites. There were no exclusively benthivorous fish selected from L377 because this step in the ontogenetic dietary shifts of perch was largely absent in fish from this lake.

L377 1998 sample

A subsample of 34 yellow perch caught in 1998 was analyzed for stable isotopes. Twenty-five were analysed for isotope ratios to confirm parasitological and dietary data showing zooplanktivory in these fish. Only three benthivorous fish were sampled because there are few of these individuals present in this system. An additional six piscivorous perch were selected from 1998.

Triangle Lake 1997 sample

Twenty-seven yellow perch were sampled from the 1997 collection for isotope studies (Table 5.1, only the non-transitional perch samples are displayed). Eight which have both zooplankton in the stomach and zooplankton derived parasites in the viscera were sampled. Six benthivores and three piscivores were also selected.

Triangle Lake 1998 sample

A subsample of 30 yellow perch captured in 1998 was selected for isotope analysis (Table 5.1). Nine zooplanktivores, fifteen benthivores and six piscivores were sampled. There was a large proportion of benthivores in this lake and fewer exclusively zooplanktivorous perch. This differs from L377 and may help to explain size differences

between the lakes. Stable isotopes should help to confirm the relative importance of the two feeding types in each lake.

Stable isotope sample preparation and analysis

A sample of muscle tissue (>1.5g wet weight) was removed from the dorsolateral region of all perch larger than ~70mm. Whole fish were used when perch size was less than ~70mm. All samples were frozen (~ -20⁰C) prior to selection for analysis. The selected subsamples were thawed, placed on filter paper and oven dried (45⁰C) for 24 hours. The dried tissue was ground to a powder with a mortar and pestle, which were sterilized with 100% ethanol before each sample was processed. Two mg of ground tissue were then placed in separate tin foil capsules. The capsules were sealed, rolled into balls and each placed in a separate well in a microtiter tray. Samples were analyzed for isotopic composition with a dual inlet isotope ratio mass spectrophotometer (VGMicromass 603E) as described by Hesslein *et al.* (1991). Briefly, this method involves the decomposition of samples to carbon dioxide and nitrogen by the modified Dumas method, which are then cryogenically separated and trapped. Standards by which C and N isotope ratios are measured are PDB and atmospheric nitrogen, respectively. Samples from 1997 were analyzed by Dr. Ray Hesslein (Department of Fisheries and Oceans, Winnipeg, Manitoba) while 1998 samples were analyzed by the National Hydrology Research Institute in Saskatoon, Canada.

Statistical analyses

Yellow perch total length was divided into four categories for statistical analysis; ≤ 60 mm, 61-80mm, 81-100mm and >100mm. Perch age was divided into five classes for analysis; 0+, 1+, 2+, 3+ and $\geq 4+$. Diet and parasites were divided into three categories

each based on stomach content observations and the intermediate host type respectively. The three categories were zooplankton, benthos and fish. MANOVAs were performed to identify significant relationships between yellow perch total length (mm), age, diet and parasite fauna and the stable isotope ratios (both d13C and d15N). ANOVAs and discriminant analysis were performed to test for significant individual relationships between each stable isotope value of sampled perch and the corresponding length, age, diet and parasite fauna of the fish. All analyses were performed with SPSS version 10.0.

RESULTS

Triangle Lake perch had more negative d13C ratios and a more positive d15N ratios that distinguished this population from those in the ELA lakes (Fig. 5.1). L240 perch showed the narrowest range of isotope values and had a higher d15N and slightly more negative d13C ratio than L239 and L377 perch (Fig. 5.1). L239 and L377 perch had similar isotopic signatures.

Figure 5.2 illustrates the isotopic ratios of L239 yellow perch grouped by size or age of the fish. As perch size and age increased, there was a trend towards less negative d13C values but with no distinct separation of d15N values. The oldest and largest perch occupied a wide range of trophic levels (Figs. 5.2a and b). When separated by apparent trophic position as revealed by diet there was greater distinction between isotope values. As perch shifted from zooplankton to benthos and then to fish there was a trend to more positive d15N and d13C values (Fig. 5.3a). When perch were categorized by apparent trophic position as revealed by determining the intermediate host sources for their parasite fauna there was the clearest distinction between isotope ratios. The apparently

Figure 5.1. Range of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of yellow perch in four Canadian Shield lakes. Boundaries represent the range of isotope values for perch in each lake.

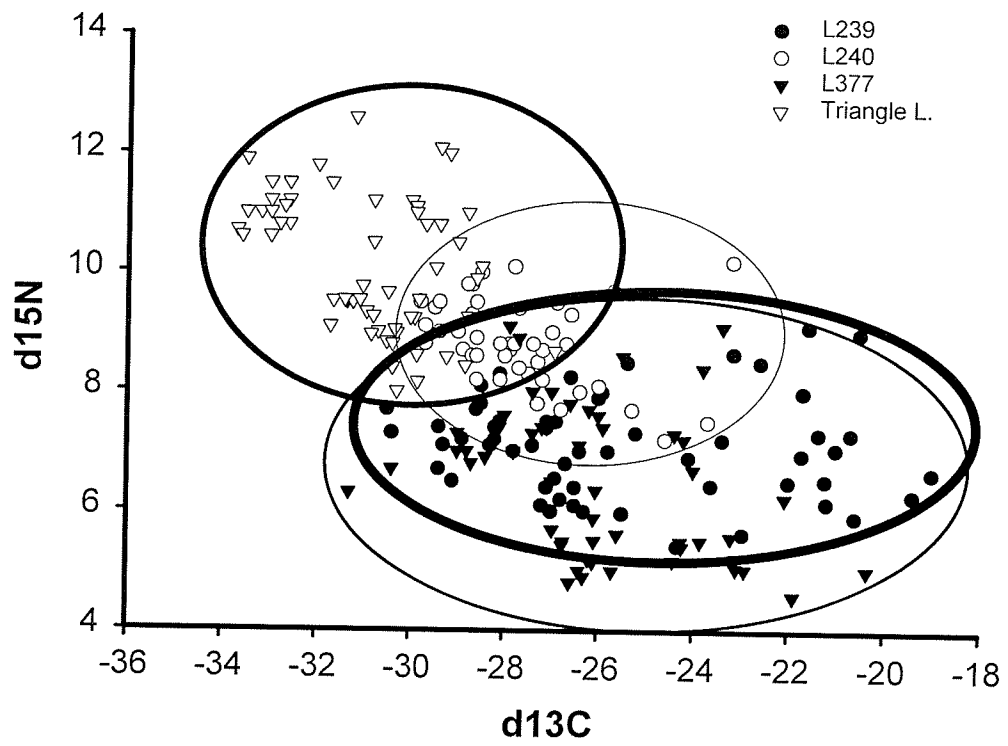
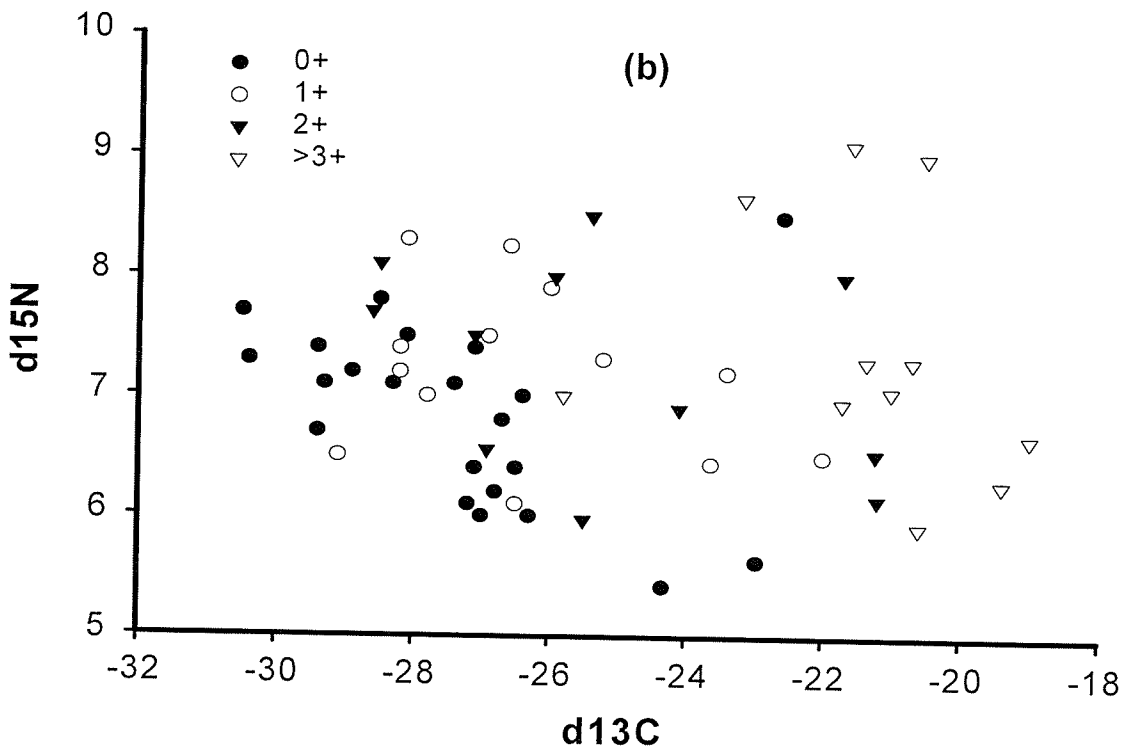
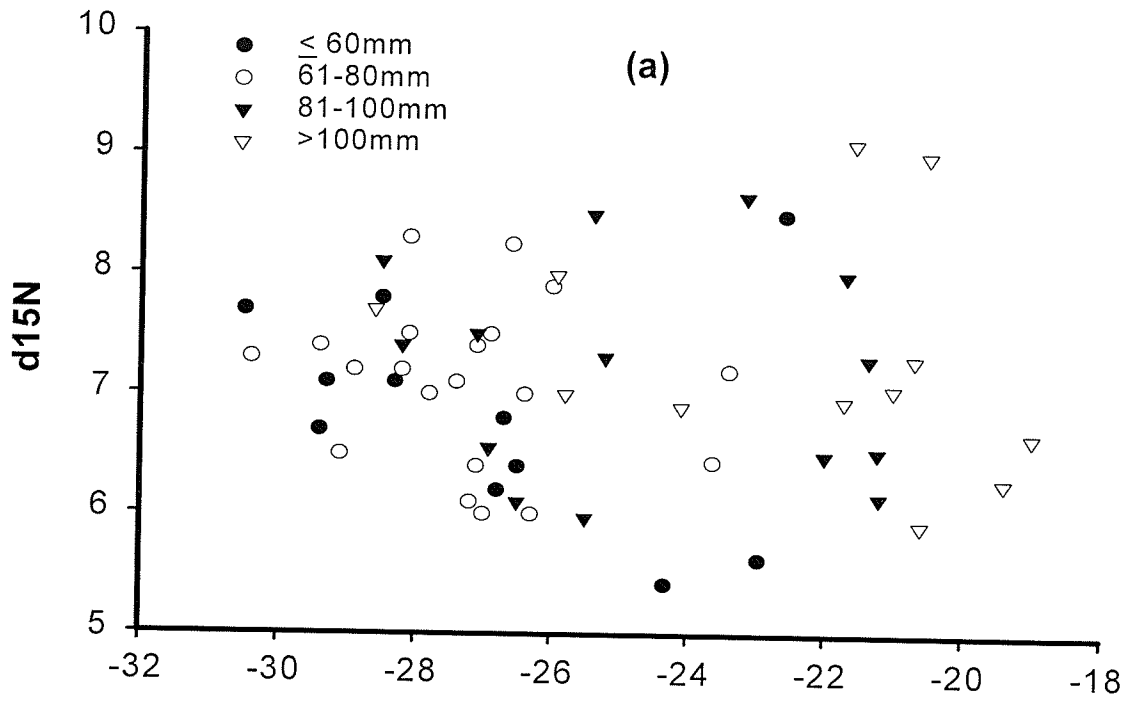


Figure 5.2. Range of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of L239 yellow perch as separated by fish (a) size and (b) age classes.



piscivorous fish are found primarily in the upper right and most zooplanktivores in the lower left of Figure 5.3b.

L240 perch showed no clear separation of either isotope value when grouped by size (Fig. 5.4a) or age (Fig. 5.4b). Diet also did not reveal any isotopically unique perch groups (Fig. 5.5a). Only the parasite fauna partitioned the perch into groups with different isotope ratios (Fig. 5.5b). The piscivores were found in the upper right, the benthivores had lower $\delta^{15}\text{N}$ values and the most negative $\delta^{13}\text{C}$ values, while the zooplanktivores had the lowest $\delta^{15}\text{N}$ values and intermediate $\delta^{13}\text{C}$ values (Fig. 5.5b).

The two largest categories of L377 perch had higher $\delta^{13}\text{C}$ values than the two smallest groups (Fig. 5.6a). Perch $\leq 60\text{mm}$ were the only fish that were also distinctly isolated by $\delta^{15}\text{N}$. There were similar age-related trends with $\delta^{13}\text{C}$ ratio but there was no age class separation by $\delta^{15}\text{N}$ ratio (Fig. 5.6b). Diet revealed two groups each of zooplanktivores and piscivores with benthivores located between these pairs (Fig. 5.7a). Piscivores had a more positive isotopic ratio than zooplanktivores in both pairs. Parasites showed a similar pattern but with fewer piscivores with lower $\delta^{15}\text{N}$ values (Fig. 7b).

The smallest Triangle Lake yellow perch had the lowest $\delta^{15}\text{N}$ values (Fig. 5.8a). The next largest perch (61-80mm) also formed a distinct group around 11‰ $\delta^{15}\text{N}$ and -33‰ $\delta^{13}\text{C}$. The two largest categories of perch showed a wider range of isotope values but typically had higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than smaller fish. Age trends were similar with 0+ perch separated into two groups as older fish occupied a wider, more isotopically positive range (Fig. 5.8b). As with L377 there were two pairings of piscivores and zooplanktivores while benthivores had intermediate isotope values (Fig. 5.9a). Additionally, there was a small group of piscivores with zooplanktivore-like $\delta^{15}\text{N}$

Figure 5.3. Range of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of L239 yellow perch as categorized by fish (a) diet and (b) parasite fauna (grouped by intermediate host type).

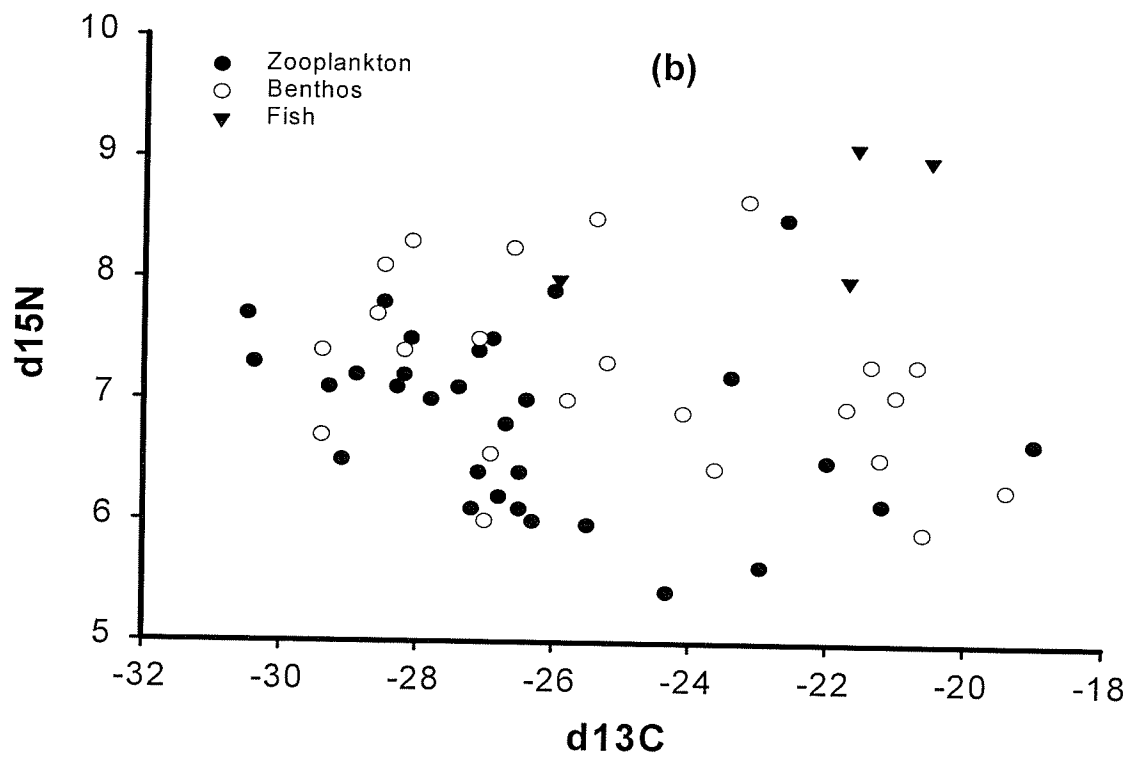
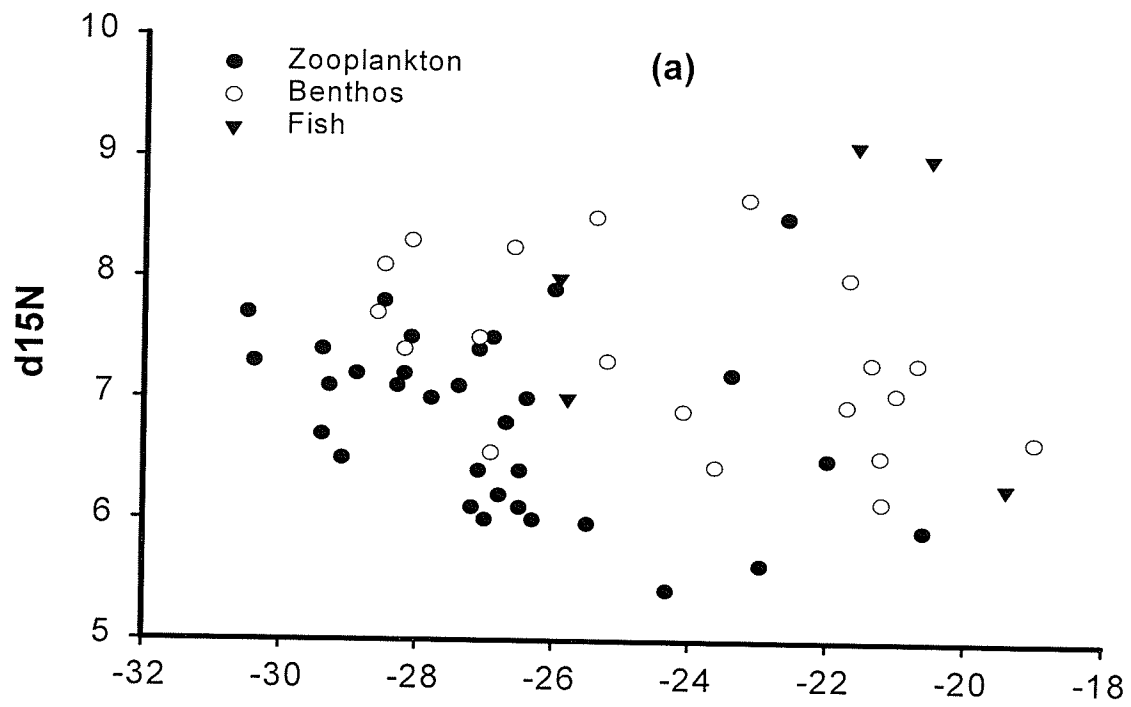


Figure 5.4. Range of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of L240 yellow perch as separated by fish (a) size and (b) age class.

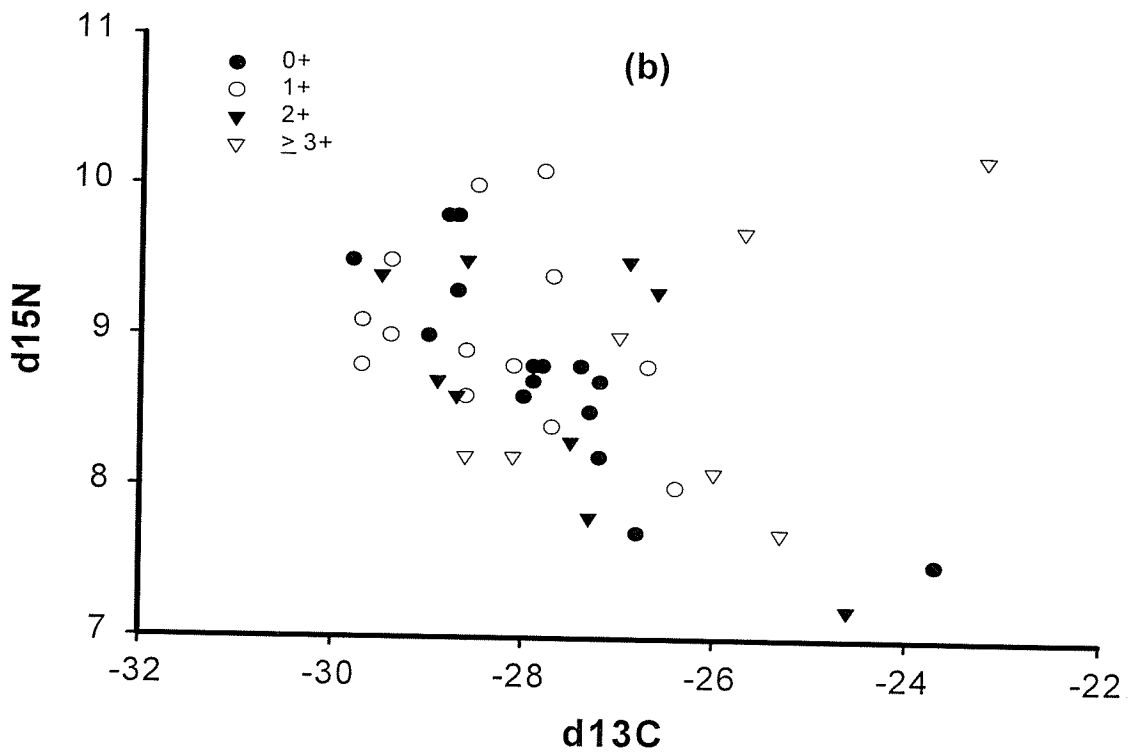
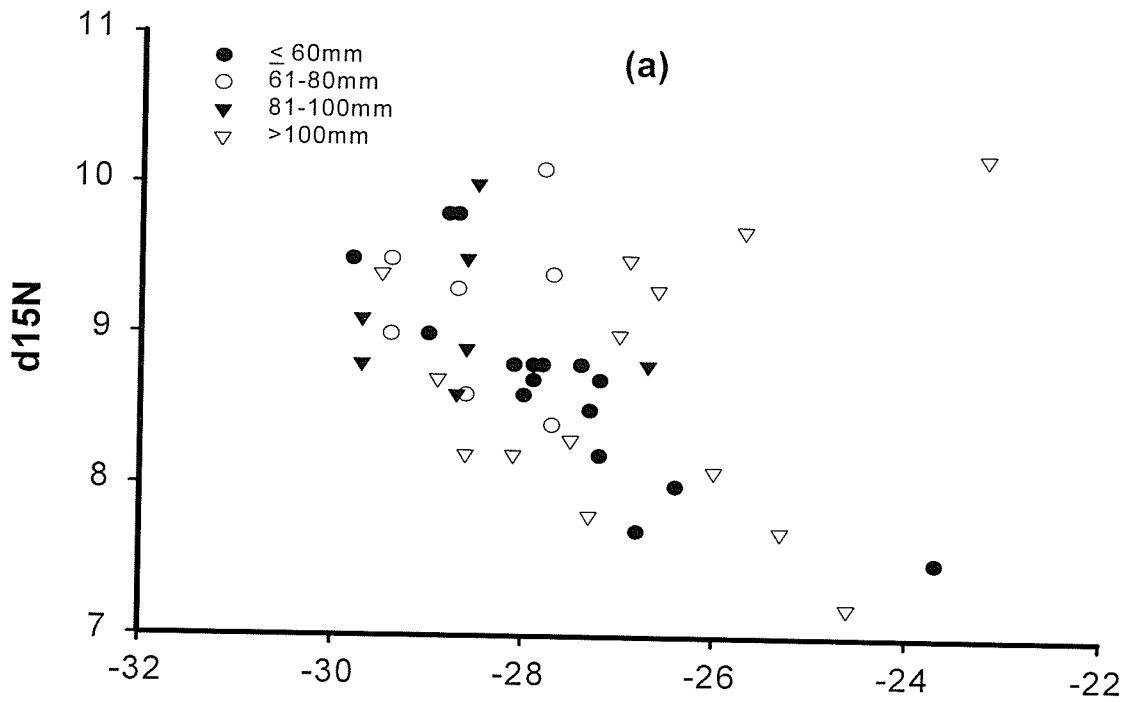


Figure 5.5. Range of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of L240 yellow perch as categorized by fish (a) diet and (b) parasite fauna (grouped by intermediate host type).

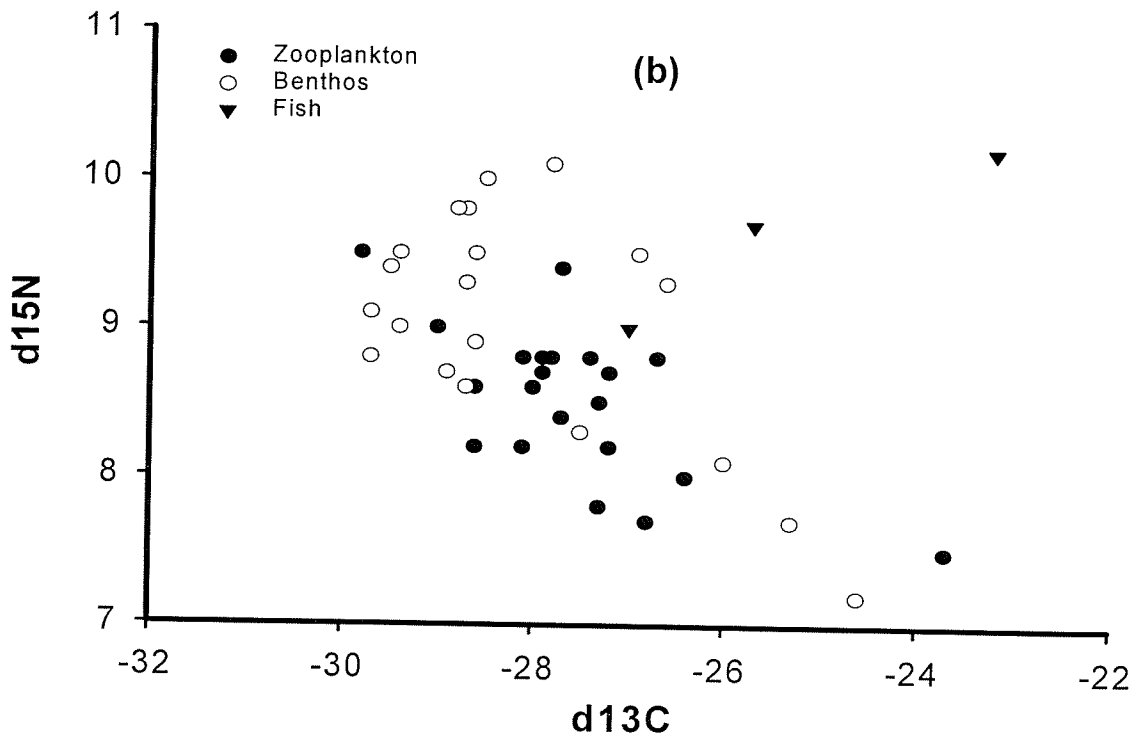
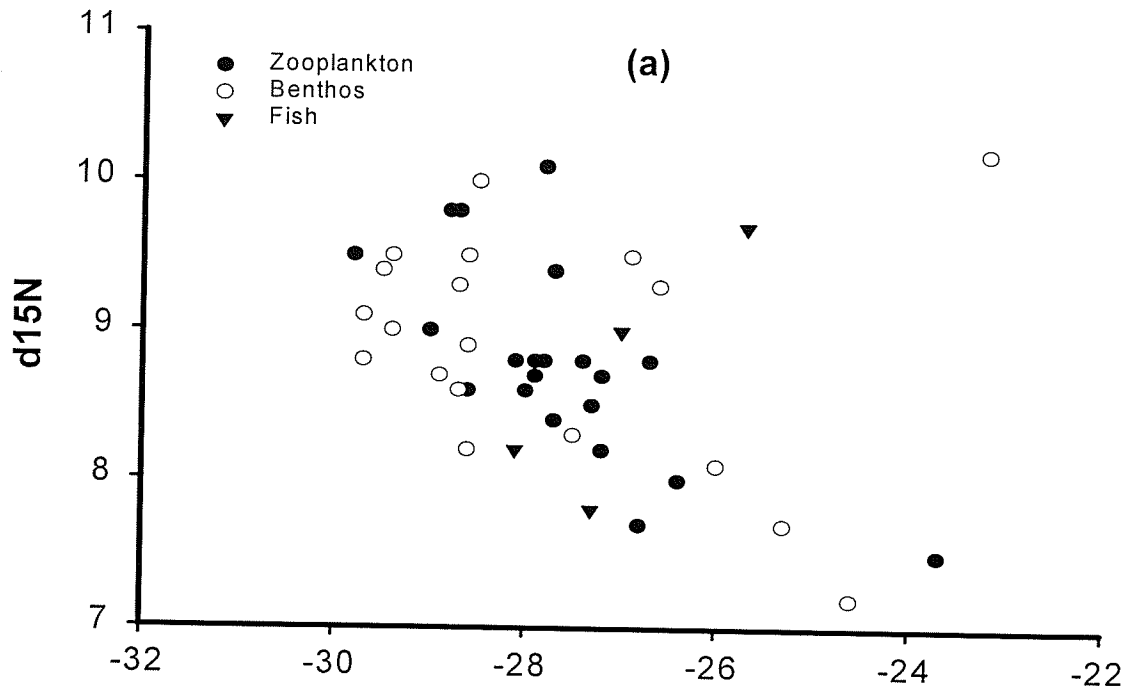


Figure 5.6. Range of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of L377 yellow perch as separated by fish (a) size and (b) age class.

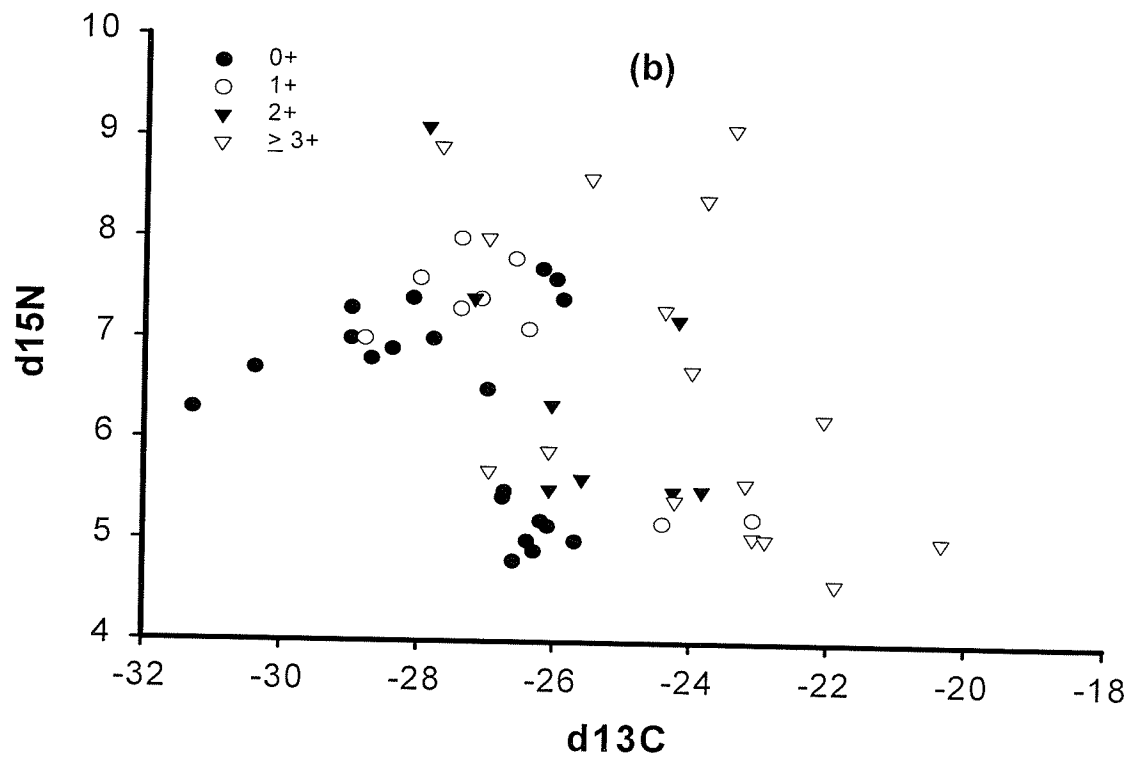
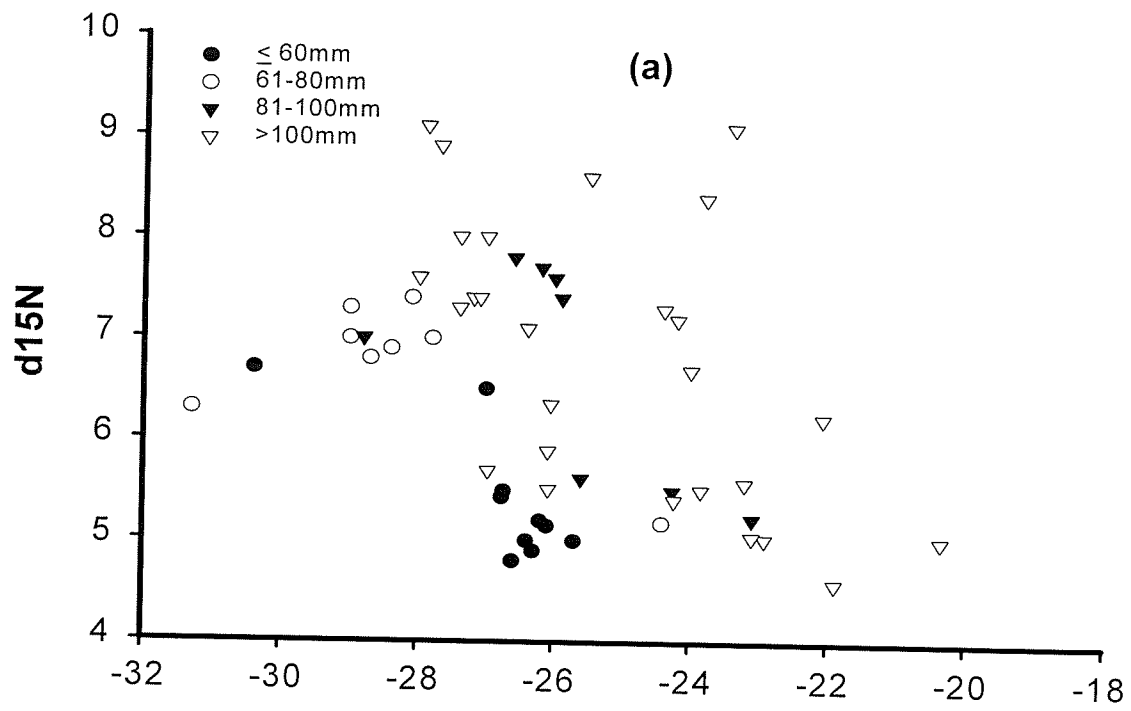


Figure 5.7. Range of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of L377 yellow perch as categorized by fish (a) diet and (b) parasite fauna (grouped by intermediate host type).

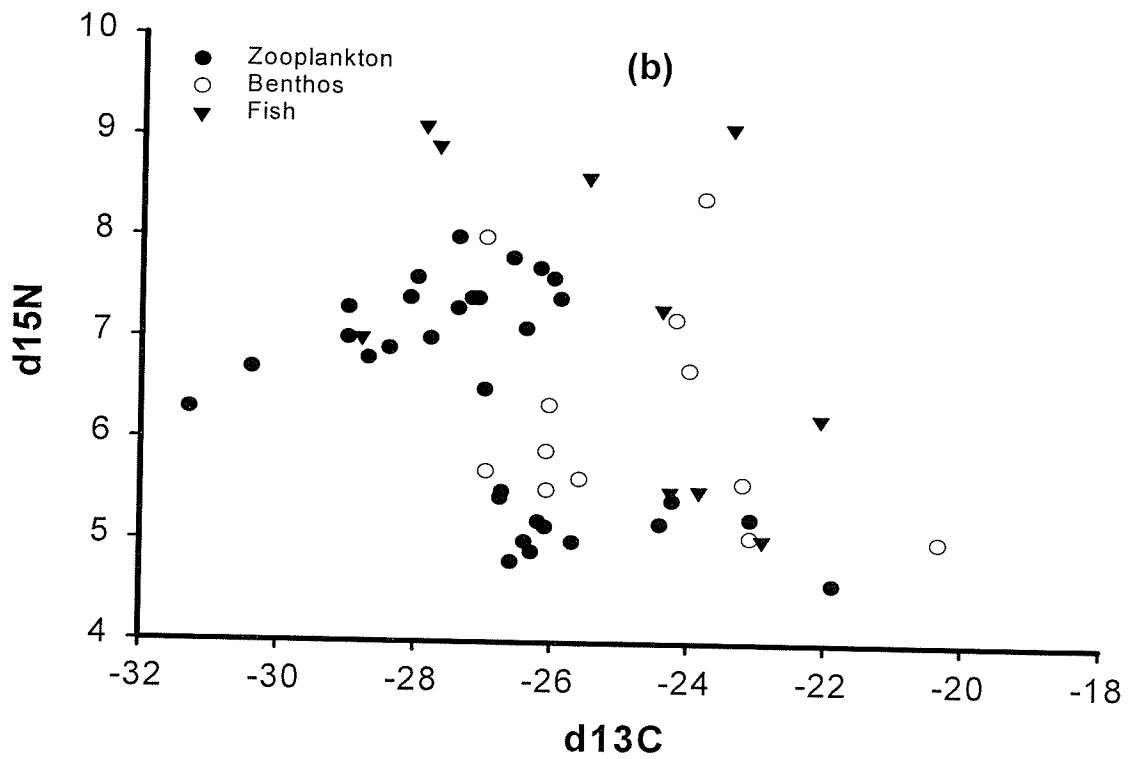
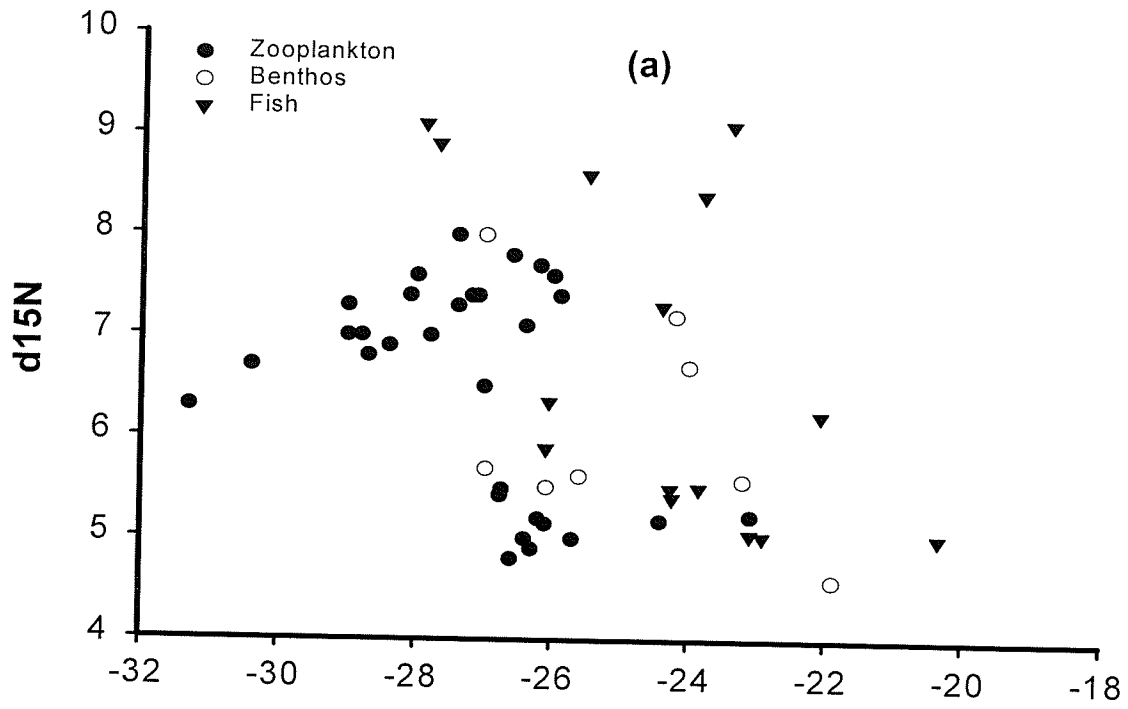


Figure 5.8. Range of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of Triangle Lake yellow perch as separated by fish (a) size and (b) age class.

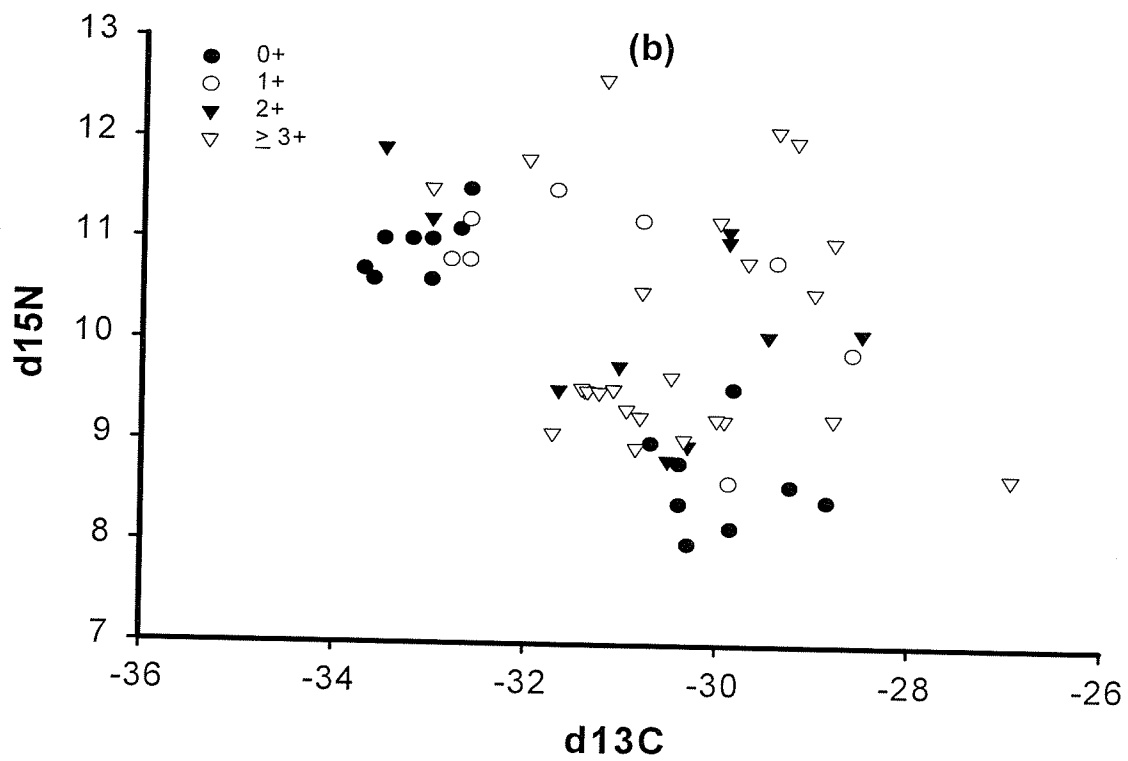
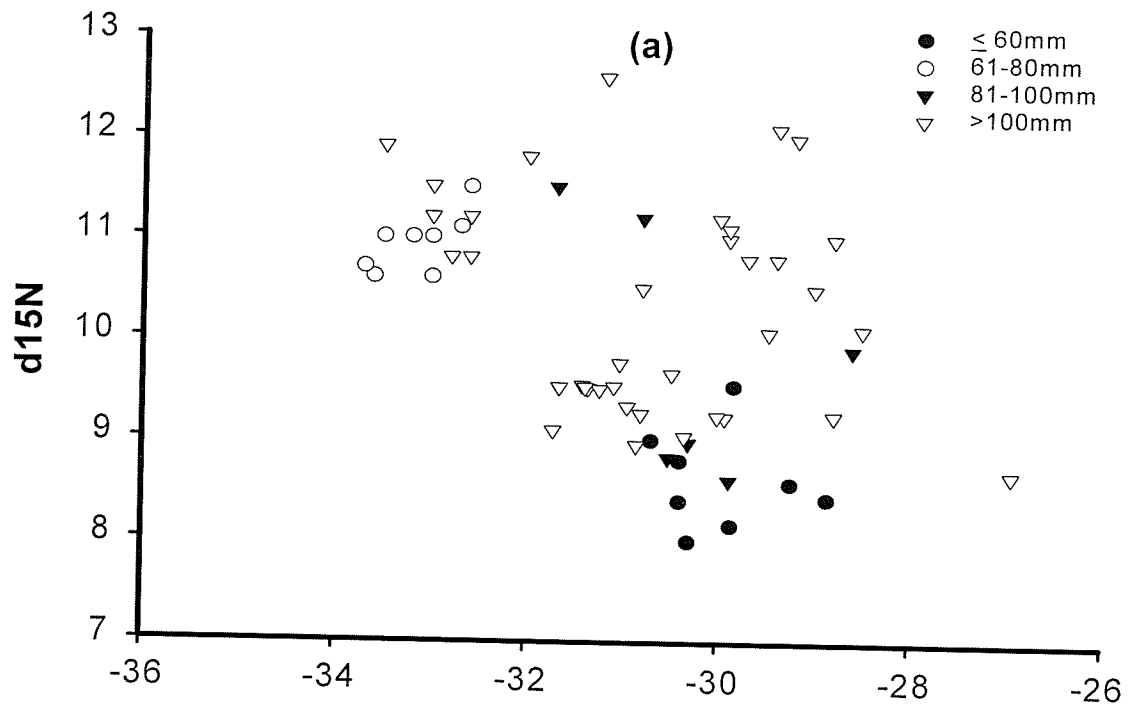
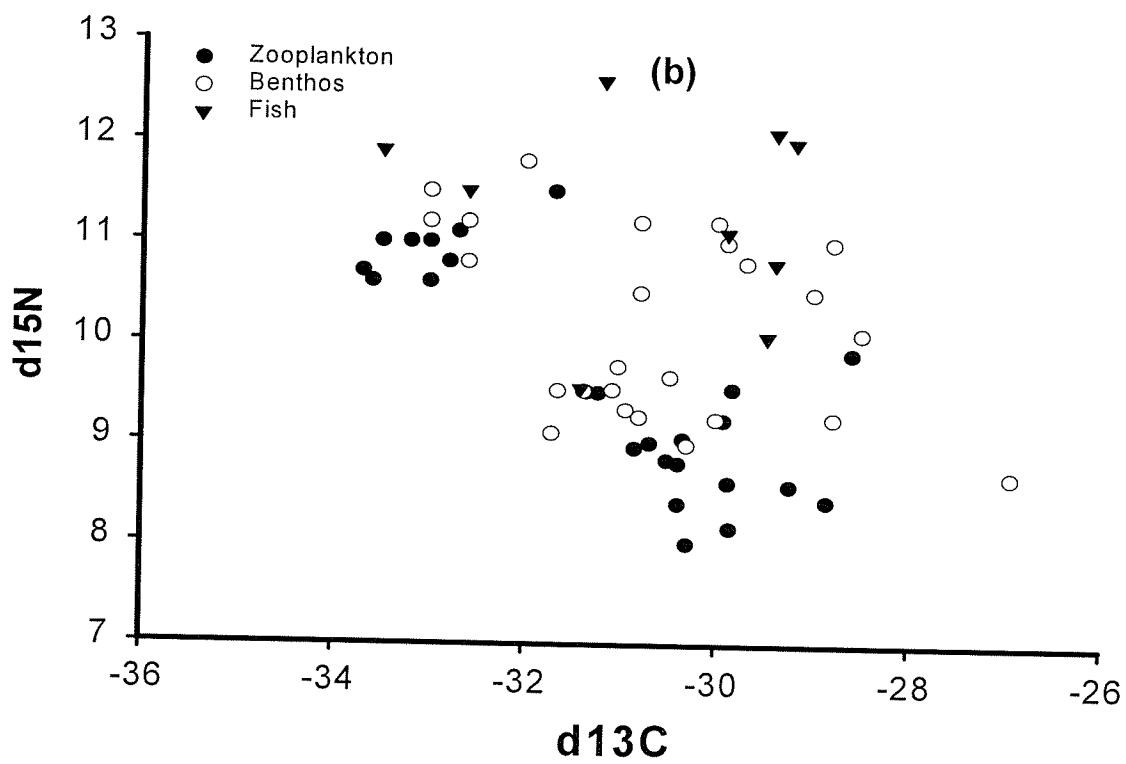
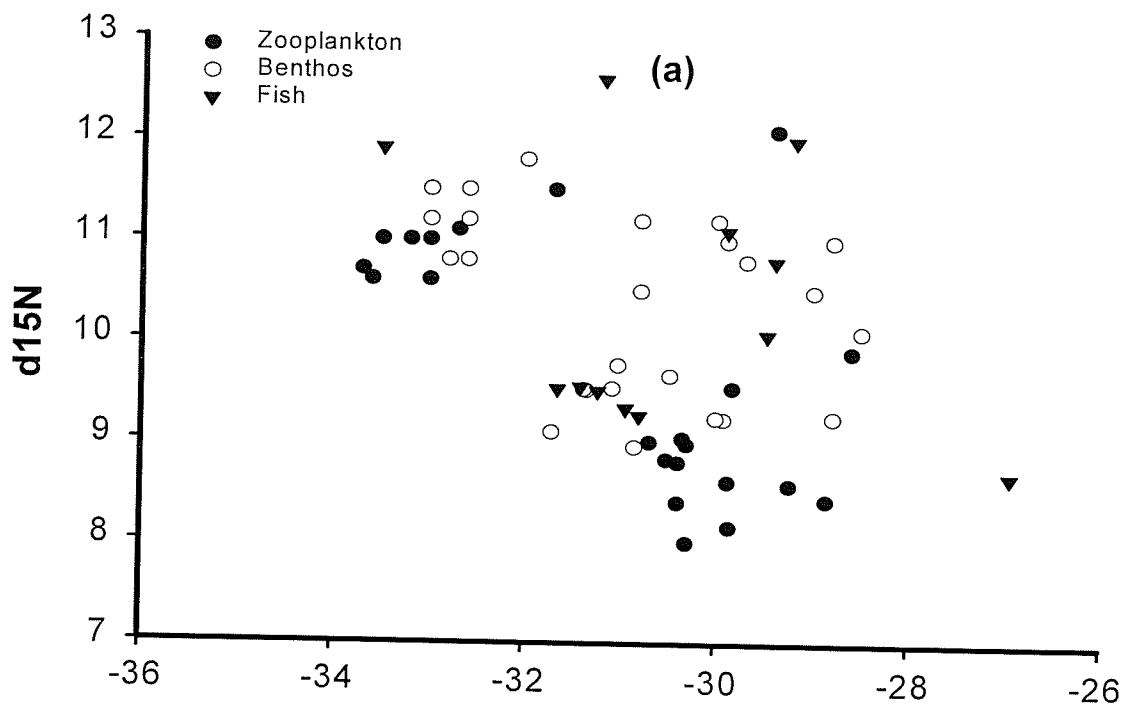


Figure 5.9. Range of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of Triangle Lake yellow perch as categorized by fish (a) diet and (b) parasite fauna (grouped by intermediate host type).



ratios. Parasite analysis, however, showed perch from that group to be either zooplanktivores or benthivores, thus separating the perch into distinct groups with zooplanktivores in the lower left and piscivores in the upper right (Fig. 5.9b).

Yellow perch total length, age, diet and parasite fauna all significantly predicted isotopic ratio in L239 and L377 (Table 5.2). Parasites in L240 and length and parasites in L239 revealed that significant MANOVAs were largely due to highly significant relationships between $\delta^{13}\text{C}$ and the measured variables (Table 5.3). Nitrogen isotope ratios were accurately predicted more significantly than carbon ratios only when parasite fauna was the predictor. Age class and diet were the poorest predictors of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values in yellow perch (Table 5.3). Table 5.4 shows the results of ANOVAs comparing the isotope ratios of the four size categories. In all sampled lakes, most significant differences in mean $\delta^{13}\text{C}$ ratio were observed between the largest and smallest size classes with the smallest classes having the most positive values. There were no significant differences in $\delta^{15}\text{N}$ ratio between size classes in L239 and L240 (Table 5.4). In both L377 and Triangle Lake the smallest perch had a significantly different $\delta^{15}\text{N}$ ratio than both the 61-80mm and the largest perch. The YOY and 1+ L239 perch have significantly different $\delta^{13}\text{C}$ values from the two oldest age classes (Table 5.5). Only YOY perch in L377 had significantly different $\delta^{13}\text{C}$ values from the two oldest age classes. There were no significant mean $\delta^{13}\text{C}$ differences between age classes in L240 or Triangle Lake. There were no significant differences in mean $\delta^{15}\text{N}$ ratio between any age classes in any of the lakes (Table 5.5). L239 perch showed a significant difference in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ ratio between fish of different dietary classes (Table 5.6). There was a significant

Table 5.2. MANOVA tests of the relationships of several yellow perch measurements with the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic ratios.

Independent Variable	Significance			
	L239	L240	L377	Triangle L.
Total Length (mm)	0.000	NS ^a	0.000	0.000
Age Class	0.000	NS	0.000	NS ^b
Diet	0.000	NS	0.000	NS ^b
Parasites	0.000	0.000	0.000	0.000

^a Of the four multivariate tests only Roy's largest root is significant ($P=0.013$)

^b Of the four multivariate tests only Roy's largest root is significant ($P=0.024$)

Table 5.3. Tests of between-subjects effects for comparison of several yellow perch measurements with either carbon (d13C) or nitrogen (d15N) isotopic ratios.

Independent Variable	Significance							
	L239		L240		L377		Triangle L.	
	d13C	d15N	d13C	d15N	d13C	d15N	d13C	d15N
Total Length (mm)	0.000	NS	0.017	NS	0.001	0.016	0.000	NS
Age Class	0.000	NS	NS	NS	0.000	NS	NS	NS
Diet	0.000	0.007	NS	NS	0.000	NS	NS	NS
Parasites	0.018	0.000	NS	0.001	0.004	0.002	NS	0.001

Table 5.4. ANOVA tests comparing the carbon and nitrogen isotopic ratios of four size classes (total length) of yellow perch in four Canadian Shield lakes. Isotope means that are not significantly different from one another in each lake have identical subscripts.

		Mean Isotopic Ratio (\pm standard deviation)			
Lake		$\leq 60\text{mm}$	61-80mm	81-100mm	$>100\text{mm}$
L239	d13C	-27.11 ± 2.63 abc	-27.25 ± 1.70 ab	-24.57 ± 2.71 acd	-22.41 ± 2.99 cd
	d15N	6.90 ± 0.90 abcd	7.08 ± 0.68 abcd	7.18 ± 0.90 abcd	7.32 ± 0.98 abcd
L240	d13C	-27.69 ± 1.34 abcd	-28.47 ± 0.76 abc	-28.64 ± 1.00 abc	-26.80 ± 1.74 ad
	d15N	8.76 ± 0.69 abcd	9.19 ± 0.58 abcd	9.10 ± 0.49 abcd	8.66 ± 0.87 abcd
L377	d13C	-26.82 ± 1.31 abc	-28.34 ± 1.91 abc	-25.81 ± 1.67 abcd	-25.12 ± 2.13 cd
	d15N	5.42 ± 0.66 ac	6.74 ± 0.71 bcd	6.73 ± 1.09 abcd	6.81 ± 1.38 bcd
Triangle L.	d13C	-29.95 ± 0.64 acd	-33.16 ± 0.41 b	-30.30 ± 1.03 acd	-30.67 ± 1.46 acd
	d15N	8.61 ± 0.49 ac	10.94 ± 0.80 bc	9.84 ± 1.26 abcd	10.31 ± 1.06 cd

Table 5.5. ANOVA tests comparing the carbon and nitrogen isotopic ratios of five age classes of yellow perch in four Canadian Shield lakes. Isotope means that are not significantly different from one another in each lake have identical subscripts.

Lake		Mean Isotopic Ratio (\pm standard deviation)				
		0+	1+	2+	3+	$\geq 4+$
L239	d13C	-27.42 ± 2.08 abc	-26.28 ± 2.17 abc	-25.11 ± 2.74 abcd	-21.66 ± 2.20 cde	-20.81 ± 1.08 de
	d15N	6.88 ± 0.76 abcde	7.20 ± 0.69 abcde	7.26 ± 0.87 abcde	7.13 ± 0.82 abcde	7.83 ± 1.43 abcde
L240	d13C	-27.81 ± 1.36 abcde	-28.33 ± 1.07 abcde	-27.62 ± 1.50 abcde	-26.08 ± 2.10 abcde	-26.53 ± 1.80 abcde
	d15N	8.84 ± 0.69 abcde	9.03 ± 0.60 abcde	8.70 ± 0.82 abcde	8.88 ± 0.97 abcde	8.53 ± 1.04 abcde
L377	d13C	-27.43 ± 1.59 abc	-26.58 ± 1.78 abcde	-25.64 ± 1.47 abcde	-24.20 ± 2.41 bcde	-24.13 ± 1.76 bcde
	d15N	6.28 ± 1.04 abcde	6.96 ± 1.04 abcde	6.52 ± 1.30 abcde	6.24 ± 1.46 abcde	6.94 ± 1.68 abcde
Triangle L.	d13C	-31.56 ± 1.74 abcde	-31.05 ± 1.62 abcde	-30.78 ± 1.56 abcde	-30.26 ± 0.88 abcde	-30.51 ± 1.47 abcde
	d15N	9.78 ± 1.26 abcde	10.60 ± 0.93 abcde	10.25 ± 1.02 abcde	10.18 ± 1.03 abcde	10.11 ± 1.26 abcde

Table 5.6. ANOVA tests comparing the carbon and nitrogen isotopic ratios of yellow perch with diet in four Canadian Shield lakes. Isotope means that are not significantly different from one another in each lake have identical subscripts.

		Mean Isotopic Ratio (\pm standard deviation)		
Lake		Zooplankton	Benthos	Fish
L239	d13C	-26.87 ± 2.42 ac	-24.17 ± 2.42 bc	-22.65 ± 3.04 abc
	d15N	6.85 ± 0.73 ac	7.38 ± 0.74 bc	7.87 ± 1.23 abc
L240	d13C	-27.69 ± 1.21 abc	-27.81 ± 1.88 abc	-27.03 ± 1.00 abc
	d15N	8.83 ± 0.68 abc	8.91 ± 0.77 abc	8.68 ± 0.85 abc
L377	d13C	-27.17 ± 1.64 abc	-24.87 ± 1.85 abc	-24.37 ± 2.03 abc
	d15N	6.52 ± 1.06 abc	6.11 ± 1.00 abc	6.76 ± 1.63 abc
Triangle L.	d13C	-31.05 ± 1.67 abc	-30.91 ± 1.40 abc	-30.48 ± 1.64 abc
	d15N	9.72 ± 1.25 abc	10.35 ± 0.89 abc	10.36 ± 1.28 abc

difference in $\delta^{13}\text{C}$ ratio between perch with zooplankton parasites and benthic parasites in L377. The $\delta^{15}\text{N}$ isotope ratio of piscivores is significantly different from both zooplanktivores and benthivores in L239, L377 and Triangle Lake and from zooplanktivores in L240 (Table 5.7). There was no significant difference between $\delta^{15}\text{N}$ ratio of zooplanktivores and benthivores in any lake.

Discriminant analysis was able to most successfully classify individual perch into their original group when the fish had been separated by parasite fauna (55-67% success) in all but L239 where separation by diet produced marginally more successful results (Table 5.8). When only zooplanktivores and piscivores are considered the percent correctly classified into their original parasite groups range from 60% in L240 to more than 75% in the other three lakes.

DISCUSSION

The distinct Triangle Lake stable isotope ratio may be a reflection of different intermediate and/or definitive host diets or of different baseline values from the ELA lakes. Different baseline values may be the result of different flushing rates (Triangle Lake has little inflow and outflow) anthropogenic influences (adjacent highway, bait fishery etc., the carbon fertilization during 1984-85) or other such parameters. The more negative $\delta^{13}\text{C}$ values in Triangle Lake may have resulted from greater importance of a different primary producer to the food chain than in the other lakes. Stable isotopes have revealed unexpectedly important C sources in tropical aquatic systems (Hamilton *et al.* 1992, Forsberg *et al.* 1993). Phytoplankton contributed only 8% of primary production in the Amazon River but accounted for at least 36.6% of the carbon in all fish species examined (Forsberg *et al.* 1993). Forsberg *et al.* (1993) hypothesized that

Table 5.7. ANOVA tests comparing the carbon and nitrogen isotopic ratios of yellow perch with parasite fauna categorized by intermediate host in four Canadian Shield lakes. Isotope means that are not significantly different from one another in each lake have identical subscripts.

Lake		Mean Isotopic Ratio (\pm standard deviation)		
		Zooplankton	Benthos	Fish
L239	d13C	-26.46 ± 2.74 abc	-24.92 ± 3.22 abc	-22.44 ± 2.39 abc
	d15N	6.86 ± 0.72 ab	7.22 ± 0.77 ab	8.52 ± 0.61 c
L240	d13C	-27.58 ± 1.19 abc	-28.04 ± 1.50 abc	-26.76 ± 2.44 abc
	d15N	8.52 ± 0.51 ab	8.99 ± 0.76 abc	9.68 ± 0.47 bc
L377	d13C	-26.91 ± 1.91 ac	-24.70 ± 1.96 bc	-25.16 ± 2.33 abc
	d15N	6.42 ± 1.10 ab	6.25 ± 1.11 ab	8.21 ± 1.18 c
Triangle L.	d13C	-31.11 ± 1.58 abc	-30.64 ± 1.50 abc	-30.84 ± 1.61 abc
	d15N	9.68 ± 1.09 ab	10.18 ± 0.93 ab	11.35 ± 1.06 c

Table 5.8. Percent of yellow perch correctly classified into their original group (groups are identical to those used in ANOVA tests) by discriminant analysis of isotope ratios and several perch measurements.

Variable	% Correctly Classified			
	L239	L240	L377	Triangle L.
Total Length (mm)	43.1	51.1	58.5	44.1
Age Class	51.7	33.3	58.5	33.9
Diet	69.0	46.7	62.3	49.2
Parasites	67.2	55.6	62.3	55.9

selective herbivory may be occurring as algae is by far the best protein source and is readily assimilated by most animals. Algae also appears to be the primary food source in North American east coast estuarine food webs (Sullivan & Moncrieff 1990) while vascular plants (*Spartina* spp.) are more important on the west coast (Kwak & Zedler 1997). Kwak & Zedler (1997) also demonstrated that there is an ecological link between the salt marsh and tidal channel that could perhaps be confirmed with a subsequent parasite study. The parasite fauna of Triangle Lake perch cannot be used to explain its distinct C ratio as the parasites are rarely determined by the diet of the intermediate hosts. Many invertebrate intermediate hosts are infected by direct penetration by an earlier parasite larval stage while infection pathways are unknown for the early life cycle stages of many other parasite species (Hoffman 1999). The fewer significant correlations between parasites and C ratios when compared with parasites and N ratios also suggest that parasites are not useful predictors of important primary producers in a food chain. The higher N isotope ratios in Triangle Lake suggest higher average trophic levels of individual perch in that population than in the other lakes. The mean length of Triangle Lake perch is greater than the other populations for most age classes older than 1+ and as such they are able to shift diets and thus trophic position at earlier ages (Chapter 2). Triangle Lake perch also live longer and thus reach much greater ultimate sizes than the ELA lakes (Chapter 2). Diet and, in particular, parasite community structure suggest higher average trophic levels for Triangle Lake perch (Chapter 2). The highly significant correlation between parasites and N ratios in Triangle in the current study could support this theory. However, since Triangle Lake is not within the ELA and has unique influences (in particular the adjacent highway) the

unknown baseline isotope ratios may differ from the ELA lakes and could explain the distinct ratios of C and N in this population.

While diet is the primary determinant of an animal's isotope ratio (Minigawa & Wada 1984, Hesslein *et al.* 1993) the methods used to predict a specific diet show different levels of accuracy when correlated with observed isotope ratios. The results of this chapter demonstrate that yellow perch food web relationship studies should not rely exclusively on stomach content analysis and/or age and size class separation. Those methods do not accurately predict individual perch position within population or lake community food webs. Trophic position, as determined by parasite infracommunity analysis, was more precise and was highly correlated with stable isotope ratios, particularly nitrogen. The diverse diet, species-rich parasite communities and well-understood parasite life cycles in yellow perch are ideal for examining these types of correlations. Predictable patterns in perch parasite assemblages are largely influenced by trophic feeding patterns, not abiotic factors (Carney & Dick 1999, Carney & Dick 2000a, Chapter 3). The significant relationship between parasites and N ratio in perch supports parasites as accurate predictors of trophic status. In fact, parasites are superior to stable isotopes in that they can be used to determine relationships of perch with prey, competitors and predators.

Stable isotope studies of freshwater and marine fish populations and aquatic ecosystems are common (Monteiro *et al.* 1991, Hamilton *et al.* 1992, Forsberg *et al.* 1993, Beaudoin *et al.* 1999, Vander Zanden *et al.* 1999b) but studies involving yellow perch populations are rare (Keough *et al.* 1996). Thorough isotopic examinations of yellow perch populations, involving large sample sizes of all age classes had not

previously been performed. This study shows that an average N or C isotopic ratio obtained from a small sample of perch (such as by Keough *et al.* 1996) cannot accurately identify the trophic relationships of the population within the aquatic system or of individual perch even when they are of similar size and age. Keough *et al.* (1996) found that the nitrogen isotopic ratio of YOY yellow perch indicated zooplanktivory and as perch size increased the ratio shifted to indicate benthivory and finally piscivory. The same trend was observed with increasing size in ELA perch but there were individuals in each size or age class that did not have nitrogen isotopic ratios typical of that group in each lake. Some of the largest individuals remained zooplanktivorous as indicated by stable isotope ratios and by their parasite infracommunities. So, while the perch population has a highly generalist diet some individual fish may be more specialized in their feeding patterns. It is unknown if environmental factors (food availability, food quality etc.) or genetics are influencing individual specialization but given that environmental factors are similar for all individuals it is possible that individual perch are genetically or behaviourally predispositioned to consume particular food types. It is also possible that these individuals are imprinted, when younger, to a specific prey type and will preferentially exploit that prey when available. Supporting laboratory experiments would help identify the major contributing factor. This specialization may also be a characteristic observed only in these smaller, nutrient poor lakes. However, the small sample size utilized by Keough *et al.* (1996) should not be considered as an accurate representation of the yellow perch populations in coastal and offshore Lake Superior food webs and individual specialization may also be revealed in large lakes through combined parasite and stable isotope studies. Similarly, pike, which

are often considered to be specialist piscivores, were found to consume a large proportion of invertebrates by dietary (Chapman *et al.* 1989) and stable isotope analysis (Beaudoin *et al.* 1999). Recent analysis of pike parasite assemblages has also suggested that pike consume large proportions of benthic invertebrates (Dick & Choudhury 1996). Preconceived concepts of marine food webs have also changed in light of stable isotope data and could be greatly enhanced with corresponding parasite data. Monteiro *et al.* (1991) used $d^{13}C$ values to confirm earlier suspicions that Southern Benguela ecosystem anchovies are largely zooplanktivorous and not phytoplanktivores as was the long-held hypothesis. Identification of zooplankton derived parasites in those anchovies would confirm the suggestion of Monteiro *et al.* (1991) and help to reject the old hypothesis.

Benthivorous perch from all study lakes were the most difficult to correctly place in their original categories by discriminant analysis of all four parameters. This is a rather broad categorization. Parasites in these systems acquired from consuming benthic intermediates can be found in invertebrates as trophically diverse as mayfly nymphs (*Spinitectus gracilis*), amphipods (*Echinorynchus salmonis*) and chironomids (*Raphidascaris acus*). The different $d^{13}C$ and $d^{15}N$ ratios of these intermediates would cause increased variation in the isotopic ratios of benthivorous perch. A larger sample size of fish with each parasite species and with particular combinations of these parasites for isotope analysis would allow for more finescale comparisons of parasite and isotope data. Casual observations of the data do reveal some trends. Fish infected with amphipod-derived parasites tend to have more negative $d^{13}C$ values and more positive $d^{15}N$ values than those infected with large benthic insect-derived parasites. Small subpopulations of perch specializing on particular prey types could be better

identified. There is also the possibility that benthic invertebrates are consuming settled pelagic algal material or terrestrial detritus that would influence $\delta^{13}\text{C}$ ratios.

Stable isotopes and parasite studies are complementary in that both are measures of the assimilated (not just ingested) diet since some digestion of intermediate host prey must occur for release of the parasites into the lumen of the intestine and subsequent migration to the organ of infection. Both long-term and short-term diets can be determined depending on the turnover rate of the tissues being examined by isotope analysis (Abelson & Hoering 1961, Parker 1964) and the life cycle of the parasite species (long or short lived). For example, slow turnover rates occur in bone collagen and fast turnover rates in the epithelial lining of the gut wall and liver, while some parasites have annual life cycles (*Bunodera sacculata* in perch) and others can persist for multiple years (*Ligula intestinalis* in spottail shiners). Combined parasite/isotope studies of a few representative species in an aquatic system can be used to make accurate predictions of overall community structure.

CHAPTER 6: Summary

PRIMARY POINTS

YELLOW PERCH MORPHOMETRICS

- Yellow perch showed the greatest range of morphometric characteristics (31-270 mm TL/ 0.19-208.5 g weight). L239 had the smallest, youngest, slowest growing perch, Triangle Lake the largest, oldest, fastest growing perch.
- Female perch were significantly larger than males from the ages of 2+ to 4+.

YELLOW PERCH DIET

Fish stomach contents

- Yellow perch consumed the greatest variety of prey types (13).
- There were more piscivorous L377 and Triangle Lake perch than in L239 and L240.
- The most zooplanktivores were in L377 and fewest in Triangle Lake.

Seasonal dietary trends

- Zooplankton and benthos were typically most prevalent and intense in the diets of perch in the summer and/or fall depending on the lake.
- Chironomids and some zooplankton showed high prevalence in the spring as well.
- Fish were typically most prevalent in the stomachs of perch in the fall.
- Empty stomachs were most common in the spring.

Age-related dietary trends

- Zooplankton prey types peaked in YOY and 1+ fish stomachs and decreased in prevalence and intensity with fish age although the rate of decrease differed between lakes (older L377 perch still had consumed large numbers of zooplankton).

- Microbenthos (chironomids) usually first appeared in 1+ perch while larger benthos (Ephemeroptera, Amphipoda) appeared a little later and increased in abundance with perch age.
- Fish were typically only present in the diet of the oldest, largest fish (usually females), however, piscivory was evident in perch as young as 1+ in L377.
- Empty stomachs were most common during the transition stage from zooplankton to benthos.

YELLOW PERCH PARASITES

Parasite fauna

- Yellow perch were infected with 17 parasite species (including a new host record for 1 species).

Seasonal trends in yellow perch infection statistics

- Numbers of *A. brevis* and *Diplostomum* sp. accumulated from spring to fall.
- Numbers of *Glugea* sp. were higher in the spring and fall and *U. adspectus* highest in the summer.
- Numbers of *B. sacculata*, and *P. pearsei* and *B. cuspidatus* (zooplankton-derived parasites) usually peaked in the summer or fall in each lake, which coincided with some peaks of zooplankton in the diet.
- *C. cooperi*, *R. acus*, *S. gracilis* and *E. salmonis* (benthic invertebrate-derived parasites) usually showed peaks that corresponded with the peaks of their respective invertebrate intermediates in perch diets.

Age related trends in yellow perch infection statistics

- *Glugea* sp. and the zooplankton-derived parasites usually decreased in numbers with perch age.
- *U. adspectus*, *A. brevis* and *Diplostomum* sp. all increased in numbers with perch age and this was related to increased area for infection by parasites in older fish.
- Benthos-derived parasites increased in numbers with perch age.
- *P. pearsei* showed increased numbers in the oldest perch despite being a zooplankton-derived parasite.

Yellow perch parasite fauna dominance, richness and diversity

- Triangle Lake perch had the highest mean species richness, prevalence, intensity and abundance of parasites
- L377 had the lowest values in all categories except number of parasite species present.
- Enteric parasites were important in Triangle and L239 perch.
- Allogenic parasites were important in Triangle and L240 perch.
- Ectoparasites were most common in Triangle Lake perch.
- L377 perch had reduced numbers of all types of parasites.
- Only L239 (2 species) and L377 (1 species) perch had any unique parasite species in this study.
- *Glugea* sp. was the dominant parasite species in all but Triangle Lake.
- *A. brevis* was dominant in Triangle Lake.
- The dominant enteric species differed in each lake but *A. brevis* and *U. adspectus* were usually the most dominant allogenic and ectoparasite, respectively.
- Total parasite percent similarity was highest between L239 and L377.

- Triangle Lake showed reduced similarity with all other lakes.
- L239 and L240, though connected, shared only 58% of their perch parasite faunas.
- Estimated richness values were higher than the observed values only for L239 and L377 (both of which had unique species).
- L240 perch had the most diverse fauna, L377 the least.
- Female perch always had more diverse assemblages than males.
- Perch ~ 2+ years-old and those sampled in the summer had the greatest parasite diversity.

Yellow perch age and length vs. infection

- Yellow perch age and length were significantly positively correlated with total species richness and all four lakes
- Total species intensity and abundance was significantly correlated with age and length in all but the Triangle Lake sample and this was entirely due to a lack of correlation between allogenic parasites and fish age and length .

Fish sex versus infection

- Female yellow perch had significantly higher total species richness, intensity and abundance than males in most lakes particularly due to higher numbers of enterics and ectoparasites in females than in males.

Parasite community predictability

- L239 and Triangle Lake perch had significantly predictable parasite assemblages.
- L240 perch older than 2+ also had significantly predictable parasite assemblages.
- L377 perch parasite faunas were entirely random

- All four yellow perch samples showed significantly more nestedness than expected by chance.

YELLOW PERCH PARASITE PATHOLOGY

***Glugea* sp. pathology**

- Mean intensities of *Glugea* sp. ranged from ~1000 in YOY to <50 in age 3+ perch
- Prevalence ranged from 56% to ~2% over the same age range.
- Heavily infected perch were typically small, emaciated, had no food in the gut and little or no visceral fat.
- Perch with mean intensities >100 xenomas/fish were usually significantly smaller than perch with lower intensity infections especially YOY perch.
- Perch gonad weights were lower in heavily infected fish than in fish with low infections prior to their first winter while visceral fat weights were reduced in heavily infected perch following the first winter.
- Overwinter mortality was also evident in perch populations.

***Apophallus brevis* pathology**

- Prevalence of *A. brevis* was 100% in Triangle Lake perch.
- Density peaked in YOY perch (~110-120 cysts/g) and decreased to <10 cysts/g in perch >2.92 years.
- Perch with high densities of this parasite showed significantly reduced length and weight compared with those with low-density infections.
- This size reduction was most evident in older 1+ perch.
- Older 0+ male perch showed decreased gonad weight.

- There was also evidence of host mortality caused by this parasite (particularly in YOY and 1+ perch).

***Raphidascaris acus* pathology**

- Density of *R. acus* cysts was highest in L240 perch from late 1+ to late 2+ years old.
- Prevalences in perch increased from 30% at age 0.92 to 100% by age 3.92
- Parasite cyst density was higher in males than females from ages 1 to 3 and higher in YOY and 4+ females than in males of the same age.
- Only percent visceral fat weight and G:F_v ratio differed significantly between perch with low and high *R. acus* densities.
- There was no evidence for mortality caused by this parasite.

STABLE ISOTOPEs

- Triangle Lake perch had distinct C and N isotope ratios from perch in the other study lakes.
- L239 and L377 perch shared the most similar range of isotope ratios.
- Perch length and age showed some correlation with ¹³C values but not ¹⁵N values in each lake.
- Older, larger perch tended to have less negative ¹³C values.
- Perch categorized by their diet and, in particular, their parasite fauna showed the greatest degree of separation.
- ¹⁵N values, especially, were well predicted by perch parasite fauna.
- The observation that parasites are the best predictors of isotope ratios in perch was supported with statistically significant tests.
- The highest degree of predictability is associated with zooplanktivores and piscivores.

- The range of isotope values exhibited by benthivores could be further explained by more detailed analysis of parasite fauna from different types of benthic invertebrates.

Some interpretation

- The maximum size and age and the growth rates of perch in these study lakes are similar to those observed in other populations of what are considered to be stunted perch.
- Low nutrients, reduced abundances of particular prey may be causes of the observed stunting, however genetics cannot be ignored as a potential cause.
- The range of prey consumed by these shield lake perch is typical of generalist perch in other systems.
- Large numbers of older zooplanktivorous perch and an earlier transition to piscivory by some perch in L377 are likely because they were outcompeted by white suckers (an efficient benthivore) for benthic prey.
- Since YOY perch had not yet developed efficient techniques for exploiting benthic invertebrates there were more fish during this transitional stage with empty stomachs.
- Not surprisingly, perch and those other fish species that had consumed the greatest variety of prey types (see below) also typically had the richest parasite faunas while those with restricted diets had small parasite faunas.
- The perch parasite assemblage observed in this study includes species typical of perch in other systems and the number of species present is typical of that observed in other small lakes.
- Typical percid and also cyprinid parasites were the major species in the parasite component communities of these Shield lakes.

- Both *Glugea* sp. and *U. adspetus* have optimum temperatures at which they can reproduce or be transmitted to other hosts, which can explain seasonal differences in infection statistics.
- Other parasites simply accumulate as perch remain exposed to 1st intermediate snails (*A. brevis* and *Diplostomum* sp.) or are dependant upon seasonal abundances of intermediate host prey (enteric parasites).
- High numbers of *P. pearsei* in the fall and in older larger perch may be a result of lateral transfer of this parasite from increased piscivory (cannibalism) by older perch in the fall.
- The age related trends of parasite infection in perch largely correspond to the ontogenetic dietary shifts observed in these fish.
- Low numbers of most parasite species in L377 was due to low numbers of piscivorous birds (allogenics) and reduced benthic invertebrate consumption (due to white sucker competition).
- Most differences in perch parasite faunal similarities were caused by differences in enteric parasites due to availability of intermediates and the presence of other fish species in some lakes (salmonids, burbot), which are contributing some of their own parasite fauna to perch. For example, the low similarity between perch parasites in L239 and L240 is partially the result of more salmonid type parasites in L239 perch.
- Parasite diversity peaks in females, older fish and the summer are all correspond to peaks in benthic-derived parasites infecting these perch.

- Predictability of these perch parasite faunas is related to the relative importance of enteric parasites in a perch population since L239 and Triangle lake and older perch in general had greater numbers and richness of enteric parasites.
- It is the instant infracommunities available from certain intermediates (mayflies for example) that ensure predictability.
- The level of predictability observed in these small, nutrient poor shield lakes is greater than that observed in larger, more productive, lacustrine systems in Canada and the U.S. These shield lake faunas also show higher correlation with perch morphometrics, age and sex than in other systems.
- Pathological effects caused by heavy infections of both *Glugea* sp. and *A. brevis* could delay perch maturation, keep those perch at a lower trophic level than uninfected perch of the same cohort and increase infected perch susceptibility to predation and overwinter mortality (decreased ability to store fat).
- Male reproduction seems to be particularly susceptible since the greatest levels of infection of these parasites occurred when male perch were maturing.
- The periods of highest *R. acus* density in males also correspond to early reproductive years and the impact of this parasite on the liver may be affecting male reproductive potential, although there was no direct evidence of this.
- The liver is an important organ that influences both visceral fat deposition and reproduction (among its many other functions) and any effect of this parasite on the liver could alter the liver's ability to allocate adequate resources to its various tasks.
- Higher density *R. acus* infections in other systems have been shown to negatively affect growth and mortality.

- The potential impact of parasites on perch population structure, recruitment and trophic status cannot be underestimated and should be considered in any population study.
- The difference in Triangle Lake perch isotope ratios could be a result of different baseline values than in the other systems (due to different flushing rates, anthropogenic influences etc.) or of differences in the diets of perch and their invertebrate prey.
- Increased numbers of piscivores in Triangle Lake would account for increased ^{15}N values.
- As mentioned earlier L239 and L377 also had the most similar parasite faunas while Triangle Lake perch parasite fauna was least similar to all other study lakes. There is some correlation of an observational nature between parasite fauna and stable isotopes. The high correlation of parasites and, in particular, ^{15}N ratios is partly because some large individual perch were still primarily zooplanktivorous (as revealed by their parasite fauna and isotopes) and not piscivorous as one might expect based on their size.
- The most important concept to understand and appreciate from this study is that not only are parasite communities excellent predictors of isotope ratio, but they are even more useful than isotope ratios in that they can reveal more precise information about prey, predators and competitors in an aquatic system.
- It is this ecosystem-level understanding gained by parasite community analyses that should promote their increased incorporation into future studies in several biological disciplines.

SECONDARY POINTS

Fish morphometrics

- Pike, cisco, burbot and white suckers were the largest of the sampled fish (>200 mm TL/100 g weight).
- White suckers showed some between lake differences with the largest in L377 and Triangle and the smallest in L239.
- Cyprinids, brook stickleback, slimy sculpins and Iowa daters were the smallest fish sampled (usually <100 mm TL/10 g weight).

Fish stomach contents

- The *Phoxinus* spp. minnows were algavores.
- The remaining cyprinid species excluding pearl dace had all consumed ≤ 7 prey types most of which were zooplankton.
- Pearl dace consumed 11 different prey types including several different benthic invertebrates.
- Zooplanktivorous cisco and piscivorous pike and burbot all consumed three prey types.
- Brook sticklebacks and Iowa darters consumed a mixture of zooplankton and microbenthos.
- Slimy sculpins and white suckers fed primarily on a variety of benthic invertebrates.

Parasite fauna

- 13 of 15 fish species were parasitized.
- 112,188 parasites infected 87% (n = 1926) of the sampled fish.
- Metacercariae of *Diplostomum* and *Apophallus brevis* were the most prevalent of all recovered species.
- *Ichthyophthirius multifiliis* and *Glugea* sp. were the most intense in their hosts.

- White suckers were infected with 11 parasite species.
- Pearl dace were infected with 10 parasite species (including new host records for 5 species).
- Slimy sculpins were infected with 9 parasite species (including new host records for 2 species).
- Northern pike were infected with 7 parasite species.
- Longnose dace and Iowa darters were each infected with 6 parasite species (each including a new host record for 1 species).
- Blacknose shiners (including a new host record for 1 species) and brook stickleback were each infected with 4 parasite species.
- Spottail shiners re infected with 3 parasite species.
- Cisco, fathead minnows and burbot were each infected with 2 parasite species.
- Northern redbelly and finescale dace were uninfected.
- Pike had a parasite fauna that indicated greater consumption of benthic invertebrates than is indicated by the diet so pike are not the exclusively piscivorous fish that they are often assumed to be.
- While most of the morphometrics and diet of these other fish is expected based on other observations, many of the observed parasite species are new host or distribution records. Few parasitological studies have included cyprinids and other smaller fish and this research has shown that there is much to still be learned from these fish.

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Appendix I

The mean and range of all morphometric and the mode and range of all meristic characteristics measured from fifteen species of fish sampled from four study lakes.

With the exception of yellow perch, all subsamples from each lake were combined into one sample for each species of fish for analysis. Yellow perch characteristics were analysed separately for each lake. All measurements were performed as described in the Chapter 2 methodology. All measurements were within ranges described for each fish species by Scott and Crossman (1973).

Appendix I-A. Morphometric and meristic measurements of 16 northern pike (*Esox lucius*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	<u>TL</u>	<u>FL</u>	<u>HL</u>	<u>PL</u>	<u>D</u>	<u>CP</u>	<u>IOW</u>	<u>Wt.</u>	<u>GWt.</u>	<u>LWt.</u>
Mean \pm ¹	255 \pm	247.5 \pm	71.25 \pm	28.0 \pm	36.5 \pm	13.5 \pm	12.25 \pm	137.6 \pm	0.74 \pm	1.78 \pm
St Dev	104.6	97.62	27.13	15.38	17.23	6.56	5.80	150.5	0.45	2.26
Range ¹	136-391	129-368	41-107	12-49	15-57	6-22	6-20	12-356	0.04- 0.13	0.12- 5.12
Mean \pm ²	704.9 \pm							2229 \pm	14.98 \pm	22.77 \pm
St Dev	51.41							261.5	3.16	5.22
Range ²	628-802							1750- 2550	9.55- 18.54	31.96- 15.51
<u>Meristic Measurements</u>	<u>GR(u)</u>	<u>GR(l)</u>	<u>DC</u>	<u>As</u>	<u>Ar</u>	<u>Pvr</u>	<u>Per</u>	<u>1Ds/r</u>	<u>2Ds</u>	<u>2Dr</u>
Mode	0	0	0	0	15	15	10	18	0	0
Range	0	0	0	0	14-16	14-16	9-12	18-19	0	0

¹ Data from 4 pike sampled during this study

² Carcasses of 12 pike were used for by other researchers and only limited morphometric data were available. All internal organs were available for the parasite survey (Chapter 2).

Appendix I-B. Morphometric and meristic measurements of 13 lake cisco (*Coregonus artedii*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.
Mean \pm St Dev	213.2 \pm 43.07	192.3 \pm 38.86	41.15 \pm 7.93	29.31 \pm 6.18	37.38 \pm 7.26	12.62 \pm 2.50	11.08 \pm 6.02	82.44 \pm 40.48	6.34 \pm 7.31	0.63 \pm 0.10
Range	142-259	127-233	29-50	20-37	25-47	8-16	6-30	24.3-136	0.03- 24.28	0.51- 0.83
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Per	1Ds/r	2Ds	2Dr
Mode	16	28	¹	0	13	12	16	12	0	0
Range	14-17	26-29	84-118	0	12-14	11-12	15-17	11-13	0	0

¹ There was no well-defined mode.

Appendix I-C. Morphometric and meristic measurements of 139 pearl dace (*Margariscus margarita*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.
Mean \pm	102.0 \pm	95.0 \pm	19.85 \pm	14.24 \pm	16.65 \pm	8.19 \pm	6.23 \pm	10.09 \pm	0.89 \pm	NA
St Dev	16.71	15.77	3.03	2.18	3.44	1.46	1.16	4.99	0.98	NA
Range	41-137	37-127	9-25	6-18	6-26	3-12	2-10	0.50- 26.25	0.01- 3.98	NA
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Pcr	1Ds/r	2Ds	2Dr
Mode	2	4	0	0	9	8	16	9	0	0
Range	1-5	3-8	0	0	8-10	7-9	12-17	9-9	0	0

Appendix I-D. Morphometric and meristic measurements of 113 black nose shiners (*Notropis heterolepis*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.
Mean \pm St Dev	56.93 \pm 6.73	51.18 \pm 7.13	12.26 \pm 4.97	8.59 \pm 1.41	8.76 \pm 1.71	4.12 \pm 0.67	3.54 \pm 0.77	1.48 \pm 0.47	0.09 \pm 0.10	NA
Range	28-67	26-62	6-53	4-11	4-14	2-5	1-4	0.11-3.16	0.001- 0.44	NA
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Per	1Ds/r	2Ds	2Dr
Mode	3	4	0	0	9	8	13	9	0	0
Range	2-4	3-11	0	0	9-10	7-8	11-14	9-9	0	0

Appendix I-E. Morphometric and meristic measurements of 29 spottail shiners (*Notropis hudsonius*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.
Mean \pm	93.17 \pm	84.72 \pm	17.38 \pm	13.66 \pm	16.03 \pm	7.03 \pm	5.76 \pm	6.93 \pm	0.30 \pm	NA
St Dev	6.86	6.56	1.01	0.94	1.64	0.42	0.51	2.01	0.31	
Range	83-109	76-98	16-20	13-17	13-19	6-8	5-7	4.44- 12.60	0.03- 1.08	NA
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Per	1Ds/r	2Ds	2Dr
Mode	2	5	0	0	9	8	15	9	0	0
Range	1-3	4-6	0	0	9-10	8-9	13-17	9-9	0	0

Appendix I-F. Morphometric and meristic measurements of eight northern redbelly dace (*Phoxinus eos*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.
Mean \pm St Dev	55.88 \pm 4.58	52.75 \pm 3.96	12.00 \pm 1.20	8.75 \pm 1.04	9.63 \pm 0.92	5.00 \pm 0.53	3.88 \pm 0.35	1.56 \pm 0.24	0.04 \pm 0.05	NA
Range	48-63	46-59	10-14	7-10	8-11	4-6	3-4	1.13-1.85	0.01- 0.15	NA
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Per	1Ds/r	2Ds	2Dr
Mode	2	8	0	0	9	8	15	9	0	0
Range	2-3	8-10	0	0	9-10	7-8	13-16	8-9	0	0

Appendix I-G. Morphometric and meristic measurements of four finescale dace (*Phoxinus neogaeus*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.
Mean \pm St Dev	70.25 \pm 5.56	66.25 \pm 4.79	15.00 \pm 2.16	10.25 \pm 0.50	12.50 \pm 1.00	5.75 \pm 0.96	4.75 \pm 0.50	3.28 \pm 0.51	0.24 \pm 0.23	NA
Range	64-77	61-72	13-18	10-11	12-14	5-7	4-5	2.88-4.02	0.03- 0.51	NA
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Per	1Ds/r	2Ds	2Dr
Mode	2	8	0	0	9	8	15,16	9	0	0
Range	2-3	8-10	0	0	9-9	7-9	15-16	9-10	0	0

Appendix I-H. Morphometric and meristic measurements of six fathead minnows (*Pimephales promelas*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.
Mean \pm	88.00 \pm	83.00 \pm	18.00 \pm	12.67 \pm	15.67 \pm	7.83 \pm	6.50 \pm	7.30 \pm	0.12 \pm	NA
St Dev	13.46	12.96	2.68	2.50	3.20	1.60	0.84	3.21	0.09	
Range	63-97	59-91	13-20	9-15	10-19	5-9	5-7	2.05-10.50	0.04-0.29	NA
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Pcr	1Ds/r	2Ds	2Dr
Mode	5	10	0	0	8	9	16,17	9	0	0
Range	5-5	8-10	0	0	8-8	8-9	16-18	9-10	0	0

Appendix I-I. Morphometric and meristic measurements of 17 longnose dace (*Rhinichthys cataractae*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.
Mean \pm	53.82 \pm	50.24 \pm	11.65 \pm	8.12 \pm	8.12 \pm	4.47 \pm	3.06 \pm	1.46 \pm	0.03 \pm	NA
St Dev	13.67	12.64	2.80	2.37	2.50	1.18	0.90	1.35	0.07	
Range	38-87	37-80	8-18	5-12	5-13	3-7	2-5	0.47-5.10	0.001-0.27	NA
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Per	1Ds/r	2Ds	2Dr
Mode	2	5	0	0	8	9	13	8	0	0
Range	1-3	4-6	0	0	8-8	7-9	12-14	8-9	0	0

Appendix I-J. Morphometric and meristic measurements of 56 white sucker (*Catostomus commersoni*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.
Mean \pm St Dev	190.1 \pm 83.67	176.4 \pm 76.89	39.52 \pm 16.36	31.46 \pm 14.08	31.14 \pm 14.59	13.79 \pm 6.04	15.11 \pm 7.27	111.1 \pm 156.0	2.22 \pm 5.29	NA
Range	46-410	46-378	12-85	7-69	7-74	2-32	2-36	0.77- 730.6	0.02- 28.48	NA
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Per	1Ds/r	2Ds	2Dr
Mode	8	12	0	0	8	10	17	12	0	0
Range	5-10	8-16	0	0	7-9	9-12	15-20	11-14	0	0

Appendix I-K. Morphometric and meristic measurements of one burbot (*Lota lota*) sampled from four Canadian Shield lakes.

All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.
	413	413	81	56	66	21	23	484.2	6.87	NA
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Pcr	1Ds/r	2Ds	2Dr
	1	7	40	0	X	X	X	X	0	0

Appendix I-L. Morphometric and meristic measurements of 26 brook stickleback (*Culea inconstans*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.
Mean \pm	48.08 \pm	48.08 \pm	12.35 \pm	7.27 \pm	8.50 \pm	2.50 \pm	2.19 \pm	0.94 \pm	0.01 \pm	0.03 \pm
St Dev	10.17	10.17	2.51	1.19	1.58	0.51	0.40	0.57	0.01	0.01
Range	31-71	31-71	8-17	5-9	6-12	2-3	2-3	0.17-2.80	0.001-0.03	0.01-0.04
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvs	Per	1Ds/r	2Ds	2Dr
Mode	3	8	0	1	10	1	10	5	0	10
Range	1-4	8-10	0	1-2	10-11	1-1	10-11	5-6	0	9-11

Appendix I-M. Morphometric and meristic measurements of 26 slimy sculpin (*Cottus cognatus*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.
Mean \pm St Dev	59.58 \pm 16.65	59.38 \pm 16.50	15.15 \pm 4.61	14.04 \pm 4.50	8.08 \pm 2.67	3.46 \pm 0.90	2.77 \pm 1.48	2.38 \pm 2.14	0.04 \pm 0.06	NA
Range	34-93	34-93	8-26	8-24	5-15	2-5	1-6	0.02-8.28	0.001- 0.22	NA
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvs	Per	1Ds/r	2Ds	2Dr
Mode	0	2	4	0	11,12	3	14	7	0	17
Range	0-2	2-6	2-5	0	10-14	3-4	13-15	7-8	0	15-18

Appendix I-N. Morphometric and meristic measurements of eight Iowa darters (*Etheostoma exile*) sampled from four Canadian Shield lakes. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.	
Mean \pm	42.00 \pm	41.63 \pm	9.75 \pm	8.25 \pm	7.38 \pm	3.63 \pm	2.38 \pm	0.56 \pm	0.02 \pm	NA	
St Dev	4.44	4.10	0.71	0.89	0.92	0.52	0.52	0.16	0.01	NA	
Range	36-49	36-48	9-11	7-10	6-9	3-4	2-3	0.37- 0.72	0.01- 0.04	NA	
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvs	Pvr	Pcr	1Ds/r	2Ds	2Dr
Mode	3	8	3	2	7	1	5	14	8	1	10
Range	2-3	6-10	3-3	2-2	6-8	1-1	5-5	13-14	8-10	0-1	9-10

Appendix I-O. Morphometric and meristic measurements of 564 yellow perch (*Perca flavescens*) sampled from L239. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.	VFWt.
Mean \pm	71.13 \pm	67.80 \pm	18.69 \pm	11.66 \pm	13.67 \pm	4.98 \pm	3.89 \pm	3.72 \pm	0.06 \pm	0.05 \pm	0.02 \pm
St Dev	17.23	16.49	4.54	2.77	4.02	1.16	0.95	4.09	0.16	0.05	0.04
Range	39-156	38-151	11-42	6-23	7-37	3-11	2-9	0.45- 44.2	0.001- 1.49	0.01- 0.49	0.00- 0.35
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvs	Pvr	Per	1Ds/r	2Ds	2Dr
Mode	6	14	3	2	7	1	5	14	13	3	13
Range	3-7	11-16	3-3	2-2	6-8	1-1	5-5	12-15	12-14	2-3	11-15

Appendix I-P. Morphometric and meristic measurements of 504 yellow perch (*Perca flavescens*) sampled from L240. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.	VFWt.
Mean \pm	79.62 \pm	75.66 \pm	20.39 \pm	12.68 \pm	15.68 \pm	5.48 \pm	4.24 \pm	6.10 \pm	0.07 \pm	0.09 \pm	0.06 \pm
St Dev	25.90	24.63	6.50	4.32	5.46	1.64	1.40	6.83	0.13	0.08	0.07
Range	35-177	33-168	9-45	4-30	6-37	3-12	2-10	0.37- 51.95	0.001- 1.35	0.01- 0.56	0.00- 1.15
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvs	Pvr	Per	1Ds/r	2Ds	2Dr
Mode	6	14	3	2	7	1	5	14	13	3	13
Range	3-7	11-16	3-4	2-2	6-8	1-1	5-5	13-15	12-14	2-3	11-14

Appendix I-Q. Morphometric and meristic measurements of 371 yellow perch (*Perca flavescens*) sampled from L377. All distance measurements are in millimetres and all weights are in grams.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.	VFWt.
Mean \pm	92.22 \pm	87.50 \pm	23.84 \pm	14.62 \pm	18.50 \pm	6.40 \pm	5.00 \pm	10.68 \pm	0.28 \pm	0.15 \pm	0.07 \pm
St Dev	33.58	31.99	8.90	5.69	7.71	2.22	1.90	14.85	0.36	0.17	0.21
Range	31-270	20-260	9-71	4-40	5-64	2-19	2-17	0.19- 208.5	0.001- 3.10	0.01- 2.16	0.00- 2.73
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvs	Pvr	Per	1Ds/r	2Ds	2Dr
Mode	6	15	3	2	7	1	5	14	13	3	13
Range	5-7	13-16	3-3	2-3	6-8	1-1	5-5	9-15	13-14	2-3	11-14

Appendix I-R. Morphometric and meristic measurements of 401 yellow perch (*Perca flavescens*) sampled from Triangle Lake. All distance measurements are in millimetres and all weights are in grams.

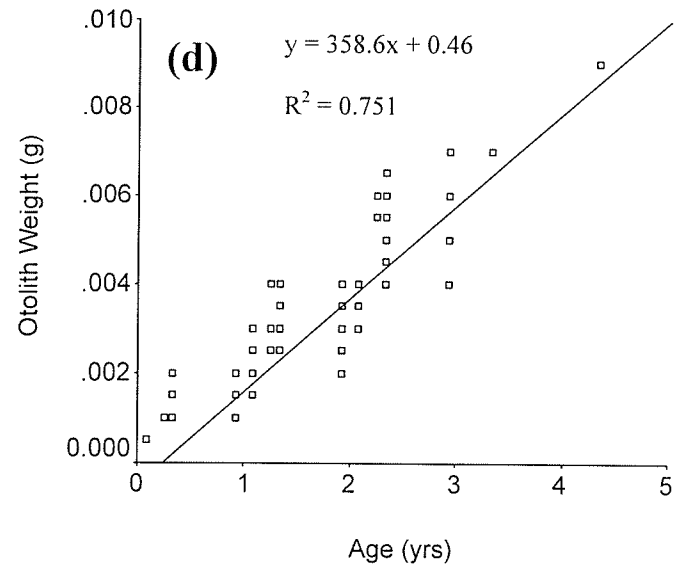
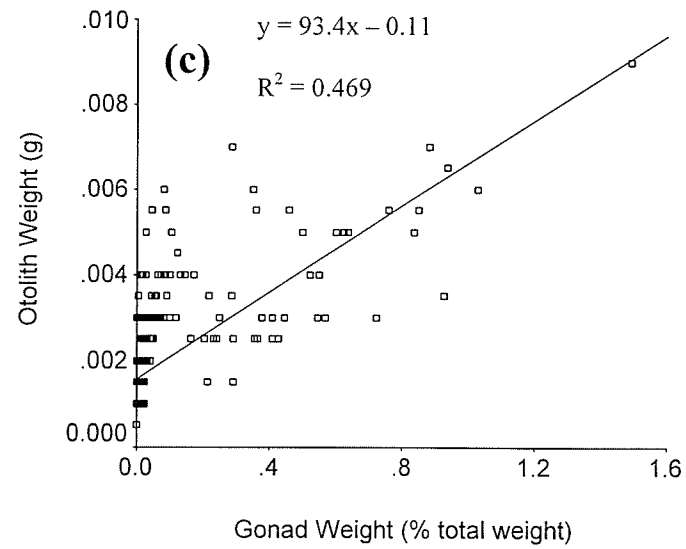
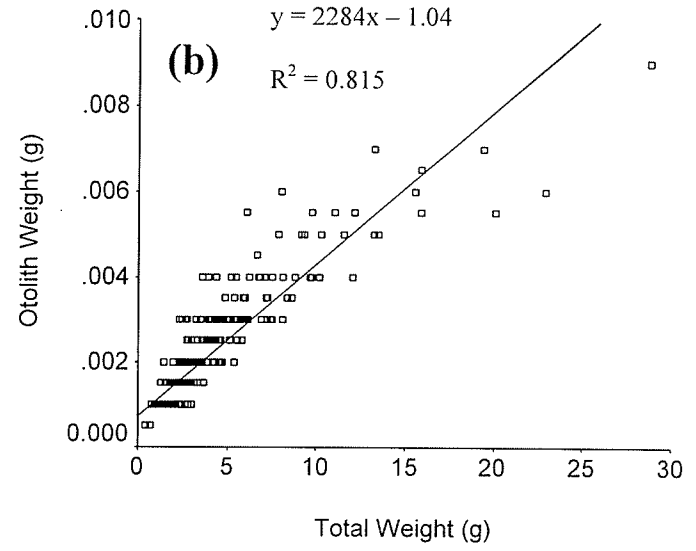
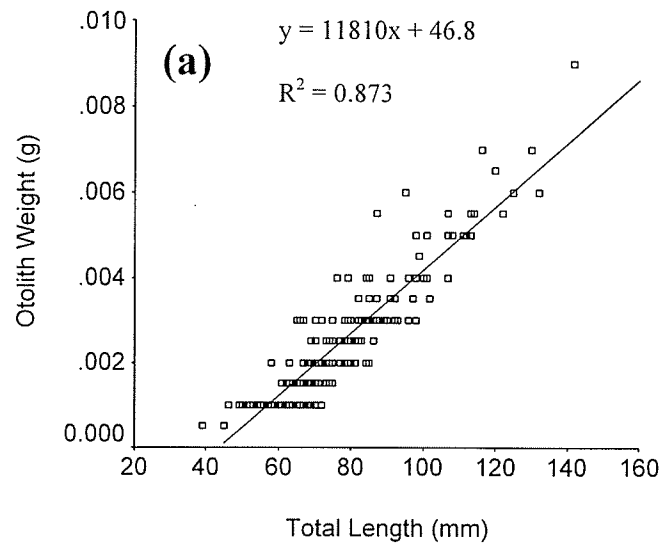
<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	GWt.	LWt.	VFWt.
Mean \pm	116.1 \pm	110.7 \pm	29.82 \pm	17.83 \pm	23.48 \pm	7.77 \pm	6.07 \pm	22.18 \pm	0.63 \pm	0.31 \pm	0.09 \pm
St Dev	45.93	43.82	11.62	6.82	10.15	2.75	2.46	25.81	1.35	0.39	0.15
Range	35-270	34-260	10-67	5-40	7-60	3-17	1-15	0.44- 219.7	0.001- 14.49	0.01- 3.38	0.00- 1.24
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvs	Pvr	Per	1Ds/r	2Ds	2Dr
Mode	6	14	3	2	8	1	5	14	13	3	13
Range	4-7	13-16	3-3	2-2	6-9	1-1	5-5	12-15	11-14	2-3	12-15

Yellow perch otolith weights were recorded to the nearest 0.001g and when both otoliths were recovered intact an average of both was. These otolith weights were linearly regressed against perch length, weight, female percent gonad and age to determine if there was any correlation between these characteristics and an increase in otolith weight. Regression analyses were performed with Microsoft Excel (Office 97 version).

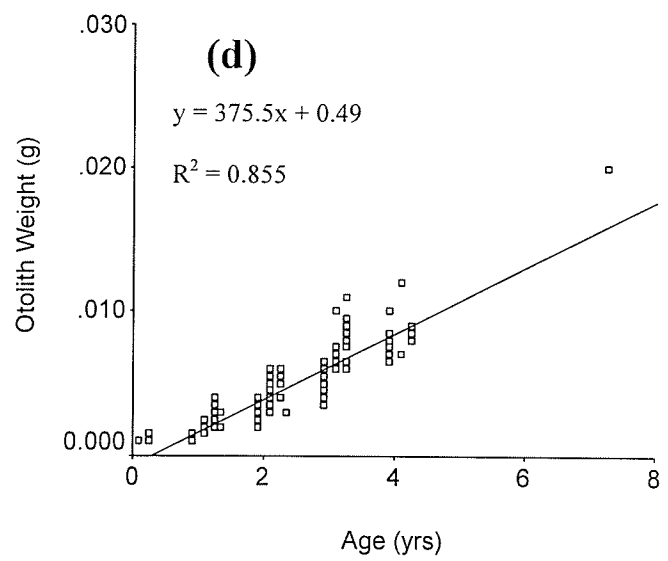
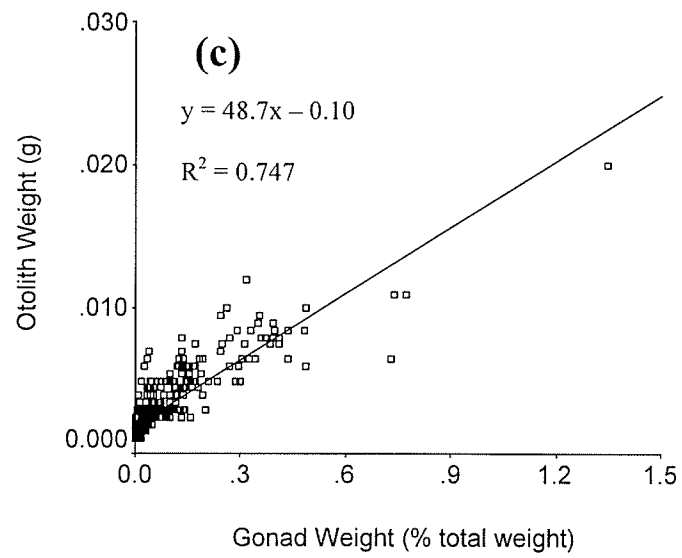
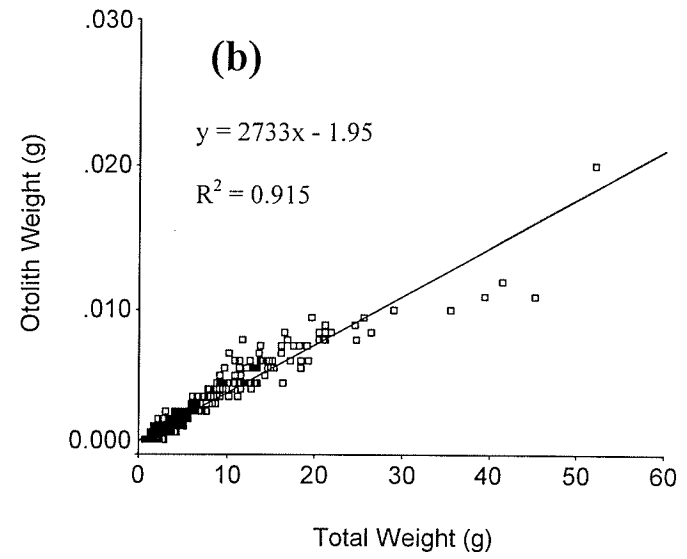
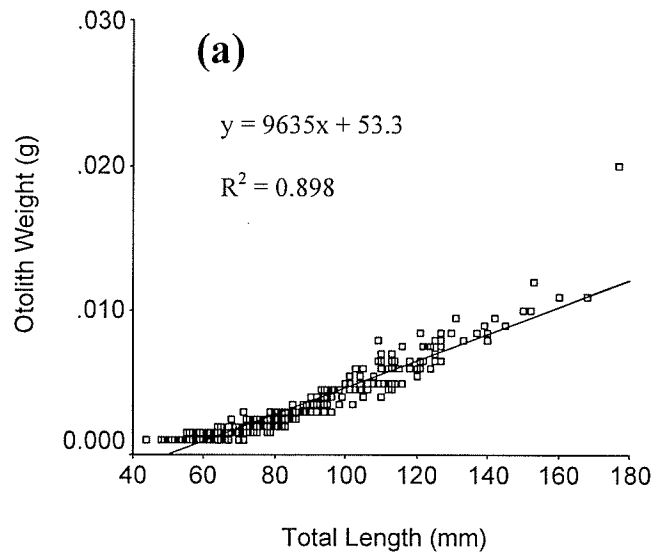
Perch length, weight and age all showed high, positive correlation with increasing otolith weights in all four lakes (r-squared values ~ 0.800) (Appendices II-A to II-D). Percent gonad weight, however, showed high positive correlation with increased otolith weight only in L240 (Appendix II-Bb).

Otolith weight, in addition to the number of annuli, can potentially be used as a powerful predictor of yellow perch age. Thus, each can be used to reinforce the age predicted by the other. Perch length and weight-at-age predictions can also be improved using both characteristics. The ovaries, although potential sinks of calcium, do not appear to affect the weight of the otoliths indicating that adequate levels of calcium are utilized for otolith growth regardless of its usage elsewhere in a fish.

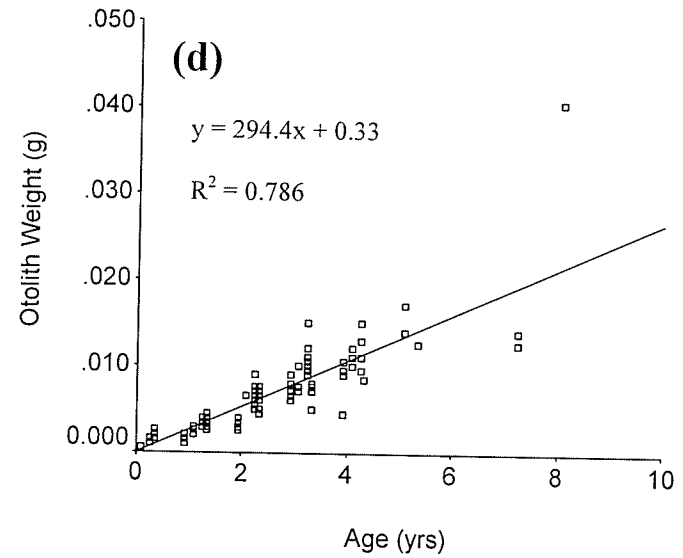
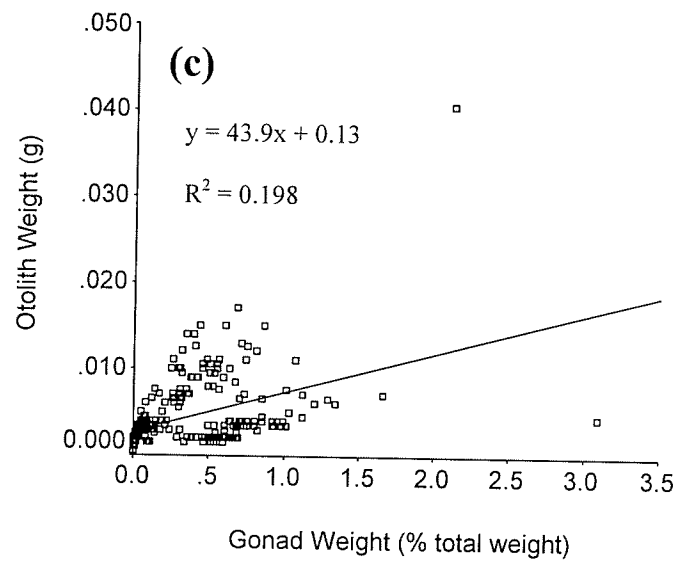
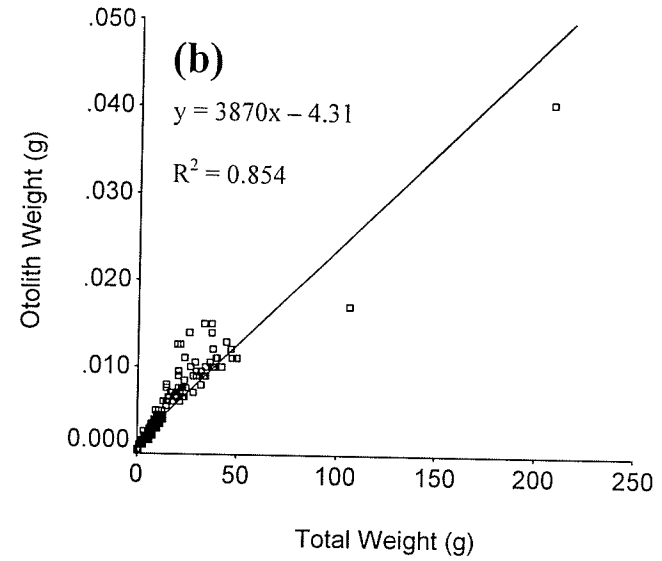
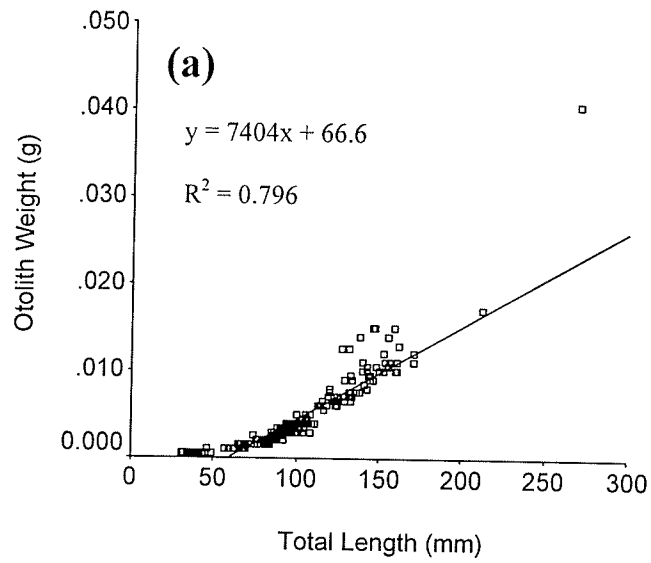
Appendix II-A. Linear regression analyses of otolith weight versus (a) total length, (b) total weight, (c) percent gonad weight, and (d) age of 381 yellow perch sampled from L239. R-squared values are included to observe the degree of correlation between each pair of measurements.



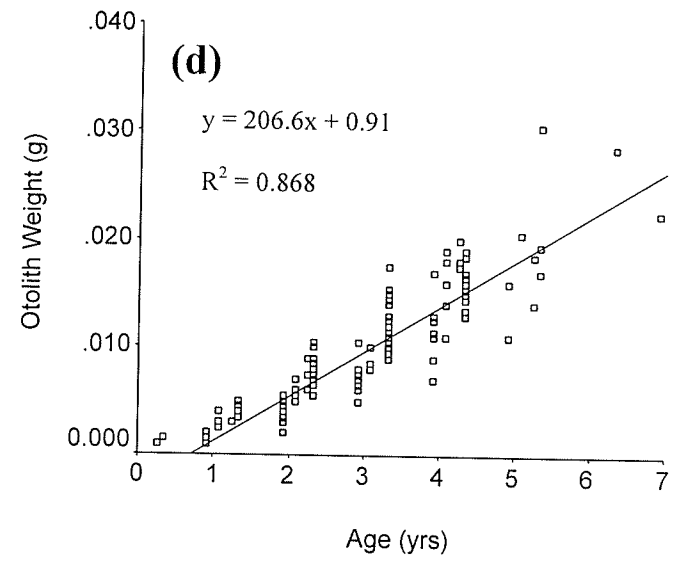
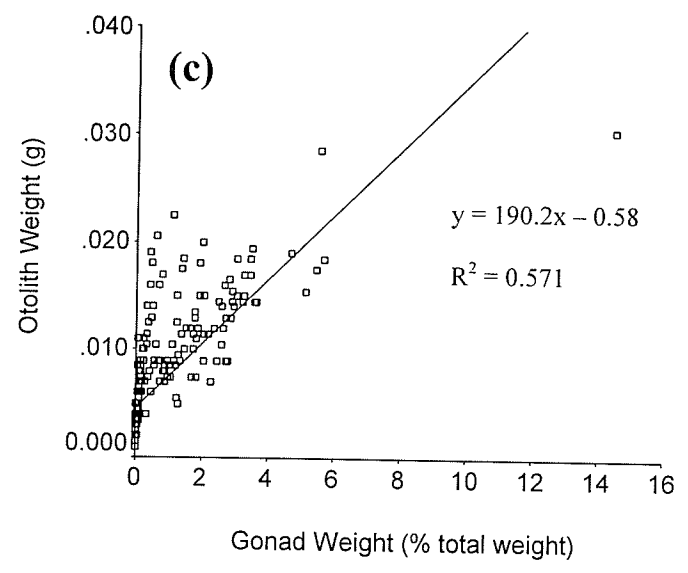
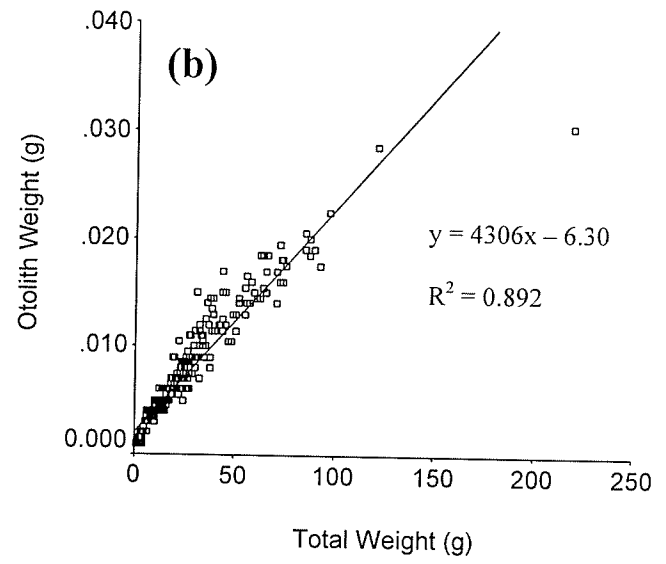
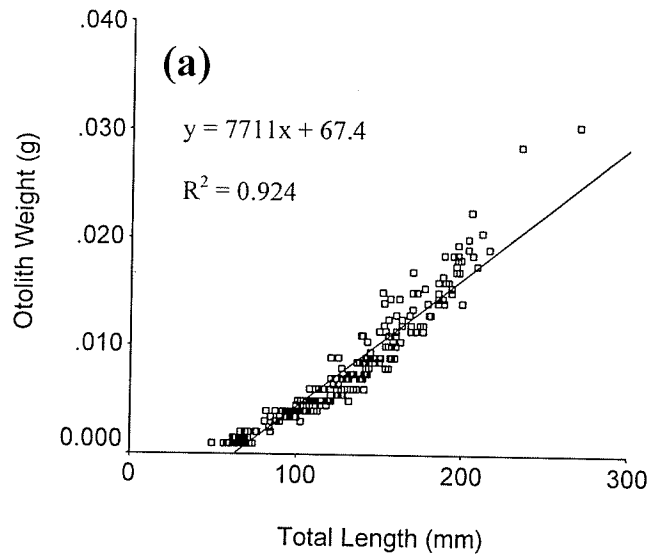
Appendix II-B. Linear regression analyses of otolith weight versus (a) total length, (b) total weight, (c) percent gonad weight, and (d) age of 406 yellow perch sampled from L240. R-squared values are included to observe the degree of correlation between each pair of measurements.



Appendix II-C. Linear regression analyses of otolith weight versus (a) total length, (b) total weight, (c) percent gonad weight, and (d) age of 302 yellow perch sampled from L377. R-squared values are included to observe the degree of correlation between each pair of measurements.



Appendix II-D. Linear regression analyses of otolith weight versus (a) total length, (b) total weight, (c) percent gonad weight, and (d) age of 301 yellow perch sampled from Triangle Lake. R-squared values are included to observe the degree of correlation between each pair of measurement.



Parasite infrapopulations and communities of 14 species of ELA fish (excluding only yellow perch) were analysed for components of richness, diversity and predictability. All measurements and statistics were recorded using the methodology described in Chapter 3 for yellow perch.

Northern pike (*Esox lucius*)

The gill monogenean, *Tetraonchus monenteron*, was the only parasite recovered from a single L239 pike and was the dominant parasite in L240 pike (Appendix III-A). The both the Jaccard and percent similarity between the two samples of pike were low (Appendix III-B). Richness was higher in L240 pike and both jackknife and bootstrap estimates were approximately two species higher than the observed values (Appendix III-C). Parasite diversity was also higher in L240 pike and overall diversity was second only to yellow perch (Appendix III-D).

Lake cisco (*Coregonus artedii*)

The enteric cestode, *Proteocephalus* sp., was dominant in the 13 lake Appendix III-A). This fish species was sampled from only one lake and so similarity measurements were not possible. The jackknife richness estimate was higher than observed number of two while the bootstrap estimate was similar (Appendix III-C). Parasite richness in cisco was among the lowest of all fish species examined, comparable with some cyprinid species. Parasite community diversity in cisco was relatively low (Appendix III-D).

Pearl dace (*Margariscus margarita*)

The allogenic metacercaria, *Posthodiplostomum minimum*, was the dominant parasite in L377 pearl dace and the cestode, *Proteocephalus* sp., was dominant in Triangle L. (Appendix III-A). Similarity between the assemblages of the two pearl dace populations was low as were the similarities of most fish species that are found in both L377 and Triangle Lake (Appendix III-B). Both jackknife and bootstrap estimates were similar to observed values in both lakes (Appendix III-C). Parasite diversity was highest in L377 pearl dace (Appendix III-D). Overall diversity, unlike richness, was not higher in pearl dace than in all other cyprinids.

Blacknose shiner (*Notropis heterolepis*)

The enteric nematode, *Rhabdochona cascadilla*, was dominant in L377 (this is the only L377 minnow where *P. minimum* was not dominant) and the larval allogenic cestode, *Ligula intestinalis*, was dominant in Triangle Lake (Appendix III-A). Parasite faunal similarity between these two populations was the lowest of all fish sampled (Appendix III-B). Richness estimates were low in both populations and were similar to the observed values (Appendix III-C). Parasite diversity was also lower in these fish than in all other hosts examined (Appendix III-D).

Spottail shiner (*Notropis hudsonius*)

The dominant spottail parasite was *P. minimum* (Appendix III-A). Richness values were low, similar to most other cyprinids and estimates accurately approximated the observed value (Appendix III-C). Alternatively, diversity of the parasite fauna in this host was second highest of all minnows sampled from L377 and had the highest cyprinid parasite faunal diversity when all lakes were combined (Appendix III-D).

Northern redbelly dace (*Phoxinus eos*) and finescale dace (*Phoxinus neogaeus*)

No parasites were recovered from six *P. eos* in two lakes (L239 and Triangle L.) and none were found in four *P. neogaeus* in two lakes (L240 and Triangle L.). Therefore, these two fish were not considered in any of these analyses.

Fathead minnow (*Pimephales promelas*)

Posthodiplostomum minimum was dominant in L377 and the eye fluke, *Diplostomum* sp., was dominant in Triangle Lake *P. promelas* (Appendix III-A). Richness estimates were among the lowest of all cyprinids (Appendix III-C) as was total parasite diversity (Appendix III-D).

Longnose dace (*Rhinichthys cataractae*)

The dominant parasite of this cyprinid was again *P. minimum* (Appendix III-A). Observed richness and richness estimates were higher than most other cyprinids while the bootstrap estimate was higher than observed for this fish species (Appendix III-C). Diversity of this host's fauna was second lowest of all L377 minnows and second highest of all total minnow diversity values (Appendix III-D)

White sucker (*Catostomus commersoni*)

The dominant white sucker parasite species in all four lakes were acanthocephalans (Appendix III-A). *Pomphorhynchus bulbocolli* was dominant in L239 and *N. cylindratus* was dominant in the three remaining lakes. The percent similarity was highest between L240 and L377 (89% similar) and lowest between L239 and Triangle Lake (35% similar) (Appendix III-B). Observed richness and richness estimates were highest in L377 suckers and lowest in L240 (Appendix III-C). Only the bootstrap estimate for Triangle Lake suckers was more than one species higher than the observed value. Parasite assemblage diversity was highest in L239 (>2 spp. per host)

and lowest in Triangle Lake (< 1 spp./fish) (Appendix III-D). Total parasite diversity in all lakes was higher only in pike and yellow perch.

Burbot (*Lota lota*)

The cestode *Proteocephalus* sp. was the dominant species (Appendix III-A). Bootstrap richness estimates cannot be calculated for just one sample so richness estimates were not determined. Burbot parasite diversity was higher than cisco, Iowa darters and most minnow species but was lower than the rest (Appendix III-D).

Brook stickleback (*Culea inconstans*)

Neascus sp., a larval trematode in the flesh was dominant in L377 and the digenean was dominant in Triangle lake sticklebacks (Appendix III-A). Percent similarity was low between the populations (Appendix III-B). Parasite richness estimates were higher in L377 *C. inconstans* but were still as low as typical cyprinid values from these systems (Appendix III-C). Parasite species diversity was also higher in L377 than in Triangle while overall diversity was only higher than Iowa darters and two cyprinid species (fathead minnow and blacknose shiner) (Appendix III-D).

Slimy sculpin (*Cottus cognatus*)

Diplostomum sp. was dominant in L240 sculpins and the nematode *S. gracilis* was dominant in L377 fish (Appendix III-A). The similarities of the parasite fauna of the two populations were higher than for minnows, stickleback and pike but were lower than most between lake comparisons of sucker populations (Appendix III-B). Parasite richness was higher in L377 than in L240 and the estimates in L377 were much higher than the observed value due to three species unique to this population (Appendix III-C).

However, diversity of the parasite fauna was higher in L240 sculpins and total diversity was higher in scuplins than in most other fish species (Appendix III-D).

Iowa darter (*Etheostoma exile*)

The unidentified Myxosporidean parasite was dominant in these fish (Appendix III-A). Observed and estimated richness of the darter parasite fauna was higher than most other samples (Appendix III-C). Diversity in darters was lower than in all but two cyprinid species (Appendix III-D).

Appendix III-A. The dominant parasites of 12 species of fish from four Canadian Shield lakes. The Berger-Parker index of dominance was used to obtain proportions.

Fish Species	Dominant Parasite (proportion)			
	L239	L240	L377	Triangle Lake
<i>Esox lucius</i>	<i>Tetronchus monenteron</i> (1.00)	<i>Tetronchus monenteron</i> (0.35)	NA	NA
<i>Coregonus artedii</i>	NA	NA	<i>Proteocephalus exiguus</i> (0.78)	NA
<i>Margariscus margarita</i>	NA	NA	<i>Posthodiplostomum minimum</i> (0.95)	<i>Proteocephalus</i> sp. (0.57)
<i>Notropis heterolepis</i>	NA	NA	<i>Rhabdochona cascadilla</i> (0.94)	<i>Ligula intestinalis</i> (0.84)
<i>Notropis hudsonius</i>	NA	NA	<i>Posthodiplostomum minimum</i> (0.89)	NA
<i>Pimephales promelas</i>	NA	NA	NA	<i>Diplostomum</i> sp. (0.87)
<i>Rhinichthys cataractae</i>	NA	NA	<i>Posthodiplostomum minimum</i> (0.72)	NA
<i>Catostomus commersoni</i>	<i>Pomphorhynchus bulbocollis</i> (0.58)	<i>Neoechinorhynchus cristatus</i> (0.64)	<i>Neoechinorhynchus cristatus</i> (0.56)	<i>Neoechinorhynchus cristatus</i> (0.89)
<i>Lota lota</i>	NA	NA	<i>Proteocephalus</i> sp. (0.97)	NA

Fish Species	Dominant Parasite (proportion)			
	L239	L240	L377	Triangle Lake
<i>Culea inconstans</i>	NA	NA	<i>Neascus</i> sp. (0.89)	<i>Digenean</i> (0.93)
<i>Cottus cognatus</i>	NA	<i>Diplostomum</i> sp. (0.41)	<i>Spinitectus gracilis</i> (0.50)	NA
<i>Etheostoma exile</i>	NA	<i>Myxosporidea</i> (0.43)	NA	NA

Appendix III-B. The Jaccard index of similarity (J) and Renkonen's percent similarity (%) of the total parasite fauna infecting six species of fish in four Canadian Shield lakes.

		Fish Species ^b Similarities						
		A	B	C	D	E	F	
Lake Comparisons ^a	1 and 2	J	0.14			0.38		
		%	0.35	NA	NA	0.55	NA	NA
	1 and 3	J				0.40		
		%	NA	NA	NA	0.63	NA	NA
	1 and 4	J				0.57		
		%	NA	NA	NA	0.35	NA	NA
	2 and 3	J				0.44		0.33
		%	NA	NA	NA	0.89	NA	0.38
	2 and 4	J				0.43		
		%	NA	NA	NA	0.69	NA	NA
	3 and 4	J		0.40	0.25	0.30	0.25	
		%	NA	0.15	0.06	0.62	0.08	NA
	All four lakes	J				0.09		
		%	NA	NA	NA	0.34	NA	NA

^a 1 = L239, 2 = L240, 3 = L377, 4 = Triangle Lake

^b A = *Esox lucius*, B = *Margariscus margarita*, C = *Notropis heterolepis*, D = *Catostomus commersoni*, E = *Culea inconstans*, F = *Cottus cognatus*

Appendix III-C. Observed total parasite species richness in ELA fish and estimates of total richness using jackknife procedures written by Krebs (1989) and bootstrap procedures written by Pisces Conservation Ltd. (1998).

	L239	L240	L377	Triangle L.
<i>Esox lucius</i>	n = 1	n = 15		
Observed richness	1	7		
Jackknife (+ SD)	1.0 + 0.0	8.9 + 5.93		
Bootstrap	0	8.6		
<i>Coregonus artedii</i>			n = 13	
Observed richness			2	
Jackknife (+ SD)			3.8 + 3.93	
Bootstrap			2.1	
<i>Margariscus margarita</i>			n = 70	n = 69
Observed richness			10	4
Jackknife (+ SD)			10.0 + 0.0	4.0 + 0.0
Bootstrap			11.4	4.4

	L239	L240	L377	Triangle L.
<i>Notropis heterolepis</i>			n = 10	n = 103
Observed richness			2	3
Jackknife (+ SD)			2.0 + 0.0	3.0 + 0.0
Bootstrap			2.3	3.2
<i>Notropis hudsonius</i>			n = 29	
Observed richness			3	
Jackknife (+ SD)			3.0 + 0.0	
Bootstrap			2.0	
<i>Pimephales promelas</i>			n = 1	n = 5
Observed richness			1	2
Jackknife (+ SD)			1.0 + 0.0	2.0 + 0.0
Bootstrap			0.0	2.5
<i>Rhinichthys cataractae</i>			n = 17	
Observed richness			5	
Jackknife (+ SD)			5.0 + 0.0	
Bootstrap			7.0	

	L239	L240	L377	Triangle L.
<i>Catostomus commersoni</i>	n = 9	n = 4	n = 37	n = 7
Observed richness	6	5	8	5
Jackknife (+ SD)	6.0 + 0.0	5.0 + 0.0	9.0 + 0.97	5.0 + 0.0
Bootstrap	6.6	5.7	8.7	6.2
<i>Culea inconstans</i>			n = 10	n = 16
Observed richness			3	2
Jackknife (+ SD)			3.9 + 2.67	2.0 + 0.0
Bootstrap			3.1	2.3
<i>Cottus cognatus</i>		n = 5	n = 21	
Observed richness		5	6	
Jackknife (+ SD)		5.0 + 0.0	8.9 + 5.03	
Bootstrap		6.9	7.4	
<i>Etheostoma exile</i>		n = 8		
Observed richness		7		
Jackknife (+ SD)		9.6 + 2.79		
Bootstrap		7.5		

Appendix III-D. Parasite diversity in 12 fish species recovered from four Canadian Shield lakes. Diversity was calculated with Simpson's (Si) and Shannon-Weiner (S/W) diversity indices. The sample size of each fish species from each lake is represented by N.

Lake Parasite Diversity										
Fish species ^a	L239		L240		L377		Triangle L.		All Lakes	
	Si	S/W	Si	S/W	Si	S/W	Si	S/W	Si	S/W
	(N)		(N)		(N)		(N)		(N)	
Pi	1.00	0.00	2.09	-0.36	NA		NA		2.02	-0.34
	(1)		(15)						(16)	
Ci	NA		NA		0.94	-0.07	NA		0.94	-0.07
					(13)				(13)	
PD	NA		NA		1.19	-0.10	0.44	-0.02	0.82	-0.06
					(70)		(69)		(139)	
BNS	NA		NA		0.32	-0.01	0.39	0.00	0.38	-0.01
					(10)		(103)		(113)	
STS	NA		NA		1.08	-0.07	NA		1.08	-0.07
					(29)				(29)	
FHM	NA		NA		1.00	0.00	0.40	0.00	0.50	0.00
					(1)		(5)		(6)	
LND	NA		NA		0.99	-0.09	NA		0.99	-0.09
					(17)				(17)	
WS	2.06	-1.14	1.53	-0.65	1.56	-0.73	0.62	-0.11	1.52	-0.72
	(9)		(4)		(37)		(7)		(57)	
Bu	NA		NA		1.06	-0.06	NA		1.06	-0.06
					(1)				(1)	
BS	NA		NA		1.11	-0.10	0.47	-0.01	0.72	-0.05
					(10)		(16)		(26)	

Lake Parasite Diversity										
Fish species ¹	L239		L240		L377		Triangle L.		All Lakes	
	Si	S/W	Si	S/W	Si	S/W	Si	S/W	Si	S/W
		(N)		(N)		(N)		(N)		(N)
SS	NA		1.66	-0.19	1.15	-0.14	NA		1.25	-0.15
			(5)		(21)				(26)	
ID	NA		0.63	-0.07	NA		NA		0.63	-0.07
			(8)						(8)	

^a Pi = pike (*Esox lucius*), Ci = cisco (*Coregonus artedii*), PD = pearl dace (*Margariscus margarita*), BNS = blacknose shiner (*Notropis heterolepis*), STS = spottail shiner (*Notropis hudsonius*), FHM = fathead minnow (*Pimephales promelas*), LND = longnose dace (*Rhynchithys cataractae*), WS = white sucker (*Catostomus commersoni*), Bu = burbot (*Lota lota*), BS = brook stickleback (*Culea inconstans*), SS = slimy sculpin (*Cottus cognatus*), ID = Iowa darter (*Etheostoma exile*).

Fish length and sex versus infection

Total species richness was correlated with total length of lake cisco, pike, Triangle Lake pearl dace, other L377 minnows and slimy sculpins (Appendix III-E). Total species intensity and abundance were both significantly correlated with length of only Triangle Lake pearl dace, other L377 minnows and sculpins. Total species richness was significantly correlated with sex of only Triangle Lake pearl dace and other minnows (Appendix III-F). Total species intensity and abundance showed significant positive correlations only with Triangle Lake pearl dace.

Parasite community predictability

Since Chi-squared (χ^2) tests for randomness were performed using only enteric parasites (and *Raphidascaris acus* larvae in perch) several hosts that had few or no enterics were omitted from this analysis. The parasite faunas of pike, pearl dace, four other cyprinid species, white sucker and slimy sculpin all do not show a significant departure from random species associations (Appendix III-G to K). There were no individual parasite species or any combination of species that were significantly different from random within any of the parasite communities of the above five hosts or groups of hosts (Appendix III-G to K). There was significantly more nestedness than expected in pike, all cyprinids and white sucker (Appendix III-L). Fill values ranged from 17.9% in pearl dace to 55.0% in cisco and T values ranged from 7.52 (highly nested) in L377 minnows to 64.89 (little nestedness) in lake cisco.

Appendix III-E. Spearman rank correlations of total length versus species richness, intensity and abundance of total parasites of several fish species from four Canadian Shield lakes. P value is given when significant (≤ 0.05), NS indicates no significance.

	Total species richness	Total species intensity	Total species abundance
<i>Coregonus artedii</i> L377 N = 11	$r_s = 0.56$ $t = 2.24$ $p = 0.05$	NS	NS
<i>Esox lucius</i> L239, L240 N = 11	$r_s = 0.73$ $t = 3.94$ $p = 0.0022$	NS	NS
<i>Margariscus margarita</i> L377 N = 70	NS	NS	NS
<i>Margariscus margarita</i> Triangle L. N = 66	$r_s = 0.33$ $t = 2.83$ $p = 0.0067$	$r_s = 0.35$ $t = 3.11$ $p = 0.0032$	$r_s = 0.34$ $t = 2.96$ $p = 0.0046$
Other Cyprinidae ^a L377 N = 46	$r_s = 0.43$ $t = 3.55$ $p < 0.0001$	$r_s = 0.45$ $t = 3.70$ $p < 0.0001$	$r_s = 0.53$ $t = 4.61$ $p < 0.0001$
Other Cyprinidae ^b Triangle L. N = 109	NS	NS	NS
<i>Catostomus commersoni</i> All lakes N = 41	NS	NS	NS
<i>Culea inconstans</i> L337, Triangle L. N = 24	NS	NS	NS
<i>Cottus cognatus</i> L240, L377 N = 19	$r_s = 0.52$ $t = 3.00$ $p = 0.0074$	$r_s = 0.62$ $t = 3.84$ $p = 0.0011$	$r_s = 0.62$ $t = 3.86$ $p = 0.0010$

^a Other cyprinids are: *Notropis heterodon*, *N. hudsonius*, *Pimephales promelas* and *Rhinichthys cataractae*

^b Other cyprinids are: *Notropis heterodon*, *Pimephales promelas*, *Phoxinus eos* and *Phoxinus neogaeus*

Appendix III-F. Mann-Whitney U test to examine the effect of sex on parasite species richness, intensity and abundance in several fish species from four Canadian Shield lakes. P value is given when significant (≤ 0.05), NS indicates no significance.

	Total species richness	Total species intensity	Total species abundance
<i>Coregonus artedii</i> L377 N = 11	NS	NS	NS
<i>Esox lucius</i> L239, L240 N = 11	NS	NS	NS
<i>Margariscus margarita</i> L377 N = 70	NS	NS	NS
<i>Margariscus margarita</i> Triangle L. N = 66	p = 0.0146	p = 0.0053	p = 0.0079
Other Cyprinidae ^a L377 N = 46	NS	NS	NS
Other Cyprinidae ^b Triangle L. N = 109	p = 0.0310	NS	NS
<i>Catostomus commersoni</i> All lakes N = 41	NS	NS	NS
<i>Culea inconstans</i> L337, Triangle L. N = 24	NS	NS	NS
<i>Cottus cognatus</i> L240, L377 N = 19	NS	NS	NS

^a Other cyprinids are: *Notropis heterodon*, *N. hudsonius*, *Pimephales promelas* and *Rhinichthys cataractae*

^b Other cyprinids are: *Notropis heterodon*, *Pimephales promelas*, *Phoxinus eos* and *Phoxinus neogeus*

Appendix III-G. Chi-square test of randomness of the parasite fauna of northern pike (*Esox lucius*) in two Canadian Shield lakes.

Parasite community ^a	Observed (number of fish)	Expected (number of fish)	X ²
Empty	0.21	1	3.01
1	0.46	1	0.64
2	0.05	0	0.05
3	0.27	0	0.27
4	0.35	1	1.23
5	0.46	1	0.64
any 2 spp.	4.51	2	1.40
> 2 spp.	9.70	10	0.01
			X ² tot.= 7.24
			X ² crit.= 14.07
			p = 0.404

^a 1, *Raphidascaris acus*; 2, *Spinitectus gracilis*; 3, *Echinorhynchus salmonis*; 4, *Proteocephalus* sp.; 5, *Triaenophorus crassus*

Appendix III-H. Chi-square test of randomness of the parasite fauna of pearl dace

(Margariscus margarita) in two Canadian Shield lakes.

Parasite community ^a	Observed (number of perch)	Expected (number of perch)	X ²
Empty	81.72	83	0.02
1	13.74	11	0.54
2	1.19	1	0.03
3	12.94	17	1.27
4	18.80	16	0.42
5	0.59	0	0.59
any 2 spp.	9.31	10	0.05
> 2 spp.	0.70	1	0.13
			X ² tot. = 3.06
			X ² crit. = 14.07
			p = 0.879

^a 1, *Allocreadium lobatum*; 2, *Pomphorhynchus bulbocolli*; 3, *Proteocephalus* sp.; 4, *Rhabdochona cascadilla*; 5, *Ligula intestinalis*

Appendix III-I. Chi-square test of randomness of the parasite fauna of four species of Cyprinidae (*Notropis heterolepis*, *N. hudsonius*, *Pimephales promelas*, *Rhinichthys cataractae*) in L377.

Parasite community ^a	Observed (number of perch)	Expected (number of perch)	X ²
Empty	32.24	32	0.00
1	0.58	1	0.31
2	0.58	1	0.31
3	0.58	0	0.58
4	21.81	22	0.00
any 2 spp.	1.20	1	0.03
> 2 spp.	0.02	0	0.02
			X ² tot. = 1.26
			X ² crit. = 12.59
			p = 0.974

^a 1, *Allocreadium lobatum*; 2, *Echinorhynchus salmonis*; 3, *Pomphorhynchus bulbocolli*; 4, *Rhabdochona cascadilla*

Appendix III-J. Chi-square test of randomness of the parasite fauna of white sucker (*Catostomus commersoni*) in four Canadian Shield lakes.

Parasite community ^a	Observed (number of perch)	Expected (number of perch)	X ²
Empty	1.80	4	2.69
1	0.34	0	0.34
2	6.75	5	0.45
3	0.07	0	0.07
4	4.61	2	1.48
5	0.07	0	0.07
6	0.70	2	2.40
7	0.10	0	0.10
any 2 spp.	25.59	26	0.01
any 3 spp.	13.97	15	0.08
> 3 spp.	3.01	3	0.00
			X ² tot.= 7.67
			X ² crit.= 18.31
			p = 0.661

^a 1, *Lissorhis* sp.; 2, *Neoechinorhynchus* sp.; 3, *Echinorhynchus salmonis*; 4, *Pomphorhynchus bulbocolli*; 5, *Proteocephalus* sp.; 6, *Isoglaridacris* sp.; 7, Nematoda

Appendix III-K. Chi-square test of randomness of the parasite fauna of slimy sculpin (*Cottus cognatus*) in two Canadian Shield lakes.

Parasite community ^a	Observed (number of perch)	Expected (number of perch)	X ²
Empty	10.36	12	0.26
1	4.61	3	0.56
2	1.35	0	1.35
3	3.11	3	0.00
4	1.88	2	0.01
any 2 spp.	4.04	5	0.23
> 2 spp.	0.65	1	0.19
			X ² tot. = 2.60
			X ² crit. = 12.59
			p = 0.857

^a 1, *Spinitectus gracilis*; 2, *Echinorhynchus salmonis*; 3, *Pomphorhynchus bulbocolli*; 4, *Schistocephalus solidus*

Appendix III-L. Nestedness of nine species of ELA fish compared with 500 randomly distributed matrices to obtain a simulated *T* value.

	Pike	Cisco	Pearl dace	L377 minnows	Triangle minnows	White sucker	Sticklebacks	Slimy sculpins	Iowa darters
Observed fill (%)	46.8	55.0	17.9	21.7	33.3	22.5	35.9	22.1	33.3
Observed <i>T</i> value	17.56	64.89	10.81	7.52	33.07	11.16	18.03	25.78	29.44
Simulated <i>T</i> value	47.56 ± 7.16	81.89 ± 40.51	42.11 ± 4.44	41.65 ± 7.48	57.37 ± 12.92	46.86 ± 5.46	34.97 ± 10.76	38.19 ± 8.94	20.16 ± 14.10
<i>P</i> value	5.64 e-05	NS	1.03 e-12	2.62 e-06	0.030	3.31 e-11	NS	NS	NS

DISCUSSION

Triangle Lake pearl dace and slimy sculpins both have fauna dominated by enteric parasites and both showed significant correlations of species richness, intensity and abundance with host size, which agrees with the predictions of Zelmer & Arai (1998). However, other L377 minnows are dominated by abundant allogenic parasites and they too show strong correlations with host size. Cisco and pike had only short-lived parasite fauna and they both showed significant correlations of parasite species richness with size but white sucker (another dominated by enterics) did not. All of the other non-perch tested were dominated by allogenic parasites and showed no correlations with size. The majority of the small suckers were obtained from L239 and L240 and these had similar enteric parasite prevalences and abundances as the large L377 suckers. It is possible that large suckers in L239 and L240 may have even higher parasite accumulations support the prediction of Zelmer and Arai (1998). A larger sample of fish from each size/age class in each lake could resolve this issue. The necessary combination of different cyprinid species which can reach different maximum sizes may result in size correlation when none is present or vice versa.

Age correlation calculations would also help to clarify if these fish species do follow the predictions established for yellow perch parasite fauna and host attribute correlations.

White sucker parasites in this study did not show any correlation with host sex. However, Triangle Lake pearl dace which display little sexual size dimorphism in this sample show a correlation between parasite richness intensity and abundance and sex. Other Triangle minnows which are almost all blacknose shiners show more females infected with *Ligula intestinalis* than males (about 40% to 10% respectively) which

explains the correlation of richness and sex. It is unknown if differential immunity of the sexes is present or if perhaps females are feeding more heavily on copepods infected with the proceroid stage of this cestode.

Predictability

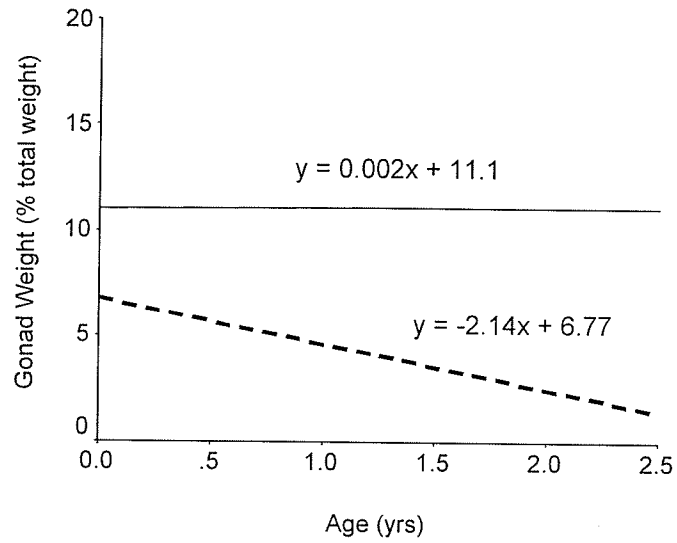
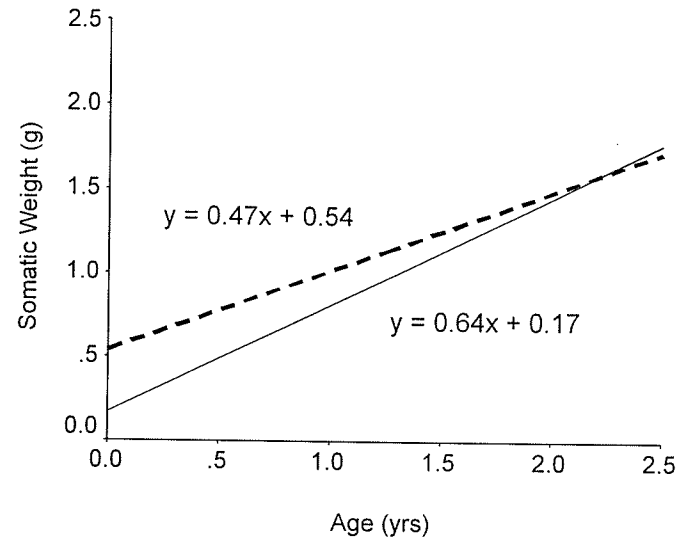
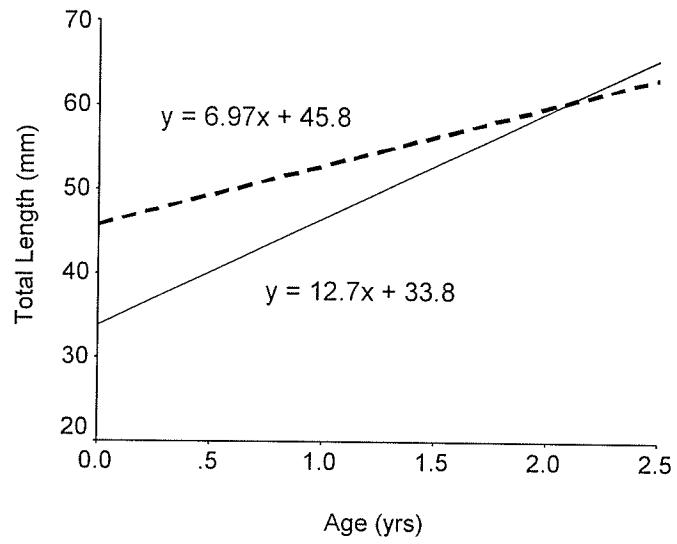
Pike, white sucker and slimy sculpin samples have host sizes and/or low parasite community similarity between lakes. The minnows share attribute similarities but have low parasite community similarity. Both of these may explain the lack of Chi-squared predictability in the non-perch in these systems (Carney & Dick 2000). Combining all the samples of each species into one X^2 test each may have masked any potential predictability. Larger samples of some species from certain lakes would be necessary to confirm parasite community randomness. For example, one might expect to see white sucker acanthocephalans or *Lissorchis attenuatum* and *Isoglaridacris* sp. paired up more often than expected by chance as amphipods and oligochaetes respectively transmit each pair to the suckers. These intermediate hosts could be providing instant infracommunities (Bush et al. 1993) to the fish host at quantities and rates controlled by the presence of each type in the diet. The individual parasite species in the fauna of the other fish are largely all acquired through different dietary items and so instant infracommunities are not transmitted by prey. In pike, both of the cestodes are likely obtained by consuming cisco so there should be some predictability associated with the rates at which they prey upon cisco. Larger samples would be needed in an attempt to confirm this. All these fish appear to be randomly selecting prey from all available types to produce random parasite communities.

The growth and development of blacknose shiners (*Notropis heterolepis*) in Triangle Lake, Ontario as measured by fish length, weight and percent gonad weight were compared between uninfected fish and individuals infected with the larval cestode *Ligula intestinalis*. *Ligula intestinalis* is obtained by consuming copepods and is passed on to piscivorous waterfowl where it matures (Hoffman 1999). It occupies the body cavity of many species of fish, particularly cyprinids. *Ligula intestinalis* was found primarily in Triangle Lake blacknose shiners. Prevalence was 43% in females and 13% in males. There was one male shiner infected with two worms but all other fish had only a single *L. intestinalis*. Worm biomass was also recorded to determine if there was increased effect on the shiners with increased parasite size.

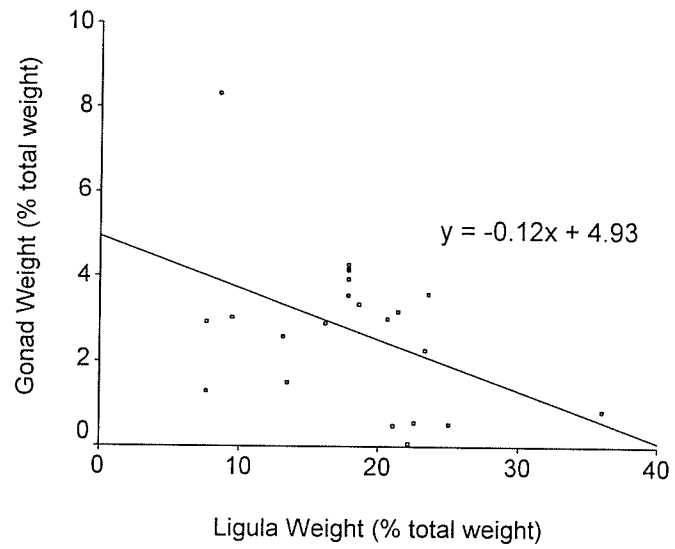
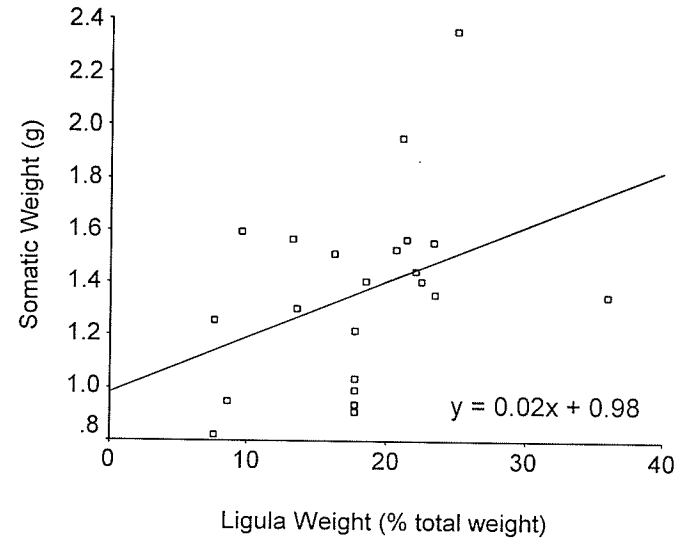
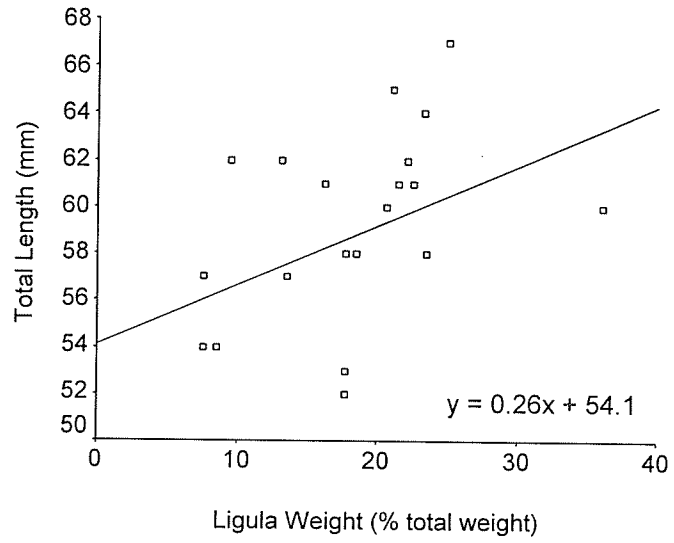
The effects of this parasite on the shiners were examined by linear regression analysis of length and weight measurements of infected versus uninfected fish. Statistical analyses were performed with Microsoft Excel (Office 97 version)

The slope of the regressions of infected fish length and weight showed a small decrease relative to the uninfected fish (Appendix IV-A). Gonad weight, however, was greatly reduced and decreased with infected fish and, thus, parasite age. All uninfected and a single infected female were mature. Szalai *et al.* (1989) observed similar effects of *L. intestinalis* on spottail shiner (*Notropis hudsonius*). In addition, an increase in worm biomass resulted in a decrease in percent gonad weight but not in length or weight (Appendix IV-B). A larger sample size of infected individuals over a greater range of age classes may reveal that length and weight are also affected by increased biomass.

Appendix IV-A. Linear regressions of Triangle Lake blacknose shiner (*Notropis heterolepis*) (a) total length, (b) somatic weight and (c) percent gonad weight versus age for uninfected fish (solid line) and fish infected with *Ligula intestinalis*. A sample size of 76 fish (50 uninfected, 26 infected) were used for total length and somatic weight calculations while only 53 females (30 uninfected, 23 infected) were used for percent gonad regression calculations.



Appendix IV-B. Linear regression scatterplots of infected blacknose shiner (a) total length, (b) somatic weight and (c) percent gonad weight versus the weight of each host's *Ligula intestinalis* infrapopulation (measured as a percent of the fish total weight).



Some preliminary morphometric and meristic characteristics, parasite community and infrapopulation statistics and dietary analysis were performed on yellow perch from four central Manitoba lakes. Total length, age and sex were recorded for 101 Lake Winnipegosis, 100 Lake Manitoba, 100 Lake Winnipeg and 40 Lake Waterhen perch obtained from the commercial fisheries through the Freshwater Fish Management Corporation. Complete necropsies and morphometric analyses as described in the Chapter 2 methodology were performed on subsamples from three of the four lakes; 21 from each of Lakes Winnipegosis and Waterhen and 20 from Lake Manitoba. Parasite infrapopulation statistics were analysed as described in Chapter 2.

Morphometrics and meristics were similar to the ranges observed by Scott and Crossman (1973). Size-at-age of the Manitoba fish (Appendix V-A) was greater than for all ELA perch (Chapter 2). The parasite community of these perch was less diverse than the ELA sample. There are two possible reasons for a smaller parasite fauna; smaller sample of perch and the fish were collected in February when many parasite species population sizes are reduced. There were two species present not observed in ELA; the copepod, *Ergasilus* sp. and *Bunodera lucioperca*. There were also greater intensities of enteric parasites than in ELA that may reflect a higher relative trophic position occupied by the Manitoba perch. This is supported by dietary analysis that shows that fish were the dominant prey type in two of the three lakes examined. Large macroinvertebrates and benthic fish dominated in Lake Waterhen perch stomachs.

Appendix V-A. Length-at-age of male and female yellow perch recovered from four central Manitoba lakes.

AGE (yrs)	Stats	Lk Winnipeg		Lk Manitoba		Waterhen Lk		Lk Winnipegosis	
		F	M	F	M	F	M	F	M
3+	N	0	0	0	0	2	0	0	0
	Mean TL (mm)	0	0	0	0	239.0	0	0	0
	St Dev	0	0	0	0	1.4	0	0	0
4+	N	0	0	0	0	17	1	6	31
	Mean	0	0	0	0	225.0	214.0	226.2	96.1
	SE	0	0	0	0	12.0	n/a	13.1	9.7
5+	N	4	0	3	0	12	2	37	1
	Mean	231.2	0	233.7	0	239.0	224.0	248.5	226.0
	SE	7.8	0	18.9	0	11.0	3.5	11.0	n/a
6+	N	17	0	5	0	4	0	15	1
	Mean	239.4	0	239.2	0	258.0	0	263.5	243.0
	SE	8.0	0	8.9	0	18.0	0	12.5	n/a
7+	N	17	1	49	1	2	0	16	1
	Mean	243.4	220	247.1	213.0	252.0	0	268.1	247.0
	SE	15.5	n/a	13.4	n/a	7.0	0	16.3	n/a

Appendix V-B. Morphometric and meristic measurements of 20 Lake Manitoba yellow perch. All distance measurements are in millimetres and all weights are in grams. Percent gonad weight is measured for females only.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	%GWt.	Age
Mean \pm	249.7 \pm	238.9 \pm	64.05 \pm	37.95 \pm	61.70 \pm	18.20 \pm	14.25 \pm	211.8 \pm	12.19 \pm	7.66 \pm
St Dev	16.34	16.00	4.63	2.72	5.25	1.15	0.85	38.37	1.95	1.29
Range	209-310	198-298	56-74	34-46	52-72	17-20	13-16	119.6- 339.3	9.15- 15.64	5-12

<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Pvr	Pcr	1Ds/r	2Ds	2Dr
Mode	6	14	3	2	7	1	5	14	14	2	13
Range	6-7	14-15	3-3	2-2	7-8	1-1	5-5	13-14	13-14	2-3	12-14

Appendix V-C. Morphometric and meristic measurements of 21 Lake Waterhen yellow perch. All distance measurements are in millimetres and all weights are in grams. Percent gonad weight is measured for females only.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	%GWt.	Age
Mean \pm	234.2 \pm	223.7 \pm	60.52 \pm	35.10 \pm	55.24 \pm	17.19 \pm	13.71 \pm	164.9 \pm	10.49 \pm	4.65 \pm
St Dev	16.18	15.97	4.65	2.61	5.64	1.29	1.31	34.32	1.54	0.92
Range	206-281	196-268	52-71	32-43	46-67	15-20	11-17	110.4- 253.9	8.33- 13.49	3-7

<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Pvr	Pcr	1Ds/r	2Ds	2Dr
Mode	6	14	3	2	7	1	5	14	13	3	13
Range	6-8	13-15	3-3	2-2	7-9	1-1	5-5	11-15	11-15	2-3	11-13

Appendix V-D. Morphometric and meristic measurements of 21 Lake Winnipegosis yellow perch. All distance measurements are in millimetres and all weights are in grams. Percent gonad weight is measured for females only.

<u>Morphometric Measurements</u>	TL	FL	HL	PL	D	CP	IOW	Wt.	%GWt.	Age	
Mean \pm St Dev	259.5 \pm 21.35	249.3 \pm 21.12	63.57 \pm 5.40	37.14 \pm 2.56	61.71 \pm 6.35	18.57 \pm 1.69	15.14 \pm 0.96	245.5 \pm 63.13	10.61 \pm 1.62	6.14 \pm 1.57	
Range	210-310	199-299	52-76	33-41	51-74	16-22	14-17	109.5- 411.6	8.15- 14.36	4-11	
<u>Meristic Measurements</u>	GR(u)	GR(l)	DC	As	Ar	Pvr	Pvr	Per	1Ds/r	2Ds	2Dr
Mode	7	14	3	2	7	1	5	14	13	3	13
Range	6-7	13-15	3-3	2-3	6-8	1-1	5-5	11-15	13-14	2-3	12- 14

Appendix V-E. Infection statistics of parasite infrapopulations of yellow perch recovered from three central Manitoba lakes. The prevalence is given followed by the mean intensity \pm standard deviation with the range in parentheses. The number of fish of each species examined from each lake is indicated by n.

Parasite	Path of infection	Site of infection	Lake Manitoba N = 20	Lake Waterhen N = 21	Lake Winnipegosis N = 21
<u>Ectoparasites</u>					
<i>Urocleidus</i> sp.	direct	gills	5.0 1.0 (5)	28.6 2.8 ± 2.1 (1-7)	4.8 2.0 (2)
<i>Ergasilus</i> sp..	direct	gills	60.0 4.8 ± 5.7 (1-21)	47.6 2.5 ± 3.9 (1-5)	76.2 4.2 ± 4.1 (1-18)
<u>Larval parasites</u>					
<i>Apophallus brevis</i>	direct	skin and flesh	55.0 2.9 ± 1.5 (1-7)	76.2 12.0 ± 11.4 (1-36)	95.2 44.4 ± 55.9 (2-242)

Appendix V-E. Continued.

Parasite	Path of infection	Site of infection	Lake Manitoba N = 20	Lake Waterhen N = 21	Lake Winnipegosis N = 21
<i>Diplostomum</i> sp.	direct	eyes	15.0	95.2	47.6
			1.0	16.1 ± 20.2	4.4 ± 4.1
			(1)	(1-90)	(1-14)
	direct	mesenteries and	10.0	4.8	52.4
<i>Posthodiplostomum</i>		visceral fat	1.0	3.0	16.5 ± 18.3
<i>minimum</i>			(1)	(3)	(1-53)
<u>Enteric parasites</u>					
<i>Bunodera</i>	mayfly ingestion	intestine	30.0	90.5	52.4
<i>lucioperca</i>			7.5 ± 13.7	58.1 ± 91.3	4.8 ± 8.5
			(1-37)	(2-328)	(1-30)
<i>Crepidostomum</i>	mayfly ingestion	intestine	10.0	38.1	23.8
<i>cooperi</i>			2.5 ± 0.7	80.1 ± 155.9	2.2 ± 0.8
			(2-3)	(2-458)	(1-3)

Appendix V-E. Continued.

Parasite	Path of infection	Site of infection	Lake Manitoba N = 20	Lake Waterhen N = 21	Lake Winnipegosis N = 21
<i>Bothriocephalus</i>	copepod ingestion	intestine	90.0	9.5	47.6
<i>cuspidatus</i>			14.7 ± 12.4 (1-49)	1.5 ± 0.7 (1-2)	3.5 ± 3.1 (1-9)
<i>Proteocephalus</i>	copepod and fish	intestine	100.0	52.4	71.4
<i>pearsei</i>	ingestion		40.5 ± 56.1 (2-233)	3.3 ± 2.2 (1-8)	8.1 ± 7.8 (1-30)
<i>Pomphorhynchus</i>	amphipod	intestine	5.0	38.1	0
<i>bulbocolli</i>	ingestion		2.0 (2)	1.8 ± 1.2 (1-4)	
Acanthocephala	amphipod	intestine	10.0	38.1	4.8
sp.	ingestion		2.0 ± 1.4 (1-3)	3.4 ± 4.8 (1-15)	1.0 (1)

Appendix V-E. Continued.

Parasite	Path of infection	Site of infection	Lake Manitoba N = 20	Lake Waterhen N = 21	Lake Winnipegosis N = 21
<u>Other parasites</u>					
<i>Raphidascaris acus</i>	chironomid and perch ingestion	liver	0	14.3 9.7 ± 7.5 (4-21)	71.4 20.4 ± 41.5 (1-172)
Nematoda sp.	benthic invertebrate ingestion	intestinal wall	90.0 4.1 ± 5.9 (1-25)	85.7 8.7 ± 8.9 (1-34)	42.9 8.7 ± 5.7 (2-16)

Appendix V-F. The percent stomach contents of yellow perch from three central Manitoba lakes. Totals may add up to more than 100% for each lake.

Prey Type	Lake Manitoba N = 20	Lake Waterhen N = 21	Lake Winnipegosis N = 21
Empty	60.0	33.3	61.9
Benthic prey			
Ephemeroptera	0.0	4.8	19.0
Odonata	0.0	4.8	0.0
Corixidae	0.0	4.8	0.0
Amphipoda	0.0	47.6	0.0
Pelagic/Benthic prey			
Fish	40.0	42.9	19.0