COMMUNITY STRUCTURE OF HELMINTH PARASITES IN WHITEFISH FROM THE CARIBOU MOUNTAINS, ALBERTA

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ABSTRACT

Spatial patterns in parasite communities of freshwater fish are often characterized as low in diversity and unpredictable. Whether or not this view is a true reflection of community patterns is unclear, in particular when comparing studies of parasite communities of fish occurring in man-altered ecosystems. To understand the structure of a fish parasite community, I first described the parasite fauna of 13 species of freshwater fish from 19 islolated lakes on the Caribou Mountains plateau in northern Alberta. After my initial broad-scale survey, I selected the diverse and complex community of parasites in whitefish, (Coregonus clupeaformis) for further analysis. This host had the most diverse parasite community of any species of fish on the plateau and was disproportionally important in the dissemination of parasites to the other species of fish.

Ten parasite species infected whitefish in the 7 large lakes on the plateau; 7 were core species (i.e found in every lake) and 9 were salmonid specialists. Parasite intensities were much higher (>100 per host) in the Caribou Mountains than elsewhere in Canada, as was community similarity (>70%). Ordination analyses showed that 48% of the variation in parasite intensities between lakes could be explained by factors associated with aquatic productivity (e.g. chlorophyll-a and total phosphorus). Low-intensity lakes were characterized by low productivity and high colour and high-intensity lakes had high productivity and low colour. Patterns of high similarity between lakes, together with the association between aquatic productivity and community structure shows that the spatial structure of parasite communities can be predicted on the basis of a common suite of specialist, core species.

PREFACE

"Grab the hook, grab the line,

Grab the bait, grab the box and wait..."

- by Speech from Arrested Development, 1992

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Chapter 1. General Introduction

Understanding the factors that lead to spatial variation in species richness and abundance has long been a central aim of community ecologists. The extent and inherent complexity of this variation has been well studied, from both ecological and evolutionary viewpoints, over scales ranging from highly localized habitats to entire biogeographical regions (reviews by Ricklefs and Schluter, 1993; Huston, 1994). However, identification of the factors and processes leading to extensive spatial variation are controversial and poorly understood (e.g. Currie et al., 1999). This is a fundamental and important shortcoming, particularly since variation in species richness and abundance is of increasing practical concern to conservation biologists and planners. The spatial context of species richness and abundance is also central to modern approaches in biogeography (Begon et al., 1996), epidemiology (Grenfall and Harwood, 1997), coevolution (Thompson, 1994), life-history variation (Stearns, 1992) and landscape ecology (Turner, 1989).

The concept of predictability is central to the idea of spatial variation in community structure. In essence, a predictable community can be defined as one where patterns in species presence, richness and (or) diversity are repeated in other communities defined at the same scale (Rosenzweig, 1995). Thus, similar sites should contain similar species. This will be especially apparent if they responded similarly to specific features of their environments, such as productivity, nutrient availability and disturbance. If they do, then species will regularly co-occur and will potentially interact. Such communities could possibly demonstrate regulated, equilibrial community structure (Sousa, 1994). If they do not, then the debate is not about what forces structure communities, but whether there is identifiable structure at all (Simberloff, 1990).

Parasite ecologists have long been interested in the extent to which hosts, or host populations, contain parasites that demonstrate predictable community structure. In general, their focus has been on questions that parallel those addressing free-living systems (reviews by Esch et al., 1990; Sousa, 1994; Poulin, 1996; Poulin, 1997). Thus, do 2 hosts collected from the same site contain similar species with similar abundances? Similarly, do hosts collected from 2 neighbouring sites (e.g. two lakes, islands, mountaintops) have similar patterns of parasite species richness and abundance? Lastly, do hosts collected from across their geographical range demonstrate predictable community structure? Many of these questions have been asked using parasite communities of fish. These hosts are usually abundant, relatively easy to collect, and they are often representative of water bodies that are themselves isolated and independent (Kennedy, 1990).

One approach has been to understand zoogeographical patterns in community structure over broad geographical ranges of their hosts (e.g. Manter, 1940; Polyanski, 1961; Price and Clancy, 1983; Rhode, 1992; Holmes, 1990; Marcogliese and Cone, 1996; Blaylock et al., 1998; Choudhary and Dick, 1998;

Carney and Dick, 1999). In general, despite often tremendous variation in community structure between widely scattered sites, factors such as host phylogeny (Halvorsen, 1971; Wooten, 1973; Anderson et al., 1990; Valtonen and Julkunen, 1995; Dubois et al., 1996), host size (Guégan and Hugueny, 1994), host geographical range (Price and Clancy, 1983), parasite host specificity (Wisniewski, 1958; Dogiel, 1961; Kennedy, 1978a; Leong and Holmes, 1981; Esch et al., 1988; Marcogliese and Cone, 1991a; Bergeron et al., 1997), chance colonization (Kennedy, a, b; Kennedy et al., 1986; Esch et al., 1988; Hartvigsen and Kennedy, 1993), host diet (Dogiel, 1964; Bergeron et al., 1997) and lake characteristics (Wisniewski, 1958; Dogiel, 1961; Marcogliese and Cone, 1991b; Bergeron et al., 1997) tend to provide underlying patterns of similarity and predictability.

A second approach has been to consider the spatial context of parasite communities at a more regional scale. Here, parasite community structure is compared between individual hosts collected from different bodies of water (e.g. fish as hosts; Hartvigsen and Kennedy, 1993; salamanders as hosts; Goater et al., 1987; birds as hosts; Bush and Holmes, 1986), different islands (e.g. lizards; Dobson, 1992 a and b; Bundy et al., 1987) and different reefs in an archipelago (Holmes, 1990). This scale of enquiry is usually referred to as a component community (Bush et al., 1997) and parallels a portion of the metacommunity of free-living organisms described by Hanski (1991). At this scale, focus is aimed at determining whether hosts collected from at least two different 'areas' have consistent patterns of species richness, diversity. Focus is then aimed at determining whether patterns are predictable on the basis of area size, distance between areas, connectivity between areas (Hartvigsen and Halvorsen, 1994) and other parameters (e.g. lake depth).

The degree to which parasite component communities in fish are predictable is controversial. There are two opposing viewpoints. The first comes from an extensive set of studies on parasite communities of a wide variety of fish in Europe. Evidence from studies on trout (Kennedy, 1978b; Hartvisen and Kennedy, 1993), arctic char (Kennedy, 1978a) and eels (Kennedy, 1990), support Kennedy's contention that the random colonization of parasite species into an area make it impossible to predict component community structure. These findings led Hartvigsen and Kennedy (1993) to conclude that "Helminth communities in freshwater fish are fundamentally stochastic...dependent on chance introductions...and extinction events". The alternative viewpoint holds that aquatic habitats with similar trophic status, limnologicial characteristics and hydrological characteristics will have similar parasite communities. For example Esch et al. (1988) concluded that "...the character of a water body...influences and determines the composition of the parasite species present".

Addressing this controversy is an important but elusive goal in parasite community ecology (Bush et al., 1995). One problem is the notorious variability in parasite population sizes between individual hosts (Poulin, 1997). Given this variation at the population level, it is not surprising to find it compounded at the community level (Aho and Bush, 1993, Ricklefs and Schluter, 1993). In addition, variation in the scope of the studies (number of host species studied), their scale (geographical size of the study area) and the taxonomic scale of species identifications (e.g. family, genus, species), makes generalizations between studies extremely difficult (Aho and Bush, 1993; Hartvigsen and Halvorsen, 1994).

One important restriction on our ability to address the controversy is that almost all studies are undertaken in anthropogenically altered habitats (Valtonen et al., 1997). Studies by Kennedy and his students characterized parasite communities as low in parasite species diversity and usually dominated by one group of parasites, the acanthocephalans. (Kennedy, 1977, 1978a; 1978b; Kennedy, 1990; Hartvigsen and Kennedy, 1993, Guégan and Kennedy, 1993; Kennedy and Guégan, 1994). However, these studies occurred in highly altered areas in Europe. The effects of adding a non-native fish species on parasite community dynamics were dramatically demonstrated by Leong and Holmes (1981). Similarity between fish infracommunities declined almost 3 fold when the acanthocephalan Metaechinorhynchus salmonis from introduced coho salmon (Onchorhynchus kisutch) was removed from the analysis. Similarly, the cestode Triaenophorus crassus was eliminated from a lake after the pike population was reduced over a period of 15 years (Doan, 1945; Lawler, 1961). Thus, the addition or elimination of a fish species through human activity can alter parasite community structure.

Changes to a lake drainage basin, including tree harvesting, dams, water diversion and disposal of industrial, domestic and agricultural waste (Mitchell and Prepas, 1990, Valtonen et al., 1997) can have a direct impact on water quality or lake productivity (Mitchell and Prepas, 1990). These changes can also affect parasite and host communities (Valtonen et al., 1997). Chemical pollution effects can be complex (Khan and Thulin, 1991), but can affect the presence and abundance of both parasite and host species (Hirschfield, 1983; Sprent, 1992; Kennedy and Bush, 1995). For instance, lake eutrophication has been identified to increase the abundance of digenetic trematodes, specifically diplostomids (Hartmann and Numann, 1977). Alterations to lake productivity have frequently been implicated to affect parasite community structure (e.g. Esch, 1971; Valtonen et al., 1997), but this link has never been explicitly tested.

Most studies are primarily descriptive and infrequently test alternatives (Currie et al., 1999). For example, the importance of determining the association between parasite component community structure in fish and trophic status, or other limnological characteristics, requires a large-scale, multi-disciplinary study. As indicated by Bush et al. (1995), multi-discipline studies of this magnitude are very rare in parasite ecology. Unfortunately, when they have been previously attempted, success has been limited (Kennedy, 1977; Kennedy, 1978a; Kennedy, 1978b; Kennedy et al., 1986; Hartvigsen and Halvorsen, 1995).

The ideal system to address this controversy should examine fish from relatively pristine temperate lakes. To reduce taxonomic identification problems, both the fish species and the parasite species should be well known, because parasite species diversity needs to be assessed for all fish species, from all lakes, in a defined geographical region. In doing so, the important fish and parasite species can be determined for the Caribou Mountains, and both scope and scale problems can be reduced. To go beyond a descriptive survey, a multi-disciplinary study is also required. This approach will provide a variety of abiotic and biotic environmental factors to evaluate their effect on parasite community structure. Also, by examining numerous lakes within one geographical region, the importance of lake size (e.g. lake area), minimum lake distance and connectiveness on parasite community structure can be analyzed (Hartvigsen and Halvorsen, 1994).

The purpose of this thesis is to examine spatial patterns of parasite community structure (between fish and between lake) in fish collected from isolated, pristine lakes in northern Alberta. Both the fish and parasite species from northern Alberta, specifically from lakes in the boreal forest, are well known throughout Canada (Millar, 1946; Millar, 1952; Smith, 1970; Margolis and Arthur, 1979; Leong and Holmes, 1981; Nelson and Paetz, 1992; McDonald and Margolis, 1995 and references within). Individuals from every fish species could be collected from all accessible lakes. Besides examining parasite faunas, fish communities, invertebrate communities, limnology and hydrology were analyzed as part of a concurrent, multi-disciplinary study involving the same lakes (Caribou Mountains Research Partnership –see below).

Objectives of the thesis

Chapter 2 characterizes the helminth fauna of all fish species (n=13) collected from every accessible lake on the Caribou Mountain plateau (n=19). The main aim is to determine the relative role of each host species in the dissemination and transmission of parasites throughout the lakes on the plateau (e.g. Leong and Holmes, 1981). This broad-scale approach also allowed me to assess patterns of host use by parasites, especially the extent to which each species was locally specific to particular hosts. In addition, parasite community patterns described in lake whitefish were compared to other North American studies (i.e. Chinniah and Threfall, 1978; Leong and Holmes, 1981; Drouin, 1982; Poole, 1985). As such, this chapter formed the foundation for the subsequent chapters.

Chapter 3 describes the spatial pattern of parasite communities of lake whitefish (Coregonus clupeaformis) collected from the 7 lakes on the plateau that contain whitefish. The approach in this chapter parallels that taken in the studies by Kennedy (1990), Valtonen et al. (1997), Poole (1985) and others on anthropogenically-altered systems. The first aim is to compare patterns of community richness, abundance and similarity among the 7 lakes in order to identify whether helminth communities form a predictable structure. The second is to determine whether variation in lake connectedness, proximity, and size played a role in determining variation in community structure between lakes.

The purpose of Chapter 4 is to determine whether variation in spatial structure described in Chapter 3 is associated with variation in the biotic and abiotic characteristics of the lakes. This chapter focuses on the extent to which communities of parasites are predictable on the basis of shared environmental variables among lakes. The multi-disciplinary nature of the CMRP enabled me to examine whether variation in limnological, morphological, hydrological and fish populations could influence the structure of the parasite component community of lake whitefish. Also, I could specifically evaluate the link between productivity and parasite community structure (Esch, 1971), because four environmental variables reflected lake productivity (Mitchell and Prepas, 1990).

Caribou Mountains Research Partnership

The Caribou Mountains Research Partnership (CMRP) provided an unique opportunity to address the shortcomings of previous studies. Initiated in 1996, the CMRP was created between the Network of Centres of Excellence for Sustainable Forest Management (SFM-NCE) and the Little Red River Cree and Tall Cree First Nations. Using a multi-disciplinary approach, CMRP combined scientific knowledge with First Nations traditional ecology to develop a co-operative management approach for managing the natural resources on the Caribou Mountains plateau. Studies included research on water quality, paleolimnology, fish, fish parasites, aquatic macroinvertebrates, vegetation, ecotourism and moose. Biological, cultural and economic sustainability issues were common themes in each project (Scrimgeour et al., 1997a).

Parasite component communities were examined in a series of boreal forest lakes that have undergone little, if any, human alteration (Scrimgeour et al., 1997a). To maximize information recovered for each individual fish, the same fish were examined in both the parasite and fisheries studies. The fish parasite study was initially designed to quantify the prevalence and abundance of parasites in the Caribou Mountains fish community (Scrimgeour et al., 1997b). However, to better understand parasite community structure, data from the fisheries, limnology and hydrology surveys were incorporated into the parasitology study. After determining whether a specific parasite community pattern was repeated between lakes, I could then use the available environmental co-variates to determine if it was possible to predict parasite community structure.

Chapter 2. Composition of the parasite fauna of fish from the Caribou Mountains, northern Alberta.

INTRODUCTION

One of the fundamental factors that affects the numbers of parasites within an assemblage is the size of the species pool that is available for colonization (Poulin, 1997). This pattern holds whether the scale of inquiry is between individual hosts in a single sample (infracommunities), between hosts collected from two or more populations (component communities), or between species of hosts collected over a part of their geographical range (review in Chapter 1). For component communities, one critical factor that will influence the size of the species pool is the structure of the host community (Holmes, 1979), and the opportunity for exchange of parasites among hosts. For example, differences in parasite species richness between populations of avocets in southern Alberta were best explained by the extent to which birds co-occurred with lesser scaup ducks (Edwards and Bush, 1989). When avocets were collected from populations containing scaup, parasite species richness approximately tripled. The extent of parasite exchange also determines patterns of species richness among parasite communities in geese (Nerasson and Holmes, 1975), grebes (Stock and Holmes, 1987), rockfish (Holmes, 1990) and salamanders (Goater et al., 1987). In each example, the most important determinant of the variation in species richness was the extent to which generalist parasites were exchanged between hosts.

The role of parasite exchange in determining variation in parasite component community structure in fish is not well known. One of the problems is that to adequately address the question, samples of all relevant hosts in the host community need to be examined for parasites. Although this approach greatly increases the scope and scale of an investigation, it is prohibitively time-consuming and expensive. Another problem is that the few studies that have examined parasite exchange have been done on fish communities collected from highly altered watersheds (Leong and Holmes, 1981; Kennedy et al., 1986b) or have been done on parasites infecting marine fishes (Holmes, 1990). Leong and Holmes (1981) documented extensive exchange between species of fish within Cold Lake, Alberta with a specific focus on one parasite species introduced when populations of its host, coho salmon, were stocked into the lake. Almost all of the exchange involved this particular parasite. Thus, the role of parasite exchange and associated patterns of host specificity were affected by the introduction of a new fish species and its parasites as suggested by other examples discussed by Dubois et al. (1996) and Bergeron et al. (1997).

The purpose of this chapter is to describe the composition of the parasite communities in all species of fish on the Caribou Mountains plateau. As such, it forms the foundation for each of the remaining chapters. My aim is to take a broad-scale, regional approach in describing the general presence and abundance of the species of parasites found in lakes on the plateau. Collections and analyses were designed to answer the following questions: Does parasite exchange contribute to differences in species richness among host species? Is the magnitude of parasite exchange associated with host phylogeny or the structure of the host community? Do different fish species contribute equally to the overall circulation of parasites within Caribou Mountain lakes?

MATERIALS AND METHODS

Study area

The region referred to as the 'Caribou Mountains' is an isolated, 4300km^2 region in the central, northern-most part of Alberta. The region is bordered to the north by the Northwest Territories (60^{0}N) and to the east by Wood Buffalo National Park (Figure 2.1). The 'mountains' actually represent a saucer-shaped plateau, demarcated on each side by a 600-700m escarpment (Lee et al., 1982). The plateau is classified as part of the Boreal Forest Natural Region, (Alberta Environmental Protection, 1998); an area that also encompasses 3 natural sub-regions, including the Subarctic, the Boreal Highlands and the Wetland Boreal (Achuff, 1994). Four areas within the Caribou Mountains are designated as 'provincially significant, environmentally-sensitive areas' together with part, or all, of eight 'regionally significant environmentally-sensitive areas' (Bilyk et al., 1996).

The topography on the plateau is rolling (Lee et al., 1982), comprised of sedimentary bedrock overlayed with till, gravel, sand and clay deposits (Smith,

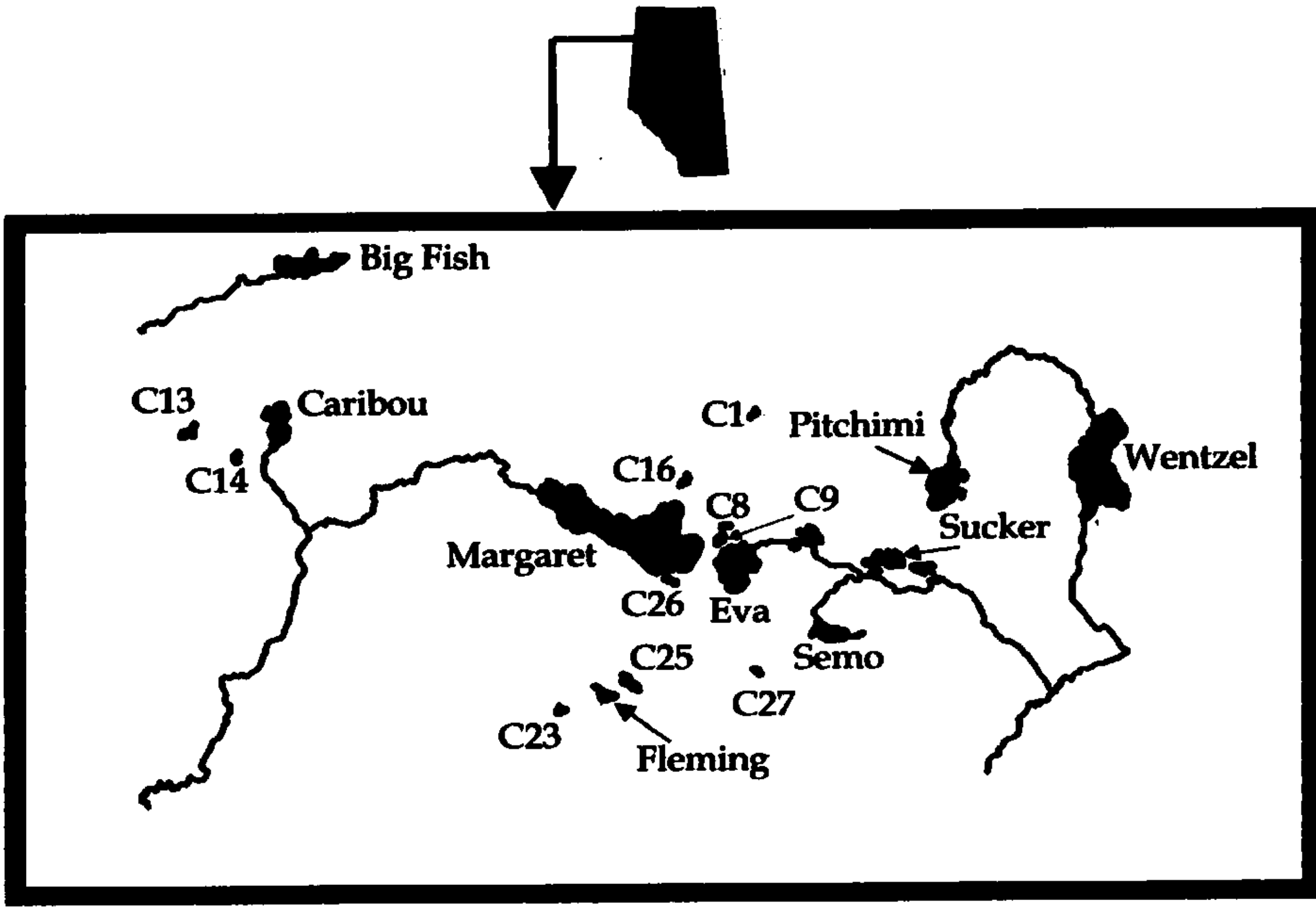

Figure 2.1. Locations of the 19 Caribou Mountains study lakes included in the freshwater fish parasite community analysis.

1970). Organic soils occur widely over the plateau, frozen at depths from 35 to 50cm below the surface. There is no evidence of permafrost in the mineral soils, which consist of grey wooded and brown wooded soils developed on glacial till (Lee et al., 1982). Summers are short and cool, with an average of 160 frost-free days (Smith, 1970). There have been no permanent settlements established in the area apart from a fishing lodge built in 1961 on the southeastern shore of Margaret Lake (Rhude, 1976). During the ice-free period, the only access to the plateau is by plane.

Both sub-arctic and arctic flora and fauna occur on the plateau (de Vries, 1997). The boreal forest is a mosaic of dense black spruce forest (Scrimgeour et al., 2000a) interspersed with pine, understory woodland herbs, birches (Betula papyrifera) and Alder (Alunus crispa) (Lee et al., 1982). Endemic and rare species of bryophytes, lichen, and vascular plants, occur on the plateau (de Vries, 1998), together with endangered species such as the woodland caribou and red throated loon.

Numerous lakes, ponds and sloughs are interspersed within the boreal forest on the plateau (Lee et al., 1982; Penner and Associates Ltd., 1999). Lake sizes range from <1m (sloughs) to 8160ha (Margaret Lake) (McEachern and Prepas, unpublished data). Maximum lake depth in the large lakes ranged from 6m in Sucker Lake to 57.9m in Wentzel (McEachern and Prepas, unpublished data). Eight of the 10 large lakes investigated are classified as oligotrophic, while Sucker and Eva are considered meso-oligotrophic (Mitchell and Prepas, 1990).

Water drainage flows off the plateau into the Arctic Ocean via the Peace River to the Mackenzie River (Lee et al., 1982).

Fish Collections

Ten small, unnamed lakes and 4 large lakes were visited between 8 July - 22 August, 1996. The nine larger lakes were sampled between 14-22 July, 1997 (Table 2.1). Access to Margaret and Eva Lakes was by foot or boat; all other lakes were accessed by floatplane. Arctic grayling (Thymallus arcticus Pallas), burbot (Lota lota Linnaeus), lake cisco (Coregonus artedii Lesueur), lake trout (Salvelinus namaycush Walbaum), lake whitefish (C. clupeaformis Mitchell), longnose sucker (Catastomus catastomus Forster), ninespine stickleback (Pungitius pungitius Linnaeus) northern pike (Esox lucius Linnaeus), pearl dace (Marariscus margarita Cope), slimy sculpin (Cottus cognatus Richardson), trout perch (Percopsis omiscomaycus Walbaum), walleye (Stizostedionis vitreum vitreum Mitchell) and white sucker (C. commersoni Lacepede) were collected with gillnets.

Each gillnet was comprised of 14 panels of different mesh sizes, ranging from 6.25 to 75mm in an exponentially increasing series (Scrimgeour et al., 1997b). Each panel was 3m long and 1.5m wide, giving a total net area of $63m^2$. Depending on the depth of each lake, up to three different net setting depths were used: <3m, 3-6m or >6m. Of the 106 nets set, seventy-seven percent were

Table 2.1. Number processed and species composition of fish collected from the Caribou Mountains study lakes in 1996 (July 8-August 22) and 1997 (14-22 July).

FISH	ARGR	BURB	CISC	LKTR	LKWH	LNSC	NNST	NRPK	PRDC	SLSC	TRPH	WALL	WHSC	Total # of Fish
LAKE (1996)														
C1								10						10
C8	1					4		10						15
C9								10						10
C13	4													4
C14								10						10
C16	3							10						13
C23	10					10			10					30
C25	8	3						10						11
C26								10						10
C27	10													10
Margaret		5												5
Eva		4												4
Semo		1												1
Wentzel		3				8							5	16
LAKE (1997)														
Margaret			12	8	25	10		6		7	4			73

Table 2.1
Continued

Eva	10		10		25	7	16	10					11	89
cke r			5		24		36	10					10	66
Big Fish			10			10		10			14		10	55
Caribou		_	10	1	7	1		6			11	10	_	46
Semo		_	10	10	18	10	_	7						55
Fleming	9	_						10						19
Pitchimi				1	16		7	10					_	28
Wentzel		_	4		20	_		6			4	10	2	46
TOTAL	55	16	61	20	135	60	59	145	10	7	33	20	38	625

ARGR = arctic grayling; BURB = burbot; CISC = lake cisco; LKTR = lake trout; LKWH = lake whitefish; LNSC = longnose sucker; NNST = ninespine stickleback; NRPK = northern pike; PRDC = pearl dace; SLSC = slimy sculpin; TRPH = trout perch; WALL = walleye; WHSC = white sucker; _ = known to occur in lake (Scrimgeour et al, 1997b), but not examined for parasites set at <3m where it was assumed fish abundance and biomass would be highest, as this is where lake water volume was highest (Scrimgeour et al., 1997b).

Gillnets were placed at random points around the perimeter of each lake. Randomization involved designating 20 points on a map of the lake's perimeter, ensuring that 4-5 points fell within the north, south, east and west quarters of each lake. The number of nets set overnight for 14-16 hours determined fishing effort per lake (Scrimgeour et al., 1997b). One unit of fishing effort was defined as one overnight net set. Thus, in relation to lake surface area and maximum depth, as few as three nets to a maximum of 16 nets were set per lake in order to obtain a representative sample of the fish community. To keep depth zones consistent, all gillnets were set parallel to the shoreline (Scrimgeour et al., 1997b).

Fish species identification and enumeration was done for the catch of each gillnet. In cases where each gillnet contained large numbers of fish, I haphazardly selected 1-5 size-matched adults. Thus, one sample of each fish species, from each lake, comprised from 8-40 adults. All fish were processed on land at the Margaret Lake Fishing Lodge. For each individual, total length, weight and sex was determined. Total length was measured as the length from the tip of the snout to the end of the caudal fin. Whole fish weight was determined with an ACCULAB V330 balance (± 0.1g) for small fish (<300g) or an ACCULAB V3000 balance (± 1g) for large fish (>300g and <3000g). Fish sex was determined by examination of gonad tissue (Scrimgeour et al., 1997b). Trout perch, slimy sculpins, ninespine stickleback, and pearl dace were frozen whole and necropsied at the University of Lethbridge.

Collection and enumeration of parasites

Fillets of lake whitefish, lake trout, artic grayling and cisco were immediately examined to obtain counts of the cysts of the cestode Triaenophorus crassus known to infect salmonids. The fillets were cut into approximately 1cm-wide strips to count those cysts buried deep within the muscles (Amundsen and Kristoffersen, 1990). After counting all T. crassus cysts, and the viscera (heart, stomach, intestine, swim bladder and liver) were stored in individual whirlpak bags, and frozen for subsequent necropsy at the University of Lethbridge.

Fish samples were thawed prior to parasite enumeration. Necropsies of internal organs followed standard protocols for fish (Arthur and Albert, 1994). To increase the manageability of the intestine and to collect specimens in good condition, the intestine was measured, then divided into five equal sections following Bush and Holmes (1986). The life-cycle stage of a parasite was classified as either immature (sex organs not fully developed and no eggs present) or mature (fully developed sex organs and/or the presence of eggs). In high intensity infections (>500 worms), dilution counts were used. Two 10mL aliquots were removed from 100mL of distilled water containing the parasites. All parasites were counted and identified separately in each aliquot. If estimates of parasite intensity in the two aliquots were not within 10% of each other, a third aliquot was examined (Bush and Holmes, 1986).

The preparation of parasites for identification followed standard procedures (Ash and Orihel, 1991). Trematodes, cestodes and acanthocephalans were removed from Petri dishes, washed in distilled water, and fixed in alcohol-formic acetic acid (AFA). Specimens were then stored in 70% ethanol, stained with acetocarmine, cleared in xylene and mounted in Canada Balsam. Nematodes were washed and stored in 5% glycerine-alcohol. Samples of nematodes were cleared in lactophenol and examined in temporary mounts under the compound microscope.

Analyses

The mean intensity (= mean number of individuals per infected fish), and prevalence (= percent of host sample infected) of each parasite species was calculated for each species of fish from each lake (Bush et al., 1997). Median intensities were also calculated as an additional indicator of central tendency for parasite counts.

Parasite exchange between hosts was evaluated two ways. First, the exchange of parasite species was determined by assessing the extent to which the same parasite life-cycle stage was recovered from at least two different host species (Leong and Holmes, 1981). Similarity was then determined using the proportion of the total number of parasite individuals of each species that were found in each host species. The aim of this analysis was to determine if the majority of each species was found in only one host, or was spread evenly among available hosts. I also determined the relative abundance of each fish species in a lake in order to determine if the regionally dominant host had the regionally dominant parasite species (Leong and Holmes, 1981).

After initially describing parasite communities in the region, I then compared whether patterns identified on the plateau reflected those patterns previously described from other lake studies in North America. For this analysis, the parasite fauna of the regionally dominant host were selected and parasite intensities were compared among studies. Only those lakes containing the dominant host were included.

Taxonomic considerations

Community-level studies rest on the accuracy of taxonomic identifications and the ability to distinguish between taxa. In this study, species identification was straightforward for a number of parasites, especially the most common ones such as Triaenophorus spp. (Chubb, 1963a and b), Diphyllobothrium spp. (Anthony, 1967), P. bulbocolli (Schmidt, 1992) and C. erraticus (Olsen, 1974). Others such as Proteocephalus spp., R. acus, N. crassus and N. rutili were clarified through the use of taxonomic keys (Yamaguti, 1961; Freze, 1969; Petrochenko, 1971) and comparison with specimens in the University of Alberta parasitology collection. Those parasites not identified to species included rare larval forms (e.g. Bothriocephalus sp. 2 from burbot) with no visible diagnostic characteristics described in keys. Thus, for the purposes of this study, all abundant and common species were identified to species. Those that were not, were rare species that contributed little to the overall exchange and dissemination of parasites on the Caribou Mountains.

RESULTS

Composition of the fish fauna

Thirteen fish species belonging to nine families were found in the Caribou Mountains. The Salmonidae were represented by four species, while the other eight families had one to two species each. Northern pike was the most widespread fish species, recovered from 16 of the 19 study lakes. Pike and (or) arctic grayling were usually the only fish species present in the small lakes (Table 2.1). One distinctive suite of fish in the large lakes consisted of northern pike, lake whitefish and lake cisco, collected from six out of the nine lakes. Other fish species had more sporadic distributions. For example, walleye and lake trout were only collected from two of the large lakes.

Composition of the parasite fauna

Of the 1686 fish collected, 625 were examined for parasites (Table 2.1). Thirty parasite species were recovered: seven digeneans, fifteen cestodes, five nematodes and three acanthocephalans (Table 2.2). All parasite species have been previously reported from Alberta (McDonald and Margolis, 1995). Eight

Table 2.2. Site location, host species and life cycles of thirty parasite species collected from thirteen freshwater fish species from the Caribou Mountains, Alberta.

			Life Cycle			
	Location	Host Species	First Host	Second Host	Definitive Host	Reference'
TREMATODA						
Alleocreadid sp. 3*	I	PRDC	snail	?	PRDC	Schell (1970)
Bunodera sp.*	C/I	TRPH	Lymnaea	na	TRPH	McDonald and Margolis (1995)
Crepidostomum farionis (Müller, 1776) Stiles and Hassall, 1898*	S/C/I	LKWH/NPRK/ WALL	fingernail clam	mayfly larvae	CISC/LKWH	Olsen (1974)
Diplostomum Spathaceum (Ruldolphi, 1819) Olsson, 1819**°	E	TRPH	snail	teleost fish	piscivorous bird	Olsen (1974)
Diplostomum baeri bucculentum (Dubois and Rausch, 1948)**	E	CISC/LKWH	snail	teleost fish	piscivorous bird	Shostak et al (1987)

Table 2.2 Continued

Diplostomum sp. 2**	E	SLSC	snail	teleost fish	piscivorous bird	Olsen (1974)
Cotylurus erraticus (Ruldolphi, 1809) Szidat, 1928 metacercaria**	H	ARGR/CISC/ LKWH/TRPH	*Valvata*	CISC/ LKWH	piscivorous bird	Olsen (1974)
CESTODA						
Bothriocephalus cuspidatus (Cooper, 1917)*	S/C/I	WALL	copepod	na	WALL	Schmidt (1992)
Bothriocephalus sp. 1*	S/C/I	LKTR	copepod	na	LKTR	Schmidt (1992))
Bothriocephalus sp. 2*	C	BURB	copepod	na	BURB	Schmidt (1992)
Glaridacris sp.*	I	LNSC/WHSC	oligochaete	na	LNSC/WHSC	Smyth (1976)
Diphyllobothrium dendriticum (Nitzsch, 1824)**	V	CISC/LKTR/ LKWH	copepod	CISC/ LKWH	piscivorous bird	Anthony (1967)

Table 2.2 Continued

Diphyllobothrium ditremum (Creplin, 1825)**	V	ARGR	copepod	ARGR	piscivorous bird	Anthony (1967)
Ligula intestinalis (Linnaeus, 1758)**	BC	WHSC	copepod	WHSC	piscivorous bird	Smyth (1976)
Proteocephalus laruei (Faust, 1920)*	S/C/I	CISC	copepod	na	CISC	Smyth (1976)
Proteocephalus neglectus (La Rue, 1911)*	S/C/I	CISC/LKWH/ NRPK/WALL	copepod	na	CISC/LKWH	Smyth (1976)
Proteocephalus parallecticus (MacLulich, 1943)*	S/C/I	LKTR	copepod	na	LKTR	Smyth (1976)
Proteocephalus pinguis (LaRue, 1911)*	S/I	NRPK	copepod	na	NRPK	Smyth (1976)
Schistocephalus solidus (Müller, 1776) Steenstrup, 1857**	BC	NNST	copepod	NNST	piscivorous bird	Smyth (1976)
Triaenophorus crassus (Forel, 1868)* (larvae)	F	CISC/LKWH/ LKTR	Diacyclops bicuspidatus thomasi	CISC/LKTR/ LKWH	NRPK	Chubb (1963)

Table 2.2 Continued

Triaenophorus crassus (Forel, 1868)* (adult)	S/I	NRPK	Diacyclops bicuspidatus thomasi	CISC/LKTR/LKWH	NRPK	Chubb (1963)
Triaenophorus nodulosus (Pallas, 1760) Rudolphi, 1819 plerocercoid*	S/I	NRPK	copepod	BURB/CISC/LKTR/LKWH	NRPK	Chubb (1963)
Triaenophorus stizostedionis (Miller, 1945)* (larvae)	BC	TRPH	copepod	TRPH	WALL	Chubb (1963)
Triaenophorus stizostedionis (Miller, 1945)* (adult)	S/C/I	WALL	copepod	TRPH	WALL	Chubb (1963)
NEMATODA						
Cystidicola farionis (Fischer, 1798) *	AB	CISC/LKTR/LKWH	amphipod	na	LKTR/LKWH	Chaubaud (1975)
Philonema sp.*	On AB	ARGR	aquatic invertebrate	?	ARGR	Chaubaud (1975)
Raphidascaris acus (Bloch, 1779) Raukkuet and Henry, 1915 larva* (larvae)	S/C/I/V	BURB/ARGR/CISC/LKTR/LKWH/NRPK/WALL	amphipod	LKWH	NRPK	Smith (1984a and b)

Table 2.2 Continued

Raphidascaris acus (Bloch, 1779)* (adult)	I	ARGR/NRPK/ WALL	amphipod	LKWH	NRPK	Smith (1984a and b)
Rhabdocona canadensis (Morevac and Arai, 1971)*	I	PRDC	?	?	PRDC	McDonald and Margolis (1995)
Rhabdocona sp. 1*	S/I	SLSC	aquatic invertebrate	?	SLSC	Shostak (1999)
ACANTHOCEPHALA						
Neoechinorhynchus crassus (Van Cleave, 1919)*	S/C/I	LKWH/LNSC/ WHSC	amphipod/ ostracod?	na	LNSC/WHSC	Petrochenko (1971)
Neoechinorhynchus rutili (Müller, 1780) Dechtiar et al. 1989*	I	LKWH	amphipod/ ostracod?	na	?	Petrochenko (1971)
Pomphorhynchus bulbocolli (Linkins in Van Cleave, 1919)*	S/C/I	CISC/LKWH/ LNSC/NRPK/ TRPH/WHSC	amphipod?	LNSC/WHSC	na	Schmidt (1992)

BC – body cavity; C – cecae; E – eye; H – heart; I – intestine; S – stomach; V – viscera; na– not applicable; ? – unknown; matures in piscivorus fish; ** - matures in piscivorus birds or mammals. o – fish host only checked for presence/absence of parasite; # - reference describing taxonomic designation; ARGR - arctic grayling; BURB - burbot; CISC - lake cisco; LKTR – lake trout; LKWH - lake whitefish; LNSC - longnose sucker; NNST - ninespine stickleback; NRPK - northern pike; PRDC - pearl dace; SLSC - slimy sculpin; TRPH - trout perch; WALL - walleye; WHSC - white sucker parasite species are known to mature in piscivorous birds (allogenic species), while twenty-two species are known to mature in piscivorous fish (autogenic species). A total of 71,499 individual parasites were collected, with 50.2% recovered from the 135 lake whitefish sampled.

Within the small lakes, both parasite and fish species diversity was low. Only 1-6 parasite species were found to infect one to three fish species (Table 2.3). In some instances, fish species were uninfected, such as arctic grayling in C16 and longnose sucker in C23. Due to the limited presence of both host and parasite species in these small lakes, the remainder of the analyses focused on the nine large lakes (Tables 2.4-2.12).

Total parasite species richness was higher in the large lakes, ranging from six in Fleming Lake to 18 in Caribou and Margaret Lakes. Species richness was lowest in burbot (2) and highest in lake whitefish (10). The mean number of parasite species ranged from one in northern pike from Fleming Lake to seven in lake whitefish from Sucker Lake. Lake trout had the highest mean number of individuals (832±1058) recovered from any one lake, 878 from Semo (Table 2.9). This high recovery was due to one species of cestode, *P. parallecticus*. Even though lake whitefish was the most abundant fish species on the plateau (Scrimgeour et al., 1997b), parasite mean intensity was not correlated with relative host density (Rho = -0.02, *P* = 0.97).

The exchange of parasites between fish in the larger lakes was low (Figure 2.2). Of the 28 species of parasites recovered from fish in the large lakes, 18 were

Table 2.3. Prevalence, mean intensity (± standard deviation) and median intensity of parasites in 5 fish species examined from 10 small unnamed lakes in the Caribou Mountains.

Host Species	C1	C8	C9	C13	C14	C16	C23	C25	C26	C27
Arctic Grayling										
n	np	1	np	4	np	3	10	8	np	10
Bunodera sp.										
prevalence (%)		nf		nf		nf	nf	13		nf
mean intensity±s.d.								54±0		
median intensity								54		
Cotylurus erraticus										
prevalence (%)		nf		nf		nf	nf	nf		80
mean intensity±s.d.										121± 109
median intensity										112
Crepidostomum farionis										
prevalence (%)		nf		25		nf	40	38		70
mean intensity±s.d.				1±0			8±7	5±8		3.3+2.4
median intensity				1			8	4		2.0
Diphyllobothrium ditremum		nf		nf		nf				
prevalence (%)							20	25		90
mean intensity±s.d.							2±1	24±33		3±2
median intensity							2	24		4
Philonema sp.		nf		nf		nf	nf	nf		
prevalence (%)										10
mean intensity±s.d.										1±0
median intensity										1

Table 2.3 Continued

Longnose Sucker										
n	np	4	np	np	np	np	10	np	np	np
Glaridacris sp.										
prevalence (%)		25					nf			
mean intensity±s.d.		4±0								
median intensity		4								
Neoechinorhynchus crassus										
prevalence (%)		75					nf			
mean intensity±s.d.		2±1								
median intensity		1								
Northern Pike										
n	10	10	10	np	10	10	np	10	10	np
Crepidostomum farionis										
prevalence (%)	10	nf	10		nf	30		nf		
mean intensity±s.d.	1±0		1±0			1±0			nf	
median intensity	1		1			1				
Proteocephalus pinguis										
prevalence (%)	20	70	nf		40	100		nf	20	
mean intensity±s.d.	38±51	315±81			2±1	51±49			4±2	
median intensity.	38	6*			1	41			4	
		3								
Raphidascaris acus										
prevalence (%)	20	10	nf		50	nf		10	nf	
mean intensity±s.d.	2±1	7±0			5±3			1±0		
median intensity	2	7			5			1		

Table 2.3 Continued

Triaenophorus crassus	nf		nf		nf	nf		nf	nf	
prevalence (%)		10								
mean intensity±s.d.		11±0								
median intensity		11								
T. nodulosus	nf		nf		nf					
prevalence (%)		10				10		nf	nf	
mean intensity±s.d.		1±0				1±0				
median intensity		1				1				
Pearl Dace	np	np	np	np	np	np	np	10	np	np
n										
Alleocreadid sp. 3										
prevalence (%)								30		
mean intensity±s.d.								4±5		
median intensity								6		
Rhabdocona canadensis										
prevalence (%)								10		
mean intensity±s.d.								1±0		
median intensity								1		

n – number of fish processed; nf – parasite not found in this host species; np - fish not present in lake; * - the high mean intensity compared to the median intensity indicated in C8 for P. pinguis, was due to one fish infected with over 2100 individuals of this particular cestode.

Table 2.4. Prevalence, mean intensity (± standard deviation) and median intensity of the parasites recovered from eight fish species in Margaret Lake.

	BURB	CISC	LKTR	LKWH	LNSC	NRPK	SLSC	TRPH
TREMATODA								
Crepidostomum farionis								
prevalence (%)	np	np	np	84	np	np	np	np
mean intensity±s.d.				22±45				
median intensity				9				
Diplostomum spathaceum								
prevalence (%)	np	np	np	np	np	np	np	75
mean intensity±s.d.								2±0
median intensity								2
Diplostomum sp. 1°								
prevalence (%)	np	50	nc	nc	np	np	np	np
mean intensity±s.d.								
median intensity								
Diplostomum sp. 2°								
prevalence (%)	np	np	np	np	np	np	100	np
mean intensity±s.d.							117±129	
median intensity							65	

Table 2.4. Continued

Cotylurus erraticus								
prevalence (%)	np	np	75	84	np	np	np	25
mean intensity±s.d.			24±33	28±22				1±0
median intensity			10	21				1
CESTODA								
Bothriocephalus sp. 1								
prevalence (%)	np	np	50	np	np	np	np	np
mean intensity±s.d.			2±1					
median intensity			2					
Bothriocephalus sp. 2								
prevalence (%)	60	np	np	np	np	np	np	np
mean intensity±s.d.	6±5							
median intensity	5							
Diphyllobothrium dendriticum								
prevalence (%)	np	100	100	100	np	np	np	np
mean intensity±s.d.		9±6	136±196	28±32				
median intensity		8	42	20				
Glaridacris sp.								
prevalence (%)	np	np	np	np	40	np	np	np
mean intensity±s.d.					3±3			
median intensity					3			

Table 2.4. Continued

Proteocephalus laruei								
prevalence (%)	np	100	np	np	np	np	np	np
mean intensity±s.d.		55±47						
median intensity		57						
P. neglectus								
prevalence (%)	np	75	np	60	np	np	np	np
mean intensity±s.d.		47±50		7±8				
median intensity		34		7				
P. parallecticus								
prevalence (%)	np	np	88	np	np	np	np	np
mean intensity±s.d.			95±86					
median intensity			99					
P. pinguis								
prevalence (%)	np	np	np	np	np	100	np	np
mean intensity±s.d.						69± 89		
median intensity						28		
Triaenophorus crassus (larvae)								
prevalence (%)	np	42	13	20	np	np	np	np
mean intensity±s.d.		1±0	1±0	2±2				
median intensity		1	1	1				

Table 2.4. Continued

T. crassus (adult)								
prevalence (%)	np	np	np	np	np	100	np	np
mean intensity±s.d.						44±22		
median intensity						46		
NEMATODA								
Cystidicola farionis								
prevalence (%)	np	np	13	72	np	np	np	np
mean intensity±s.d.			1±0	3±3				
median intensity			1	4				
Rhabdocona sp. 1								
prevalence (%)	np	np	np	np	np	np	50	np
mean intensity±s.d.							7±7	
median intensity							4	
Raphidascaris acus (larvae)								
prevalence (%)	100	np	80	36	np	97	np	np
mean intensity±s.d.	47±39		11±12	4±5		2±1		
median intensity	26		7	2		3		

Table 2.4 Continued

ACANTHOCEPHALA								
Neoechinorhynchus crassus								
prevalence (%)	np	np	np	np	40	np	np	np
mean intensity±s.d.					4±4			
median intensity					3			
Pomphorhynchus bulbocolli								
prevalence (%)	np	np	np	np	20	np	np	np
mean intensity±s.d.					3±1			
median intensity					3			

np - not present, nc - not collected; o – fish host only checked for presence/absence of parasite

Table 2.5. Prevalence, mean intensity (± standard deviation) and median intensity of the parasites recovered from eight fish species in Eva Lake.

	ARGR	BURB	CISC	LKWH	LNSC	NRPK	NNST	WHSC
TREMATODA								
Crepidostomum farionis								
prevalence (%)	10	np	np	28	np	np	np	np
mean intensity±s.d.	1±0			7±8				
median intensity	1			3				
Diplostomum sp. 1°								
prevalence (%)	nc	np	70	nc	np	np	np	np
mean intensity±s.d.								
median intensity								
Cotylurus erraticus								
prevalence (%)	50	np	40	88	np	np	np	np
mean intensity±s.d.	3±2		2±2	90±176				
median intensity	2		1	10				
CESTODA								
Bothriocephalus sp. 2								
prevalence (%)	np	75	np	np	np	np	np	np
mean intensity±s.d.		4±0						
median intensity		4						

Table 2.5 Continued

<u>Diphyllobothrium dendriticum</u>								
prevalence (%)	np	np	100	100	np	np	np	np
mean intensity±s.d.			68±33	298±207				
median intensity			74	227				
<u>Diphyllobothrium ditremum</u>								
prevalence (%)	100	np	np	np	np	np	np	np
mean intensity±s.d.	72±50							
median intensity	54							
<u>Glaridacris</u> sp.								
prevalence (%)	np	np	np	np	57	np	np	45
mean intensity±s.d.					3±2			2±
median intensity					3			1
<u>Proteocephalus laruei</u>								
prevalence (%)	np	np	100	np	np	np	np	np
mean intensity±s.d.			104±141					
median intensity			67					
<u>P. neglectus</u>								
prevalence (%)	np	np	np	72	np	np	np	np
mean intensity±s.d.				15±13				
median intensity				12				

Table 2.5 Continued

P. pinguis								
prevalence (%)	np	np	np	np	np	100	np	n
mean intensity±s.d.						34± 20		
median intensity						36		
Schistocephalus solidus								
prevalence (%)	np	np	np	np	np	np	13	n
mean intensity±s.d.							1±0	
median intensity							1	
Triaenophorus crassus (larvae)								
prevalence (%)								
mean intensity±s.d.	np	np	100	68	np	np	np	n
median intensity			7±4	15±25				
			6	9				
T. crassus (adult)								
prevalence (%)	np	np	np	np	np	90	np	n
mean intensity±s.d.						8±9		
median intensity						4		
NEMATODA								
Cystidicola farionis								
prevalence (%)	np	np	20	80	np	np	np	n
mean intensity±s.d.			1±0	6±6				
median intensity			1	4				

Table 2.5 Continued

Raphidascaris acus (larvae)								
prevalence (%)	90	np	90	84	np	27	np	np
mean intensity±s.d.	6±11		5±4	26±33		7±6		
median intensity	5		4	8		4		
Raphidascaris acus (adult)								
prevalence (%)	10	np	np	np	np	11	np	np
mean intensity±s.d.	1±0					1±0		
median intensity	1					1		
ACANTHOCEPHALA								
Neoechinorhynchus crassus								
prevalence (%)	np	np	np	60	14	np	np	100
mean intensity±s.d.				4±4	1±0			14±15
median intensity				2	1			10
Pomphorhynchus bulbocolli								
prevalence (%)	np	np	np	np	np	np	np	9
mean intensity±s.d.								1±0
median intensity								1

nc – not collected; np - not present; o – fish host only checked for presence/absence of parasite

Table 2.6. Prevalence, mean intensity (± standard deviation) and median intensity of the parasites recovered from five fish species in Sucker Lake.

	CISC	LKWH	NNST	NRPK	WHSC
TREMATODA					
Crepidostomum farionis					
prevalence (%)	np	63	np	np	np
mean intensity±s.d.		20±44			
median intensity		4			
Diplostomum sp. 1°					
prevalence (%)	60	nc	np	np	np
mean intensity±s.d.					
median intensity					
Cotylurus erraticus					
prevalence (%)	20	100	np	np	np
mean intensity±s.d.	2±0	194±246			
median intensity	2	82			
CESTODA					
Diphyllobothrium dendriticum					
prevalence (%)	100	100	np	np	np
mean intensity±s.d.	21±12	146±151			
median intensity	18	93			

Table 2.6 Continued

Glaridacris sp.					
prevalence (%)	np	np	np	np	20
mean intensity±s.d.					2±1
median intensity					2
Proteocephalus laruei					
prevalence (%)	20	np	np	np	np
mean intensity±s.d.	9±0				
median intensity	9				
P. neglectus					
prevalence (%)	np	67	np	10	np
mean intensity±s.d.		8±9		2±0	
median intensity		4		2	
P. pinguis					
prevalence (%)	np	np	np	100	np
mean intensity±s.d.				29±46	
median intensity				10	
Schistocephalus solidus					
prevalence (%)	np	np	58	np	np
mean intensity±s.d.			1±0		
median intensity			1		

Table 2.6 Continued

Triaenophorus crassus (larvae)					
prevalence (%)	60	92	np	np	np
mean intensity±s.d.	2±2	6±5			
median intensity	[illegible]	4			
T. crassus (adult)					
prevalence (%)	np	np	np	100	np
mean intensity±s.d.				18±22	
median intensity				14	
NEMATODA					
Cystidicola farionis					
prevalence (%)	20	42	np	np	np
mean intensity±s.d.	2±0	7±14			
median intensity	2	2			
Raphidascaris acus (larvae)					
prevalence (%)	60	75	np	20	np
mean intensity±s.d.	2±1	7±6		1±0	
median intensity	3	6		1	
Raphidascaris acus (adult)					
prevalence (%)	np	np	np	10	np
mean intensity±s.d.				1±0	
median intensity				1	

Table 2.6 Continued

ACANTHOCEPHALA

Neoechinorhynchus crassus					
prevalence (%)	np	17	np	np	90
mean intensity±s.d.		4±2			25±31
median intensity		4			3
N. rutili					
prevalence (%)	np	4	np	np	np
mean intensity±s.d.		7±0			
median intensity		7			
Pomphorhynchus bulbocolli					
prevalence (%)	np	30	np	np	100
mean intensity±s.d.		4±5			13±11
median intensity		2			6

np - not present; nc - not collected; o – fish host only checked for presence/absence of parasite

Table 2.7. Prevalence, mean intensity (± standard deviation) and median intensity of the parasites recovered from five fish species in Big Fish Lake.

	CISC	LNSC	NRPK	TRPH	WHSC
TREMATODA					
Bunodera sp.					
prevalence (%)	np	np	np	50	np
mean intensity±s.d.				3±2	
median intensity				2	
Crepidostomum farionis					
prevalence (%)	np	np	np	np	np
mean intensity±s.d.					
median intensity					
Diplostomum sp. 1°					
prevalence (%)	60	np	np	np	np
mean intensity±s.d.					
median intensity					
Diplostomum spathaceum					
prevalence (%)	np	np	np	100	np
mean intensity±s.d.				70±41	
median intensity				75	
Cotylurus erraticus					
prevalence (%)	90	np	np	18	np
mean intensity±s.d.	10±9			3±1	
median intensity	8			1	

Table 2.7 Continued

CESTODA					
Diphyllobothrium dendriticum					
prevalence (%)	100	np	np	np	np
mean intensity±s.d.	149±84				
median intensity	124				
Glaridacris sp.					
prevalence (%)	np	50	np	np	np
mean intensity±s.d.		4±3			
median intensity		5			
Proteocephalus laruei					
prevalence (%)	50	np	np	np	np
mean intensity±s.d.	8±7				
median intensity	7				
P. neglectus					
prevalence (%)	40	np	10	np	np
mean intensity±s.d.	2±2		1±0		
median intensity	2		1		
P. pinguis					
prevalence (%)	np	np	100	np	np
mean intensity±s.d.			146±183		
median intensity			81		

Table 2.7 Continued

Triaenophorus crassus (larvae)					
prevalence (%)	100	np	np	np	np
mean intensity±s.d.	30±26				
median intensity	26				
Table 2.4.4 Continued					
T. crassus (adult)					
prevalence (%)	np	np	100	np	np
mean intensity±s.d.			38±36		
median intensity			28		
NEMATODA					
Cystidicola farionis					
prevalence (%)	10	np	np	np	np
mean intensity±s.d.	2±0				
median intensity	2				
Raphidascaris acus (larvae)					
prevalence (%)	70	np	80	np	np
mean intensity±s.d.	7±10		8±15		
median intensity	3		4		
R. acus (adult)					
prevalence (%)	np	np	20	np	np
mean intensity±s.d.			2±0		
median intensity			2		

Table 2.7 Continued

ACANTHOCEPHALA

Neoechinorhynchus crassus					
prevalence (%)	np	10	np	np	np
mean intensity±s.d.		1±0			
median intensity		1			
Pomphorhynchus bulbocolli					
prevalence (%)	20	80	np	np	80
mean intensity±s.d.	5±0	3±1			15±17
median intensity	2	2			9

np - not present; o – fish host only checked for presence/absence of parasite

Table 2.8. Prevalence, mean intensity (± standard deviation) and median intensity of the parasites recovered from nine fish species in Caribou Lake.

	CISC	LKTR	LKWH	LNSC	NNST	NRPK	TRPH	WALL	WHSC
TREMATODA									
Bunodera sp.									
prevalence (%)	np	np	np	np	np	np	55	np	np
mean intensity±s.d.							1±1		
median intensity							2		
Crepidostomum farionis									
prevalence (%)	np	np	14	np	np	np	np	np	np
mean intensity±s.d.			58±23						
median intensity			70						
Diplostomum sp. 1°									
prevalence (%)	30	np	np	np	np	np	np	np	np
mean intensity±s.d.									
median intensity									
Diplostomum spathaceum									
prevalence (%)	np	np	nc	np	np	np	91	np	np
mean intensity±s.d.							2±1		
median intensity							2		

Table 2.8 Continued

Cotylurus erraticus									
prevalence (%)	50	np	100	np	np	np	22	np	np
mean intensity±s.d.	3±3		55±68				3±1		
median intensity	2		16				3		
CESTODA									
Bothriocephalus sp. 1									
prevalence (%)	np	100	np	np	np	np	np	np	np
mean intensity±s.d.		18±0							
median intensity		18							
B. cuspidatus									
prevalence (%)	np	np	np	np	np	np	np	100	np
mean intensity±s.d.								61±81	
median intensity								21	
Diphyllobothrium dendriticum									
prevalence (%)	100	np	100	np	np	np	np	np	np
mean intensity±s.d.	9±7		11±8						
median intensity	7		10						

Table 2.8 Continued

Proteocephalus laruei									
prevalence (%)	20	np	np	np	np	np	np	np	np
mean intensity±s.d.	3±2								
median intensity	3								
P. neglectus									
prevalence (%)	60	np	86	np	np	np	np	90	np
mean intensity±s.d.	7±5		65±75					8±10	
median intensity	5		42					5	
P. pinguis									
prevalence (%)	np	np	np	np	np	100	np	np	np
mean intensity±s.d.						69±90			
median intensity						46			
Triaenophorus crassus (larvae)									
prevalence (%)	70	np	57	np	np	np	np	np	np
mean intensity±s.d.	2±2		6±7						
median intensity	1		3						
T. crassus (adult)									
prevalence (%)	np	np	np	np	np	67	np	np	np
mean intensity±s.d.						31±29			
median intensity						17			

Table 2.8 Continued

T.nodulosus (adult)									
prevalence (%)	np	np	np	np	np	50	np	np	np
mean intensity±s.d.						7±7			
median intensity						3			
T. stizostedionis (larvae)									
prevalence (%)	np	np	np	np	np	np	18	np	np
mean intensity±s.d.							3±1		
median intensity							2		
T. stizostedionis (adult)									
prevalence (%)	np	np	np	np	np	np	np	20	np
mean intensity±s.d.								1±0	
median intensity								1	
NEMATODA									
Cystidicola farionis									
prevalence (%)	np	np	43	np	np	np	np	np	np
mean intensity±s.d.			8±12						
median intensity			1						

Table 2.8 Continued

Raphidascaris acus (larvae)									
prevalence (%)	10	np	86	np	np	67	np	20	np
mean intensity±s.d.	2±0		1±1			12±5		1±0	
median intensity	2		1			12		1	
Raphidascaris acus (adult)									
prevalence (%)	np	np	np	np	np	17	np	10	np
mean intensity±s.d.						1±0		1±0	
median intensity						1		1	
ACANTHOCEPHALA									
Pomphorhynchus bulbocolli									
prevalence (%)	np	np	np	np	np	np	7	np	100
mean intensity±s.d.							1±0		47±0
median intensity							1		47

np - not present; nc – not collected; o – fish host only checked for presence/absence of parasite

Table 2.9. Prevalence, mean intensity (± standard deviation) and median intensity of the parasites recovered from seven fish species in Semo Lake.

	BURB	CISC	LKTR	LKWH	LNSC	NNST	NRPK
TREMATODA							
Crepidostomum farionis							
prevalence (%)	np	np	np	67	np	np	np
mean intensity±s.d.				11±10			
median intensity				8			
Diplostomum sp. 1°							
prevalence (%)	np	70	nc	nc	np	np	np
mean intensity±s.d.							
median intensity							
Cotylurus erraticus							
prevalence (%)	np	np	90	67	np	np	np
mean intensity±s.d.			24±29	29±31			
median intensity			18	15			
CESTODA							
Bothriocephalus sp. 1							
prevalence (%)	np	np	70	np	np	np	np
mean intensity±s.d.			8±6				
median intensity			7				

Table 2.9 Continued

Bothriocephalus sp. 2							
prevalence (%)	100	np	np	np	np	np	np
mean intensity±s.d.	4±0						
median intensity	4						
Diphyllobothrium dendriticum							
prevalence (%)	np	90	100	100	np	np	np
mean intensity±s.d.		4±3	85±104	55±100			
median intensity		4	45	20			
Glaridacris sp.							
prevalence (%)	np	np	np	np	50	np	np
mean intensity±s.d.					3±2		
median intensity					3		
Proteocephalus laruei							
prevalence (%)	np	100	np	np	np	np	np
mean intensity±s.d.		14±7					
median intensity		14					
P. neglectus							
prevalence (%)	np	90	np	83	np	np	np
mean intensity±s.d.		11±7		26±50			
median intensity		11		6			

Table 2.9 Continued

P. parallecticus							
prevalence (%)	np	np	90	np	np	np	np
mean intensity±s.d.			832±1058				
median intensity			345				
P. pinguis							
prevalence (%)	np	np	np	np	np	np	100
mean intensity±s.d.							113±69
median intensity							100
Triaenophorus crassus (larvae)							
prevalence (%)	np	80	40	72	np	np	np
mean intensity±s.d.		3±1	1±1	4±3			
median intensity		3	1	2			
T. crassus (adult)							
prevalence (%)	np	np	np	np	np	np	86
mean intensity±s.d.							84±58
median intensity							87
T. nodulosus							
prevalence (%)	np	np	np	np	np	np	71
mean intensity±s.d.							20±19
median intensity							10

Table 2.9 Continued

NEMATODA							
Cystidicola farionis							
prevalence (%)	np	np	50	56	np	np	np
mean intensity±s.d.			3±2	3±2			
median intensity			3	3			
Raphidascaris acus (larvae)							
prevalence (%)	100	10	90	44	np	np	86
mean intensity±s.d.	1±0	1±0	12±10	4±4			1±1
median intensity	1	1	9	3			1
Raphidascaris acus (adult)							
prevalence (%)	np	np	10	np	np	np	np
mean intensity±s.d.			1±0				
median intensity			1				
ACANTHOCEPHALA							
Neoechinorhynchus crassus							
prevalence (%)	np	np	np	np	100	np	np
mean intensity±s.d.					5±6		
median intensity					4		

np - not present; nc - not collected; o – fish host only checked for presence/absence of parasite

Table 2.10. Prevalence, mean intensity (± standard deviation) and median intensity of the parasites recovered from two fish species in Fleming Lake.

	ARGR	NRPK
TREMATODA		
Crepidostomum farionis		
prevalence (%)	33	np
mean intensity±s.d.	15±7	
median intensity	16	
Cotylurus erraticus		
prevalence (%)	78	np
mean intensity±s.d.	42±38	
median intensity	29	
CESTODA		
Diphyllobothrium ditremum		
prevalence (%)		
mean intensity±s.d.	56	np
median intensity	16±10	
	12	
Triaenophorus nodulosus (adult)		
prevalence (%)	np	40
mean intensity±s.d.		3±1
median intensity		3
NEMATODA		
Philonema sp.		
prevalence (%)	10	np
mean intensity±s.d.	1±0	
median intensity	1	
Raphidascaris acus (adult)		
prevalence (%)	np	10
mean intensity±s.d.		1±0
median intensity		1

np - not present

Table 2.11. Prevalence, mean intensity (± standard deviation) and median intensity of the parasites recovered from four fish species in Pitchimi Lake.

	LKTR	LKWH	NNST	NRPK
TREMATODA				
Crepidostomum farionis				
prevalence (%)	np	69	np	20
mean intensity±s.d.		42±53		2±1
median intensity		21		2
Cotylurus erraticus				
prevalence (%)	np	100	np	np
mean intensity±s.d.		34±36		
median intensity		20		
CESTODA				
Bothriocephalus sp. 1				
prevalence (%)	100	np	np	np
mean intensity±s.d.	37±0			
median intensity	37			
Diphyllobothrium dendriticum				
prevalence (%)	np	100	np	np
mean intensity±s.d.		48±43		
median intensity		45		

Table 2.11 Continued

Proteocephalus neglectus				
prevalence (%)	np	50	np	np
mean intensity±s.d.		19±32		
median intensity		7		
P. parallecticus				
prevalence (%)	100			
mean intensity±s.d.	4880±0	np	np	np
median intensity	4880			
P. pinguis				
prevalence (%)	np	np	np	100
mean intensity±s.d.				248±304
median intensity				94
Triaenophorus crassus (larvae)				
prevalence (%)	np	63	np	np
mean intensity±s.d.		7±5		
median intensity		7		
T. crassus (adult)				
prevalence (%)	np	np	np	50
mean intensity±s.d.				3±4
median intensity				1

Table 2.11 Continued

T. nodulosus (adult				
prevalence (%)	np	np	np	100
mean intensity±s.d.				45±39
median intensity)				36
NEMATODA				
Cystidicola farionis				
prevalence (%)	np	50	np	np
mean intensity±s.d.		3±3		
median intensity		3		
Raphidascaris acus (larvae)				
prevalence (%)	100	94	np	20
mean intensity±s.d.	3±0	4±4		2±1
median intensity	3	3		2
Raphidascaris acus (adult)				
prevalence (%)	np	np	np	10
mean intensity±s.d.				1±0
median intensity				1

Table 2.11 Continued

ACANTHOCEPHALA				
Pomphorhynchus bulbocolli				
prevalence (%)	np	np	np	20
mean intensity±s.d.				3±2
median intensity				3

np – not present

Table 2.12. Prevalence, mean intensity (± standard deviation) and median intensity of the parasites recovered from eight fish species in Wentzel Lake.

	BURB	CISC	LKWH	LNSC	NRPK	TRPH	WALL	WHSC
TREMATODA								
Crepidostomum farionis								
prevalence (%)	np	np	95	np	np	np	10	np
mean intensity±s.d.			26±32				1±0	
median intensity			8				1	
Diplostomum spathaceum								
prevalence (%)	np	np	np	np	np	50	np	np
mean intensity±s.d.						2±1		
median intensity						2		
Diplostomum sp. 1°								
prevalence (%)	np	0	nc	np	np	np	np	np
mean intensity±s.d.								
median intensity								
Cotylurus erraticus								
prevalence (%)	np	np	95	np	np	np	np	np
mean intensity±s.d.			210±196					
median intensity			137					

Table 2.12 Continued

CESTODA

Bothriocephalus cuspidatus								
prevalence (%)	np	np	np	np	np	np	100	np
mean intensity±s.d.							77±103	
median intensity							31	
Bothriocephalus sp. 2								
prevalence (%)	100	np	np	np	np	np	np	np
mean intensity±s.d.	6±3							
median intensity	7							
Diphyllobothrium dendriticum								
prevalence (%)	np	75	100	np	np	np	np	np
mean intensity±s.d.		11±5	195±125					
median intensity		8	176					
Glaridacris sp.								
prevalence (%)	np	np	np	np	np	np	np	20
mean intensity±s.d.								3±0
median intensity								3
P. neglectus								
prevalence (%)	np	75	95	np	np	np	40	np
mean intensity±s.d.		19±20	45±58				7±6	
median intensity		15	18				4	

Table 2.12 Continued

P. pinguis								
prevalence (%)	np	np	np	np	100	np	np	np
mean intensity±s.d.					40±23			
median intensity					42			
Triaenophorus crassus (larvae)								
prevalence (%)	np	50	65	np	np	np	np	np
mean intensity±s.d.		4±4	3±1					
median intensity		4	3					
T. crassus (adult)								
prevalence (%)	np	np	np	np	50	np	np	np
mean intensity±s.d.					21±19			
median intensity					14			
T.stizostedionis (larvae)								
prevalence (%)	np	np	np	np	np	25	np	np
mean intensity±s.d.						1±0		
median intensity						1		
T.stizostedionis (adult)								
prevalence (%)	np	np	np	np	np	np	30	np
mean intensity±s.d.							7±9	
median intensity							4	

Table 2.12 Continued

NEMATODA								
Cystidicola farionis								
prevalence (%)	np	25	65	np	np	np	np	np
mean intensity±s.d.		1±0	3±3					
median intensity		1	1					
Raphidascaris acus (larvae)								
prevalence (%)	33	np	100	np	50	np	80	np
mean intensity±s.d.	1±0		12±11		5±4		4±6	
median intensity	1		7		4		2	
Raphidascaris acus (adult)								
prevalence (%)	np	np	np	np	np	np	10	np
mean intensity±s.d.							4±0	
median intensity							4	
ACANTHOCEPHALA								
Neoechinorhynchus crassus								
prevalence (%)	np	np	5	25	np	np	np	50
mean intensity±s.d.			1±3	2±1				3+0
median intensity			12	2				3

Table 2.12 Continued

Pomphorhynchus bulbocolli								
prevalence (%)	np	np	np	np	np	np	np	50
mean intensity±s.d.								6±0
median intensity								6

np - not present; nc - not collected; o – fish host only checked for presence/absence of parasite

host specialists (Table 2.2). For example, many of the rare parasite species such as *Schistocephalus solidus*, *Ligula intestinalis* and *Bunodera* sp. and the abundant parasite species such as *Proteocephalus pinguis* and *P. parallecticus*, were restricted to one species of host. One exception involved exchange of parasite species among the four salmonids, especially between lake whitefish and cisco. Of the seven species found in cisco, six were shared with lake whitefish. A second exception involved the exchange of parasites among the two catastomids. All three parasite species infecting catastomids were exchanged between both longnose and white suckers (Figure 2.2). These results indicated that when parasite species were exchanged, it tended to occur between phylogenically-related hosts.

However, even when parasite species were exchanged between fish species from the same family, the actual number of parasite individuals being exchanged was limited (Figure 2.3). For example, 93% of *Cystidicola farionis* individuals and 99.5% of *Crepidostomum farionis* individuals were recovered from lake whitefish, even though these two parasite species could infect all four members of the Family Salmonidae. This same pattern was also seen in the parasite exchange between suckers. For instance, *N. crassus* was predominately found in white suckers. Thus, despite the exchange of species, the majority of parasite individuals were restricted to one host, showing that most of the parasite species in the Caribou Mountains were either strict host specialists or specialists of salmonids.

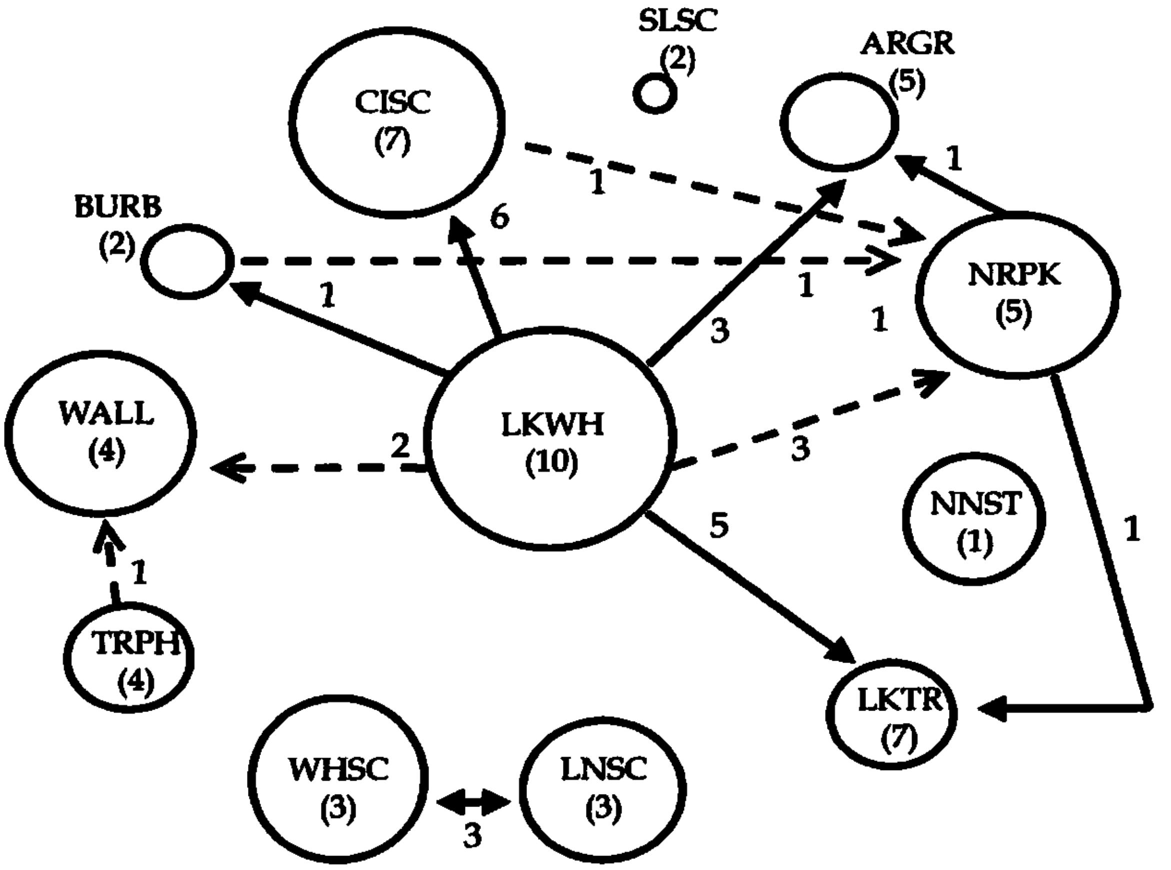

Figure 2.2. Parasite exchange and accumulation in those Caribou Mountain Lakes that contained lake whitefish. The size of each circle represents the relative abundance of each fish species. Numbers in brackets indicate total parasite species richness. Parasite exchange consists of two or more fish species sharing the same life cycle stage of a parasite species (solid lines). The broken lines indicate parasite accumulation through the diet whereby the parasite becomes sexually mature in the second host. The number of parasite species being exchanged is indicated on the line. ARGR = arctic grayling; BURB = burbot; CISC = lake cisco; LKTR = lake trout; LKWH = lake whitefish; LNSC = longnose sucker; NNST = ninespine stickleback; NRPK = northern pike; SLSC = slimy sculpin; TRPH = trout perch; WALL = walleye.

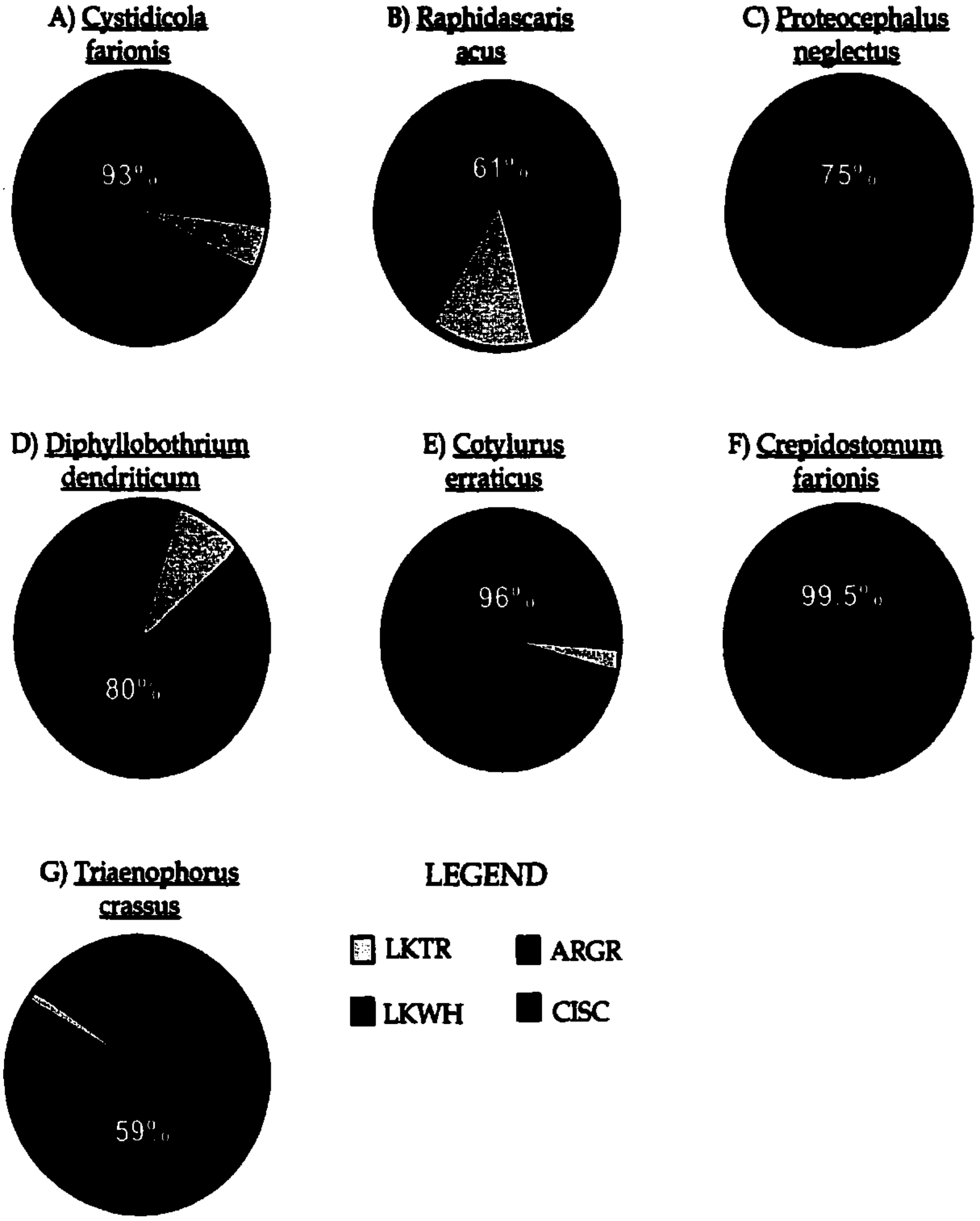

Figure 2.3. The percentage of individual parasites shared in parasite exchange with lake whitefish. A-G indicate individual parasite species being exchanged, and the percentage found in each fish host species. The number in each graph represents the percentage recovered from lake whitefish.

The results from lake whitefish, a regionally common fish species, were chosen to compare to those of other studies involving lake whitefish off the plateau (Table 2.13). Parasite intensities in Caribou Mountain whitefish ranged from 1±0 to 298±207 (Tables 2.3 to 2.12). The mean intensity of parasites such as *T. crassus*, *R. acus* and *D. dendriticum* were approximately three, eight and 17 times higher respectively on the plateau than elsewhere (Table 2.13). Compared to Leong and Holmes (1981), the prevalence of *C. erraticus* in Cold Lake was about half of that in Caribou Mountains lakes. In contrast to the common species, *P. bulbocolli*, one rare parasite in Caribou Mountain lake whitefish was almost 3x more prevalent and 53x more abundant in a southern, Alberta reservoir (Drouin, 1982). All parasites recovered from the plateau were identified in the other studies, except *P. neglectus* and *N. crassus*. Overall, all seven whitefish lakes on the plateau had higher parasite intensities for at least one parasite species, than the other whitefish populations that have been studied.

DISCUSSION

The regional composition of the parasite faunas of the 13 fish species in the Caribou Mountains comprised 30 species, 15 of which were cestodes. Of the 30 species recovered, eight were allogenic species and 22 were autogenics. In addition, 18 species were host specialists. The pattern of high species richness, dominance by cestodes with mixed life-cycle strategies and dominance by

Table 2.13. Comparison of the range of prevalence (mean intensities) found in studies examining lake whitefish (Coregonus clupeaformis) in Canada.

	Curent study		Poole (1985) Manitoba		Leong and Holmes (1981) Alberta	Drouin (1982) Alberta		Chinniah and Threfall (1978) Labrador	
Parasite	lowest	highest	lowest	highest		lowest	highest	lowest	highest
TREMATODA									
Crepidostomum cooperi	np	np	2.6(2.5)	2.7(22)	np	np	np	(1)	3(4) *
C. farionis	14(6.6)	95(58.2)	—	1.3(1)	0.2(1)	np	np	5(1)	(27)
Cotylurus erraticus	67(21.8)	100(209.8)	np	np	48.7~	np	np	np	np
Diplostomum spathecum			np	np	1.4(1)	1(1)	6(1)	np	np
Phyllodistomum coregoni	np	np	np	np	1.9(2.9)	np	np	21(1)	(11)
Prosorhychoides pusilla	np	np	—	1.3(1)	np	np	np	np	np

Table 2.13 Continued

CESTODA

Bothriocephalus cuspidatus	np	np	—	1.3(1)	np	np	np	np	np
Cyanthocephalus truncatus	np	np	np	np	72.8(28.2)	np	np	np	np
Diphyllobothrium dendriticum	100(10.7)	100(298)	9.1(4)	56(17.6)	np	33(1.4)	78.2(6.5)	np	np
Diphyllobothrium sp.	—	—	np	np	0.1(1)	np	np	5(1)	(42)
Proteocephalus exiguus	np	np	6.1(1.5)	53.9(65.4)	14.3(12.7)	—	1(1)	np	np
P. neglectus	50(7.4)	95(65.3)	np	np	np	np	np	np	np
P. tumidocollus	np	np	np	np	np	np	np	47(1)	(138)
Proteocephalus sp. Type 1	np	np	np	np	np	np	np	5(2)	(10)
Proteocephalus sp. Type 2	np	np	np	np	np	np	np	3(2)	(10)

Table 2.13 Continued

Proteocephalus spp.	—	—	—	—	12.8(18.1)	—	—	np	np
Triaenophorus crassus	57(2.2)	92(17.9)	51.5(2.5)	86.7(5.5)	np	np	np	16(1)	(9)
NEMATODA									
Anisakidae larvae	np	np	np	np	np	1(1)	10(1.3)	np	np
Capillaria salvelini	np	np	np	np	np	np	np	20(1)	(10)
Cystidicola farionis	42(2.8)	83(7.7)	np	np	76.1(12.6)	np	np	np	np
Raphidascaris acus	36(1.3)	100(25.7)	6.1(1.5)	76(3.2)	np	np	np	np	np
Raphidascaris sp.	np	np	np	np	np	np	np	—	1(2)
Rhabdocona milleri	np	np	—	4(2.7)	np	np	np	np	np
Spinitectus gracilis	np	np	7.7(2.2)	75.8(28.2)	np	np	np	np	np

specialists, contrasts with the results from other studies done at a similar scale (Poole, 1985, Kennedy et al., 1986b). For example, Kennedy et al. (1986b) recovered only 13 parasite species (three generalists and ten specialists) from the 12 host fish species present on Jersey Island. Three of the host species were completely uninfected and trematodes were noticeably absent. Only one parasite species was classified as allogenic and the most common and abundant parasite species was an acanthocephalan. Unfortunately, those few studies that are comparable, come from hosts collected from human-altered water bodies, so it is premature to make conclusions regarding the uniqueness of these patterns of infection.

Almost all of the parasites in the Caribou Mountains were restricted to the seven larger lakes. Only pearl dace and their parasites were unique to one small lake, C25. Even in the few cases where species occurred in both large and small lakes, their mean intensities were much lower in the latter. For example, P. pinguis was 100% prevalent in eight of the nine large lakes, and had mean intensities ranging between 29 – 248. Prevalence was never >70% in the smaller lakes, and mean intensities were rarely >50. A similar pattern of low prevalence and low mean intensity was observed in the smaller lakes for Crepidostomum farionis, and T. crassus in pike and D. dendriticum in arctic grayling. There are likely to be many factors that limit parasite species richness and intensity in the smaller lakes. However, the simplest explanation for this pattern, as suggested by Holmes (1979), is the link between host presence and parasite presence.

Evidence for the intuitive link between parasite presence and host presence is provided by the three species of Triaenophorus spp. in the larger lakes. In lakes containing both trout perch and walleye, T. stizostedionis was always present and abundant (Caribou and Wentzel Lakes), but not when walleye were missing (Margaret and Big Fish Lakes). Triaenophorus nodulosus occurred only in lakes that contained pike and burbot, while T. crassus was recovered when lake whitefish and northern pike co-existed. Clearly, the structure of the host community influenced the structure of the parasite component community, a feature well-recognized in other studies (Holmes, 1979; Marcogliese and Cone, 1991a; Chen and Xu, 1995; Nie, 1996). Thus, those factors that limit the colonization and success of fish in the small lakes (e.g. winterkill, distance between lakes, predation by pike) likely also play an important role in their colonization by parasites.

One defining characteristic of the parasite fauna of fish in the Caribou Mountains was the high degree of parasite specialization and thus by definition, their low rates of parasite exchange. This pattern differs markedly from the generalist-dominated systems described by Valtonen et al. (1997) in Finnish lakes and by Holmes (1990) and Blaylock et al. (1998) in marine archipelagos. Specialists also dominated the parasite communities in fish from Cold Lake, Alberta when the introduced acanthocephalan was removed from analyses (Leong and Holmes, 1981). However, in the few instances when exchange occurred in the Caribou Mountain lakes, it involved phylogenetically-related hosts (Dubois et al., 1996; Bergeron et al., 1997) within the salmonid and catastomid families. For instance, six of the seven species that occurred in lake whitefish also infected lake cisco, and the three species that occurred in white suckers, also occurred in long-nosed suckers. This pattern of exchange within the salmonids and catostomids was identical to the pattern described by Leong and Holmes (1981) involving the same species of fish from Cold Lake, Alberta. Moreover, in those instances when parasite species were exchanged, the majority of individuals were found in only one host species.

All of the parasite species in the Caribou Mountains have been reported in other studies involving fish collected from northern, temperate lakes (McDonald and Margolis, 1995 and references within); thus, none were endemic to the area. The only parasite that has been reported elsewhere, but not found in the Caribou Mountains, was the nematode Spinitectus gracilis. This species was abundant in whitefish from Manitoba (Poole, 1985) in lakes where exchange occurred between walleye and the percid, yellow perch. Percids were conspicuously absent in lakes in the Caribou Mountains, but their absence apparently did little to restrict parasite species richness and community structure.

The most important distinguishing characteristic of the parasite faunas in the Caribou Mountains appears to be the relatively high intensities found in some lakes compared to other Canadian studies. Although the comparisons were limited to the parasites of whitefish, intensities for most species were up to two orders of magnitude higher in the Caribou Mountains. For example, the mean intensity of D. dendriticum in Eva was 17x higher than that reported in any of the 7 lakes studied by Poole (1985). Even the lowest intensity lake (Margaret), had a higher mean intensity than reported elsewhere. In addition, the mean intensity of larval T. crassus tended to be up to 3x higher than that reported elsewhere (e.g. Chinnah and Threfall, 1978; Leong and Holmes, 1981; Drouin, 1982; Poole, 1985). The nematode R. acus and the cestode, P. neglectus also had relatively higher mean intensities in the Caribou Mountains than those reported elsewhere (e.g. Chinnah and Threfall, 1978; Leong and Holmes, 1981; Drouin, 1982; Poole, 1985). The high mean intensities may reflect a shared environmental characteristic(s) between lakes that each parasite species is responding to, and thus enabling successful establishment.

In summary, the parasite fauna sampled from fish in the Caribou Mountains is rich in number of species, at least in the larger lakes that contain a diverse host community. Most parasites were host specialists and thus, the exchange of parasites among hosts was low and should contribute little towards parasite community structure. Finding mean parasite intensities at least 2x higher on the plateau was a key difference between fish examined in the Caribou Mountains and other studies. Factors contributing to this high variation in intensity will be addressed in later chapters.

Chapter 3. Helminth component community structure of lake whitefish (Coregonus clupeaformis) from seven northern-Alberta lakes.

INTRODUCTION

Comparing the structure of communities of helminths from hosts collected from two or more localities is a common line of inquiry in parasite ecology. Questions at this scale focus on the predictability of community structure between hosts collected from two different areas or, in parasitic terms, component communities (reviews by Kennedy, 1990; Sousa, 1994; Poulin, 1997). There are currently two views describing the structure of parasite communities sampled at this scale. One holds that parasite component communities are unstructured assemblages, developing primarily by chance colonization and transmission events. Evidence for this view comes from extensive studies done by Kennedy and his students on fish collected in Europe (Kennedy, 1977, 1978a; 1978b; Kennedy, 1990; Hartvigsen and Kennedy, 1993, Guégan and Kennedy, 1993; Kennedy and Guégan, 1994). For example, Hartvigsen and Kennedy (1993) examined parasite communities in brown trout (Salmo trutta) collected from ten reservoirs in southwest England. Of the thirteen helminth species identified, species composition varied extensively between reservoirs. Also, none of the parasite species were found in >60% of hosts. Helminths rarely, if ever co-occurred and intensities seldomly exceeded ten individuals per host. Based on a large number of similar studies, Kennedy (1990) concluded that in the case of fish helminth communities, the individual characteristics and history of a lake overwhelmed any regional factors that might promote similarity and predictability between any two fish helminth communities.

The alternative view holds that parasite component communities are structured assemblages and that this structure is predictable (e.g. Esch et al., 1988; Holmes, 1990; Valtonen et al., 1997; Choudary and Dick, 1998). Valtonen et al. (1997) examined four lakes in Finland and identified 38 parasite species infecting roach (Rutilis rutilis) and 42 infecting perch (Perca fluviatilis). Parasite intensities ranged from 33-153 parasites per fish. Thirteen helminth species were present in >60% of the hosts. Valtonen et al. (1997) concluded that regional factors led to similar parasite communities in the different lakes, and that the similarity was due primarily to the predictable presence and abundance of a suite of common parasite species.

Resolving these two contrasting views, or at least determining the conditions under which one view overrides the other, is important in assessing whether parasite component communities are predictable (Hartvigsen and Halvorsen, 1994). One shortcoming of previous studies is that most focus on only one host species, thereby restricting their scope. The inability to predict parasite community structure in one host species may not occur for all species. Another host species in the area may have a predictable parasite community, but this host species was not examined. Another shortcoming is that most evaluations of parasite component community structure are descriptive and do not test specific hypotheses. Apart from Kennedy's (1978a) assessment of distance and lake area in determining component community structure in arctic char in Norway, there are few specific tests of the factors that may determine parasite component community structure (Hartvigsen and Halvorsen, 1994; Bergeron et al., 1997).

Perhaps the most important shortcoming is that the majority of empirical and theoretical studies examining fish parasite component communities have occurred in anthropogenically-altered water systems. Virtually all detailed studies have been done on fish collected from lakes in Great Britain (e.g. Kennedy, 1990), mainland Europe (e.g. Hartvigsen and Halvorsen, 1994; Valtonen et al., 1997), Eastern North America (e.g. Poole, 1985; Marcogliese and Cone, 1991b; Dubois et al., 1996; Marcogliese and Cone, 1996; Bergeron et al., 1997) and China (e.g. Nie, 1998). Each region has been characterized by various forms of anthropogenic change, from direct alterations to fish populations (introduction of non-natives, stocking, and exploitation) to indirect effects in the form of eutrophication and pollution. Each of these factors, alone and in combination, has been shown to alter fish parasite community structure (review by Snieszko, 1974; Hirschfield et al., 1983; Scott and Dobson, 1989; Marcogliese et al., 1990; Khan and Thulin, 1991; Sprent, 1992; Valtonen et al., 1997).

The objective of this study is to examine spatial structure of parasite component communities in whitefish (Coregonus clupeaformis) collected from the seven lakes on the Caribou Mountains where they are known to occur

(Chapter 2). In this region, lake whitefish have the richest parasite communities and they share common parasite species to other hosts than any other on the plateau (Chapter 2). My first aim is to take a descriptive, broad-scale approach to evaluate between-lake differences in parasite species richness and abundance in the seven lakes. I then used predictions based on metacommunity ecology (e.g. Hanski, 1991) to assess whether variation in community structure was associated with variation in lake area, distance between lakes or connectedness between lakes. Finally, I used standard classification analyses (ter Braak, 1986) to assess whether sub-sets of lakes can be grouped on the basis of their parasite communities.

MATERIALS AND METHODS

Collection of data

The general characteristics of the 19 study lakes on the Caribou Mountains Plateau, and their associated fish species are described in Chapter 2. Collection sites, processing procedures and the methods used to describe general features of parasite infracommunities (parasite prevalence, abundance, and intensity) are described in Chapter 2. Figure 3.1 indicates the seven lakes containing lake whitefish in the Caribou Mountains and their shared river systems. The number of fish examined per lake varied from 9-25 (Table 2.1). Despite the low sample sizes, 90% of the parasite species identified from each locality were recovered

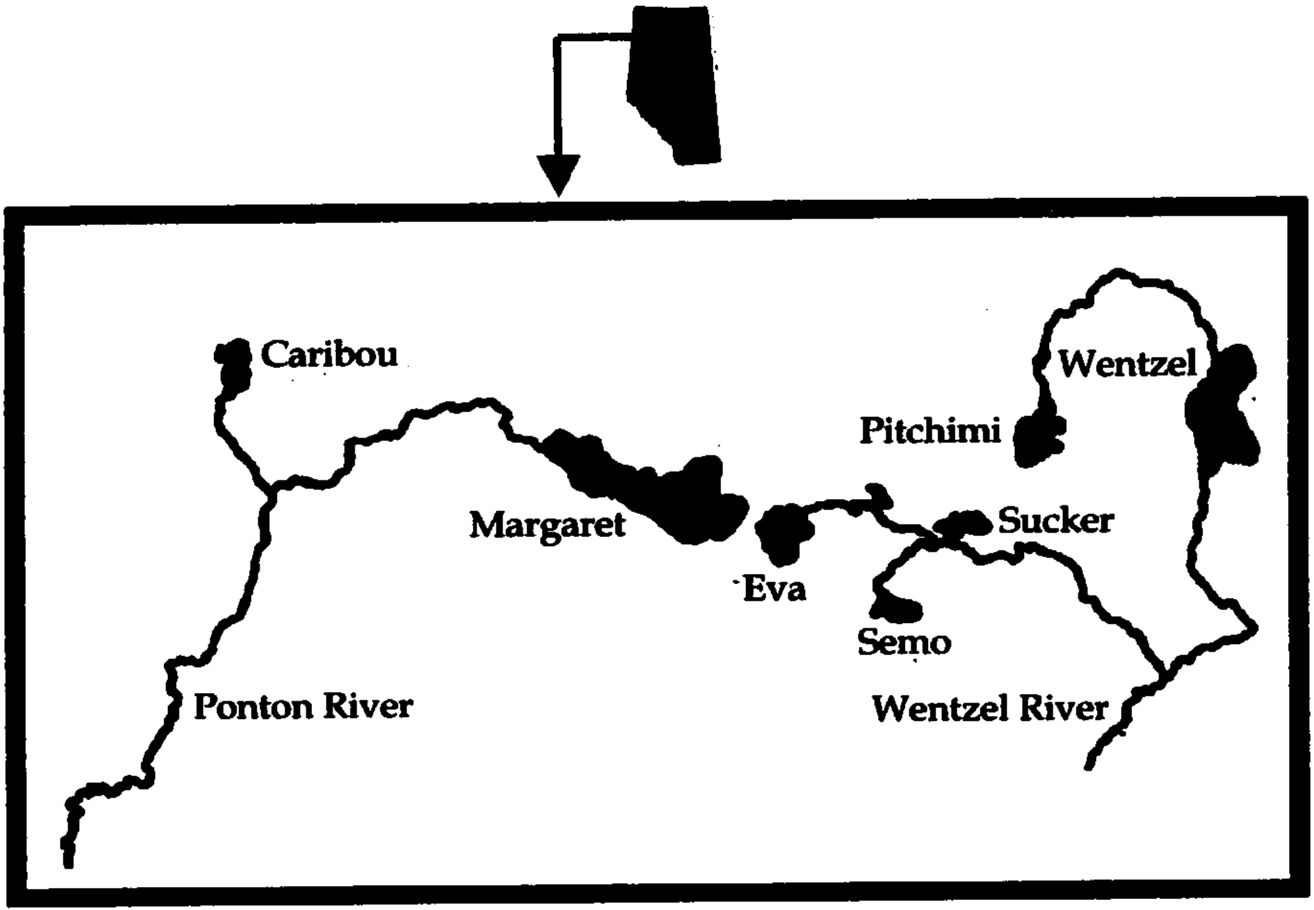

Figure 3.1. Caribou Mountain lakes where lake whitefish (Coregonus clupeaformis) were collected and examined for parasites.

after examining just six fish, as determined by cumulative species richness curves (Begon et al., 1996).

Data Analyses

Parasite component community structure was described in three ways: traditional descriptors (e.g. species richness, mean abundance and mean intensity), community similarity and cluster analyses. Total component community richness equaled the total number of species of parasite per whitefish per lake. Mean intensity is defined as the mean number of parasites of a given species per infected host (Bush et al., 1997). Measures of dominance, species richness and evenness also followed standard definitions (Begon et al., 1996). Dominance was calculated as the abundance (the number of parasite individuals of a specific species in a single host) of the parasite divided by the sum of the abundances of all parasites in that host species (Bush et al., 1997). An index of species diversity was provided by the reciprocal of Simpson's index, which measures the proportion of the parasite component community each parasite species comprised per lake $D = 1/\Sigma(p_i)^2$, where p_i represents the proportion of species i in the sample (Begon et al., 1996). The index of evenness measured the equability of a parasite species distribution within a lake ($E = D/S$ where D represents the value from the reciprocal of Simpson's index and S indicates species richness in the component community richness (Begon et al., 1996).

I further designated each species of parasite into qualitative categories corresponding to their life-cycle strategy, their status as host specialists or generalists (from Chapter 2) and their pattern of occurrence and abundance. Esch et al. (1988) defined autogenic species as parasites that complete their life-cycles within a water body by using fish as definitive hosts. In contrast, allogenic species can complete part of their life-cycle outside the confines of a lake by using birds or mammals as definitive hosts. Following Stock and Holmes (1987), core parasite species were those with a prevalence >70% and satellite species occurred in <30% of the hosts.

Parasite component community similarity between lakes was estimated using Jaccard's index and Percent Similarity. Jaccard's index was used to compare the presence/absence of species occurring in two lakes $J = 100(c/(a + b - c))$, where a is the number of taxa in the first sample, b is the number of taxa in the second sample and c is the taxa shared between the two samples) (Begon et al., 1996). Percent similarity compared the mean abundances of the lake whitefish parasite component communities in each lake $PS = 1 - (0.5(|p_{ia} - p_{ib}|))$, where p_{ia} and p_{ib} indicate the proportions of taxon i in samples a and b, respectively; Hurlbert, 1978).

Lastly, cluster analyses were used to analyze community similarity between hosts collected from the seven different lakes. One dendogram was based on Jaccard's index, the other based on Percent Similarity. Euclidean distances and Ward's linkage were used to create the dendograms using PC-ORD (Version 2.0; McCune and Mefford, 1995).

Factors affecting component community structure

Standard, non-parametric correlation analyses (Spearman's tests) were used to evaluate associations between component community structure and lake area, minimum lake distance and lake connectivity. Estimates of lake area were from McEachern and Prepas (unpublished data). Minimum lake distances were determined in kilometers from a 1:250,000 regional map of the Caribou Mountains.

The seven lakes in the Caribou Mountains are located within two separate watersheds (Figure 3.1). Margaret Lake and Caribou Lake drain into the Ponton River, while the remaining five lakes (Sucker, Semo, Pitchimi, Eva and Wentzel) are linked via the Wentzel River (Figure 3.1). If connectivity is an important determinant of component community structure, lakes within a watershed should share more parasites and thus have higher community similarity. To evaluate this, I used a method modified from Blaylock et al. (1998). First, mean percent similarity was calculated between 20 randomly-selected pairs of fish within a watershed (regardless of their exact lake of origin). This value was compared with mean percent similarity values calculated between another 20 randomly-selected pairs of fish where for each pair, one fish came from one watershed and the second came from the other. This analysis was done initially using all 10 parasites infecting lake whitefish; it was then repeated with autogenic species alone.

RESULTS

General patterns of infection

Ten parasite species were found in the 135 lake whitefish examined (Table 3.1). Seven of the 10 species were found in each of the seven lakes. The three species that were more erratic in their occurrence in the Caribou Mountains were all acanthocephalans (Table 3.1). For the set of seven species found in each lake, variation between lakes in mean intensity and prevalence was high. For six of these species, differences between the lake with the lowest mean intensity and the highest, was approximately one order of magnitude. The exception was the mean intensity of Cystidicola farionis, which tended to be relatively similar among lakes. This result suggests that parasites could be aggregated within their whitefish populations within a lake.

Two of the 10 helminth species were allogenic, using piscivorous birds as definitive hosts (C. erraticus, D. dendriticum). The other 8 species were autogenic, using piscivorous fish as definitive hosts. Based on patterns of exchange outlined in Chapter 2, 8 of the 10 species were designated as coregonid specialists. The exceptions were two acanthocephalans P. bulbocolli and N. crassus, maturing in catastomids. Thus, it was not surprising to recover a high number of salmonid specialists from lake whitefish. The frequency distribution

Table 3.1. Summary infection characteristics of ten species of helminths recovered from lake whitefish collected from seven lakes in the Caribou Mountains in northern Alberta. Data are presented as mean ± standard deviation, with percent prevalence noted below. The number of whitefish sampled per lake is indicated below each lake name.

Parasite	Status**	Margaret (25)	Eva (25)	Sucker (24)	Caribou (7)	Semo (18)	Pitchimi (16)	Wentzel (20)
TREMATODA								
Crepidostomum farionis#	C	22.1±44.6 (884)	6.6±7.9 (28)	19.6±43.6 (63)	58.2±23.3 (14)	11.4±9.8 (67)	42.1±53.3 (69)	26.4±32.3 (95)
Cotylurus erraticus*	C	28.0±22.2 (84)	89.8±176.4 (88)	194.0±245.5 (100)	54.7±67.8 (100)	21.8±30.7 (67)	34.0±36.2 (100)	209.8±195.7 (95)
CESTODA								
Diphyllobothrium dendriticum*	C	28.0±31.8 (100)	298.0±207.2 (100)	146.2±150.7 (100)	10.7±7.6 (100)	54.7±100.0 (100)	48.3±43.0 (100)	195.1±124.8 (100)
Proteocephalus neglectus#	C	7.4±8.2 (60)	14.7±12.6 (72)	8.1±8.5 (67)	65.3±74.9 (86)	26.3±50.3 (83)	18.6±31.5 (50)	45.0±58.0 (95)
Triaenophorus crassus^	C	2.2±1.6 (60)	17.9±24.8 (68)	6.0±5.0 (92)	5.5±7.1 (57)	3.8±3.4 (72)	7.0±5.2 (63)	2.5±1.3 (65)
NEMATODA								
Cystidicola farionis#	C	3.4±2.9 (72)	6.0±6.3 (83)	6.6±13.6 (42)	7.7±11.6 (43)	2.8±2.3 (56)	3.3±2.6 (50)	3.2±3.2 (65)

Table 3.1 Continued

Raphidascaris acus^	C	4.1±4.6 (36)	25.7±33.4 (84)	6.7±5.7 (75)	1.3±0.5 (86)	4.4±3.8 (44)	3.5±3.6 (94)	11.6±11.0 (100)
ACANTHOCEPHALA								
Neoechinorhynchus crassus^	S	np	3.5±3.5 (60)	3.8±1.5 (15)	np	np	np	0.6±2.7 (5)
N. rutili^	S	np	np	7.0±0.0 (4)	np	np	np	np
Pomphorhynchus bulbocolli^	S	np	np	4.4±4.9 (30)	np	np	np	np

= matures in lake whitefish; ^ = larval stage maturing in piscivorous fish; * = larval stage maturing in piscivorous birds; ** = parasite either a core species (C) or a satellite species (S).; np = not present

of parasite species in the total sample of 135 whitefish was bimodal (Figure 3.2). In general, the left-hand mode (satellite species) corresponded to the three acanthocephalans, while the right-hand mode (core species) corresponded to the remaining 7 species.

Adult whitefish collected from the Caribou Mountains harboured, on average 4.6±1.5 (range = 1-7) parasite species and 80.6±85.8 (range = 12-441) individuals (Table 3.2). In general, species richness (7-10) and mean number of species per host (5-6) was consistent between lakes. However, there was extensive variation in the intensity of individuals per host between lakes (Table 3.2). Much of this variation was associated with variation in parasite dominance. In six of the seven lakes, one of the two allogenic species (either larvae of the trematode C. erraticus or larvae of the cestode D. dendriticum) dominated the parasite communities. Dominance estimates were positively correlated with the standard deviation of parasite counts (Rho = 0.85, P = 0.02). Thus, the intensity of the two dominant allogenic species in a lake tended to affect the overall structure of the parasite community; when dominance of an allogenic was high (Eva, Sucker and Wenztel Lakes), Simpson's diversity index was low and evenness was low (Table 3.2). Although the two allogenics still dominated the low intensity lakes, their intensities were relatively low. These lakes had correspondingly high values of Simpson's index and evenness.

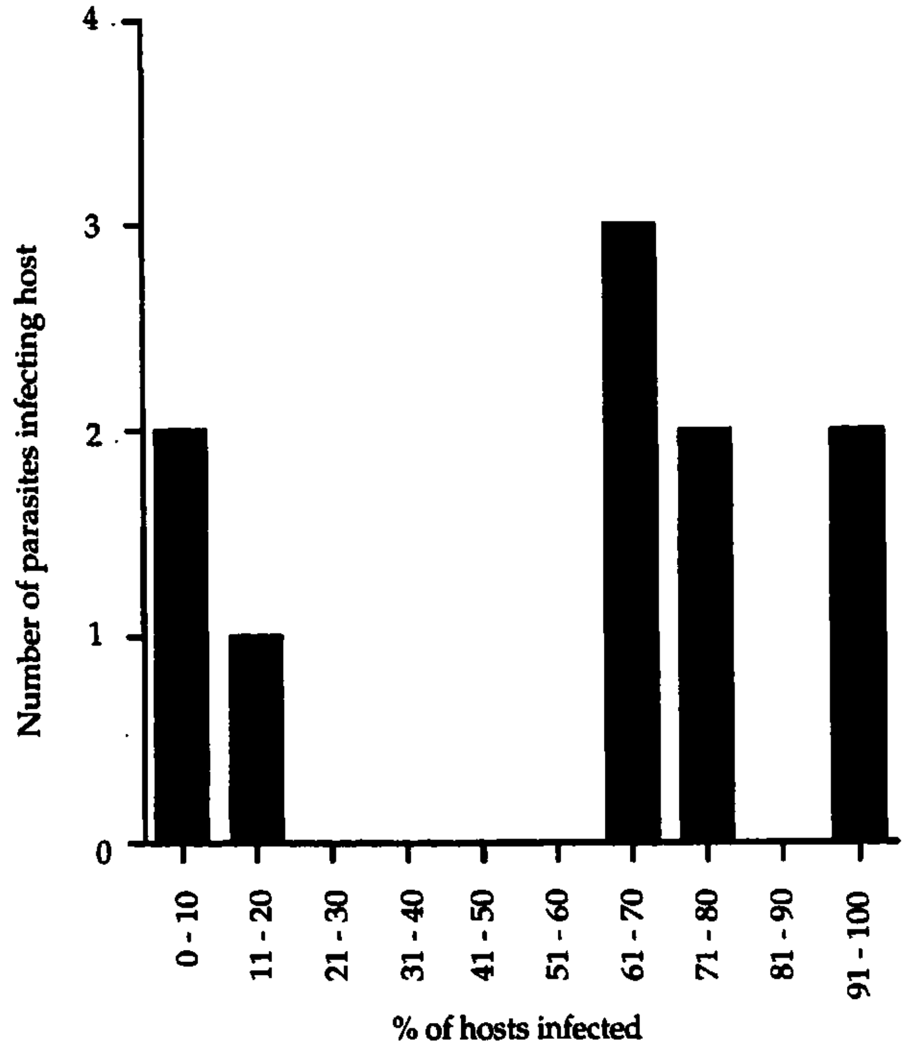

Figure 3.2. A frequency distribution of intestinal parasite species in 135 lake whitefish to determine core and satellite parasite species. Parasites occurring in <30% of hosts are considered rare (satellite), while those parasites found in >60% are considered common (core).

Table 3.2. Summary characteristics of the diversity patterns of parasite communities in lake whitefish collected from seven lakes in the Caribou Mountains Standard deviation values are included when required..

	Margaret	Eva	Sucker	Caribou	Semo	Pitchimi	Wentzel
species richness	7	8	10	7	7	8	8
mean number of parasite species per host	5 ± 2	6 ± 1	6 ± 1	6 ± 1	5 ± 1	5 ± 1	6 ± 1
mean number of parasite individuals per host	81 ± 86	431 ± 383	372 ± 386	179 ± 73	105 ± 140	130 ± 77	473 ± 346
Simpson's index	3.9	1.8	2.3	3.6	3.0	3.8	2.8
dominant species	Di	Di	Cot	Pro	Di	Di	Cot
dominance	0.35	0.72	0.52	0.31	0.52	0.37	0.42
Evenness index	0.56	0.23	0.23	0.52	0.42	0.47	0.35

Cot – *Cotylurus erraticus*; Di – *Diphyllobothrium dendriticum*; Pro – *Proteocephalus neglectus*

Patterns of similarity

On average, values for Jaccard's index ranged from 0.47 to 1.00 (x=0.80±0.03) and Percent Similarity from 0.39 to 0.93 (x=0.65±0.03). The high values for Jaccard's similarity were expected (Table 3.3), because 7 of the 10 parasite species occurred in each lake (Table 3.1). Of the 21 combinations of lake pairs, 4 contained identical combinations of species, 9 differed by the presence/absence of one species and 2 by the presence/absence of 2 species. Thus, reductions from 100% similarity can only be explained by the erratic occurrence of the 3 rare species of acanthocephalans. Values for Percent Similarity were lower, primarily reflecting variation in intensity of the dominant allogenic species. A lake pair with a high value for Jaccard's index did not necessarily correspond to a high value for Percent Similarity. For example, the Jaccard's index for Margaret and Eva Lakes was 88%, but Percent Similarity was only 39%. This indicates that although the two lakes shared all but one species (the acanthocephalan, N. crassus), the two lakes had different patterns of parasite intensity.

Cluster analysis based on qualitative and quantitative similarities produced similar results (Figure 3.3). For qualitative similarity (Figure 3.3a), lakes segregated according to the presence or absence of the satellite acanthocephalans. Margaret, Caribou, Semo and Pitchimi Lakes formed one cluster (no acanthocephalans), while Eva, Wentzel and Sucker Lakes formed a second cluster (with acanthocephalans). In general, the latter cluster of lakes

Table 3.3. Similarity comparison between parasite component communities of lake whitefish collected from seven Caribou Mountains lakes using Jaccard's index (above diagonal) and percent similarity (below diagonal).

	Margaret	Eva	Sucker	Caribou	Semo	Pitchimi	Wentzel
Margaret	X	0.88	0.70	1.00	1.00	0.88	0.88
Eva	0.39	X	0.80	0.88	0.88	1.00	0.78
Sucker	0.71	0.60	X	0.70	0.70	0.80	0.70
Caribou	0.68	0.44	0.44	X	1.00	0.88	0.88
Semo	0.66	0.74	0.61	0.52	X	0.88	0.88
Pitchimi	0.93	0.61	0.63	0.65	0.71	X	0.47
Wentzel	0.82	0.64	0.88	0.51	0.71	0.79	X

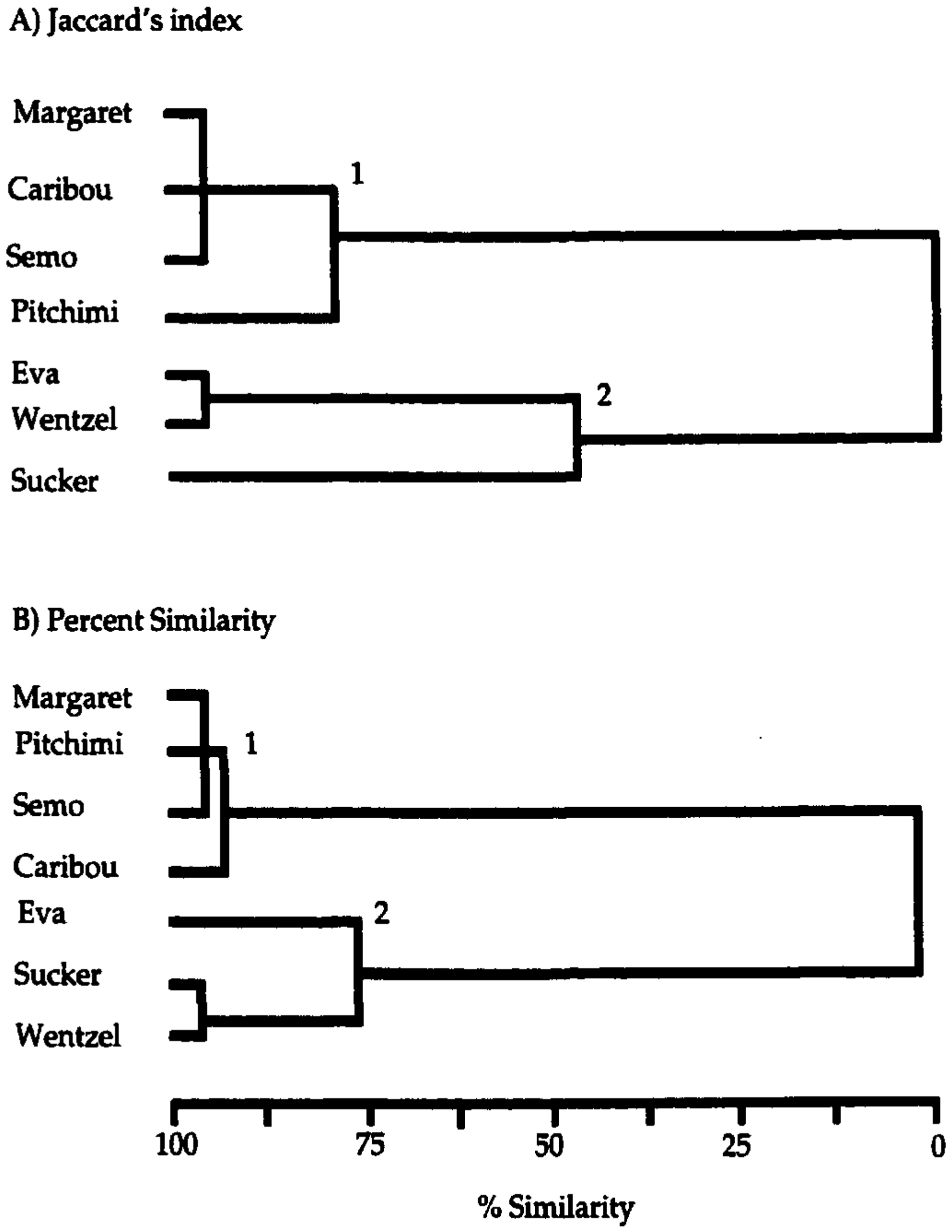

Figure 3.3. Cluster analysis of lake whitefish (Coregonus clupeaformis) parasite component communities from seven lakes in the Caribou Mountains, Alberta. A) Jaccard's index. B) Percent Similarity.

tended also to have high overall parasite intensities (Fig. 3.3b), clustering together in terms of quantitative similarity as well.

Factors affecting parasite community structure

The mean number of helminth species per whitefish was not associated with lake area (Rho = -0.11, P = 0.82) or with the minimum distance between lakes (Rho = 0.75, P = 0.052). The mean number of individuals per whitefish was also not affected by lake area (Rho = 0.04, P = 0.93) or distance between lakes (Rho = 0.68, P = 0.09). There was also no indication that lakes that were closer together had higher Jaccard's index (Rho = 0.20, P = 0.40) or Percent Similarity (Rho = -0.14, P = 0.55). Also, non-significant correlations were determined when the analyses were repeated without the 2 allogenic species (ranges for Rho = 0.07 to 0.61 and P = 0.88 to 0.14).

There was no clear relationship between lake connectivity and community similarity (Table 3.4). Although there was a general tendency for fish from the Wentzel watershed to have more similar helminth communities, this difference disappeared when the 2 allogenic species were removed. Analysis without the allogenics is most appropriate, since bird definitive hosts can disperse parasites between lakes, independent of lake connectedness. Thus, when only the 8 autogenic species were considered, community similarity between any 2 individuals was similar whether fish were compared within a watershed, or between the two watersheds (Table 3.4).

Table 3.4. Analysis of lake connectivity between seven lakes located on the Caribou Mountains Plateau in northern Alberta. Lakes were compared within the same watershed to those in another watershed using mean Percent Similarities ± standard error.

Parasite Group	Within Watershed		Between Watersheds
	Ponton River	Wentzel River	
all 10 species	0.394 ± 0.06	0.641 ± 0.04	0.474 ± 0.06
8 autogenic species	0.352 ± 0.06	0.378 ± 0.05	0.322 ± 0.06

DISCUSSION

The parasite component community of lake whitefish was characterized by high species diversity (5-6 species/host), high similarity (>80% presence/absence and >60% intensities), and the domination of two allogenic core species (C. erraticus and D. dendriticum). Cotylurus erraticus and D. dendriticum were present in all lakes and in >90% of the fish examined. This community pattern contrasts with the dominating view of component communities of freshwater fish parasites (review by Kennedy, 1990), where emphasis is on communities with low species diversity (1-2 species/host), low similarity (<25%), the absence of cores species, and the domination of one or two generalists (Kennedy, 1990; Hartvigsen and Kennedy, 1993; Carney and Dick, 1999).

One important distinguishing characteristic of the component communities in whitefish of the current study is the presence of a suite of seven species that were present in each lake. These species represented one of two modes of the bimodal species frequency distribution of parasites of whitefish in the Caribou Mountains. Moreover, the average intensity of these species was correlated with their prevalence, indicating that common species were also abundant. Both of these characteristics are fundamental assumptions of Hanski's (1982) core/satellite species hypothesis. This hypothesis has received much attention from parasite ecologists (e.g. Bush and Holmes, 1986; Stock and Holmes, 1987) but in general, has found been tested infrequently in studies of parasite communities in freshwater fish. Kennedy (1990) concluded that the core/satellite hypothesis was inappropriate in most fish/parasite systems due to the stochastic and unpredictable nature of colonization. Clearly, the results from this study, together with those in Valtonen et al. (1997) that also document domination by core species, suggest that this view is premature.

Another distinguishing characteristic is the minor role of acanthocephalans in whitefish from the Caribou Mountains. In general, there were only three species of acanthocephalans, their occurrence in the different lakes was erratic and their intensities low compared to the other groups. These results contrast with those of Leong and Holmes (1981) on whitefish in Cold lake Alberta, and also contrast with the extensive series of studies by Kennedy and his colleagues in Europe (Kennedy, 1977; 1978a; 1978b; Kennedy et al., 1986b; Kennedy, 1990; Hartvigsen and Kennedy, 1993; Guégan and Kennedy, 1993; Kennedy and Guégan, 1994). Interestingly, similar patterns of erratic occurrence and low intensity seems to hold with the acanthocephalans among lakes in the Caribou Mountains, further suggesting that it is the characteristics of the remaining species that distinguish these component communities from those studied by others.

A third distinguishing characteristic is in the importance of the life-history characteristics of the seven common species. Esch et al. (1988) suggested that allogenic species should have a greater potential to increase their distribution than autogenic parasites. While an allogenic species can be transported across inhospitable areas between lakes by their definitive hosts (Esch et al., 1988), it is more difficult for an autogenic species to successfully colonize an isolated lake (Kennedy, 1993). Thus, when core species are present, they should be allogenic ones. In contrast, the core species in whitefish comprised a combination of allogenic and autogenic species. These results suggest that conditions in the Caribou Mountain lakes are suitable for the colonization of both types of parasites, and thus, each can contribute approximately equally to the structure of component communities.

Perhaps the most striking distinguishing characteristic of the component communities in whitefish is their high similarity. In general, values for both qualitative and quantitative similarity were up to 3x higher than similar studies reported in the literature. For example, Hartvigsen and Kennedy (1993) indicated a mean similarity of 0.07, approximately 9x lower than our study. Other studies such as Nie et al (1998) and Salgado-Maldonado and Kennedy(1997) had mean Jaccard's index values 2 and 6x lower. Although Kennedy et al. (1986b) identified a mean Percent Similarity >60%, this value was based on a parasite species diversity of only 2-3 per fish species. One freshwater study that did indicate lake similarity to be >70% was Valtonen et al (1997). Unfortunately, the 2 studies are not strictly comparable because protozoans and ectoparasites were not included in our study. Repeating analyses by Valtonen et al. (1997) using only endoparasites would likely lower their similarity values. The only other known studies with comparable similarity values involved communities of parasites in marine fish (Holmes, 1990; Blaylock et al., 1997) and tropical freshwater fish (Kennedy, 1995; Salgado-Maldonado and Kennedy, 1997). Yet in these studies, high similarity values were attributed to the extremely high rates of exchange of generalist parasites, especially larval trematodes (Salgado-Maldonado and Kennedy, 1997). Despite these differences, it appears that component communities in lake whitefish share more characteristics of parasite communities described by Valtonen et al. (1997) and in marine fish, than those examined by Kennedy (Kennedy, 1977, 1978a; 1978b; Kennedy et al., 1986b; Kennedy, 1990; Hartvigsen and Kennedy, 1993, Guégan and Kennedy, 1993; Kennedy and Guégan, 1994).

Thus, it is the combined characteristics of high similarity, domination by core species with a mixture of life-cycle strategies (both autogenics and allogenics), and the absence of a role for acanthocephalans that distinguishes component communities in whitefish from the Caribou Mountain Lakes from other studies. The most simple explanation for these contrasting patterns is my choice of study location and (or) host species. Being a relatively pristine environment, the Caribou Mountains may contain parasite communities not representative of lakes off the plateau. Yet results from Chapter 2 suggest that this is unlikely because all of the lake whitefish parasites recovered were identified in other Canadian studies (McDonald and Margolis, 1995). However, I also recognize that lake whitefish communities in some lakes in the Caribou Mountains have extremely high intensities relative to other sites in Canada

(Chapter 2). Clearly, these high-intensity species play a major role in conferring structure and similarity to the component communities in whitefish on the plateau. Thus, the processes leading to high parasite intensity (Chapter 4) may be the single most important factor in distinguishing these communities from the stochastic and unpredictable communities described by Kennedy.

It is also clear that in my choice of host species, I chose the one with the richest and most diverse parasite assemblage (Chapter 2). Helminth communities in the other 11 host species, with the possible exception of lake cisco, were less diverse with more sporadic parasite distributions than those infecting lake whitefish. Thus, while whitefish component communities may contrast with studies depicted by Kennedy (Kennedy, 1977, 1978a; 1978b; Kennedy, 1990; Hartvigsen and Kennedy, 1993, Guégan and Kennedy, 1993; Kennedy and Guégan, 1994; Salgado-Maldonado and Kennedy, 1997), the parasite communities in other fish species in the Caribou Mountains probably do not.

Alternatively, it is possible that the hosts and their respective parasite communities selected by Kennedy are not indicative of parasite communities in other fish species. The distinctive pattern of dominating acanthocephalans combined with stochastic occurrences of other species under investigation, and the high recovery of generalists, may be unique to Britain or to other highly-altered sites. The low similarity and other characteristics of the communities described by Kennedy may also be due to complications imposed by anthropogenic effects. Parasite ecologists should be aware that studies on anthropogenic systems might not accurately reflect parasite community structure. For example, pulp and paper effluent has been reported to affect both host and parasite species diversity (Valtonen et al., 1997). Reservoirs and introduced fish species, both common alterations in temperate freshwaters (e.g. Hartvigsen and Kennedy, 1993), and the absence of salmonids, specifically coregonids in polluted waterbodies (Hakkari, 1992), have affected the parasite community structure in altered waterbodies (MacKenzie et al., 1995; Lafferty, 1995; Valtonen et al., 1997). More evidence from pristine systems is needed before determining whether Kennedy's description of parasite component communities can be applied to other geographic locations.

Despite the presence of core species in every lake and high similarity, there was still much variation in parasite intensity between the lakes. The cluster analyses depicted two distinctive lake types. The first included whitefish with low-intensity infections and no acanthocephalans (Margaret, Semo, Pitchimi and Caribou). The other included fish with high overall intensities and three acanthocephalans (Eva, Sucker and Wentzel). The associations maintained between lakes whether using parasite presence/absence or intensity data were unusual. Most studies indicate a shuffling of lakes between clusters when comparing Jaccard's index and Percent Similarity values (Bailey and Margolis, 1987; Hartvigsen and Kennedy, 1993; Holmes, 1990; Blaylock et al., 1998). The metacommunity analyses demonstrated factors such as lake size, lake distance and connectivity had little predictive value in distinguishing these two types of lakes. Those factors potentially leading to variation in intensities between lakes will be examined in Chapter 4.

My interpretations could be influenced by the broad-scale approach undertaken in this study. Thus, in order to emphasize spatial variation, I have necessarily restricted my analysis of temporal variation. Kennedy (1993) suggested that the understanding of component community structure on a temporal scale is lacking since the majority of studies occur for <3 years. Annual variation could obscure these patterns, especially with respect to the different transmission patterns of individual parasite species (Holmes, 1990). For example, the plerocercoid stage of T. crassus can remain viable for several years in lake whitefish (Rosen and Dick, 1984), but will only survive up to one year as an adult in northern pike (Shostak and Dick, 1987). Thus, without examining the longevity differences, if any, of allogenic and autogenic transmission stages, the high abundance values for both allogenics may merely indicate accumulation over time, with a slow generation turn-over (Holmes, 1990).

It has been suggested that parasite component community similarity is determined by regional factors that promote similarity versus local factors that lead to distinctions between water bodies (Kennedy, 1990; Aho and Bush, 1993). Unlike Kennedy (1990), both regional and local factors seem to play a role in defining the structure of the parasite component community of lake whitefish in the current study. Specific factors that are distributed regionally enable the presence of both allogenic and autogenic core species in all seven lakes. However, local effects are likely affecting the intensity levels indicated by the two lake clusters. It may be that in pristine environments, regional and local factors are not overriding each other, but are balanced in such a manner as to enhance parasite transmission.

Unlike Hartvigsen and Kennedy (1993), the Caribou Mountains lakes were not chosen to reduce variation and enhance similarity between parasite component communities. However, evidence of high similarity and species diversity patterns observed in this study and in Valtonen et al. (1997), suggest that Kennedy may be premature in concluding that fish parasite communities are species poor, and that it would be rare for two lakes to have similar component communities. Due to differences in fish species, patterns of exchange and anthropogenic influences, it is also premature to directly compare results from Valtonen et al. (1997) to those reported here. Thus, patterns in fish parasite component communities are complicated, and as suggested by Sousa (1994), it is too early to make broad generalizations.

Chapter 4. Predictability of parasite component communities in lake whitefish (Coregonus clupeaformis) from seven lakes in northern, Alberta.

INTRODUCTION

The identification of factors determining the diversity of parasite communities has been a prominent goal for parasite ecologists since the early studies by Wisniewski (1958) and Dogiel (1961, 1964). Studies that involve fish as hosts continue to be a central focus (review in Chapter 1). A number of factors have been shown to confer predictability to fish parasite communities, including the structure of the host community (Holmes, 1979), physical characteristics of ecosystems (Marcogliese and Cone, 1991b), and historical and phylogenetic events (Halvorsen, 1971; Esch et al., 1988). However, based on evidence from a large number of studies involving parasites of freshwater fish, Kennedy (1990) concluded that the stochastic and erratic occurrence of fish parasites, together with the uniqueness of individual water bodies, prevented any form of predictability between two samples. This view of unpredictable, stochastic communities, particularly for parasites of fish, pervades the literature on the ecology of parasite communities (reviews by Kennedy; 1990; Esch and Fernandez, 1994; Chapters 1 and 3).

One of the factors that was first considered to play an important role in shaping parasite component communities of fish was the trophic status of a lake (Wisniewski, 1958; Kennedy, 1978a). The prediction was that as lakes become more productive, the dominant parasite species shifted from ones that completed their life-cycles in fish (autogenic species) to ones that completed their life-cycles in birds (allogenic species). Esch (1971) extended this idea, indicating that parasite species diversity and intensities should increase as lake productivity increased. Thus, high parasite intensities in fish should be associated with eutrophic lakes where allogenic species dominate. However, the link between lake productivity and parasite component community structure has rarely been explicitly tested. Those few studies that have considered this question, have done so on fish collected from highly-altered ecosystems (Chubb, 1963; Halvorsen, 1971; Kennedy, 1978a, 1978b). One problem is that factors that are known to be associated with productivity (e.g. Chlorophyll-a, phosphorous concentrations) are rarely included in parasitological surveys, nor are other physico-chemical variables such as lake size, pH and temperature. Bush et al., (1997) point out that the omission of large-scale, multidisciplinary projects that incorporate parasitism into standard limnological and hydrogeographical studies is a major shortcoming.

The main objective of this chapter is to describe, and evaluate, species – environment associations for the parasite component communities of whitefish collected from seven pristine lakes in the Caribou Mountains, Alberta. Thus, this chapter extends the approach taken in Chapters 2 and 3 by examining whether a suite of 25 environmental factors could be used to predict parasite component community structure. Because several of the variables were specifically selected as indicators of aquatic productivity, a final objective was to test Esch's (1971) hypothesis regarding aquatic productivity and parasite community structure.

MATERIALS AND METHODS

Study area and collection procedures

For a general description of the Caribou Mountains Plateau and for detailed descriptions of the seven lakes that contain lake whitefish, see Chapters 2 and 3, respectively. Details concerning collection sites, fish processing procedures and the methods used to calculate component community characteristics are also outlined in Chapter 3.

Collection of environmental predictor variables

The environmental variables were collected as part of the Caribou Mountains Research Partnership (CMRP) (Scrimgeour et al., 1997a). Within 24 hr of the fish collections, the lakes were also sampled for benthic invertebrates (Scrimgeour et al., 1997b) and limnological and hydrological characteristics (McEachern and Prepas, unpublished data). Five morphometric characteristics of the lakes were also determined: lake area (ha), watershed area (ha), lake volume ($10^3 m^3$), maximum lake depth (m) and mean lake depth (m). These variables were estimated from 1:50,000 topographic, 1:15,000 Province of Alberta Phase 3 Forest Inventory and bathymetric maps (Dinsmore et al., 1999).

Temperature (°C) was measured using a YSI 50B oxygen probe situated approximately 5cm from the lake bottom (Dinsmore et al., 1999).

Water chemistry variables were collected using standard protocols. Unstable water chemistry variables were analyzed within 24 hr of collection to obtain the most accurate measurement before degradation. These included: colour, pH, total alkalinity, chlorophyll-a (Chl-a) and total phosphorus (TP). Using pre-filtered water, colour (mg Pt/L) was determined with a Milton Roy 1001 spectrophotometer at 440nm (Cuthbert and del Giorgio, 1992). Water pH was measured in the field using a Fisher Scientific Accumet 925m (Scrimgeour et al., 2000a). Total alkalinity (mg/L) was determined with a Mettler DL21 titrator, in accordance with the methodology of the American Public Health Association (1994). Chl-a (µg/L) was calculated by first filtering water on Whatman GF/C filters at approximately 50kPa and then measured using Ostrofsky's ethanol extraction method (Bergman and Peters, 1980). Total phosphorus (µg/L) was determined from unfiltered water samples using the potassium sulfate technique (Stainton et al., 1977).

Other water chemistry variables that were used included: total nitrogen (TN), dissolved organic carbon (DOC), volatile suspended solids (VSS), non-volatile suspended solids (NVSS) and calcium (Ca). TN (µg/L) was measured by combining measurements of $NO_3^- + NO_2^-$ and NH_4^+. Water samples tested for $NO_3^- + NO_2^-$ and NH_4^+ were filtered with pre-washed Gelman DM-450 membranes (pore size = 0.45µm) and then analyzed with a Technicon autoanalyzer (Scrimgeour et al, 2000). Dissolved inorganic carbon (mg/L) was determined with an Ionics 1505 carbon analyzer (Curtis and Prepas, 1993). Volatile suspended solids (mg/L), NVSS (mg/L) and Ca (mg/L) were measured following the protocols of Cole (1994). Each lake was sampled for limnological and hydrological characteristics once in July.

Four variables were used to describe characteristics of the lake fish populations (Scrimgeour et al., 1997b). Host species richness indicated the number of different fish species in a lake. Total fish density measured total fish abundance per lake by including all the fish species present. Relative fish density was estimated by dividing the number of lake whitefish caught by total fish density. Mean condition indicated the relative weight of a fish to its length (mean condition = weight (g)/total length (mm)) (Scrimgeour et al., 1997b). A high condition value indicated a fish that was heavier (e.g. may have a higher fat content) than a similar-sized fish that weighed less. Finally, 4 characteristics of the parasite component community of lake whitefish were considered: mean number of species per host, mean number of individuals per host, parasite species diversity (reciprocal of Simpson's Index) and parasite species dominance (data from Chapter 3).

Multivariate analyses

I used Canonical Correspondence Analysis (CCA) to characterize associations between lake environmental variables and characteristics of the parasite component communities. CCA is a common type of multivariate analysis (Stevensen et al., 1989; Allen and Peet, 1990; McCune and Mefford, 1995; Williams et al., 1997) that is used to 1) infer species-environment relationships and 2) detect patterns that are best explained by a particular set of environmental variables. CCA was also chosen to permit comparisons with Scrimgeour et al. (2000), who examined the same set of lakes in the Caribou Mountains lakes for invertebrate species-environment associations. CCA was performed on the statistical package PC-ORD (Version 2.0) (McCune and Mefford, 1995). The highest canonical coefficients indicated those environmental variables with the most influence on parasite community structure.

To determine whether the correlations between the environmental variables and the first two ordination axes were significantly higher than expected by chance, a Monte Carlo test was performed (Gauch, 1982, McCune and Mefford, 1995). The null hypothesis was that there was no association between the environmental variables and parasite community structure. To test the null hypothesis, data are randomly shuffled within the columns of the parasite species dataset and the species-environment correlations are regenerated (McCune and Mefford, 1995). One random shuffling was classified as one Monte Carlo iteration. For each ordination analysis, 100 iterations of the Monte Carlo test were run. A species-environment association was significant when few (e.g. less than 10) numbers were randomly generated above the actual value. A P value ≤ 0.05 was considered significant.

Although rare species are often considered to lead to ecological noise (Gauch, 1982), rarity is relative to sample size and size of the study area. Thus, rare parasite species (in this case, the 3 acanthocephalans; Chapter 3) were included in the analyses. The CCA was first done on all 10 parasite species. It was then repeated without the two allogenic species, D. dendriticum and C. erraticus (Chapter 3). The reason for this is that these two allogenic species are unlikely to be directly influenced by fluctuations in water chemistry (Esch et al., 1988), partly because their bird definitive hosts can carry on the life-cycle outside the confines of a lake. Thus, it is possible that these two abundant, and often dominant (Chapter 3) species might mask species-environment patterns occurring with the autogenic species (Esch et al., 1988). For analyses, parasite intensities were log-transformed in order to reduce the effects of highly variable species intensities (Gauch, 1982). The environmental data were not transformed.

RESULTS

Most of the 25 biotic and abiotic characteristics that were measured varied extensively between the seven lakes (Table 4.1). High variation was especially apparent for the morphometric characteristics, features associated with parasite intensity, and those associated with aquatic productivity. Thus, TP ranged from 13.3 - 40.0µg/L, TN from 411.5 - 610µg/L and Chl-a ranged from 2.1 - 15.6µg/L. The exceptions were variables such as water temperature, pH and fish species richness that tended to vary little between the lakes (Table 4.1).

Table 4.1. Abiotic and biotic characteristics of seven study lakes in the Caribou Mountains, Alberta. Where applicable, mean (± standard deviation) is provided. Data provided by McEachern (in press) and Scrimgeour et al (1997).

	Margaret	Eva	Semo	Pitchimi	Wentzel	Sucker	Caribou*
Morphometric Characteritsics							
lake area (ha)	8160	1706	536	1334	3819	268	1428
watershed area (ha)	74023	3696	3218	11519	80898	832	11572
lake volume ($10^3 m^3$)	1509600	88920	55564	105386	301701	24365	101388
maximum lake depth (m)	61.0	21.3	33.5	19.8	57.9	12.8	24.4
mean lake depth (m)	18.5	5.2	11.6	7.9	7.9	5.5	7.1
Environmental Characteristics							
temperature (°C)	12.0±5.2	14.7±3.1	13.2±5.6	13.7±4.9	14.3±4.0	14.5±15.0	17.1
colour (mg Pt/L)	209.6±104.7	8.1±1.5	104.7±5.9	106.8±3.0	173.9±8.9	31.3±17.8	168.5
pH	7.4±0.2	8.1±0.8	7.4±0.3	8.1±0.5	7.4±0.3	8.2±0.0	7.8
TP (µg/L)	13.3±2.5	39.5±9.2	21.5±4.9	26.0±8.5	17.5±0.7	40.0±2.8	24.0

Table 4.1 Continued

TN (µg/L)	510.0±56.7	546.0±164.0	411.5±31.8	536.0±48.1	570.0±25.5	610.0±131.5	554
Chl a (µg/L)	5.1±3.6	15.6±8.5	4.7±2.1	6.0±0.04	2.1±0.1	14.0±11.9	4.3
Ca (mg/L)	6.5±0.2	9.9±0.04	10.4±0.3	12.5±0.1	8.7±6.4	11.8±0.2	14.7
Tot. Al. (mg/L)	16.3±5.0	38.3±2.1	36.8±2.1	45.0±2.1	29.3±15.9	44.3±1.1	51.8
VSS (mg/L)	0.73±0.4	3.8±1.1	0.8±0.4	1.1±0.4	0.4±0.1	3.2±1.1	0.9
NVSS (mg/L)	0.23±0.3	1.2±0.3	1.0±0.7	0.8±0.7	0.2±0.1	0.4±0.5	0.8
DOC (mg/L)	16.7±0.0	8.6±1.5	13.2±0.4	16.5±0.2	21.4±2.3	11.4±0.6	18.7
Biotic Characteristics							
# LKWH examined for parasites	25	25	18	16	20	24	7
host species richness	7	7	6	5	9	4	8
total fish density	247	226	72	225	243	79	116
relative whitefish density	0.33	0.33	0.16	0.65	0.21	0.43	0.06
mean condition of LKWH	0.97	0.81	0.76	0.91	0.96	0.92	0.94

Table 4.1 Continued

Characteristics of Parasite Component Community							
# spp./host	4.6	5.8	4.9	5.2	6.2	5.9	5.6
# inds./host	80.6	430.6	105.1	130.0	473.3	371.9	179.0
spp. diversity	3.9	1.8	3.0	3.8	2.8	2.3	3.6
parasite species dominance	0.35	0.72	0.52	0.37	0.42	0.52	0.31

TP = total phosphorus; TN = total nitrogen; Chl a = chlorophyll a; Ca = calcium; Tot. Al. = total alkalinity; VSS = volatile suspended solids; NVSS = non-volatile suspended solids; DOC = dissolved organic carbon; * = only one measurement taken. # = number; LKWH = lake whitefish; spp. = number of parasite species; inds. = parasite abundance

The overall CCA ordination of the seven lakes using 25 environmental variables is shown in Figure 4.1. For clarity, only the six variables that explained a significant proportion of the variation in the first two axes are presented (Figure 4.1). Overall, 48% of the variation in parasite intensities was explained by these two axes. Of this total variation, Axis 1 explained 70% of the total variance, while Axis 2 explained 20%. The Monte Carlo test indicated that both axes were significant ($P \leq 0.01$). The first axis was correlated with four variables, but specifically with TP ($r = 0.72$), and Chl-a ($r = 0.69$). The second axis was correlated with colour ($r = -0.58$) and calcium ($r = 0.47$). The species-environment correlation was high for both axes (1.0 and 0.99).

When the analysis was repeated without the two allogenic species (*D. dendriticum* and *C. erraticus*), there was only a moderate improvement in the amount of variation explained by Axis 1 (73%), while Axis 2 remained unchanged (20%). The Monte Carlo Test was significant for both axes ($P \leq 0.02$). Axis 1 was associated with the same two variables, TP ($r = 0.74$) and Chl-a ($r = 0.71$). Axis 2 was associated with colour ($r = -0.60$) but the correlation was weakened for calcium ($r = 0.37$). The species-environment correlation for both axes was 0.99.

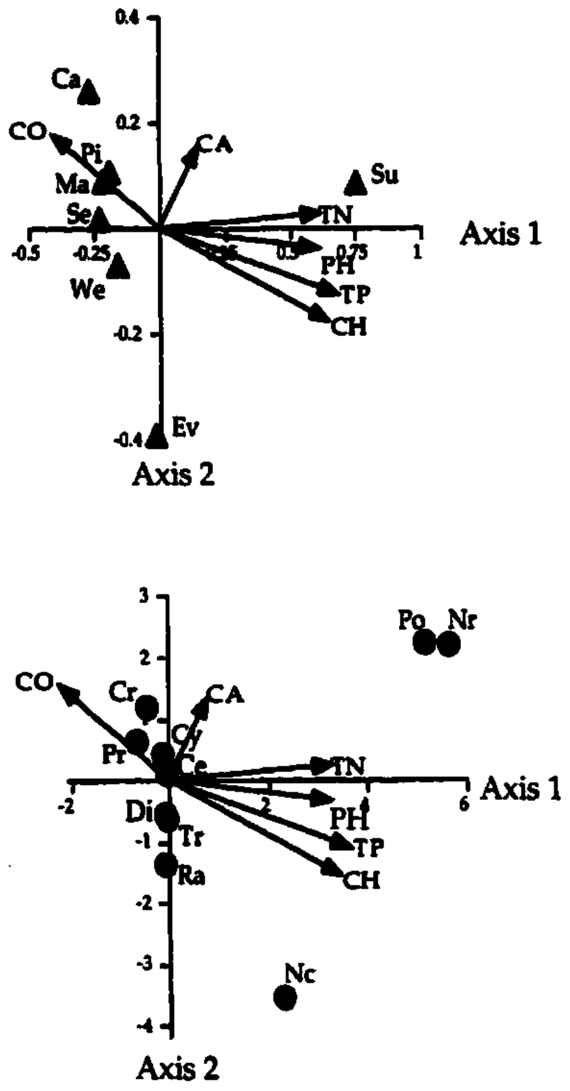

Figure 4.1. Canonical Correspondance Analysis (CCA) for seven lakes and 10 lake whitefish parasite species in the Caribou Mountains. The significant environmental variables are the same for both graphs: CA = calcium, CH = chlorophyll- a, CO = colour, PH = pH, TP = total phosphorus and TN = total nitrogen. A) Lakes: Ca = Caribou, Ev = Eva, Ma = Margaret, Pi = Pitchimi, Se = Semo, Su = Sucker and We = Wentzel. B) Parasites: Cr = Crepidostomum farionis, Cy = Cystidicola farionis, Ce = Cotylurus erraticus, Di = Diphyllbothrium dendriticum, Nc = Neoechinorhynchus crassys, Nr = N. rutuli, Po = Pomphorhynchus bulbocolli, Pn = Proteocephalus neglectus, Ra = Raphidascaris acus and Tr = Triaenophorus crassus.

Environmental co-variates with lakes

Based on parasite intensity data summed across whitefish within a lake, Margaret, Semo, Caribou and Pitchimi Lakes were distinct and strongly associated with high colour (Figure 4.1a). Thus, lakes high in colour tended to have parasite component communities that were low in mean intensity. The remaining three lakes (Eva, Sucker and Wentzel) did not form a similarly distinct cluster based on a single environmental factor (Figure 4.1a). Thus, Eva and Wentzel Lakes were negatively associated with calcium, while only Eva Lake was negatively associated with colour. In contrast, Sucker Lake was positively associated with the three lake productivity variables (TN, Chl-a and TP) and pH. These results show that low-intensity lakes could be clustered together based on a single predictor variable (colour), whereas the high-intensity lakes had more complex associations with the environmental variables.

Environmental co-variates with parasite species

Based on the intensities of individual parasites, P. neglectus and Crepidostomum farionis were positively correlated with colour (Figure 4.1b). Triaenophorus crassus, R. acus and D. dendriticum were negatively correlated with calcium and colour. Cotylurus erraticus and Cystidicola farionis were not clearly associated with any environmental variables. The three acanthocephalan species were weakly associated with the suite of predictor variables that were linked to aquatic productivity (TN, TP, Chl-a and pH).

DISCUSSION

The structure of parasite component communities in lake whitefish was affected by two opposing environmental gradients, both of which were associated to aquatic productivity. One gradient was defined primarily by colour, and secondarily by calcium concentration. The other was defined by characteristics that are known to be directly linked to aquatic productivity (TP and Chl-a). Four lakes (Margaret, Semo, Pitchimi and Caribou) were distinct and clustered due to a combination of high colour, low productivity, the absence of larval acanthocephalans (Chapter 3) and low parasite intensities. The other three lakes (Eva, Sucker and Wentzel) tended to have low colour, high productivity, high parasite intensities and acanthocephalans. These results, particularly those for the four low-intensity lakes, support Esch's (1971) hypothesis regarding parasite community structure and aquatic productivity. The implication is that parasite communities in whitefish contain components that are predictable on the basis of aquatic productivity. Thus, my results, based on parasite communities of fish collected from these seven pristine lakes, contrast with Kennedy's (1990) assertion that parasite communities are unpredictable and stochastic assemblages.

The strongest predictor of parasite component community structure in whitefish was colour. This was an unexpected result, partly because colour is only indirectly linked to aquatic productivity (Cole, 1994). Thus, if aquatic productivity alone was the most important predictor variable, then those features that are directly linked to productivity would be expected to show the strongest patterns. However, colour indicates the level of humic material in the water, reaching maximum values in ecosystems where muskegs or bogs dominate the watershed (Mitchell and Prepas, 1990). Interestingly, five of the seven lakes in the Caribou Mountains were highly coloured relative to 26 other lakes in northern Alberta (Mitchell and Prepas, 1990; Dinsmore et al., 1999), reflecting the presence of humic acids originating from the surrounding muskeg that characterizes this sub-arctic region (see chapter 2). Thus, one of the unusual (and perhaps unique) features of the Caribou Mountain lakes is their relatively high colour.

However, colour is also related to water transparency, the depth whereby 1% of available light is suitable for photosynthesis (Mitchell and Prepas, 1990). Thus, water colouration is known to be negatively correlated with primary productivity (Mitchell and Prepas, 1990), a pattern that is especially apparent with Eva and Sucker Lakes. Eva and Sucker Lakes had colour values <30, whereas all other lakes were >100 (Table 4.1). Both lakes were also highest in TP and Chl-a concentrations. The ordination results show that parasite intensities reflected these opposing environmental gradients. Thus, Eva and Sucker lakes contained fish with high intensities of species such as D. dendriticum, C. erraticus, T. crassus and R. acus. In contrast, Margaret, Semo, Pitchimi and Caribou Lakes tended to harbour whitefish with low intensities of these four species, but high intensities of Crepidostomum farionis and P. neglectus. These results, together with the fact that the four lakes formed a distinct cluster (Chapter 3 and Figure 4.1a), suggest that the predictive power of variables associated with aquatic productivity is less clear as parasite intensities increase. It should be noted that this result may simply be a feature of the positive correlation between mean parasite intensity and its associated variation (Anderson and Gordon, 1982). Thus, as mean intensity increases (especially for allogenic species that are a feature of the productive lakes), variation around the mean increases, and the strength of species-environmental correlations is likely to be weakened.

Esch et al. (1988) suggested that the distinction between low-intensity and high-intensity lakes could be partly explained by parasite life-histories. Thus, in productive lakes, allogenic species that use birds as definitive hosts should dominate. This expected pattern was not consistent in the Caribou Mountain Lakes where autogenic species such as T. crassus, P. neglectus and R. acus could also dominate the high-productivity lakes. An alternative explanation for the distinction between low-intensity and high-intensity lakes may be in the intermediate hosts that dominant species then to share in high-intensity lakes. Copepods are a first intermediate host for D. dendriticum, T. crassus and R. acus. For each of these species, high-intensity infections occurred in lakes with low colour (Figure 4.1b; Eva, Sucker and Wentzel). Thus, if copepod biomass is highest in lakes with low colour and thus with high primary productivity, then a response by the copepods should equate to a response by the parasites they carry. There is no information available on zooplankton biomass in the Caribou Mountain Lakes, but Scrimgeour et al. (2000a) showed the biomass of oligochaete and chironomid larvae was positively correlated with phosphorus and free-living nematodes were positively correlated with total inorganic nitrogen. Thus, in general, aquatic invertebrate biomass tends to be highest in the more productive lakes in the Caribou Mountains. My preliminary evidence suggests that parasites respond similarly, at least those that use copepods as first intermediate hosts. A long-term study by Marcogliese et al. (1990) showed that parasite intensities in mayflies from Gull Lake, Michigan increased as cultural eutrophication increased. When eutrophication was reversed, parasite intensities decreased rapidly.

It should be expected that each of the ten species that infect whitefish has different levels of tolerance to increased productivity. For instance, in four Finnish lakes, the presence and abundance of molluscs decreased once the system surpassed a suitable range of productivity because of intolerable nutrient loading levels (Valtonen et al., 1997). Another unanswered question concerns the relationship between lake whitefish parasites and their piscivorous fish definitive hosts. Do the species/environment associations described above apply only to parasite stages infecting their intermediate hosts, or do they also affect stages in their definitive hosts? In addition, the effect of temporal scale on spatial patterns needs to be addressed in future studies to determine how parasite species react to fluctuating water chemistry variables over time.

Hartvigsen and Kennedy (1993) concluded that predicting parasite component community structure would only be possible if a suite of environmental variables could be identified and their associations clarified. In the Caribou Mountains, seven lakes were classified as either low in colour and high in productivity or high in colour and low in productivity. Of the ten parasite species examined, five common species were clearly associated with at least one environmental variable. Thus, a portion of the spatial structure of parasite communities in lake whitefish can be predicted, based on a suite of specialist, core species interacting with aquatic productivity.

Chapter 5. General Conclusions

Communities of parasites in fish in the Caribou Mountains range from being low in species diversity and simple, to being high in species diversity and complex. At one extreme, fish such as trout perch were infected with only four parasite species and their intensities never exceeded 10 per host. At the other extreme, fish such as whitefish were infected with 10 parasite species and their intensities commonly exceeded 50 per host. It should not be surprising that this variation in diversity should occur between hosts, given the wide diversity in parasite community structure in fish reported in other studies (e.g. Kennedy, 1990; Valtonen et al., 1997). Perhaps what is surprising, is the variety of parasite species that occur within such a restricted spatial scale (19 lakes in $4300km^2$).

In my attempt to resolve the stochastic versus deterministic views of parasite community structure, I selected the host that was regionally common and had the highest parasite species richness. The parasite community structure of lake whitefish in seven lakes in the Caribou Mountains can be characterized as both high in species diversity. There were 10 parasite species, eight of which matured in fish, and two that matured in piscivorous birds. Species richness was comparable to other Canadian studies in Manitoba (n = 10, Poole, 1985), Alberta (n = 11, Leong and Holmes, 1981) and Labador (n = 10, Chinniah and Threfall, 1978). No endemic species were recovered and all parasite species have been found previously in whitefish.

Although species richness was similar, there were three factors that distinguished the parasite component communities in Caribou Mountain Lakes whitefish from other studies on freshwater fish. First, almost all of the species were specialists. Those few species that were exchanged between hosts, only did so between other salmonids, particularly lake cisco. Second, a suite of 7sevem core species was found in all lakes, each of which usually had high intensities (>50). In general, the presence of any core species contrasts with Kennedy's (1990) assertion that core species are absent from parasite communities in freshwater fish, and confirms, that Hanski's (1982) core-satellite species hypothesis is appropriate for parasites of freshwater fish. Lastly, the similarity in parasite community composition and species intensities between lakes was higher (>70%) than that reported from comparable studies (10-30%) in Europe and North America. Thus, it appears that parasite communities in whitefish in the Caribou Mountains are more similar to the high diversity, high similarity systems described for fish collected from marine habitats (e.g. Holmes, 1990; Blaylock et al., 1998.) than to the low diversity, low similarity system typically described for freshwater habitats (e.g. Hartvigsen and Kennedy, 1993).

The above three factors may be the consequence of the unusually high-intensities of parasite species in whitefish in the Caribou Mountains. Compared to four other studies involving populations of whitefish, parasite intensities were at least three times higher for five of the six species in lakes in the Caribou Mountains. Clearly, high intensity infections will affect descriptors of parasite community structure, such as species diversity and dominance. More importantly, because the high intensity species also occurred in every lake, high values for community similarity should be expected. Thus, the identification of the factors leading to high intensity and high similarity are important in evaluating the degree to which parasite communities in lake whitefish are predictable.

Results from chapter 4 are among the first to address whether specific environmental factors co-vary with features of parasite community structure, such as intensity. Of the 25 environmental variables examined, five were significantly associated with parasite intensity, especially colour and productivity (total phosphorus and chlorophyll-a). Four low-intensity lakes were characterized by low productivity and high colour, while 3 high-intensity lakes had high productivity and low colour. These environmental variables explained 48% of the variation in intensity of five common parasite species. These results show that lake productivity and colour influences the intensity of a suite of common parasite species, and the species-environment associations can be predicted.

Before the controversy surrounding the predictability of parasite communities in fish can be resolved, anthropogenic alterations to the environment is one key issue to address. One possible explanation for the differences between the Caribou Mountains study and other studies such as those by Kennedy (Kennedy, 1977, 1978a; 1978b; Kennedy et al, 1986b; Kennedy, 1990; Hartvigsen and Kennedy, 1993, Guégan and Kennedy, 1993; Kennedy and Guégan, 1994) is that my study occurred in a pristine area. Most empirical and theoretical tests have been done on fish communities affected by direct impacts to fish populations (e.g. commercial and recreational fishing), and (or) changes to the water drainage basin, such as eutrophication, the damming of rivers, and forest harvesting. Alone or in combination, human alterations can impact parasite transmission and colonization (Mitchell and Prepas, 1990; Valtonen et al., 1997), making it difficult to identify the true structure of the community, thus weakening direct comparisons between studies. With my study considered as one replicate in a pristine environment, more studies in pristine areas are required to clarify how my results compare to those from anthropogenically-altered habitats. Unfortunately, few pristine areas remain that can be compared at the same spatial scale.

Results from this study suggest that the presence of five common parasite species can be predicted through their association with colour and lake productivity variables. Since a system of this magnitude cannot be maintained in a laboratory, one possibility to better understand the species-environment associations would be to experimentally alter the productivity levels in a group of lakes at the same spatial scale. Another alternative for future studies would be to examine the effects of natural disturbances on lake productivity, and then monitor changes in parasite community structure over time. The effect of phosphorus fluctuations on the presence and intensity of common parasite species may depend on the rate phosphorus levels change over a period of time. For instance, phosphorus levels may increase every spring due to an algal bloom with a steady decline over the summer, or increase immediately after a forest fire with no new input until another disturbance some years later. Conversely, restoration of a eutrophic or polluted waterbody to an oligotrophic one should parallel a decline in abundant parasites. Ideally, future studies should focus on a host common within a pristine area that has defined borders, where the host is infected with both allogenic and autogenic species and the area is accessible for long-term monitoring.

Thus, the generalization that "Helminth communities in freshwater fish are fundamentally stochastic...dependant on chance introductions...and extinction events" (Hartvigsen and Kennedy, 1993), may be premature. My results suggest that a sub-set of the component community, five common parasite species, is associated with a combination of five specific abiotic environmental variables, some of which are tied directly to aquatic productivity. The association between parasite community structure and aquatic productivity was first suggested by Esch (1971), but has not previously been tested. These findings imply that some aspects of the parasite community in fish are predictable, despite their notorious variability. In ecology, the use of ordination techniques to associate environmental change to community change is becoming more popular. For example, Scrimgeour et al. (2000b) correlated an increase in benthic macroinvertebrates biomass to high lake productivity in the Caribou

Mountains. My results suggest that species-environment associations described by (Scrimgeour et al., 2000a; Scrimgeour et al., 2000b) can also be used for fish parasites.

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