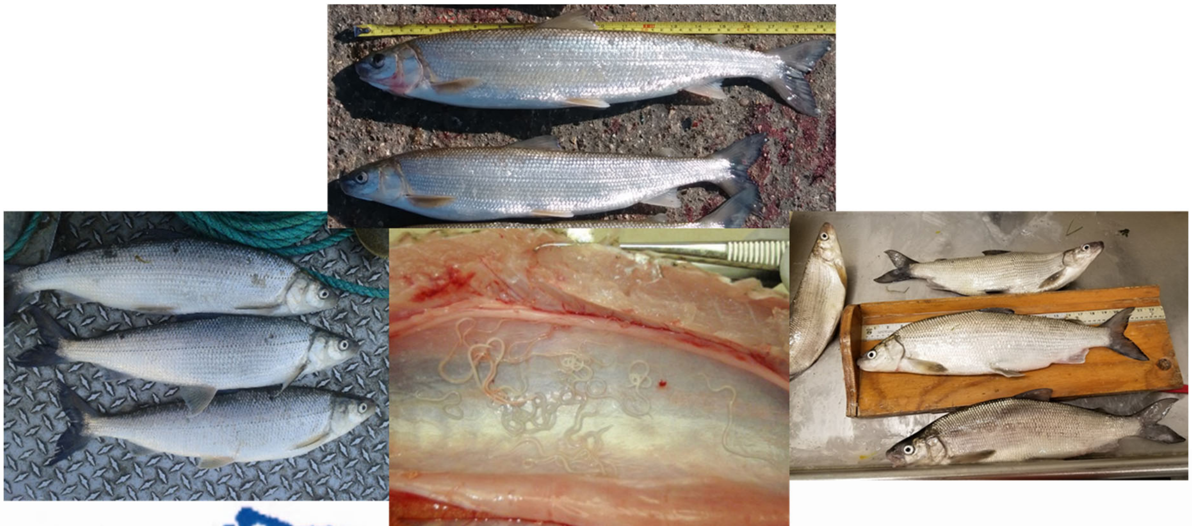
Parasites of Coregonines in the Genera *Coregonus* and *Prosopium* (Salmonidae, Coregoninae) in the Great Lakes



Great Lakes Fishery Commission

Miscellaneous Publication 2022-01

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Great Lakes Fishery Commission
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Cover photographs of three common whitefish species and the parasite *Cystidicola* sp. Left: Cisco (*Coregonus artedi)* from Lake Superior (Michigan DNR Fisheries Division). Top: Round Whitefish (*Prosopium cylindraceum)* from Ottawa County, Lake Michigan (Michigan DNR Fisheries Division). Right: Lake Whitefish (*Coregonus clupeaformis*) from Green Bay, Wisconsin (Lydia Doerr, Michigan DNR Fisheries Division). Bottom: *Cystidicola* sp. (nematode) infecting a Lake Whitefish swimbladder (Courtney Harrison and Thomas Loch, Michigan State University Aquatic Animal Health Laboratory).

Parasites of Coregonines in the Genera *Coregonus* and *Prosopium* (Salmonidae, Coregoninae) in the Great Lakes

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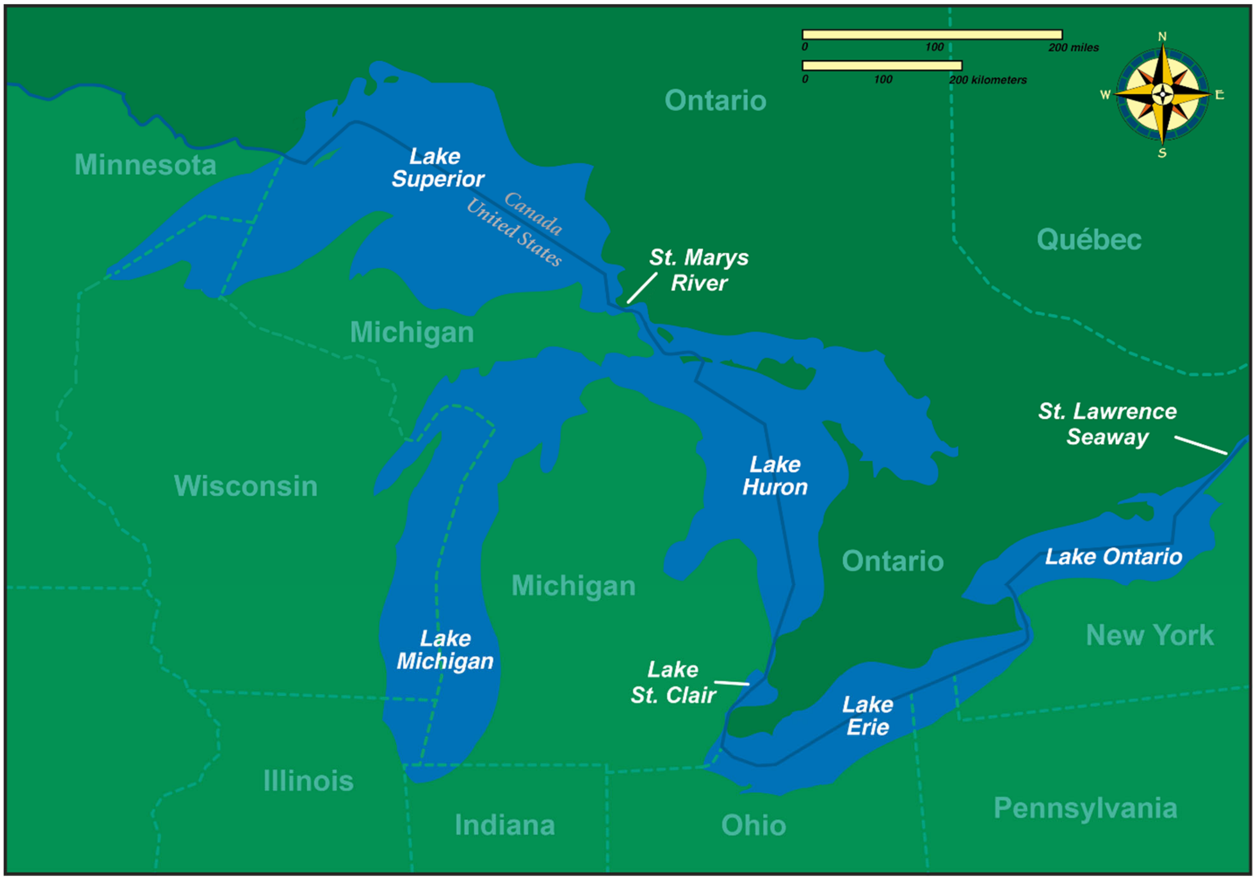
Frontispiece. The Laurentian Great Lakes showing locations referenced in the text.



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EXECUTIVE SUMMARY

This document describes and summarizes the parasites of ciscoes and whitefishes within the subfamily Coregoninae in the Great Lakes and their connecting waters. Our report is based on information from the literature and our personal observations about mastigophorans, ciliophorans, myxozoans, digenetic trematodes, monogeneans, cestodes, nematodes, acanthocephalans, leeches, copepods, and molluscs of coregonines from 1898 through 2020. Parasites are reported in Longjaw Cisco (*Coregonus alpenae*), Cisco (*C. artedi*), Lake Whitefish (*C. clupeaformis*), Bloater (*C. hoyi*), Deepwater Cisco (*C. johannae*), Kiyi (*C. kiyi*), Blackfin Cisco (*C. nigripinnis*), *C. prognathus* (nomem dubium), Shortnose Cisco (*C. reighardi*), Shortjaw Cisco (*C. zenithicus*), Round Whitefish (*Prosopium cylindraceum*), and Pygmy Whitefish (*P. coulteri*). A total of 62 different studies reported on some aspect of one or more parasite species infecting these coregonine species from the Great Lakes. Our emphasis is on the parasites of *C. artedi*, *C. clupeaformis*, *C. hoyi*, and *P. cylindraceum* since many individuals of these species were examined for parasites in two or more lakes. The largest number of parasite species found in these coregonines was 24 from Lake Superior in *C. artedi*, 29 from Lake Huron in *C. clupeaformis*, 15 from Lake Superior in *C. hoyi*, and 20 from Lake Huron in *P. cylindraceum*. In total, we found 26 species of parasites reported in 11 studies of *P. cylindraceum*, 26 species in 22 studies of *C. hoyi*, 35 species in 36 studies of *C. artedi*, and 38 species in 35 studies of *C. clupeaformis*. *Epistylis* spp., *Trichodina* spp., *Chloromyxum* sp., *Henneguya zschokkei*, *Diplostomum* spp., *Ichthyocotylurus erraticus*, *Discocotyle sagittata*, *Proteocephalus longicollis*, *Eubothrium salvelini*, *Cyathocephalus truncatus*, *Diphyllobothrium* spp., *Triaenophorus crassus*, *Cystidicola farionis*, *Echinorhynchus salmonis*, *Ergasilus* spp., and *Salmincola* spp. caused pathology to one or more coregonine species. Plerocercoids of *Diphyllobothrium* might infect humans if they eat poorly cooked infected coregonines.

The most important parasite groups based on number of species for the four main species are *Coregonus artedi* (cestodes (32.2%), acanthocephalans (17.6%), digeneans (17.5%), copepods (14.7%)); *C. clupeaformis* (cestodes (18.4%), acanthocephalans (18.3%), digeneans (15.7%), nematodes (15.7%)); *C. hoyi* (cestodes (24%), acanthocephalans (24%), digeneans (20%), copepods (16%)); and *Prosopium cylindraceum* (acanthocephalans (19.2%), cestodes (19.1%), nematodes (19.1%), digeneans (15.2%)). The percentage of parasitic species that complete their life cycles in the four main coregonines (autogenic) ranged from 75-90% compared to 10-25% of the parasitic species found in these same fish that complete their life cycles in piscivorous birds or mammals (allogenic). Parasite faunas were similar for these four fish species. Cestodes, acanthocephalans, and some trematodes and nematodes are acquired in the diet of coregonines while monogeneans, copepods, and molluscs that have direct life cycles and larval trematodes directly penetrate fish.

Sorenson's Coefficient of Similarity for the parasite communities for each coregonine species varied among the Great Lakes and ranged from 0.24 to 0.64 for *Coregonus artedi*, from 0.31 to 0.69 for *C. clupeaformis,* from 0.14 to 0.62 for *C. hoyi*, and from 0.17 to 0.59 for *Prosopium cylindraceum*. The similarity coefficients for all parasite data combined into communities for all Great Lakes among the four major species ranged from a low of 0.57 (*C. artedi*, *P. cylindraceum*) to a high of 0.75 (*C. hoyi*, *P. cylindraceum*). Most similarity coefficients for the parasite communities of *C. artedi*, *C. clupeaformis*, *C. hoyi*, and *P. cylindraceum* showed congruence among the Great Lakes. Our analyses showed higher similarity coefficients within the Great Lakes for each coregonine species we evaluated than coefficients for the same species from lakes outside the Great Lakes basin, indicating that the parasite communities of these four coregonine species are more similar to one another in the Great Lakes than in other waters.

INTRODUCTION

Ciscoes and whitefishes (Salmonidae, Coregoninae) are found throughout the northern U.S. and Canada. Taxonomically, they are a group of perplexing species and subspecies. Scott and Crossman (1973) recognized 18 species of coregonines in North America, in three genera: *Coregonus* (14 species), *Prosopium* (3 species), and *Stenodus* (1 species). Historical cisco species of the Laurentian Great Lakes (Great Lakes) included the Cisco (*Coregonus artedi*), Bloater (*C. hoyi*), Deepwater Cisco (*C. johannae*), Kiyi (*C. kiyi*), Blackfin Cisco (*C. nigripinnis*), Shortnose Cisco (*C. reighardi*), Shortjaw Cisco (*C. zenithicus*), and Longjaw Cisco (*C. alpenae*) (see Eshenroder et al. 2016). The species *C. johannae* and *C. alpenae* are currently considered either extinct or their populations have introgressed with other species. Thus there are now only six ciscoes extant in the Great Lakes, and the status of two of these is uncertain (Eshenroder et al. 2016). Todd (1981) concluded that *C. prognathus* has no taxonomic validity and should be considered a nomen dubium with a scientific name of unknown or doubtful application. Of the whitefishes, the Lake Whitefish (*C. clupeaformis*), Pygmy Whitefish (*Prosopium coulteri*), and Round Whitefish (*P. cylindraceum*) occur in one or more of the Great Lakes. Ciscoes are difficult to identify because they are phenotypically diverse and exhibit more similarity among lakes than within lakes (Eshenroder et al. 2016). Individuals in the genus *Stenodus* do not occur in the Great Lakes.

Coregonines are an important component of fish communities in the Great Lakes. They transfer energy from the benthic food webs to the upper-level pelagic food webs and vice versa (Eshenroder and Burnham-Curtis 1999; Nalepa et al. 2005; Stockwell et al. 2014). Of the coregonine species, *Coregonus clupeaformis* provides the most important fishery from an economic perspective in Lakes Superior, Huron, and Michigan. It is estimated that *C. clupeaformis* alone had an annual commercial value yield of US$16.6 million (Mohr and Ebener 2005; Madenjian et al. 2006; Ebener et al. 2008). The recreational harvests of *C. artedi*, *C. clupeaformis*, and *Prosopium cylindraceum* from Michigan waters of the Great Lakes were more than 125,000, 55,000, and 3,600 pounds, respectively, during 2016-2018 (Michigan DNR, Fisheries Division, unpublished data). Thus, coregonines are an integral component of both the fish community and fisheries of the Great Lakes, and knowledge of coregonine parasites and diseases will help advance our understanding of their biology.

Numerous studies documented the parasites of coregonines outside of the Great Lakes. Some early important studies of the parasites of coregonines in Canada can be found in Miller (1945a, b; 1946; 1952), Welch (1952), Lawler and Scott (1954), and Lawler (1970). Surveys about the parasites of coregonines in Canada include Dechtiar (1972a, b), Arthur et al. (1976), Chinniah and Threlfall (1978), Watson and Dick (1979), Dick and Rosen (1981), Leong and Holmes (1981), Arai and Mudry (1983), Stewart and Bernier (1999), Goater et al. (2005), and Pietrock and Hursky (2011). There are a few anecdotal parasitological studies of the four main coregonine species (*Coregonus artedi, C. clupeaformis*, *C. hoyi*, *Prosopium cylindraceum*) in Maine (Meyer 1954), Wisconsin (Cross 1938; Fischthal 1953), the Pacific Northwest (Pratt and McCauley 1961), and Alaska (Schmidt 1965). Studies of the parasites of coregonines have occurred in Russia (Bauer 1970; Fagerholm and Valtonen 1980) and Finland (Rahkonen and Valtonen 1987; Rintamaki and Valtonen 1988; Valtonen et al. 1988; Pulkkinen and Valtonen 1998, 1999; Pulkkinen et al. 1999; Karvonen and Valtonen 2004).

Published studies concerning the coregonine parasites in the Laurentian Great Lakes provide a body of unsummarized information, including the occurrence of parasite species, their prevalence and intensity, if the coregonines or their parasites were extirpated locally, and insights on if a coregonine parasite ever occurred in one or more Great Lakes. Loch and Faisal (2011) reviewed the parasites of *Coregonus clupeaformis* from the Great Lakes and included articles and records published in 1988 or before, except Faisal et al. (2010) and some records from the Aquatic Animal Health Laboratory (AAHL) at Michigan State University (MSU). Muzzall and Whelan (2011) listed the parasites of fish, including coregonines, from the Great Lakes and their connecting waters. Our study summarizes previously published information to provide a foundation and new information about parasites infecting 11 coregonine species, including *Coregonus clupeaformis*, along with an analysis of the parasites infecting all coregonine species in the Great Lakes. The objectives of our study are to

1. Summarize the available information about the parasites of the genera *Coregonus* and *Prosopium* in the Great Lakes and their connecting waters
2. Describe the occurrence and distribution of parasites of coregonines in the Great Lakes to allow for future comparative analyses
3. Specify and discuss parasites that cause pathology to coregonine species
4. Document the larval parasites infecting coregonines that can be transferred to humans or other vertebrates
5. Compare the parasite communities of *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* in the Great Lakes
6. Compare and contrast the parasite communities of *C. artedi*, *C. clupeaformis*, and *P. cylindraceum* in the Great Lakes to those in Canadian, Russian, and Finnish lakes

METHODS

Information for this document is gleaned from available literature about the parasites of coregonines in the Great Lakes and their connecting waters and is presented as a host species-parasite list. The parasite data are organized by taxonomic group and parasite species, lake or river, site of infection, prevalence, infection intensity (mean intensity and/or mean abundance), and reference. When the site of infection for a parasite is not provided in the original record, the site typical of infection for that parasite on that species from other records is given in brackets. Prevalence values are rounded to the nearest whole number. We emphasize that some information is difficult to interpret in the original sources and may be interpreted differently depending on the investigator. Prevalence and infection intensity (mean intensity and/or mean abundance) are defined as the percentage of fish infected in a sample, the mean number of individual parasites per infected fish, and the mean number of individual parasites per examined fish, respectively. The association of some parasitological studies with a specific Great Lake may be conjecture, but we did our best to understand the data and the authors' interpretation at the time of publication. The compiled information covers the period 1898 through 2020. Studies of viruses, bacteria, fungi, and Sea Lamprey (*Petromyzon marinus*) marking of coregonines are not included.

Coregonine Species Examined for Parasites

An alphabetical list of common names of coregonines used in this publication and their scientific names and present status in the Great Lakes are given in Table 1. Scientific names of coregonines are used in this document to avoid confusion among common names of coregonines. The coregonines *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* and their parasites are the main objects of our analysis because they were examined in two or more Great Lakes. See Table 1 to interpret which coregonine species were examined for parasites because of their presence or absence in the Great Lakes.

Table 1. A list of common and scientific names of Great Lakes coregonines used in this document and their status in each Great Lake based on information from Eshenroder et al. (2016).

Species		**Lake**				
Common Name	**Scientific Name**	**Superior**	**Huron**	**Michigan**	**Erie**	**Ontario**
Blackfin Cisco	*Coregonus nigripinnis*	Uncertain	Extinct	Extinct	Never present	Never present
Bloater	*Coregonus hoyi*	Extant	Introgressed	Extant	Never present	Reintroduced
Cisco	*Coregonus artedi*	Extant	Extant	Extant	Extirpated	Extant
Deepwater Cisco	*Coregonus johannae*	Never present	Extinct	Extinct	Never present	Never present
Kiyi	*Coregonus kiyi*	Extant	Introgressed	Extirpated	Never present	Extirpated
Lake Whitefish	*Coregonus clupeaformis*	Extant	Extant	Extant	Extant	Extant
Longjaw Cisco	*Coregonus alpenae*	Never present	Introgressed	Extinct	Extinct	Never present
Pygmy Whitefish	*Prosopium coulteri*	Extant	Never present	Never present	Never present	Never present
Round Whitefish	*Prosopium cylindraceum*	Extant	Extant	Extant	Extant	Extant
Shortjaw Cisco	*Coregonus zenithicus*	Extant	Introgressed	Extirpated	Never present	Never present
Shortnose Cisco	*Coregonus reighardi*	Uncertain	Introgressed	Extinct	Never present	Extinct

The coregonine species with the largest number of individuals examined for parasites was *Coregonus clupeaformis* followed by *C. artedi* and *C. hoyi* (Table 2). Few *Prosopium cylindraceum* were examined from the Great Lakes. Fewer than 76 individuals were examined for each of *C. alpenae*, *C. johannae*, *C. kiyi*, *C. nigripinnis*, *C. reighardi*, *C. zenithicus*, and *P. coulteri.* The largest number of coregonines examined for parasites was from Lake Huron, primarily due to the number of *C. clupeaformis* examined followed by *P. cylindraceum*, *C. artedi*, and *C. hoyi*. The next largest number of individuals examined was from Lake Michigan, primarily *C. hoyi* and *C. clupeaformis*. Most coregonines examined from Lake Superior were individuals of *C. artedi* followed by *C. clupeaformis*. Few coregonines were examined from Lakes Erie and Ontario, and those examined were primarily *C. artedi* and *C. clupeaformis*.

Table 2. Estimated number of individuals of coregonine species examined for parasites in the Great Lakes based on a review of the published literature. Np1 = number of coregonine species examined in one paper not provided, so we designated the number of fish examined as one. Np2 = number of coregonine species examined in two papers were not provided, so we designated the number of fish examined as two. Npp = coregonine species never present in a Great Lake.

	Lake					
Species	**Superior**	**Huron**	**Michigan**	**Erie**	**Ontario**	**Total**
Coregonus alpenae	24	1	Npp	0	Npp	25
Coregonus artedi	990	483	57	115	112	1,757
Coregonus clupeaformis	295	1,264	773	48	137	2,517
Coregonus hoyi	162	371	1,154	Npp	4	1,691
Coregonus johannae	0	0	Np1	Npp	Npp	1
Coregonus kiyi	24	Np2	24	Npp	26	76
Coregonus nigripinnis	0	24	Np2	Npp	Npp	26
Coregonus reighardi	0	0	Np2	Npp	Np1	3
Coregonus zenithicus	25	0	0	Npp	Npp	25
Prosopium coulteri	35	Npp	0	Npp	Npp	35
Prosopium cylindraceum	113	512	23	0	0	648
Total	**1,668**	**2,657**	**2,036**	**163**	**280**	**6,804**

We emphasize the number of individuals of each coregonine species examined was an estimate and not an actual number examined for several reasons. In some articles, the number of individuals examined was not provided and was not possible to estimate. In each of these articles, the number of fish examined for each species was designated as one. Other factors played a role regarding the number of fish examined for parasites. In some articles, each fish was examined comprehensively for parasites, and, in other articles, only one organ/site was examined (such as gills, gall bladder, swimbladder, intestine). For example, Bowen and Stedman (1990) examined only the branchial cavities of 8,347 individuals of *Coregonus hoyi*, and Hudson et al. (1994) examined only the gills of 386 individuals of *Prosopium cylindraceum*, thereby increasing the number examined. In doing this, the authors were looking for one target parasite species. We do not have an issue with the authors for this approach.

Additionally, the number of coregonines examined systematically for mastigophorans, ciliophorans, and myxozoans is not known. For example, the number of coregonines examined for different parasites in fish in different sites might be different in the same article. Furthermore, we needed to discern if the same fish were used in two or more different articles by the same authors. Additionally, we needed to determine if fish involved in two or more articles were different fish, such as the 12 *Coregonus kiyi* examined by Vergeer (1928) and the 12 *C. kiyi* mentioned by Vergeer (1942).

Parasite Species, Taxonomy, Synonyms, and Helminth Developmental Stages

When a parasite species such as *Crepidostomum farionis* was reported in a fish species and the same genus (*Crepidostomum* sp.) was also found, we counted it as only one species when quantitative information was presented. Furthermore, when a parasite species was reported as an adult in a fish species and as a larval/immature stage in the same fish species, this parasite was counted only in the adult parasite category. We were conservative in counting the number of parasites in the adult and larval/immature groups for digeneans, cestodes, and nematodes. Common parasite species mentioned in this document are those that have a prevalence of 25% or higher in one or more samples. We considered a genus not identified to species but having a prevalence of 25% or better to be common, even though it may consist of two or more species.

The following references formed the basis of the higher classification system we used for parasite species: Mastigophora, Ciliophora, Myxozoa (Lom and Dykova 1992); Digenea (Yamaguti 1953; Schell 1985; Gibson 1996); Monogenea (Yamaguti 1963a; Schell 1985); Cestoda (Wardle and Mcleod 1952; Yamaguti 1959); Nematoda (Yamaguti 1961; Anderson 1992); Acanthocephala (Yamaguti 1963b; Amin 2002); Hirudinea (Klemm 1972, 1991); and Copepoda (Hudson et al. 2003). Hoffman (1999) was consulted for information about the taxonomic status of several parasite species if there was ambiguity in the above sources. Current accepted scientific names are used for each parasite species, as the scientific names of many parasite species changed during the period examined in this document. We emphasize that investigators should check the status of these current scientific names when work is done on each parasite species. Important synonyms for some parasites used in this document are *Proteocephalus longicollis* (= *P. exiguus*, *P. laruei*, *P. wickliffi*); *Salmincola corpulentus* (= *Achtheres corpulentus*, *S. extumescens*, *S. inermis*); and *S. extensus* (= *A. coregoni*, *S. wisconsinensis*). Also, nematodes identified earlier as *Cystidicola stigmatura* in coregonid hosts from the Great Lakes are in fact *C. farionis*. However, in the tables reporting on the parasites of coregonine species, *Proteocephalus exiguus*, *P. laruei*, and *P. wickliffi*, as well as *C. farionis* and *C. stigmatura*, are listed as separate species because of the large amount of data generated for each species in several studies in the Great Lakes. We had difficulty combining prevalences or intensities for two or more of these species in the same article. When quantitative data are presented, *P. longicollis* represents *P. exiguus*, *P. laruei*, and *P. wickliffi* and *Cystidicola farionis* represents *C. stigmatura*. Thus, each observation of *P. longicollis* and *C. farionis* is counted as only one species.

Helminth developmental stages were divided into larval, immature, and adult stages. Larval stages are poorly developed and encysted and do not occur in the digestive tract. Also, larval stages of some genera of digenetic trematodes (such as *Diplostomum* and a few other helminth species) do not encyst but were still considered larvae if they were not in the digestive tract. Immature helminths found in the digestive tract were not classified as larvae nor were they considered adults. Adult helminths mature in their fish hosts, no matter where they infect the fish. Autogenic parasite species are helminths that mature in fish, and allogenic parasite species are helminths that mature in piscivorous birds and mammals. This separation of developmental stages and the autogenic-allogenic dichotomy is useful to characterize and compare the parasite communities of the four main coregonine species.

Sorenson's Coefficient of Parasite Community Similarity for Coregonine Species

Species-richness is the number of parasite species and distinct genera (parasite genera reported in a fish but a species for that genus was not given in the original article) infecting a coregonine species. Sorenson's Coefficient of Similarity (Dice 1945; Sørensen 1948) was used to determine how similar the parasite communities were in *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* in the Great Lakes and some Canadian provinces by consideration of the presence or absence of a parasite species in each fish species. This coefficient does not account for the abundance of each parasite species found, which would be difficult to do because, in most articles, the total number of individuals of each parasite species in each coregonine species is often not provided.

Sorenson's Coefficient of Similarity is estimated as

$$\boldsymbol{CCs} = 2c/(S_1 + S_2)$$

where c is the number of species that occur in both communities (host fish species being compared), S_1 is the number of species in host fish species 1 (community 1), and S_2 is the number of species in host fish species 2 (community 2).

As the number of parasite species and distinct genera that infect coregonine species being compared increases, so does the calculated value (range 0.00-1.00), indicating the parasite communities are more similar. Furthermore, the coefficients below and above 0.5 indicate the pairwise parasite communities are less or more similar, respectively.

RESULTS

The first method used to examine Great Lakes coregonine parasite communities was an analysis of each coregonine species. This section details the findings of this approach.

Coregonine Species Analysis

Coregonus artedi

Larval, immature, and adult life stages of 35 parasite species from 7 taxonomic groups were reported in *Coregonus artedi* in the Great Lakes, St. Marys River, and Lake St. Clair (Table 3). Researchers reported two Myxozoa, two adult Digenea, four larval/immature Digenea, one Monogenea, five adult Cestoda, seven larval/immature Cestoda, two adult Nematoda, one larval/immature Nematoda, six adult Acanthocephala, and five Copepoda in *C. artedi*. Common parasite species of *C. artedi* are *Chloromyxum* sp., *Henneguya* sp., *Crepidostomum farionis*, *Phyllodistomum* sp., *Ichthyocotylurus erraticus*, *Diplostomum* sp., *Discocotyle sagittata*, *Cyathocephalus truncatus*, *Proteocephalus longicollis*, *Diphyllobothrium ditremum*, *D. laruei*, *D. oblongatum*, *Triaenophorus crassus*, *Cystidicola farionis*, *Echinorhynchus lateralis*, *E. leidyi*, *E. salmonis*, and *Salmincola corpulentus*. A total of 46 studies reported on the parasites of *C. artedi* from these waters. The number of parasitological studies conducted was highest in Lake Superior followed by Lake Michigan. The oldest and most recent studies of the parasites of *Coregonus artedi* were published or conducted in 1911 and 2017, respectively. Most individuals of *C. artedi* were examined from Lake Superior followed by Lake Huron (Table 2).

Table 3. Reported parasites of *Coregonus artedi* from Lakes Superior (LS), Huron (LH), Michigan (LM), Erie (LE), Ontario (LO), St. Clair (LSC), and the St. Marys River (SMR), based on published literature and personal observation of the authors. If the site of infection for a parasite was not provided in the original record, the site typical of infection for that parasite on that fish from other records is in brackets. Prevalence reported as a percentage with the number (in parentheses) represented by total number of fish examined. Infection intensity reported as L = light intensity (1-9 worms/fish); M = medium intensity (10-49 worms/fish); H = high intensity (>50 worms/fish) or as mean intensity defined as the mean number of parasites per infected fish and noted as * or as mean abundance defined as the mean number of parasites per examined fish and noted as **. NC = number of parasites not counted; NP = information not provided. Number (in parentheses) after intensity is maximum intensity value.

Taxonomic Group (Bold) and Parasite Species	Lake/ River	Site of Infection	Prevalence	Infection Intensity	Reference
Myxozoa					
Chloromyxum sp.	LS	[Coelom, gall bladder, kidney, liver]	2 locations: 38% (139), 54% (13)	NC	Hoff et al. 1997
Henneguya zschokkei	LS	[Muscle]	1% (139)	<1** (NP)	Hoff et al. 1997
	LH	Muscle	2% (101)	H	Dechtiar et al. 1988
Henneguya sp.	LS	Gills	14% (36)	H	Dechtiar and Lawrie 1988
	LS	Gills	39% (13)	1.5* (NP)	Hoff et al. 1997
Unidentified myxozoan	LH	NP	5% (79)	NP	Bangham 1955
Adult Digenea					
Crepidostomum farionis	LS	Gall bladder	1% (250)	NP	Warren 1952
	LS	Intestine, gall bladder	28% (36)	H	Dechtiar and Lawrie 1988
Phyllodistomum sp.	LH	Ureters	49% (101)	L	Dechtiar et al. 1988
Larval/Immature Digenea					
Clinostomum marginatum	LS	[Several non-intestinal sites]	1% (139)	<1** (NP)	Hoff et al. 1997
Diplostomum flexicaudum	LH	[Eye]	NP (101)	NP	Dechtiar and Berst 1978
Diplostomum spathaceum	LS	Eye	14% (36)	L	Dechtiar and Lawrie 1988
	LH	Eye	2% (101)	L	Dechtiar et al. 1988
	LO	Eye	12% (25)	L	Dechtiar and Christie 1988
Diplostomum sp.	LS	[Several non-intestinal sites]	2% (139)	<1** (NP)	Hoff et al. 1997
	LH	[Several non-intestinal sites]	61% (79)	NP	Bangham 1955
Ichthyocotylurus erraticus	LS	Heart	22% (36)	M	Dechtiar and Lawrie 1988
	LH	Pericardium	NP	NP	Hughes 1928
	LH	[Heart]	NP (101)	NP	Dechtiar and Berst 1978
	LH	Heart	10% (101)	L	Dechtiar et al. 1988
	LO	Heart	40% (25)	L	Dechtiar and Christie 1988

Taxonomic Group (Bold) and Parasite Species	Lake/ River	Site of Infection	Prevalence	Infection Intensity	Reference
Ichthyocotylurus sp.	LS	[Several non-intestinal sites]	2 locations: 6% (139), 23% (13)	<1** (NP), <1** (NP)	Hoff et al. 1997
	LE	[Several non-intestinal sites]	50% (6)	NP	Dechtiar 1972a
Monogenea					
Discocotyle sagittata	LS	Gills	83% (36)	L-M	Dechtiar and Lawrie 1988
	LS	[Gills]	2 locations: 2% (139), 15% (13)	<1** (NP), <1** (NP)	Hoff et al. 1997
	LH	Gills	11% (79)	NP	Bangham 1955
	LH	[Gills]	NP (101)	NP	Dechtiar and Berst 1978
Adult Cestoda					
Bothriocephalidae gen. sp.	LO	NP	NP (66)	NP	Pritchard 1931
Cyathocephalus truncatus	LS	[Pyloric caeca]	2 locations: 1% (139), 69% (13)	<1** (NP), 2** (NP)	Hoff et al. 1997
	LH	Pyloric caeca	100% (5)	11.4* (NP)	Dechtiar and Loftus 1965
	LH	[Pyloric caeca]	NP (101)	NP	Dechtiar and Berst 1978
	LH	Intestine	44% (101)	M	Dechtiar et al. 1988
Eubothrium crassum	LS	Intestine	2% (200)	NP	Warren 1952
	LH	[Intestine, pyloric caeca]	4% (79)	NP	Bangham 1955
	LE	Intestine	1% (78)	L	Bangham and Hunter 1939
Eubothrium salvelini	LS	[Intestine, pyloric caeca]	2 locations: 6% (139), 8% (13)	<1** (NP), <1** (NP)	Hoff et al. 1997
	LH	[Intestine, pyloric caeca]	NP (101)	NP	Dechtiar and Berst 1978
Proteocephalus exiguus	LM	Intestine	NP	NP	LaRue 1911
	LM	Intestine	NP	NP	LaRue 1914
	LS	Intestine	77% (200)	NP	Warren 1952
	LS	Intestine	64% (36)	L-M	Dechtiar and Lawrie 1988
	SMR	Intestine	61% (38)	NP	Muzzall 1984
	LH	Intestine	11% (79)	NP	Bangham 1955
	LH	Intestine	12% (101)	M	Dechtiar et al. 1988
	LE	Intestine	NP	NP	Hunter and Bangham 1933

Taxonomic Group (Bold) and Parasite Species	Lake/ River	Site of Infection	Prevalence	Infection Intensity	Reference
	LE	Digestive tract	33% (78)	L-H	Bangham and Hunter 1939
	LO	Intestine	12% (25)	M	Dechtiar and Christie 1988
Proteocephalus laruei	LS	Intestine	78% (36)	M-H	Dechtiar and Lawrie 1988
	LH	Intestine	90% (79)	NP	Bangham 1955
	LH	Intestine	44% (101)	M	Dechtiar et al. 1988
	LO	Intestine	80% (25)	M	Dechtiar and Christie 1988
Proteocephalus exiguus/*Proteocephalus laruei* mixed infections	LS	[Intestine]	2 locations: 98% (139), 100% (13)	97** (NP), 98** (NP)	Hoff et al. 1997
Proteocephalus wickliffi	LE	Intestine	NP	NP	Hunter and Bangham 1933
	LE	Digestive tract	12% (78)	L	Bangham and Hunter 1939
Proteocephalus sp.	LM	Pyloric caeca, intestine	63% (8)	2.2* (5)	Authors, personal observation, 2017
	LS	Pyloric caeca, intestine	91% (22)	23.5* (161)	Authors, personal observation, 2017
	LH	[Pyloric caeca, intestine]	NP (101)	NP	Dechtiar and Berst 1978
Larval/Immature Cestoda					
Bothriocephalid plerocercoids	LM	Under peritoneum	6 locations (42)	2-4** (14)	Vergeer 1928
	LS	Under peritoneum	(NP) (24)	<3** (11)	Vergeer 1928
	LH	Under peritoneum	(NP) (195)	2-2** (8)	Vergeer 1928
	LE	Under peritoneum	(NP) (27)	4.0-5.5** (13)	Vergeer 1928
	LO	Cysts attached to stomach wall	21% (66)	NP	Pritchard 1931
Diphyllobothrium ditremum	LS	Stomach wall	22% (36)	M	Dechtiar and Lawrie 1988
	LS	[Stomach wall]	2 locations: 28% (139), 31% (13)	<1** (NP), <1** (NP)	Hoff et al. 1997
	LH	Stomach wall	47% (101)	L	Dechtiar et al. 1988
	LO	Stomach wall	16% (25)	L	Dechtiar and Christie 1988

Taxonomic Group (Bold) and Parasite Species	Lake/ River	Site of Infection	Prevalence	Infection Intensity	Reference
Diphyllobothrium laruei	LS	Stomach, peritoneum, under peritoneum lining flesh	NP	NP	Vergeer 1942
	LS	[Stomach, peritoneum, under peritoneum lining flesh]	NP	NP	Sutton 1969
	LM	Stomach, peritoneum, under peritoneum lining flesh	NP	4.0	Vergeer 1942
	LH	Stomach, peritoneum, under peritoneum lining flesh	NP	NP	Vergeer 1942
	LE	Stomach, peritoneum, under peritoneum lining flesh	NP	NP	Vergeer 1942
	LO	Stomach, peritoneum, under peritoneum lining flesh	NP	NP	Vergeer 1942
Diphyllobothrium oblongatum	LM	[Stomach wall]	NP	NP	Thomas 1947
	LS	Stomach wall	78% (200)	NP	Warren 1952
Diphyllobothrium sp.	LS	External stomach wall, pyloric caeca, viscera	NP (345)	Total viscera 2.4-38.4** (NP), stomach <1.0-16.7** (NP)	Swanson and Pratt 1977
	LH	Stomach and associated muscles	68% (79)	NP	Bangham 1955
	LH	[External stomach wall, pyloric caeca, viscera]	NP (101)	NP	Dechtiar and Berst 1978
Eubothrium crassum	LE	Mesentery	4% (78)	L	Bangham and Hunter 1939
Eubothrium sp.	SMR	Intestine	11% (38)	NP	Muzzall 1984
Proteocephalus ambloplitis	LS	[Gonads, viscera]	1% (139)	<1** (NP)	Hoff et al. 1997
Triaenophorus crassus	LS	Muscle	NP	NP	Hoffman 1941
	LS	[Muscle]	<10% (NP)	NP	Johnson 1946
	LS	Muscle	6% (350 fillets)	1* (1)	Klick 1946
	LS	Muscle	21% (200)	NP	Warren 1952
	LS	Muscle	22% (36)	M	Dechtiar and Lawrie 1988
	LH	Muscle	77% (79)	NP	Bangham 1955
	LH	Muscle	47% (101)	L	Dechtiar et al. 1988

Taxonomic Group (Bold) and Parasite Species	Lake/ River	Site of Infection	Prevalence	Infection Intensity	Reference
Triaenophorus sp.	LS	[Muscle]	NP	NP	Cooper 1918
	LS	Muscle	<10%	NP	Johnson 1946
	LS	Dorsal muscle tissue close to skin	6 locations: 3% (59)-14% (50)	NP (5)	Swanson and Pratt 1977
Rhyncobothrid cestode	LO	NP	NP	NP	Pritchard 1931
Adult Nematoda					
Cystidicola farionis	LM	[Swimbladder]	NP	NP	Ward and Magath 1916
	LS	Swimbladder	60% (30)	NP	Smith 1978
	LS	Swimbladder	61% (89)	52 (NP)	Lankester and Smith 1980
	LS	Swimbladder	64% (36)	39* (NP)	Dextrase 1987
	LS	Swimbladder	69% (36)	H	Dechtiar and Lawrie 1988
	LS	[Swimbladder]	2 locations: 26% (139), 100% (13)	2.9** (NP), 54.0** (NP)	Hoff et al. 1997
	LH	Swimbladder	44% (101)	M	Dechtiar et al. 1988
	LO	[Swimbladder]	NP	NP	Skinker 1930
	LO	[Swimbladder]	NP	NP	Skinker 1931
Cystidicola stigmatura	LM	[Swimbladder]	NP	NP	Ward and Magath 1916
	LS	Swimbladder	8% (13)	37* (37)	Klick 1946
	LS	Swimbladder	72% (200)	NP	Warren 1952
	LH	Swimbladder	4% (79)	NP	Bangham 1955
	LH	[Swimbladder]	NP (101)	NP	Dechtiar and Berst 1978
	LSC	[Swimbladder]	NP	NP	Ward and Magath 1916
	LO	Swimbladder	58% (NP)	NP (480)	Ekbaum 1936
	LE	[Swimbladder]	NP	NP	Ward and Magath 1916
	LE	[Swimbladder]	NP	NP	Hunter and Bangham 1933
	LE	Swimbladder	1% (78)	L	Bangham and Hunter 1939
Cystidicola sp.	LS	[Swimbladder]	<10% (NP)	NP	Johnson 1946
	LS	Swimbladder	8 locations: 31% (62)-60% (50)	NP (>100)	Swanson and Pratt 1977
	LO	Swimbladder	41% (66)	NP	Pritchard 1931

Taxonomic Group (Bold) and Parasite Species	Lake/ River	Site of Infection	Prevalence	Infection Intensity	Reference
Sterliadochona ephemeridarum	LS	Intestine	19% (36)	L	Dechtiar and Lawrie 1988
Sterliadochona sp.	LS	[Stomach, intestine]	1% (139)	<1** (NP)	Hoff et al. 1997
Larval/Immature Nematoda					
Philometra sp.	LH	Encysted in coelom	6% (79)	NP	Bangham 1955
Adult Acanthocepala					
Echinorhynchus lateralis	LS	Intestine	56% (36)	H	Dechtiar and Lawrie 1988
	LS	[Intestine]	46% (13)	1.2** (NP)	Hoff et al. 1997
	LS	Intestine	9% (22)	1.5* (2)	Authors, personal observation, 2017
Echinorhynchus leidyi	LS	Intestine	30% (200)	NP	Warren 1952
Echinorhynchus salmonis	LS	Intestine	42% (36)	H	Dechtiar and Lawrie 1988
	LS	[Intestine]	2 locations: 14% (139), 8% (13)	<1** (NP), <1** (NP)	Hoff et al. 1997
	SMR	Intestine	10% (38)	NP	Muzzall 1984
	LH	Intestine	5% (79)	NP	Bangham 1955
	LH	Intestine	9% (101)	M	Dechtiar et al. 1988
	LH	[Intestine]	NP (101)	NP	Dechtiar and Berst 1978
	LE	[Intestine]	83% (6)	NP	Dechtiar 1972a
	LO	Intestine	92% (25)	M	Dechtiar and Christie 1988
Neoechinorhynchus crassus	LS	[Intestine]	2 locations: 1% (139), 8% (13)	<1** (NP), <1** (NP)	Hoff et al. 1997
Neoechinorhynchus cylindratus	LS	Intestine	<1% (200)	NP	Warren 1952
Neoechinorhynchus tumidus	LS	Intestine	17% (36)	L	Dechtiar and Lawrie 1988
Neoechinorhynchus sp.	LO	Stomach	22% (66)	NP	Pritchard 1931
Immature Acanthocephala					
Echinorhynchus salmonis	LH	Encysted	8% (79)	NP	Bangham 1955
Copepoda					
Achtheres pimelodi	LM	Gills	NP	NP	Pearse 1924
Argulus sp.	LH	[Outer surface, fins]	5% (79)	NP	Bangham 1955
Ergasilus caeruleus	LM	Gills	NP	NP	Pearse 1924
Ergasilus sp.	LS	[Gills]	1% (139)	<1** (NP)	Hoff et al. 1997
Salmincola corpulentus	LS	Gill chamber	65% (200)	NP	Warren 1952
	LS	Gills	22% (36)	L	Dechtiar and Lawrie 1988

Taxonomic Group (Bold) and Parasite Species	Lake/ River	Site of Infection	Prevalence	Infection Intensity	Reference
	LS	[Gills, gill cavity, operculum]	2 locations: 46% (139), 31% (13)	<1** (NP), <1** (NP)	Hoff et al. 1997
	LH	Gill cavity	24% (79)	NP	Bangham 1955
	LH	Gills	3% (101)	L	Dechtiar et al. 1988
	LE	[Gills, gill cavity, operculum]	NP	NP	Tidd 1931
	LO	Gill cavity, operculum	15% (66)	Usually 1 (NP)	Pritchard 1931
	LO	Gills	NP (16)	NP	Mueller 1940
Salmincola extensus	LS	Fins	7% (250)	NP	Warren 1952
	LH	Body surface, fins	14% (79)	NP	Bangham 1955
Salmincola sp.	LS	Gill cavity area	7 locations: 24% (25)-50% (55)	(NP) 1-2	Swanson and Pratt 1977
	LS	Loose in petri dish	5% (22)	1* (1)	Authors, personal observation, 2017

The largest number of parasite species infecting *Coregonus artedi* was reported from Lake Superior (24) followed by Lake Huron (18) (Table 4). Most parasite species in *C. artedi* from Lake Superior were cestodes followed by acanthocephalans. Cestodes were also the most common parasite group in *C. artedi* from the other lakes. The fewest parasite species were reported from Lake Erie followed by Lakes Michigan and Ontario.

Generally, the parasite communities of *Coregonus artedi* were similar among Lakes Superior, Michigan, and Huron. Three of the ***CCs*** values for *C. artedi* were above 0.50, indicating that these pairwise communities were more similar to one another than the seven coefficients below 0.50 (Table 5). The highest ***CCs*** values involved the parasite communities of Lakes Superior and Michigan (0.64) followed by Lakes Michigan and Huron (0.57). The lowest ***CCs*** value involved the parasite communities of Lakes Michigan and Ontario (0.14). The number of parasite species shared in these pairwise coefficients ranged from a low of 2 in three pairwise lake comparisons to a high of 9 in Lakes Michigan and Superior. The species *Proteocephalus longicollis*, *Diphyllobothrium laruei*, *Cystidicola farionis* and bothriocephalid plerocercoids occurred in all Great Lakes, *Echinorhynchus salmonis* and *Salmincola corpulentus* occurred in four Great Lakes, and *Diplostomum spathaceum*, *Ichthyocotylurus erraticus*, *Eubothrium crassum*, and *Diphyllobothrium ditremum* occurred in three Great Lakes.

Table 4. Number of parasite species in each taxonomic group reported and number of parasitological studies conducted on *Coregonus artedi* in each Great Lake.

Taxonomic Group	Lake				
	Superior	Huron	Michigan	Erie	Ontario
Myxozoa	0	1	2	0	0
Adult Digenea	0	1	1	0	0
Larval/Immature Digenea	2	3	1	1	2
Monogenea	0	1	1	0	0
Adult Cestoda	4	3	1	2	2
Larval/Immature Cestoda	7	4	3	3	3
Adult Nematoda	2	1	1	1	1
Larval/Immature Nematoda	0	0	0	0	0
Acanthocephala	6	1	0	1	1
Hirudinea	0	0	0	0	0
Copepoda	3	3	2	1	1
Mollusca	0	0	0	0	0
Total Species	**24**	**18**	**12**	**9**	**10**
Number of Studies	**15**	**6**	**8**	**6**	**6**

Table 5. Sorenson's coefficients of parasite community similarity and number of shared parasite species (in parentheses) in *Coregonus artedi* from the Great Lakes.

Lake	Lake				
	Superior	Huron	Michigan	Erie	Ontario
Superior	-	0.57 (8)	0.64 (9)	0.00 (0)	0.24 (2)
Huron	0.57 (8)	-	0.52 (7)	0.00 (0)	0.27 (2)
Michigan	0.64 (9)	0.52 (7)	-	0.00 (0)	0.14 (2)
Erie	0.00 (0)	0.00 (0)	0.00 (0)	-	0.00 (0)
Ontario	0.24 (2)	0.27 (2)	0.14 (2)	0.00 (0)	-

Coregonus clupeaformis

Larval, immature, and adult life stages of 38 parasite species from 11 taxonomic groups were reported in *Coregonus clupeaformis* in all Great Lakes and Lake St. Clair (Table 6). Researchers reported two Mastigophora, one Ciliophora, one Myxozoa, two adult Digenea, four larval/immature Digenea, one Monogenea, four adult Cestoda, three larval/immature Cestoda, four adult Nematoda, two larval/immature Nematoda, seven adult Acanthocephala, two Hirudinea, four Copepoda, and one Mollusca in *C. clupeaformis*. Common parasite species of *C. clupeaformis* are *Crepidostomum farionis*, *Phyllodistomum coregoni*, *Diplostomum flexicaudum*, *D. spathaceum*, *Ichthyocotylurus erraticus*, *Discocotyle sagittata*, *Bothriocephalus* sp., *Cyathocephalus truncatus*, *Proteocephalus longicollis*, *Diphyllobothrium* sp., *Triaenophorus crassus*, *Pseudocapillaria salvelini*, *Cystidicola farionis*, *Sterliadochona ephemeridarum*, *Acanthocephalus dirus*, *Echinorhynchus lateralis*, *E. salmonis*, *Neoechinorhyncus salmonis*, *N. tumidus*, and *Achtheres pimelodi*. The occurrence of a glochidium (larval mollusc) on one *Coregonus clupeaformis* from Lake Huron is the only such report on a coregonine in the Great Lakes. A total of 49 studies reported on the parasites of *C. clupeaformis* from these waters. The number of parasitological studies conducted was highest in Lake Huron followed by Lake Michigan. The oldest and most recent studies of the parasites of *C. clupeaformis* were published or conducted in 1898 and 2017, respectively, with the largest number of individuals examined from Lake Huron followed by Lake Michigan (Table 2). The fewest parasitological studies of *C. clupeaformis* occurred in Lake Ontario.

Table 6. Reported parasites of *Coregonus clupeaformis* from Lakes Superior (LS), Huron (LH), Michigan (LM), Erie (LE), Ontario (LO), St. Clair (LSC) based on published scientific literature and personal observation of the authors. If the site of infection for a parasite was not provided in the original record, the site typical of infection for that parasite on that fish from other records is in brackets. Prevalence reported as a percentage with the number (in parentheses) represented by total number of fish examined. Infection intensity reported as L = light intensity (1-9 worms/fish); M = medium intensity (10-49 worms/fish); H = high intensity (>50 worms/fish) or as mean intensity defined as the mean number of parasites per infected fish and noted as * or as mean abundance defined as the mean number of parasites per examined fish and noted as **. NP = information not provided. Number (in parentheses) after intensity is maximum intensity value.

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
Mastigophora					
Cryptobia sp.	LM	Gills	NP	NP	Michigan State University Aquatic Animal Health Laboratory (MSU-AAHL) in Loch and Faisal 2011
	LH	Gills	NP	NP	MSU-AAHL in Loch and Faisal 2011
Epistylis sp.	LM	Gills, skin	NP	NP	MSU-AAHL in Loch and Faisal 2011
	LH	Gills, skin	NP	NP	MSU-AAHL in Loch and Faisal 2011
Ciliophora					
Trichodina sp.	LM	Gills	NP	NP	MSU-AAHL in Loch and Faisal 2011
	LM	Skin	NP	NP	MSU-AAHL in Loch and Faisal 2011
	LH	Gills	NP	NP	MSU-AAHL in Loch and Faisal 2011
Myxozoa					
Henneguya sp.	LS	Muscle	5% (21)	8 (8)	Olds 2012

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
Adult Digenea					
Crepidostomum farionis	LS	Gall bladder	26% (23)	L-M	Dechtiar and Lawrie 1988
	LS	Gall bladder	4% (45)	1* (1)	Authors, personal observation, 2017
	LH	[Gall bladder]	NP (39)	NP	Collins and Dechtiar 1974
Phyllodistomum coregoni	LS	Ureters	35% (23)	L-M	Dechtiar and Lawrie 1988
	LH	Ureters	39% (90)	L	Dechtiar et al. 1988
	LO	Ureters	24% (22)	L	Dechtiar and Christie 1988
Unidentified digeneans	LE	Digestive tract	3% (30)	L	Bangham and Hunter 1939
Larval/Immature Digenea					
Diplostomum flexicaudum	LH	[Eyes]	NP (90)	NP	Dechtiar and Berst 1978
	LE	[Eyes]	25% (4)	NP	Dechtiar 1972a
Diplostomum spathaceum	LM	Eye	23% (31)	1.4 (3)	Olds 2012
	LS	Eye	2 locations: 3% (32), 30% (30)	4.0 (4), 2.3 (6)	Olds 2012
	LH	NP	NP (39)	NP	Collins and Dechtiar 1974
	LH	Eye	20% (90)	L	Dechtiar et al. 1988
	LH	Eye	10% (30)	2.5 (4)	Olds 2012
	LO	Eye	8% (22)	L	Dechtiar and Christie 1988
Diplostomum sp.	LH	NP	71% (99)	NP	Bangham 1955
Diplostomum sp./*Tylodelphys* sp. mixed infections	LH	Eyes	NP	NP	LaRue et al. 1926
Tylodelphys sp./*Diplostomum* sp. mixed infections	LH	Eyes	NP	NP	LaRue et al. 1926
Ichthyocotylurus erraticus	LS	Heart	39% (23)	L-M	Dechtiar and Lawrie 1988
	LH	[Heart]	NP (39)	NP	Collins and Dechtiar 1974
	LH	[Heart]	NP (90)	NP	Dechtiar and Berst 1978
	LH	Heart	19% (90)	L	Dechtiar et al. 1988
	LE	Heart	100% (11)	941* (1,903)	PMM, unpublished data
	LO	Heart	60% (22)	L	Dechtiar and Christie 1988
Ichthyocotylurus sp.	LM	Ventricle, bulbous	45% (NP)	L-H	MSU-AAHL in Loch and Faisal 2011
	LH	Ventricle, bulbous	30% (NP)	L-H	MSU-AAHL in Loch and Faisal 2011

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
Monogenea					
Discocotyle sagittata	LS	Gills	43% (23)	L-M	Dechtiar and Lawrie 1988
	LS	[Gills]	4 locations: 11% (9), 10% (21), 31% (32), 30% (30)	1.0 (1), 4.0 (4), 3.0 (9), 2.7 (7)	Olds 2012
	LH	[Gills]	NP (90)	NP	Dechtiar and Berst 1978
	LH	Gills	17% (90)	L	Dechtiar et al. 1988
Adult Cestoda					
Bothriocephalus sp.	LM	Gastric mucosa	11% (649)	4.9* (NP), 0.5**	Faisal et al. 2011
	LS	Pyloric caeca, intestine	31% (45)	1.9* (5)	Authors, personal observation, 2017
	LH	Gastric mucosa	12% (635)	7.0* (NP), 0.8**	Faisal et al. 2011a
Cyathocephalus truncatus	LM	Intestine	NP	NP	Cooper 1918
	LM	Anterior intestine	13% (8)	7* (7)	Amin 1977
	LM	Pyloric caeca	10% (649)	31.6* (NP), 3.2**	Faisal et al. 2011a
	LM	[Intestine, pyloric ceca]	10% (31)	10 (20)	Olds 2012
	LS	Intestine	NP	NP	Linton 1898
	LS	Pyloric caeca	35% (23)	M	Dechtiar and Lawrie 1988
	LS	[Intestine, pyloric caeca]	4 locations: 44% (9), 14% (21), 63% (32), 10% (30)	120.3 (408), 6.7 (12), NP, 9.5 (29)	Olds 2012
	LS	Intestine	24% (45)	2.0* (6)	Authors, personal observation, 2017
	LH	Stomach, pyloric caeca, intestine	NP	NP	Cooper 1918
	LH	[Intestine, pyloric caeca]	NP	NP	Cooper 1921
	LH	[Intestine, pyloric caeca]	40% (99)	NP	Bangham 1955
	LH	[Intestine, pyloric caeca]	NP (90)	NP	Dechtiar and Berst 1978
	LH	Pyloric caeca	17% (90)	M	Dechtiar et al. 1988
	LH	Pyloric caeca, anterior intestine	24% (34)	1.4* (NP)	French et al. 2005
	LH	Pyloric caeca	16% (635)	66.8* (NP), 10.8**	Faisal et al. 2011

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
	LH	[Intestine, pyloric caeca]	13% (30)	111.2 (306)	Olds 2012
	LO	Pyloric caeca	96% (113)	NP (>10)	Hart 1931b
	LO	Intestine	NP	NP	Wardle 1933
	LO	Intestine	16% (22)	M	Dechtiar and Christie 1988
Eubothrium salvelini	LS	[Intestine, pyloric caeca]	2 locations: 10% (21), 3% (32)	2 (2), 8 (8)	Olds 2012
	LH	[Intestine, pyloric caeca]	NP (90)	NP	Dechtiar and Berst 1978
	LE	Digestive tract	3% (30)	L	Bangham and Hunter 1939
Proteocephalus exiguus	LM	Anterior intestine	13% (8)	4* (4)	Amin 1977
	LM	[Intestine, pyloric caeca]	29% (31)	NP	Olds 2012
	LS	Intestine	43% (23)	L-M	Dechtiar and Lawrie 1988
	LS	[Intestine, pyloric caeca]	3 locations: 56% (9), 56% (32), 22% (30)	7.6 (25), 14.1 (50), 22 (30)	Olds 2012
	LH	[Intestine, pyloric caeca]	65% (99)	NP	Bangham 1955
	LH	[Intestine, pyloric caeca]	85% (30)	13.6 (70)	Olds 2012
	LE	[Intestine, pyloric caeca]	NP	NP	Hunter and Bangham 1933
	LE	Digestive tract	50% (30)	L-H	Bangham and Hunter 1939
	LO	Intestine	12% (22)	M	Dechtiar and Christie 1988
Proteocephalus laruei	LS	Intestine	83% (23)	H	Dechtiar and Lawrie 1988
	LH	[Intestine, pyloric caeca]	2% (99)	NP	Bangham 1955
	LH	Intestine	6% (90)	M	Dechtiar et al. 1988
	LO	Pyloric caeca, intestine	NP (113)	NP	Hart 1931b
	LO	Intestine	NP	NP	Wardle 1933
Proteocephalus sp.	LM	Intestine	24% (79)	3.3* (14)	Authors, personal observation, 2017
	LS	Intestine	60% (45)	8.6* (44)	Authors, personal observation, 2017
	LSC	Intestine	2% (100)	2.5* (3)	Authors, personal observation, 2017
	LH	[Intestine]	NP (90)	NP	Dechtiar and Berst 1978
	LH	[Intestine]	5% (30)	70 (70)	Olds 2012

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
Larval/Immature Cestoda					
Diphyllobothrium sp.	LS	Stomach wall	30% (23)	L-M	Dechtiar and Lawrie 1988
	LH	[Stomach wall, intestinal wall]	1% (99)	NP	Bangham 1955
	LH	[Stomach wall, intestinal wall]	NP (90)	NP	Dechtiar and Berst 1978
	LH	Intestinal wall	2% (90)	M	Dechtiar et al. 1988
	LO	Stomach wall	NP	NP	Mueller 1940
	LO	Stomach wall	28% (22)	L	Dechtiar and Christie 1988
Proteocephalus sp.	LS	Intestine	8% (30)	NP	Olds 2012
	LO	[Stomach]	100%	NP (1)	Hart 1931a
Schistocephalus sp.	LE	Pericardial cavity	3% (30)	L	Bangham and Hunter 1939
Triaenophorus crassus	LS	Muscle	NP	NP	Hoffman 1941
	LS	Muscle	26% (23)	M	Dechtiar and Lawrie 1988
	LH	[Muscle]	18% (99)	NP	Bangham 1955
	LH	Muscle	8% (90)	L	Dechtiar et al. 1988
	LO	Muscles	8% (22)	L	Dechtiar and Christie 1988
Adult Nematoda					
Pseudocapillaria salvelini	LS	Intestine	30% (23)	L	Dechtiar and Lawrie 1988
Cystidicola farionis	LM	[Swimbladder]	NP	NP	Ward and Magath 1916
	LM	Swimbladder	Range 3-35% (649)	Range 1-3 (NP)	Faisal et al. 2010
	LM	[Swimbladder]	23% (31)	2 (6)	Olds 2012
	LS	Swimbladder	58% (126)	16* (NP)	Lankester and Smith 1980
	LS	Swimbladder	87% (23)	M	Dechtiar and Lawrie 1988
	LS	[Swimbladder]	3 locations: 5% (21), 3% (32), 33% (30)	38 (38), 118 (118), 33, (6)	Olds 2012
	LH	Swimbladder	68% (122)	NP	Smith 1978
	LH	Swimbladder	2 locations: 71% (73), 62% (42)	11* (NP), 9* (NP)	Lankester and Smith 1980
	LH	Swimbladder	8% (90)	L	Dechtiar et al. 1988
	LH	Swimbladder	Range 10-100% (635)	Range 1-31 (NP)	Faisal et al. 2010
	LH	[Swimbladder]	40% (30)	7.2 (39)	Olds 2012
	LO	Swimbladder	52% (22)	M	Dechtiar and Christie 1988

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
Cystidicola stigmatura	LM	[Swimbladder]	NP	NP	Ward and Magath 1916
	LH	[Swimbladder]	13% (99)	NP	Bangham 1955
	LH	[Swimbladder]	NP	NP	Ko and Anderson 1969
	LH	[Swimbladder]	NP (39)	NP	Collins and Dechtiar 1974
	LH	[Swimbladder]	NP (90)	NP	Dechtiar and Berst 1978
	LSC	[Swimbladder]	NP	NP	Ward and Magath 1916
	LE	[Swimbladder]	NP	NP	Ward and Magath 1916
	LE	[Swimbladder]	NP	NP	Hunter and Bangham 1933
	LE	Swimbladder	10% (30)	L	Bangham and Hunter 1939
	LO	Swimbladder	>50% (NP)	(NP)	Mueller 1940
Cystidicola sp.	LS	Swimbladder	29% (45)	22.5* (119)	Authors, personal observation, 2017
	LO	Swimbladder	42% (113)	NP (8)	Hart 1931b
Sterliadochona ephemeridarum	LS	Intestine	30% (23)	M	Dechtiar and Lawrie 1988
	LH	Intestine	31% (90)	L	Dechtiar et al. 1988
	LO	Intestine	56% (22)	L	Dechtiar and Christie 1988
Spinitectus gracilis	LH	[Intestine]	NP (39)	NP	Collins and Dechtiar 1974
	LH	[Intestine]	NP (90)	NP	Dechtiar and Berst 1978
Larval/Immature Nematoda					
Cystidicola farionis	LS	Swimbladder	43% (7)	1* (NP)	Dextrase 1987
Philometra sp.	LH	[Body cavity]	1% (99)	NP	Bangham 1955
Raphidascaris acus	LH	Encysted in liver, spleen	19% (90)	M	Dechtiar et al. 1988
Spinitectus gracilis	LH	[Intestine]	8% (99)	NP	Bangham 1955
Adult Acanthocephala					
Acanthocephalus dirus	LM	Intestine	21% (649)	18.4* (NP), 3.8**	Faisal et al. 2011a
	LM	[Intestine]	26% (31)	1.9 (4)	Olds 2012
	LS	[Intestine]	4 locations: 100% (9), 5% (21), 38% (32), 44% (30)	12.2 (35), 2.0 (2), 18.3 (115), 23.6 (80)	Olds 2012
	LH	[Intestine]	NP (39)	NP	Collins and Dechtiar 1974
	LH	Intestine	36% (635)	32.8* (NP), 11.9**	Faisal et al. 2011a
	LH	[Intestine]	70% (30)	18.1 (95)	Olds 2012
	LO	Intestine	28% (22)	L	Dechtiar and Christie 1988
Echinorhynchus lateralis	LS	Intestine	33% (45)	3.2* (12)	Authors, personal observation, 2017

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
Echinorhynchus salmonis	LM	Intestine	NP	NP	Pearse 1924
	LM	Intestine	100% (8)	22 (56)	Amin and Burrows 1977
	LM	Intestine	1% (649)	5.0* (NP), 0.1**	Faisal et al. 2011
	LS	Intestine	87% (23)	M-H	Dechtiar and Lawrie 1988
	LS	[Intestine]	2 locations: 44% (9), 25% (32)	21.8 (41), 5.3 (13)	Olds 2012
	LS	Intestine	13% (45)	1.5* (2)	Authors, personal observation, 2017
	LH	[Intestine]	69% (99)	NP	Bangham 1955
	LH	[Intestine]	NP (39)	NP	Collins and Dechtiar 1974
	LH	[Intestine]	NP (90)	NP	Dechtiar and Berst 1978
	LH	Intestine	17% (90)	M-H	Dechtiar et al. 1988
	LH	Intestine	8% (635)	4.8* (NP), 0.4**	Faisal et al. 2011a
	LH	[Intestine]	5% (30)	1 (1)	Olds 2012
	LE	Digestive tract	63% (30)	L-M	Bangham and Hunter 1939
	LE	NP	100% (4)	NP	Dechtiar 1972a
	LO	Intestine	100% (22)	M	Dechtiar and Christie 1988
Echinorhynchus sp.	LO	Posterior intestine	96% (113)	NP	Hart 1931b
Neoechinorhynchus rutili	LS	[Intestine]	2 locations: 5% (21), 3% (32)	6 (6), 3 (3)	Olds 2012
Neoechinorhynchus salmonis	LS	[Intestine]	3 locations: 33% (9), 10% (21), 16% (32)	10 (18), 4 (7), 8 (13)	Olds 2012
Neoechinorhynchus tumidus	LM	Intestine	6% (649)	7.4* (NP), 0.5**	Faisal et al. 2011
	LS	Intestine	30% (23)	L	Dechtiar and Lawrie 1988
	LS	Intestine	7% (45)	2.3* (4)	Authors, personal observation, 2017
	LS	[Intestine]	5% (21)	1 (1)	Olds 2012
	LH	[Intestine]	NP (39)	NP	Collins and Dechtiar 1974
	LH	Intestine	13% (90)	L	Dechtiar et al. 1988
	LH	Intestine	11% (635)	8.6* (NP), 0.9**	Faisal et al. 2011a
	LH	[Intestine]	15% (30)	2 (2)	Olds 2012
	LE	[Intestine]	25% (4)	NP	Dechtiar 1972a
	LO	Intestine	16% (22)	L	Dechtiar and Christie 1988
Neoechinorhynchus sp.	LS	Intestine	20% (45)	4.6* (28)	Authors, personal observation, 2017

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
Neoechinorhynchus sp.	LSC	Intestine	100% (2)	1.0* (1)	Authors, personal observation, 2017
Pomphorhynchus bulbocolli	LH	Intestine	2% (90)	L	Dechtiar et al. 1988
Immature Acanthocephala					
Echinorhynchus sp.	LE	Coelom	3% (30)	L	Bangham and Hunter 1939
Hirudinea					
Piscicola milneri	LM	[External surface, gills]	NP	NP	Meyer 1940
	LM	[External surface, gills]	NP	NP	Meyer 1946
	LH	[External surface, gills]	NP	NP	Meyer 1946
Piscicola punctata	LM	[External surface, gills]	NP	NP	Meyer 1940
Copepoda					
Achtheres pimelodi	LE	Gills	25% (4)	NP	Dechtiar 1972a
Ergasilus caeruleus	LH	[Gills]	NP (39)	NP	Collins and Dechtiar 1974
Salmincola corpulentus	LH	[Gills, gill arches]	2% (99)	NP	Bangham 1955
	LH	Gills	11% (90)	L	Dechtiar et al. 1988
	LO	Gills	<1% (113)	NP	Hart 1931b
	LO	Gill arches	8% (22)	L	Dechtiar and Christie 1988
Salmincola extensus	LE	[Fins, body]	NP	NP	Tidd 1931
	LO	Fins, body	<1% (113)	NP	Hart 1931b
Salmincola sp.	LS	Base of pectoral fin	2% (45)	1* (1)	Authors, personal observation, 2017
Mollusca					
Unidentified glochidium	LH	Pectoral fin	NP (NP)	NP (NP)	Hart 1931a

The largest number of parasite species infecting *Coregonus clupeaformis* was reported from Lake Huron (29) followed by Lake Superior (22) (Table 7). Six species of digeneans, six species of cestodes, and four acanthocephalan species infected *C. clupeaformis* from Lake Huron. Six species of cestodes and six acanthocephalan species infected *C. clupeaformis* from Lake Superior. The number of parasite species in *C. clupeaformis* from Lakes Michigan, Erie, and Ontario ranged from 10 to 14, with Lake Erie having the fewest.

Table 7. Number of parasite species in each taxonomic group reported and number of parasitological studies conducted on *Coregonus clupeaformis* from each Great Lake.

	Lake				
Taxonomic Group	**Superior**	**Huron**	**Michigan**	**Erie**	**Ontario**
Mastigophorans, Ciliophorans, Myxozoans	1	**3**	3	0	0
Adult Digenea	2	2	0	0	0
Larval/Immature Digenea	2	4	2	2	2
Monogenea	1	1	0	0	0
Adult Cestoda	4	4	3	2	2
Larval/Immature Cestoda	2	2	0	1	2
Adult Nematoda	3	3	1	1	2
Larval/Immature Nematoda	0	2	0	0	0
Acanthocephalans	6	4	3	2	3
Hirudinea	0	1	2	0	0
Copepoda	1	2	0	2	2
Mollusca	0	1	0	0	0
Total Species	**22**	**29**	**14**	**10**	**13**
Number of Studies	**7**	**14**	**11**	**6**	**4**

The parasite community in *C. clupeaformis* from Lake Ontario was most similar to the parasite communities in the other Great Lakes while the parasite community from Lake Erie showed the least similarity to the other lakes. The highest ***CCs*** values involved Lakes Superior and Ontario (0.69) followed by Lakes Superior and Huron (0.63), and Lakes Huron and Ontario (0.62) (Table 8). The lowest ***CCs*** value involved Lakes Superior and Erie (0.31). The number of parasite species shared by *C. clupeaformis* ranged from a low of 4 in Lakes Michigan and Erie to a high of 16 in Lakes Superior and Huron. *Proteocephalus longicollis*, *Cystidicola farionis*, *Echinorhynchus salmonis*, and *Neoechinorhynchus tumidus* infected *Coregonus clupeaformis* in all Great Lakes. The parasites *Diplostomum spathaceum*, *Cyathocephalus truncatus*, and *Acanthocephalus dirus* infected fish in four lakes and *Phyllodistomum coregoni*, *Bothriocephalus* sp., *Diphyllobothrium* sp., *Triaenophorus crassus*, and *Sterliadochona ephemeridarum* infected fish in three lakes.

Table 8. Sorenson's coefficients of parasite community similarity and number of shared parasite species (in parentheses) in *Coregonus clupeaformis* from the Great Lakes.

	Lake				
Lake	**Superior**	**Huron**	**Michigan**	**Erie**	**Ontario**
Michigan	0.44 (8)	0.47 (10)	-	0.33 (4)	0.52 (7)
Superior	-	0.63 (16)	0.44 (8)	0.31 (5)	0.69 (12)
Huron	0.63 (16)	-	0.47 (10)	0.36 (7)	0.62 (13)
Erie	0.31 (5)	0.36 (7)	0.33 (4)	-	0.52 (6)
Ontario	0.69 (12)	0.62 (13)	0.52 (7)	0.52 (6)	-

Coregonus hoyi

Larval, immature, and adult life stages of 26 parasite species from eight taxonomic groups were reported in *Coregonus hoyi* in four of the Great Lakes (Table 9). Researchers reported one Myxozoa, two adult Digenea, three larval/immature Digenea, one Monogenea, four adult Cestoda, three larval/immature Cestoda, one adult Nematoda, six adult Acanthocephala, one Hirudinea, and four Copepoda in *C. hoyi*. Common parasite species of *C. hoyi* are *Henneguya* sp., *Crepidostomum farionis*, *Phyllodistomum* sp., *Diplostomum* sp., *Ichthyocotylurus erraticus*, *Discocotyle sagittata*, *Bothriocephalus* sp., *Cyathocephalus truncatus*, *Proteocephalus longicollis*, *Diphyllobothrium ditremum*, *Triaenophorus crassus*, *Cystidicola farionis*, *Acanthocephalus dirus*, *Echinorhynchus salmonis*, *Neoechinorhynchus rutili*, and *Salmincola corpulentus*. A total of 25 studies reported on the parasites of *C. hoyi* from these waters. The number of parasitological studies conducted was highest in Lake Superior followed by Lake Huron. Individuals of *C. hoyi* were not examined from Lake Erie, and only four individuals were examined from Lake Ontario. The oldest and most recent studies of the parasites of *C. hoyi* were published or conducted in 1924 and 2017, respectively, with the largest number of individuals examined from Lake Michigan followed by Lake Huron.

Table 9. Reported parasites of *Coregonus hoyi* from Lakes Superior (LS), Huron (LH), Michigan (LM), and Ontario (LO) based on published scientific literature and personal observation of the authors. If the site of infection for a parasite was not provided in the original record, the site typical of infection for that parasite on that fish from other records is in brackets. Prevalence reported as a percentage with the number (in parentheses) represented by total number of fish examined. Infection intensity reported as L = light intensity (1-9 worms/fish); M = medium intensity (10-49 worms/fish) or as mean intensity defined as the mean number of parasites per infected fish and noted as * or as mean abundance defined as the mean number of parasites per examined fish and noted as **. NP = information not provided. Number (in parentheses) after intensity is maximum intensity value.

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
Myxozoa					
Henneguya sp.	LS	Gills	38% (8)	M	Dechtiar and Lawrie 1988
	LS	Gills	2 locations: 19 (30), 23 (22)	7.3 (16), 3.0 (10)	Olds 2012
Adult Digenea					
Crepidostomum farionis	LM	[Intestine]	NP (647)	NP	DeGiusti 1965
	LS	Intestine	63% (8)	M	Dechtiar and Lawrie 1988
Crepidostomum sp.	LM	[Intestine]	NP (647)	NP	DeGiusti 1965
Phyllodistomum sp.	LH	Ureters	45% (55)	L	Dechtiar et al. 1988
Unidentified digeneans	LH	Intestine	<1% (166)	1* (1)	Lundahl and Hoeberling 1967
Larval/Immature Digenea					
Diplostomum flexicaudum	LH	[Eye]	NP (59)	NP	Dechtiar and Berst 1978
Diplostomum spathaceum	LM	Eye	7% (30)	1 (1)	Olds 2012
	LH	Eye	4% (55)	L	Dechtiar et al. 1988
Diplostomum sp.	LH	[Eye]	51% (47)	NP	Bangham 1955
Ichthyocotylurus erraticus	LH	[Heart]	NP (59)	NP	Dechtiar and Berst 1978
	LH	Heart	27% (55)	L	Dechtiar et al. 1988
Monogenea					
Discocotyle sagittata	LS	Gills	75% (8)	L	Dechtiar and Lawrie 1988
	LS	Gills	6% (30)	1.5 (2)	Olds 2012
	LH	[Gills]	11% (47)	NP	Bangham 1955
	LH	[Gills]	NP (59)	NP	Dechtiar and Berst 1978
	LH	Gills	18% (55)	L	Dechtiar et al. 1988
Octocotylidae	LM	[Gills]	5% (647)	NP	DeGiusti 1965
Adult Cestoda					
Bothriocephalus sp.	LS	Pyloric caeca, intestine	36% (14)	2.4* (6)	Authors, personal observation, 2017
Cyathocephalus truncatus	LM	[Pyloric caeca, intestine]	NP	NP	Pearse 1924
	LM	[Pyloric caeca, intestine]	NP (647)	NP	DeGiusti 1965
	LM	Pyloric caeca	5% (238)	NP	Olson 1973
	LM	Intestine	1% (79)	1* (1)	Amin 1977
	LM	Pyloric caeca	16% (158)	1.6* (6)	Muzzall and Madenjian 2013
	LM	[Pyloric caeca, intestine]	33% (30)	2.7 (8)	Olds 2012
	LS	[Pyloric caeca, intestine]	2 locations: 19% (30), 9% (22)	3 (8), 8 (13)	Olds 2012

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
	LH	Intestine	11% (166)	0.3** (NP)	Lundahl and Hoeberling 1967
	LH	[Pyloric caeca, intestine]	NP (59)	NP	Dechtiar and Berst 1978
	LH	Pyloric caeca, anterior intestine	52% (31)	4.6** (NP)	French et al. 2005
	LH	Intestine	9% (55)	L	Dechtiar et al. 1988
Eubothrium salvelini	LM	Rectum	1% (79)	1* (1)	Amin 1977
	LM	[Pyloric caeca, intestine]	13% (30)	6 (15)	Olds 2012
	LM	Intestine, rectum	19% (158)	8.3* (81)	Muzzall and Madenjian 2013
Proteocephalus exiguus	LS	Intestine	50% (8)	L	Dechtiar and Lawrie 1988
	LS	[Pyloric caeca, intestine]	2 locations: 36% (30), 41% (22)	11 (25), 20 (11)	Olds 2012
	LH	[Pyloric caeca, intestine]	28% (47)	NP	Bangham 1955
Proteocephalus laruei	LS	Intestine	63% (8)	M	Dechtiar and Lawrie 1988
	LH	[Pyloric caeca, intestine]	68% (47)	NP	Bangham 1955
Proteocephalus sp.	LM	[Pyloric caeca, intestine]	NP (647)	NP	DeGiusti 1965
	LS	Intestine	100% (14)	22.4* (103)	Authors, personal observation, 2017
	LS	[Pyloric caeca, intestine]	23% (22)	46 (169)	Olds 2012
	LH	Intestine	33% (166)	3** (NP)	Lundahl and Hoeberling 1967
	LH	[Pyloric caeca, intestine]	NP (59)	NP	Dechtiar and Berst 1978
Larval/Immature Cestoda					
Bothriocephalid plerocercoids	LO	Unclear	NP	NP	Pritchard 1931
Diphyllobothrium ditremum	LS	Stomach, intestinal wall	50% (8)	M	Dechtiar and Lawrie 1988
Diphyllobothrium sp.	LM	[Body cavity, stomach wall]	51% (647)	NP	DeGiusti 1965
	LM	Body cavity	23% (238)	NP	Olson 1973
	LS	[Body cavity, stomach wall]	NP	NP	Swanson and Pratt 1977
	LH	[Body cavity, stomach wall]	55% (47)	NP	Bangham 1955
	LH	Body cavity, stomach wall	71% (166)	6** (NP)	Lundahl and Hoeberling 1967

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
	LH	[Body cavity, stomach wall]	NP (59)	NP	Dechtiar and Berst 1978
	LH	Stomach wall	36% (55)	L	Dechtiar et al. 1988
Triaenophorus crassus	LS	Muscles	38% (8)	M	Dechtiar and Lawrie 1988
	LH	[Muscles]	36% (47)	NP	Bangham 1955
	LH	Muscles	47% (55)	L	Dechtiar et al. 1988
Adult Nematoda					
Cystidicola farionis	LM	[Swimbladder]	90% (30)	27.1 (112)	Olds 2012
	LM	Swimbladder	48% (158)	5.2* (36)	Muzzall and Madenjian 2013
	LS	Swimbladder	98% (43)	NP	Smith 1978
	LS	Swimbladder	98% (44)	223* (NP)	Lankester and Smith 1980
	LS	Swimbladder	75% (8)	M	Dechtiar and Lawrie 1988
	LS	[Swimbladder]	2 locations: 39% (30), 41% (22)	24.8 (95), 21.3 (78)	Olds 2012
	LH	Swimbladder	85% (123)	16.7** (NP)	Lundahl and Hoeberling 1967
	LH	Swimbladder	1 (100%)	NP	Smith 1978
	LO	[Swimbladder]	NP	NP	Skinker 1930
	LO	[Swimbladder]	NP	NP	Skinker 1931
Cystidicola stigmatura	LM	Swimbladder	71% (238)	NP	Olson 1973
	LH	[Swimbladder]	9% (47)	NP	Bangham 1955
	LH	Swimbladder	85% (123)	16.7** (84)	Lundahl and Hoeberling 1967
	LH	[Swimbladder]	NP (59)	NP	Dechtiar and Berst 1978
Cystidicola sp.	LM	[Swimbladder]	40% (647)	NP	DeGiusti 1965
	LS	Swimbladder	7% (14)	6* (6)	Authors, personal observation, 2017
	LO	Swimbladder	40% (NP)	NP	Pritchard 1931
Adult Acanthocephala					
Acanthocephalus dirus	LM	Intestine	1% (158)	1.5* (2)	Muzzall and Madenjian 2013
	LM	[Intestine]	83% (30)	13.8 (76)	Olds 2012
	LS	[Intestine]	2 locations: 19% (30), 27% (22)	5 (9), 9 (36)	Olds 2012
Echinorhynchus lateralis	LS	Intestine	14% (14)	2* (2)	Authors, personal observation, 2017
Echinorhynchus leidyi	LH	[Intestine]	9% (47)	NP	Bangham 1955
Echinorhynchus salmonis	LM	[Intestine]	99% (647)	NP	DeGiusti 1965
	LM	Posterior intestine, some “broke” into body cavity and attached to mesenteries	95% (238)	NP	Olson 1973

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
	LM	Intestine	1% (79)	1* (1)	Amin 1977
	LM	Digestive tract	96% (79)	12.5** (54)	Amin and Burrows 1977
	LM	Intestine, rectum	23% (158)	2.7* (27)	Muzzall and Madenjian 2013
	LS	Intestine	50% (8)	L	Dechtiar and Lawrie 1988
	LS	[Intestine]	45% (30)	5.8 (12)	Olds 2012
	LH	[Intestine]	38% (47)	NP	Bangham 1955
	LH	Intestine	78% (166)	12.4** (145)	Lundahl and Hoeberling 1967
	LH	[Intestine]	NP (59)	NP	Dechtiar and Berst 1978
	LH	Intestine	9% (55)	M	Dechtiar et al. 1988
Neoechinorhynchus rutili	LH	Intestine	29% (55)	L	Dechtiar et al. 1988
Neoechinorhynchus tumidus	LM	[Intestine, rectum]	3% (30)	1 (1)	Olds 2012
	LM	Intestine, rectum	2% (158)	7* (7)	Muzzall and Madenjian 2013
	LS	[Intestine, rectum]	2 locations: 10% (30), 5% (22)	3.3 (7), 1.0 (1)	Olds 2012
	LH	[Intestine, rectum]	NP (59)	NP	Dechtiar and Berst 1978
	LH	Intestine	5% (55)	L	Dechtiar et al. 1988
Hirudinea					
Piscicola milneri	LM	[Outer surface, gills]	NP	NP	Pearse 1924
Unidentified leech	LM	Dentary	<1% (238)	NP	Olson 1973
Copepoda					
Achtheres sp.	LM	Gill cavity	11% (238)	NP	Olson 1973
Salmincola corpulentus	LM	[Gills]	NP	NP	Buttner and Hamilton 1976
	LM	[Gills]	17% (30)	1.2 (2)	Olds 2012
	LM	Branchial rim	1% (158)	1.5* (2)	Muzzall and Madenjian 2013
	LS	Gills	38% (8)	L	Dechtiar and Lawrie 1988
	LS	[Gills]	13% (30)	1 (1)	Olds 2012
	LH	Branchial cavities	16% (1,051)	1.9* (5)	Bowen and Stedman 1990
	LO	Gill cavity, operculum	5% (20)	Usually 1	Pritchard 1931
Salmincola extensus	LH	[Fins, body]	2% (47)	NP	Bangham 1955
Salmincola thymalli	LS	[Fins, body]	10% (30)	1 (1)	Olds 2012
Salmincola sp.	LM	[Fins, body]	5% (647)	NP	DeGiusti 1965
	LM	Fins, body	3% (238)	NP	Olson 1973

The number of parasite species found in *Coregonus hoyi* was similar in Lakes Superior (15), Huron (13), and Michigan (14) (Table 10). Furthermore, the number of digeneans, monogeneans, cestodes, nematodes, acanthocephalans, leeches, and copepods was the same or similar in these lakes. Species of cestodes and acanthocephalans were most common in *C. hoyi* in these lakes. Only two helminth species were reported in *C. hoyi* from Lake Ontario.

Table 10. Number of parasite species in each taxonomic group reported and number of parasitological studies conducted on *Coregonus hoyi* in each Great Lake.

	Lake				
Taxonomic Group	**Superior**	**Huron**	**Michigan**	**Erie**	**Ontario**
Myxozoa	1	0	0	0	0
Adult Digenea	1	1	1	0	0
Larval/Immature Digenea	0	2	1	0	0
Monogenea	1	1	1	0	0
Adult Cestoda	3	2	3	0	0
Larval/Immature Cestoda	2	1	1	0	1
Adult Nematoda	1	1	1	0	1
Larval/Immature Nematoda	0	0	0	0	0
Acanthocephalans	4	3	3	0	0
Hirudinea	0	0	1	0	0
Copepoda	2	2	2	0	0
Mollusca	0	0	0	0	0
Total Species	**15**	**13**	**14**	**0**	**2**
Number of Studies	**14**	**8**	**6**	**0**	**3**

Parasite communities in *Coregonus hoyi* were very similar in Lakes Superior, Michigan, and Huron. Only six pairwise coefficients could be calculated for the parasite communities of *C. hoyi* in the Great Lakes: Lakes Superior, Huron, and Michigan (Table 11). Parasite pairwise coefficients were highest for Lakes Superior and Michigan (0.62) followed by Lakes Superior and Huron (0.57). The number of parasite species shared by *C. hoyi* ranged from a low of two in three pairwise lake comparisons to a high of nine in Lakes Superior and Michigan. *Cystidicola farionis* and *Salmincola corpulentus* occurred in four Great Lakes; *Discocotyle sagittata*, *Cyathocephalus truncatus*, *Proteocephalus longicollis*, *Echinorhynchus salmonis*, and *Neoechinorhynchus tumidus* occurred in three lakes; and *Diphyllobothrium* sp. and *Acanthocephalus dirus* occurred in two lakes.

Table 11. Sorenson's coefficients of parasite community similarity and number of shared parasite species (in parentheses) in *Coregonus hoyi* from the Great Lakes.

	Lake				
Lake	**Superior**	**Huron**	**Michigan**	**Erie**	**Ontario**
Michigan	0.62 (9)	0.52 (7)	-	0.00 (0)	0.14 (2)
Superior	-	0.57 (8)	0.62 (9)	0.00 (0)	0.24 (2)
Huron	0.57 (8)	-	0.52 (7)	0.00 (0)	0.27 (2)
Erie	0.00 (0)	0.00 (0)	0.00 (0)	-	0.00 (0)
Ontario	0.24 (2)	0.27 (2)	0.14 (2)	0.00 (0)	-

Coregonus kiyi

A total of 76 individuals of *Coregonus kiyi* were examined for parasites in Lakes Superior, Huron, Michigan, and Ontario from four studies published in 1928, 1931, 1940, and 1942 (Table 12). Only bothriocephalid plerocercoids, *Diphyllobothrium laruei*, *Cystidicola stigmatura*, *Cystidicola* sp., and *Salmonicola corpulentus* were reported in *C. kiyi*.

Table 12. Reported parasites of *Coregonus kiyi* from Lakes Superior (LS), Huron (LH), Michigan (LM), and Ontario (LO) based on published scientific literature and personal observation of the authors. If the site of infection for a parasite was not provided in the original record, the site typical of infection for that parasite on that fish from other records is in brackets. Prevalence reported as a percentage with the number (in parentheses) represented by total number of fish examined. Infection intensity reported as mean intensity defined by the mean number of parasites per infected fish and noted as * or mean abundance defined as the mean number of parasites per examined fish and noted as **. NP = information not provided. Number (in parentheses) after intensity is maximum intensity value.

Taxonomic Group (Bold) and Parasite	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
Larval/Immature Cestoda					
Bothriocephalid plerocercoids	LM	Under peritoneum of stomach	NP (12)	<1** (1)	Vergeer 1928
	LS	Under peritoneum of stomach	NP (12)	<1** (2)	Vergeer 1928
	LH	[Under peritoneum of stomach]	NP	NP	Pritchard 1931
	LO	Under peritoneum of stomach	NP (12)	2** (6)	Vergeer 1928
Diphyllobothrium laruei	LM	Outside stomach	8% (12)	1* (1)	Vergeer 1942
	LS	Outside stomach	NP (12)	8 plerocercoids found	Vergeer 1942
	LO	Outside stomach	NP (12)	21 plerocercoids found	Vergeer 1942

Taxonomic Group (Bold) and Parasite	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
Adult Nematoda					
Cystidicola stigmatura	LO	Swimbladder	NP	NP	Mueller 1940
Cystidicola sp.	LO	Swimbladder	20% (NP)	NP	Pritchard 1931
Copepoda					
Salmincola corpulentus	LH	[Gills]	NP	NP	Pritchard 1931

Coregonus zenithicus

Bothriocephalid plerocercoids, *Diphyllobothrium laruei*, *Diphyllobothrium* sp., and *Salmincola corpulentus* were reported in *Coregonus zenithicus* only from Lake Superior in four studies published in 1928, 1942, 1977, and 2003 (Table 13). Otherwise, the records for this species are scant.

Table 13. Reported parasites of *Coregonus zenithicus* from Lake Superior based on published scientific literature. If the site of infection for a parasite was not provided in the original record, the site typical of infection for that parasite on that fish from other records is in brackets. Prevalence reported as a percentage with the number (in parentheses) represented by total number of fish examined. Infection intensity reported as mean abundance defined as the mean number of parasites per examined fish and noted as **. NP = information not provided. Number (in parentheses) after intensity is maximum intensity value.

Taxonomic Group (Bold) and Parasite Species	Site of Infection	Prevalence	Infection Intensity	Reference
Larval/Immature Cestoda				
Bothriocephalid plerocercoids	Under stomach peritoneum	NP (12)	<1** (1)	Vergeer 1928
Diphyllobothrium laruei	Outside stomach	NP (12)	2 found	Vergeer 1942
Diphyllobothrium sp.	[Outside stomach, viscera]	NP	NP	Swanson and Pratt 1977
Copepoda				
Salmincola corpulentus	Gills	NP	NP	Hudson et al. 2003

Coregonus reighardi

Only three individuals of *Coregonus reighardi* were examined for parasites in Lakes Huron and Ontario (Table 14). *Cystidicola farionis*, *Cystidicola* sp., *Echinorhynchus* sp., and *Salmincola corpulentus* were reported in *Coregonus reighardi* based on three studies published in 1930 and 1931.

Table 14. Reported parasites of *Coregonus reighardi* from Lakes Huron (LH) and Ontario (LO) based on published scientific literature. If the site of infection for a parasite was not provided in the original record, the site typical of infection for that parasite on that fish from other records is in brackets. Prevalence reported as a percentage with the number (in parentheses) represented by total number of fish examined. NP = information not provided.

Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
Adult Nematoda					
Cystidicola farionis	LO	[Swimbladder]	NP	NP	Skinker 1930
	LO	[Swimbladder]	NP	NP	Skinker 1931
Cystidicola sp.	LO	Swimbladder	45% (NP)	NP	Pritchard 1931
Adult Acanthocephala					
Echinorhynchus sp.	LO	Intestine	45% (NP)	NP	Pritchard 1931
Copepoda					
Salmincola corpulentus	LH	Gill cavity, operculum	NP	NP	Pritchard 1931

Coregonus alpenae

Individuals of *Coregonus alpenae* were examined for parasites in Lakes Superior and Huron only, with *Diplostomum* sp., *Triaenophorus* sp., *Cystidicola stigmatura*, and *Echinorhynchus salmonis* being reported (Table 15). Only 25 individuals were examined in two studies published in 1946 and 1955.

Table 15. Reported parasites of *Coregonus alpenae, C. johannae, C. nigripinnis,* and *C. prognathous* (nomem dubium) from Lakes Superior (LS), Huron (LH), and Michigan (LM) based on published scientific literature and personal observations of the authors. If the site of infection for a parasite was not provided in the original record, the site typical of infection for that parasite on that fish from other records is in brackets. Prevalence reported as a percentage with the number (in parentheses) represented by total number of fish examined. Infection intensity defined as the mean number of parasites per infected fish and noted as *. NP = information not provided. Number (in parentheses) after intensity is maximum intensity value.

Coregonus spp.	Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
C. alpenae	**Larval/Immature Digenea**					
	Diplostomum sp.	LH	[Eye, viscera]	100% (1)	NP	Bangham 1955
	Larval/Immature Cestoda					
	Triaenophorus sp.	LS	Muscle	NP (24)	1* (1)	Klick 1946
	Adult Nematoda					
	Cystidicola stigmatura	LS	[Swimbladder]	92% (24)	NP (>50)	Klick 1946
	Adult Acanthocephala					
	Echinorhynchus salmonis	LH	[Intestine]	100% (1)	NP	Bangham 1955

Coregonus spp.	Taxonomic Group (Bold) and Parasite Species	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
C. johannae	**Immature Nematoda**					
	Dichelyne cotylophora	LM	Viscera	NP	NP	Pearse 1924
	Copepoda					
	Salmincola corpulentus	LM	Gills	NP	NP	Pearse 1924
C. nigripinnis	**Adult Cestoda**					
	Proteocephalus exiguus	LM	Intestine	NP	NP	LaRue 1911
	Larval/Immature Cestoda					
	bothriocephalid plerocercoids	LH	Under peritoneum of stomach	NP	NP	Vergeer 1928
	Diphyllobothrium laruei	LH	Stomach	8% (12)	1* (1)	Vergeer 1942
C. prognathus	**Adult Cestoda**					
	Proteocephalus exiguus	LM	Intestine	NP	NP	LaRue 1911
		LM	Intestine	NP	NP	LaRue 1914

Coregonus johannae

Dichelyne cotylophora and *Salmincola corpulentus* were the only parasites reported in *Coregonus johannae* examined from Lake Michigan in one study published in 1924 (Table 15).

Coregonus nigripinnis

Individuals of *Coregonus nigripinnis* were found infected only with *Proteocephalus longicollis* (= *P. exiguus*), bothriocephalid plerocercoids, and *Diphyllobothrium laruei* from Lakes Huron and Michigan in three studies published in 1942 or before (Table 15).

Unknown *Coregonus* spp.

All parasite species found in unidentified species of *Coregonus* spp. from Lake Michigan (Table 16) involving three studies published in 1918, 1924 and 1965 were reported in identified species of *Coregonus* spp. in one or more Great Lakes.

Table 16. Reported parasites of *Coregonus* spp. from Lake Michigan based on published literature. If the site of infection for a parasite was not provided in the original record, the site typical of infection for that parasite on that fish from other records is in brackets. Prevalence reported as a percentage with the number (in parentheses) represented by total number of fish examined. NP = information not provided.

Taxonomic Group (Bold) and Parasite Species	Site of Infection	Prevalence	Infection Intensity	Reference
Adult Cestoda				
Proteocephalus exiguus	Intestine	NP	NP	Pearse 1924
Proteocephalus sp.	Intestine	NP	NP	Pearse 1924
Adult Nematoda				
Cystidicola stigmatura	Swimbladder	NP	NP	Pearse 1924
Cystidicola sp.	[Swimbladder]	40% (647)	NP	DeGiusti 1965
Adult Acanthocephala				
Echinorhynchus leidyi	Intestine	NP	NP	Pearse 1924
Echinorhynchus salmonis	Intestine	NP	NP	Pearse 1924

Prosopium cylindraceum

Larval, immature, and adult life stages of 26 parasite species from 8 taxonomic groups were reported in *Prosopium cylindraceum* from Lakes Superior, Huron, and Michigan and the St. Marys River (Table 17), with most species occurring in Lake Huron (20) and Lake Superior (17). (Table 18). Researchers reported one Myxozoa, two adult Digenea, two larval/immature Digenea, two Monogenea, three adult Cestoda, two larval/immature Cestoda, three adult Nematoda, two larval/immature Nematoda, five adult Acanthocephala, one Hirudinea, and three Copepoda in *P. cylindraceum*. Common parasite species of *P. cylindraceum* are *Crepidostomum farionis*, *Diplostomum spathaceum*, *Ichthyocotylurus erraticus*, *Tetraonchus variabilis*, *Eubothrium salvelini*, *Cystidicola farionis*, *Camallanus oxycephalus*, *Acanthocephalus dirus*, *Echinorhynchus lateralis*, *E. salmonis*, *Salmincola corpulentus*, and *S. thymalli*. A total of 15 studies reported on the parasites of *P. cylindraceum* from these waters. The oldest and most recent studies were published or conducted in 1928 and 2005, respectively, with the largest number of individuals examined from Lake Huron followed by Lake Superior.

Table 17. Reported parasites of *Prosopium cylindraceum* from Lakes Superior (LS), Huron (LH), and Michigan (LM) and the St. Marys River (SMR) based on published scientific literature. If the site of infection for a parasite was not provided in the original record, the site typical of infection for that parasite on that fish from other records is in brackets. Prevalence reported as a percentage with the number (in parentheses) represented by total number of fish examined. Infection intensity reported as L = light intensity (1-9 worms/fish); M = medium intensity (10-49 worms/fish) or as mean intensity defined as the mean number of parasites per infected fish and noted as *. NP = information not provided. Number (in parentheses) after intensity is maximum intensity value.

Taxonomic Group (Bold) and Parasite Species	Lake/ River	Site of Infection	Prevalence	Infection Intensity	Reference
Myxozoa					
Henneguya sp.	LS	[Muscle, gills]	6% (19)	8 (8)	Olds 2012
Adult Digenea					
Crepidostomum farionis	LS	Intestine	27% (56)	M	Dechtiar and Lawrie 1988
	LH	[Intestine]	27% (22)	NP	Bangham 1955
Phyllodistomum sp.	LS	Ureters	18% (56)	M	Dechtiar and Lawrie 1988
	LH	Ureters	7% (43)	L	Dechtiar et al. 1988
Larval/Immature Digenea					
Diplostomum spathaceum	LM	[Eye]	13% (23)	5.3 (9)	Olds 2012
	LS	Eye	73% (56)	L	Dechtiar and Lawrie 1988
	LH	Eye	21% (43)	L	Dechtiar et al. 1988
	LH	[Eye]	19% (32)	4.3 (18)	Olds 2012
Diplostomum sp.	LH	[Eye, viscera]	95% (22)	NP	Bangham 1955
Ichthyocotylurus erraticus	LS	Heart	36% (56)	L	Dechtiar and Lawrie 1988
	LH	[Heart]	NP (2)	NP	Hughes 1928
Ichthyocotylurus sp.	LH	Heart	14% (43)	L	Dechtiar et al. 1988
Monogenea					
Discocotyle sagittata	LS	Gills	21% (56)	L	Dechtiar and Lawrie 1988
	LH	[Gills]	5% (22)	NP	Bangham 1955
Tetraonchus variabilis	LS	Gills	NP	NP	Dechtiar 1972c
	LS	Gills	27% (56)	M	Dechtiar and Lawrie 1988
	LH	Gills	NP	NP	Dechtiar 1972c
	LH	Gills	70% (43)	L	Dechtiar et al. 1988
Adult Cestoda					
Cyathocephalus truncatus	LH	Intestine	14% (43)	L	Dechtiar et al. 1988
	LH	Pyloric caeca, anterior intestine	8% (26)	0.5* (NP)	French et al. 2005
Eubothrium salvelini	LM	[Pyloric caeca, intestine]	35% (23)	3.8 (10)	Olds 2012
	LS	Intestine	11% (56)	M	Dechtiar and Lawrie 1988
Proteocephalus exiguus	LH	[Pyloric caeca, intestine]	18% (22)	NP	Bangham 1955
	LH	[Pyloric caeca, intestine]	3% (32)	0.1 (3)	Olds 2012

Taxonomic Group (Bold) and Parasite Species	Lake/ River	Site of Infection	Prevalence	Infection Intensity	Reference
Larval/Immature Cestoda					
Triaenophorus crassus	LH	Muscle	7% (43)	L	Dechtiar et al. 1988
Triaenophorus nodulosus	LH	Liver	9% (43)	L	Dechtiar et al. 1988
Adult Nematoda					
Pseudocapillaria salvelini	LS	Intestine	16% (56)	L	Dechtiar and Lawrie 1988
Cystidicola farionis	LS	Swimbladder	53% (17)	16* (NP)	Lankester and Smith 1980
	LS	Swimbladder	25% (20)	7* (NP)	Dextrase 1987
	LS	Swimbladder	59% (56)	M	Dechtiar and Lawrie 1988
	LH	Swimbladder	7% (43)	L	Dechtiar et al. 1988
Cystidicola stigmatura	LH	[Swimbladder]	5% (22)	NP	Bangham 1955
Spinitectus gracilis	LS	Intestine	18% (56)	M	Dechtiar and Lawrie 1988
Larval/Immature Nematoda					
Camallanus oxycephalus	SMR	Posterior intestine	100% (1)	1* (1)	Muzzall 1984
Philometra sp.	LH	[Body cavity]	5% (22)	NP	Bangham 1955
Adult Acanthocephala					
Acanthocephalus dirus	LM	[Intestine]	53% (23)	1.3 (3)	Olds 2012
	LS	[Intestine]	2 locations: 12% (17), 50% (2)	2.5 (4), 5.0 (5)	Olds 2012
	LH	[Intestine]	3% (32)	0.01 (1)	Olds 2012
Echinorhynchus lateralis	LS	Intestine	34% (56)	L	Dechtiar and Lawrie 1988
Echinorhynchus salmonis	LS	Intestine	41% (56)	M	Dechtiar and Lawrie 1988
	LH	[Intestine]	23% (22)	NP	Bangham 1955
	LH	Intestine	7% (43)	M	Dechtiar et al. 1988
Neoechinorhynchus tumidus	LH	[Intestine]	9% (22)	NP	Bangham 1955
	LH	Intestine	7% (43)	L	Dechtiar et al. 1988
Pomphorhynchus bulbocolli	LH	Intestine	7% (43)	L	Dechtiar et al. 1988
Immature Acanthocephala					
Pomphorhynchus bulbocolli	LS	Intestine	14% (56)	L	Dechtiar and Lawrie 1988
Hirudinea					
Piscicola milneri	LS	Fins	4% (56)	L	Dechtiar and Lawrie 1988
Copepoda					
Ergasilus nerkae	LH	Gills	<1% (386)	1* (1)	Hudson et al. 1994
Salmincola corpulentus	LS	Gills	63% (56)	L	Dechtiar and Lawrie 1988
	LH	Gills	23% (43)	L	Dechtiar et al. 1988
	LH	[Gills]	5% (22)	NP	Bangham 1955

Taxonomic Group (Bold) and Parasite Species	Lake/ River	Site of Infection	Prevalence	Infection Intensity	Reference
Salmincola thymalli	LS	[Gills]	2 locations: 6% (17), 50% (2)	2.00 (2), 0.13 (13)	Olds 2012
	LH	Gills	Relatively common	Relatively common	C. Bowen, personal observation, in Hudson et al. 2003
	LH	[Gills]	34% (32)	0.2 (22)	Olds 2012
Salmincola sp.	LH	NP	36% (22)	NP	Bangham 1955

Table 18. Number of parasite species in each taxonomic group reported in scientific literature and number of parasitological studies conducted on *Prosopium cylindraceu*m in each Great Lake.

Taxonomic Group	Lake				
	Superior	Huron	Michigan	Erie	Ontario
Myxozoa	1	0	0	0	0
Adult Digenea	2	2	0	0	0
Larval/Immature Digenea	2	2	1	0	0
Monogenea	2	2	0	0	0
Adult Cestoda	1	2	1	0	0
Larval/Immature Cestoda	0	2	0	0	0
Adult Nematoda	3	1	0	0	0
Larval/Immature Nematoda	0	1	0	0	0
Acanthocephala	3	4	1	0	0
Hirudinea	1	0	0	0	0
Copepoda	2	4	0	0	0
Mollusca	0	0	0	0	0
Total Species	**17**	**20**	**3**	**0**	**0**
Number of Studies	**4**	**7**	**1**	**0**	**0**

Most species of parasites reported in *Prosopium cylindraceum* from Lakes Superior and Michigan were acanthocephalans, cestodes, nematodes, and digeneans (Table 18). The number of these parasite species in all groups was the same or similar in *P. cylindraceum* in these lakes. Cestodes were more common in Lake Huron. Individuals of *P. cylindraceum* were not examined from Lakes Erie and Ontario. The lowest number of parasite species was three in Lake Michigan.

Parasite communities of *Prosopium cylindraceum* were most similar between Lakes Superior and Huron and least similar between Lakes Huron and Michigan. Sorenson's Coefficient of Similarity between Lakes Huron and Michigan was 0.17, between Lakes Michigan and Superior was 0.30, and between Lakes Superior and Huron was 0.59. A total of 11 parasite species were shared in the parasite communities of *P. cylindraceum* from Lakes

Superior and Huron. *Diplostomum spathaceum* occurred in *P. cylindraceum* in three Great Lakes. *Crepidostomum farionis*, *Phyllodistomum* sp., *Ichthyocotylurus erraticus*, *Discocotyle sagittata*, *Tetraonchus variabilis*, *Eubothrium salvelini*, *Cystidicola farionis*, *Salmincola corpulentus*, and *S. thymalli* occurred in two Great Lakes.

Prosopium coulteri

Cystidicola farionis was the only parasite species reported in *Prosopium coulteri* examined from Lake Superior in one study published in 1987 (Table 19).

Table 19. Reported parasite of *Prosopium coulteri* from Lake Superior based on published scientific literature. Prevalence reported as a percentage with the number (in parentheses) represented by total number of fish examined. Infection intensity reported as mean intensity defined as the mean number of parasites per infected fish and noted as *. Number (in parentheses) after intensity is the maximum intensity value.

Taxonomic Group (Bold) and Parasite	Lake	Site of Infection	Prevalence	Infection Intensity	Reference
Immature Nematoda					
Cystidicola farionis	LS	Swimbladder	20% (35)	1* (NP)	Dextrase 1987

Parasite Taxonomic Group Analysis

The second method used to examine Great Lakes coregonine parasite communities was an analysis of each taxonomic group of parasites. This section details the findings of this approach.

Mastigophorans, Ciliophorans, Myxozoans

At least five species of mastigophorans, ciliophorans, and myxozoans were reported in coregonines from the Great Lakes (Tables 3, 6, 9, 17). *Cryptobia* sp., *Epistylis* sp., and *Trichodina* sp. occurred on the gills and skin of *Coregonus clupeaformis* from Lakes Huron and Michigan. Two species of myxozoans (*Chloromyxum* sp., *Henneguya zschokkei*) were reported in non-intestinal sites in *Coregonus artedi*, with *Chloromyxum* sp. and *H. zschokkei* infecting fish from Lake Superior; the latter species was also found in Lake Huron. *Chloromyxum* sp. had the highest prevalence of myxozoans found, occurring in *Coregonus artedi* from Lake Superior. It is not known if the *Henneguya* sp. found in *C. artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* from Lake Superior is *H. zschokkei* or a separate species. An unidentified species of myxozoan was reported in various tissues of *C. artedi* from Lake Huron.

Digenetic Trematodes

At least two species of adult digeneans were reported in coregonines from the Great Lakes (Tables 3, 6, 9, 17). *Crepidostomum farionis* was reported in the intestine and gall bladder of *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* from Lakes Superior, Huron, and Michigan, with its highest prevalence in *C. hoyi* from Lake Superior. *Phyllodistomum coregoni* infected the ureters of *C. clupeaformis* from Lakes Superior, Huron, and Ontario, with its highest intensity in *C. clupeaformis* from Lake Huron. It is not known if *Crepidostomum* sp. in *Coregonus hoyi* from Lake Michigan, *Phyllodistomum* sp. in *C. artedi* and *C. hoyi* from Lake Huron, the unidentified digeneans in *C. clupeaformis* from Lake Erie, and *C. hoyi* from Lake Huron are separate species from *Crepidostomum farionis* and *Phyllodistomum coregoni*.

Five species of larval digeneans were reported in coregonines from the Great Lakes. *Clinostomum marginatum* was found only in *Coregonus artedi* from Lake Superior. *Diplostomum flexicaudum* infected *C. artedi* and *C. hoyi* from Lake Huron and *C. clupeaformis* from Lakes Huron and Erie. *Diplostomum spathaceum* is a common larval digenean infecting *C. artedi* from Lakes Superior, Huron, and Ontario; *C. clupeaformis* in all Great Lakes except Lake Erie; *C. hoyi* from Lakes Huron and Michigan; and *P. cylindraceum* from Lakes Superior, Huron, and Michigan. *Diplostomum spathaceum* had its highest prevalence (73%) in *Prosopium cylindraceum* from Lake Superior. *Diplostomum* sp. was reported in *C. artedi*, *C. clupeaformis*, *C. hoyi*, and *P. cylindraceum* from Lake Huron and in *C. artedi* from Lake Superior. It is not known how common *Tylodelphys* sp. is in coregonines from the Great Lakes because fish brain tissue, a site that *Tylodelphys* sp. can infect, is not commonly examined for parasites. *Ichthyocotylurus erraticus* commonly infected *C. artedi* from Lakes Superior, Huron, and Ontario; *C. clupeaformis* in all Great Lakes except Lake Michigan; *C. hoyi* from Lake Huron; and *P. cylindraceum* from Lakes Superior and Huron. *Ichthyocotylurus erraticus* had its highest prevalence (100%) and mean intensity (941) in *C. clupeaformis* from Lake Erie. *Ichthyocotylurus* sp. was reported in *C. artedi*, *C. clupeaformis*, and *P. cylindraceum* from all Great Lakes except Lake Ontario.

Monogeneans

Two species of monogeneans were reported in coregonines from the Great Lakes. *Discocotyle sagittata* was the most common, infesting *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* from Lakes Superior and Huron (Tables 3, 6, 9, 17). *Tetraonchus variabilis* was found only on *P. cylindraceum* from Lakes Superior and Huron. Monogeneans in the family Octocotylidae infected *C. hoyi* from Lake Michigan, and its probable identification is addressed in the Discussion.

Cestodes

Five species of adult cestodes were reported in coregonines from the Great Lakes (Tables 3, 6, 9, 17). Individuals of *Bothriocephalus* sp. infected *Coregonus clupeaformis* from Lakes Superior, Huron, and Michigan and *C. hoyi* from Lake Superior. *Cyathocephalus truncatus* (species name sometimes misspelled *truncates*) is a common cestode occurring in the four major coregonine species in all Great Lakes except Lake Erie. *Cyathocephalus truncatus* had its highest prevalence (100%) in *Coregonus artedi* and mean intensity (120.3) in *C. clupeaformis* from Lake Huron. *Eubothrium crassum* was reported in *C. artedi* from Lakes Superior and Huron in three studies published before 1956. *Eubothrium salvelini* occurred in *C. artedi* from Lakes Superior and Huron; *C. clupeaformis* from Lakes Superior, Huron, and Erie; *C. hoyi* from Lakes Superior and Huron; and *Prosopium cylindraceum* from Lake Huron. *Eubothrium salvelini* had its highest prevalence (35%) in *P. cylindraceum* from Lake Huron and highest mean intensity (8.3) in *C. hoyi* from Lake Michigan.

Proteocephalus longicollis (= *P. exiguus*, *P. laruei*, *P. wickliffi*) is a common cestode maturing in all four major coregonines and other coregonine species from the Great Lakes. If *P. longicollis* is separated by its synonyms, *P. exiguus* (also found in the St. Marys River) infected *Coregonus artedi* and *C. clupeaformis* from all Great Lakes; *C. hoyi* from Lakes Superior and Huron; *C. nigripinnis*, *C. prognathus*, and *Coregonus* sp. from Lake Michigan; and *Prosopium cylindraceum* from Lake Huron. *Proteocephalus exiguus* had its highest prevalence (85%) in *C. clupeaformis* from Lake Huron and highest mean intensity (20) in *C. hoyi* from Lake Superior. *Proteocephalus laruei* infected *C. artedi* and *C. clupeaformis* from Lakes Superior, Huron, and Ontario and *C. hoyi* from Lakes Superior and Huron. *Proteocephalus laruei* had its highest prevalence (90%) in *C. artedi* from Lake Huron, but mean intensities were unreported in any studies. *Proteocephalus wickliffi* infected *C. artedi* only from Lake Erie in studies published in 1933 and 1939. Unidentified individuals of *Proteocephalus* were reported in *C. artedi* and *C. clupeaformis* from Lake St. Clair and *C. hoyi* from Lakes Superior, Huron, and Michigan.

Nine species of larval/immature cestodes were reported in coregonines from the Great Lakes. Bothriocephalid plerocercoids were found in *Coregonus artedi* from all Great Lakes, *C. hoy*i from Lake Ontario, and *C. kiyi* from Lakes Michigan and Huron. All studies reporting on these plerocercoids were published before 1932. Plerocercoids of *Eubothrium crassum* and *Eubothrium* sp. were found in *C. artedi* from Lake Erie and the St. Marys River, respectively. *Proteocephalus ambloplitis* infected *C. artedi* from Lake Superior. One rhyncobothrid cestode infected *C. artedi* from Lake Ontario, and *Schistocephalus* sp. infected *C. clupeaformis* from Lake Erie. It is not known what genus or species the rhyncobothrid cestode refers to, and it is not involved in any numerical presentation of the autogenic-allogenic data.

Plerocercoids of *Diphyllobothrium ditremum*, *D. laruei*, and *D. oblongatum* were reported in coregonines from the Great Lakes. *Diphyllobothrium ditremum* infected *Coregonus artedi* from Lakes Superior, Huron, and Ontario and *C. hoyi* from Lake Superior. *Diphyllobothrium laruei* infected *C. artedi* from all Great Lakes; *C. kiyi* from Lakes Superior, Michigan, and Ontario; *C. nigripinnis* from Lake Huron; and *C. zenithicus* from Lake Superior. *Diphyllobothrium laruei* had its highest prevalence (85%) in *C. artedi* from Lakes Huron, Michigan, Ontario, and Erie. *Diphyllobothrium oblongatum* was reported in *C. artedi* from Lakes Superior and Michigan. Studies reporting these *Diphyllobothrium* species infecting coregonines were published in 1969 or earlier. Plerocercoids of *Diphyllobothrium* not identified to species were found in *C. artedi*, *C. clupeaformis*, and *C. hoyi* from Lakes Superior, Huron, Ontario, and St. Clair in studies from 1973 to 1988.

Plerocercoids of *Triaenophorus* sp. were reported in the four major coregonines (*Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, *Prosopium cylindraceum*). *Triaenophorus crassus* was reported in *C. artedi* from Lakes Superior and Huron; *C. clupeaformis* from Lakes Superior, Huron, and Ontario; *C. hoyi* from Lakes Superior, Huron, and Michigan; and *P. cylindraceum* from Lake Huron. *Triaenophorus crassus* had its highest prevalence (77%) in *C. artedi* from Lake Huron. *Triaenophorus nodulosus* infected only *P. cylindraceum* from Lake Huron. Unidentified individuals of *Triaenophorus* were reported in *C. artedi* from Lake Superior.

Nematodes

Four species of adult nematodes were found in coregonines from the Great Lakes (Tables 3, 6, 9, 17). *Pseudocapillaria salvelini* infected *Coregonus clupeaformis* and *Prosopium cylindraceum* from Lake Superior. *Cystidicola farionis* is a common parasite of *Coregonus artedi* and *C. clupeaformis* from Lakes Superior, Huron, Michigan, and Ontario; *C. hoyi* from Lakes Superior, Michigan, and Ontario; *C. reighardi* from Lake Ontario; *Coregonus* sp. from Lake Michigan; *P. cylindraceum* from Lakes Superior and Huron; and *P. coulteri* from Lake Superior. *Cystidicola farionis* had its highest prevalence (100%) in *Coregonus artedi* and highest mean intensity (24.8) in *C. hoyi* from Lake Superior. *Cystidicola stigmatura* was reported in *Coregonus artedi* in all Great Lakes and Lake St. Clair; *C. clupeaformis* from Lakes Huron, Michigan, Erie, and St. Clair; *C. hoyi* from Lakes Huron and Michigan; *C. alpenae* from Lake Superior; *Coregonus* sp. from Lake Michigan; and *P. cylindraceum* from Lake Huron. *Cystidicola stigmatura* had its highest prevalence (87%) in *Coregonus clupeaformis* and its highest mean intensity (223) in *C. hoyi* from Lake Superior. We believe the true identity of *Cystidicola stigmatura* in the coregonines mentioned in the text above is *Cystidicola farionis* (see Discussion). *Cystidicola* sp. was reported in *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, *C. kiyi*, *C. reighardi*, and *Coregonus* sp. from Lakes Superior, Michigan, and Ontario. *Sterliadochona ephemeridarum* was reported in *C. artedi* from Lake Superior and *C. clupeaformis* from Lakes Superior, Huron, and Ontario. *Spinitectus gracilis* infected *C. clupeaformis* from Lake Huron and *P. cylindraceum* from Lake Superior.

Dichelyne cotylophora, *Philometra* sp., *Raphidascaris acus*, *Spinitectus gracilis*, and *Camallanus oxycephalus* were represented as larval/immature nematodes. *Dichelyne cotylophora* was reported in *Coregonus johannae* from Lake Michigan. *Philometra* sp. infected *C. artedi*, *C. clupeaformis*, and *Prosopium cylindraceum* from Lake Huron. *Raphidascaris acus* and *Spinitectus gracilis* infected *C. clupeaformis* from Lake Huron. *Camallanus oxycephalus* infected *Coregonus hoyi* from the St. Marys River.

Acanthocephalans

A total of 10 species of acanthocephalans were reported in coregonines from the Great Lakes (Tables 3, 6, 9, 17). Adults of *Acanthocephalus dirus* were common in *Coregonus clupeaformis* from Lakes Superior, Huron, Michigan, and Ontario and *C. hoyi* and *Prosopium cylindraceum* (also from Lake Huron) from Lakes Superior and Michigan. Adults of *Pomphorhynchus bulbocolli* were found in *C. clupeaformis* from Lake Huron, and immature individuals occurred in *Prosopium cylindraceum* from Lake Superior.

Three species of acanthocephalans infecting coregonines are in the genus *Echinorhynchus*, and five species are in the genus *Neoechinorhynchus*. *Echinorhynchus lateralis* was a common parasite of *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* from Lake Superior. *Echinorhynchus leidyi* was found in *C. artedi* from Lake Superior and in *C. hoyi* from Lake Huron. *Echinorhynchus salmonis* was the most common acanthocephalan species found, infecting *C. artedi* from Lakes Superior, Huron, Erie, and Ontario and the St. Marys River; *C. clupeaformis* from all Great Lakes; *C. hoyi* from Lakes Superior, Huron, and Michigan; and *P. cylindraceum* from Lakes Superior and Huron. In some samples, *E. salmonis* had prevalences of 100% and mean intensities greater than 20. *Neoechinorhynchus crassus* and *N. cylindratus* have been reported only in *C. artedi* from Lake Superior. *Neoechinorhynchus salmonis* was found only in *C. clupeaformis* from Lake Superior. *Neoechinorhynchus rutili* was found in *C. clupeaformis* from Lake Superior and *C. hoyi* from Lake Huron. *Neoechinorhynchus tumidus* was the most common species of the genus found and was reported in *C. artedi* from Lake Superior; *C. clupeaformis* from all Great Lakes; *C. hoyi* from Lakes Superior, Huron, and Michigan; and *P. cylindraceum* from Lake Huron.

Hirudineans

Only two species of leeches were reported in coregonines from the Great Lakes (Tables 6, 9, 17). *Piscicola milneri* infested *Coregonus clupeaformis* from Lakes Huron and Michigan, *C. hoyi* from Lake Michigan, and *Prosopium cylindraceum* from Lake Superior. *Piscicola punctata* was reported on *C. clupeaformis* from Lake Michigan. Studies reporting leeches from coregonines in the Great Lakes were published in the 1940s and 1988.

Copepods

Seven species of copepods were reported on coregonines from the Great Lakes (Tables 3, 6, 9, 17). *Achtheres pimelodi* infested *Coregonus artedi* from Lake Michigan and *C. clupeaformis* from Lake Erie. *Argulus* sp. was found only once in *C. artedi* from Lake Huron. Two species of *Ergasilus* were reported, with *Ergasilus. caeruleus* infesting *C. artedi* from Lake Michigan and *C. clupeaformis* from Lake Huron and *E. nerkae* infesting *Prosopium cylindraceum* from Lake Huron.

Three species of *Salmincola* were reported on coregonines from the Great Lakes. *Salmincola corpulentus* was the most common species of this genus found and infested *Coregonus artedi* from all Great Lakes except Lake Michigan, *C. clupeaformis* from Lakes Huron and Ontario, *C. hoyi* from all Great Lakes except Lake Erie, *Prosopium cylindraceum* from Lakes Superior and Huron, *C. kiyi* from Lake Huron, *C. johannae* from Lake Michigan, and *C. reighardi* from Lake Huron. *Salmincola extensus* was reported in *C. artedi* from Lakes Superior and Huron, *C. clupeaformis* from Lakes Erie and Ontario, and *C. hoyi* and *P. cylindraceum* from Lake Huron. *Salmincola thymalli* infested *C. hoyi* from Lake Superior and *P. cylindraceum* from Lakes Superior and Huron.

Coregonine Species, Parasite Communities, and Studies by Lake and Connecting Waters

The number and percentage of parasite species and genera with species not identified by taxonomic group for the four major coregonine species (*Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, *Prosopium cylindraceum*) are in Table 20. The number for each fish species represents the total parasite number for all Great Lakes and connecting waters. The numbers of mastigophorans and ciliophorans were drastically different among the coregonines, as they were reported only in or on *Coregonus clupeaformis*. The number and percentage of myxozoans were similar in *C. artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum*. The percentages of digeneans, monogeneans, adult cestodes, adult nematodes, larval/immature nematodes, acanthocephalans, and copepods were similar in the four fish species. The largest dissimilarity of helminth groups by number and percentage in the four coregonine species involved larval/immature cestodes, with *C. artedi* having higher numbers and percentages than the other three fish species. Only one nematode species (*Cystidicola farionis*) was reported in *Coregonus hoyi*. The most important parasite groups, based on number of species found from highest to lowest percentage by coregonine species, are *C. artedi* (cestodes, acanthocephalans and digeneans tied, copepods), *C. clupeaformis* (acanthocephalans and cestodes similar with digeneans and nematodes tied), *C. hoyi* (acanthocephalans, cestodes, digeneans, copepods), and *P. cylindraceum* (acanthocephalans, cestodes and nematodes similar, digeneans).

Table 20. Number and percentage (in parentheses) of parasite species by major taxonomic group for *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* in the Great Lakes and connecting waters for all parasite species data combined.

Taxonomic Group	***Coregonus artedi***	***Coregonus clupeaformis***	***Coregonus hoyi***	***Prosopium cylindraceum***
Mastigophora	0 (0%)	2 (5.3%)	0 (0%)	0 (0%)
Ciliophora	0 (0%)	1 (2.6%)	0 (0%)	0 (0%)
Myxozoa	2 (5.7%)	1 (2.6%)	1 (3.9%)	1 (3.9%)
Adult Digenea	2 (5.7%)	2 (5.3%)	2 (7.6%)	2 (7.7%)
Larval/Immature Digenea	4 (11.4%)	4 (10.5%)	3 (11.5%)	2 (7.7%)
Monogenea	1 (2.9%)	1 (2.6%)	1 (3.9%)	2 (7.7%)
Adult Cestoda	5 (14.3%)	4 (10.5%)	4 (15.4%)	3 (11.5%)
Larval/Immature Cestoda	7 (20%)	3 (7.9%)	3 (11.5%)	2 (7.7%)
Adult Nematoda	2 (5.7%)	4 (10.5%)	1 (3.9%)	3 (11.5%)
Larval/Immature Nematoda	1 (2.9%)	2 (5.3%)	0 (0%)	2 (7.7%)
Adult Acanthocephala	6 (17.1%)	7 (18.5%)	6 (23%)	5 (19.2%)
Hirudinea	0 (0%)	2 (5.3%)	1 (3.9%)	1 (3.9%)
Copepoda	5 (14.3%)	4 (10.5%)	4 (15.4%)	3 (11.5%)
Mollusca	0 (0%)	1 (2.6%)	0 (0%)	0 (0%)
Total	**35 (100%)**	**38 (100%)**	**26 (100%)**	**26 (100%)**

A total of 15 parasite species were reported in *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum*. The species are *Henneguya* sp., *Crepidostomum farionis*, *Diplostomum spathaceum*, *Ichthyocotylurus erraticus*, *Discocotyle sagittata*, *Cyathocephalus truncatus*, *Eubothrium salvelini*, *Proteocephalus longicollis*, *Triaenophorus crassus*, *Cystidicola farionis*, *Echinorhynchus lateralis*, *E. salmonis*, *Neoechinorhynchus tumidus*, *Salmincola corpulentus*, and *S. extensus.* Six parasite species (*Diplostomum flexicaudum*, *Diphyllobothrium* sp., *Philometra* sp., *Acanthocephalus dirus*, *E. lateralis*, *Piscicola milneri*) infected three of these coregonine species. The number of helminth species (digeneans, monogeneans, cestodes, nematodes, acanthocephalans) ranged from 20 (*Coregonus hoyi*) to 27 (*C. artedi*). The number of autogenic parasite species ranged from 16 (*C. hoyi*) to 21 (*C. clupeaformis*), with the percentage of each species ranging from 74% (*C. artedi*) to 90% (*Prosopium cylindraceum*) (Table 21). The number of allogenic species was much lower, with a range from 2 (*P. cylindraceum*) to 7 (*C. artedi*), and the percentage of each range was from 10% (*P. cylindraceum*) to 26% (*C. artedi*). Parasite species found only in *P. cylindraceum* and not in *Coregonus* spp. in the Great Lakes were *Tetraonchus variabilis*, *Triaenophorus nodulosus*, *Pomphorhynchus bulbocolli*, and *Ergasilus nerkae*.

Table 21. Total numbers of trematode, monogenean, cestode, nematode, and acanthocephalan species and number and percentage (in parentheses) of autogenic and allogenic species in *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* from the Great Lakes.

Coregonine Species	**Number Helminth**	**Autogenic Helminth**	**Allogenic Helminth**
Coregonus artedi	27	20 (74%)	7 (26%)
Coregonus clupeaformis	27	21 (78%)	6 (22%)
Coregonus hoyi	20	16 (80%)	4 (20%)
Prosopium cylindraceum	21	19 (90%)	2 (10%)

The greatest number of parasite species were reported in *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* from Lakes Superior and Huron followed by Lake Michigan (Table 22). The lowest number of parasites in these four coregonine species was reported from Lakes Erie and Ontario, likely because (1) the fewest numbers of individuals of *C. clupeaformis* and *C. hoyi* were examined from Lakes Erie and Ontario, (2) individuals of *C. hoyi* have not been examined from Lake Erie, and (3) *P. cylindraceum* was not examined from Lakes Erie and Ontario. Only *C. artedi* and *C. clupeaformis* were examined for parasites in all Great Lakes.

Table 22. Number of parasite species of *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* in the Great Lakes.

Lake	***Coregonus artedi***	***Coregonus clupeaformis***	***Coregonus hoyi***	***Prosopium cylindraceum***
Michigan	7	14	13	3
Superior	27	24	14	19
Huron	20	27	16	20
Erie	7	11	0	0
Ontario	10	14	3	0

The number of studies reporting on the parasites of the four main coregonine species from the Great Lakes ranged from 14 (*Prosopium cylindraceum*) to 47 (*Coregonus clupeaformis*) (Table 23). Most studies reporting on the parasites of *C. artedi* were from Lake Superior (15) followed by Lake Michigan (8). A total of 17 studies reported on the parasites of *C. clupeaformis* from Lake Huron followed by 12 studies from Lake Michigan. A total of 8 studies reported on the parasites of *C. hoyi* from Lake Michigan followed by 7 studies from Lake Huron. A total of 8 studies reported on the parasites of *P. cylindraceum* from Lake Huron followed by 5 studies from Lake Superior. When the number of studies reporting on the parasites of these four coregonine species are combined by Great Lake, most studies were conducted in Lake Huron followed by Lakes Superior and Michigan.

Table 23. Number of studies reporting on parasites of *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* in the Great Lakes and connecting waters.

Lake/Connecting Water	*Coregonus artedi*	*Coregonus clupeaformis*	*Coregonus hoyi*	*Prosopium cylindraceum*	Total
Lake Superior	15	7	6	5	33
Lake Huron	7	17	7	8	39
Lake Michigan	8	12	8	1	29
Lake Erie	7	6	0	0	13
Lake Ontario	7	5	4	0	16
Great Lakes Total	**44**	**47**	**25**	**14**	**130**
Lake St. Clair	1	2	0	0	3
Saint Marys River	1	0	0	1	2
Overall Total	**46**	**49**	**25**	**15**	**135**

When the parasitological studies are arranged in 10-year intervals conducted individually on the four main coregonine species, the number for each coregonine species ranges from 11 (*Prosopium cylindraceum*) to 36 (*Coregonus artedi*) (Table 24). Nearly all of these studies are now 30+ years old, as most of them on *C. artedi* and *C. clupeaformis* were published from 1911 through 1989. Similarly, most studies of *C. hoyi* and *P. cylindraceum* were conducted during 1970-1979 and 1980-1989, respectively. The number of parasitological studies conducted on *C. artedi*, *C. clupeaformis*, *C. hoyi*, and *P. cylindraceum* in Table 23 is higher than the number of studies on these coregonine species in 10-year intervals in Table 24 because some studies reported on the parasites of two or more of these coregonine species. Only 13 studies were conducted on the parasites of *C. artedi*, *C. clupeaformis*, *C. hoyi*, and *P. cylindraceum* from the Great Lakes after 2000.

Table 24. Number of studies reporting on parasites of *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* in the Great Lakes and connecting waters in 10-year intervals. Studies (author(s)/year) are identified in the footnotes in alphabetical order from the oldest to the most recent studies.

10-Year Interval	***Coregonus artedi***	***Coregonus clupeaformis***	***Coregonus hoyi***	***Prosopium cylindraceum***	**Total**
1890-1899	0	1[a]	0	0	**1**
1900-1909	0	0	0	0	**0**
1910-1919	4[b]	2	0	0	**6**
1920-1929	3	3	1[c]	1[d]	**8**
1930-1939	7	5	3	0	**15**
1940-1949	6	4	0	0	**10**
1950-1959	2	1	1	1	**5**
1960-1969	2	3	2	0	**7**
1970-1979	4	5	7	1	**17**
1980-1989	6	5	3	5	**19**
1990-1999	1	0	1	1	**3**
2000-2009	0	1	1	1[e]	**3**
2010-2019	1[f]	5[f]	3[f]	1	**10**
2020-2029	0	0	0	0	**0**
Total	**36**	**35**	**22**	**11**	**104**

[a]Linton 1898.
[b]LaRue 1911.
[c]Pearse 1924.
[d]Hughes 1928.
[e]French et al. 2005.
[f]Authors, personal observation, 2017.

Nearly all studies of the other coregonine species are more than 70 years old. At least eight parasite species in *Coregonus alpenae*, *C. johannae*, *C. kiyi*, *C. nigripinnis*, *C. prognathus*, *C. reighardi*, *C. zenithicus*, and *Prosopium coulteri* were reported in 12 studies: Trematoda (*Diplostomum* sp.), Cestoda (*Triaenophorus* sp., bothriocephalid plerocercoids, *Diphyllobothrium laruei*, *Proteocephalus longicollis*), Nematoda (*Cystidicola farionis*), Acanthocephala (*Echinorhynchus salmonis*), Copepoda (*S. corpulentus*). Ten of these studies were published during 1911-1955. Additional studies of the parasites of *C. johannae*, *C. nigripinnis*, and *C. prognathus* from Lake Michigan were published during 1911-1924.

Parasite Similarity among Coregonine Species

There was a high degree of similarity in parasites of the four coregonine species (*Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, *Prosopium cylindraceum*). We calculated ***CCs*** values for all parasite data combined from all Great Lakes to determine how similar the parasite communities were among the four major coregonine species (Table 25). These coefficients and number of parasite species common to these species-pair analyses were all above 0.50 and ranged from a low involving *Coregonus artedi*-*Prosopium cylindraceum* (0.57, 17 shared parasite species) to a high involving *C. hoyi* and *P. cylindraceum* (0.75, 19 shared parasite species). As expected, the ***CC_s*** values were highest when the number of parasite species shared between species were the highest. The large sample sizes for each coregonine species and the large number of parasitological studies conducted were largely responsible for these high coefficients, as these two factors play a role in increasing the number and variety of parasites found in coregonines. The parasite communities of *P*. *cylindraceum* were involved in both the two highest coefficients and the lowest coefficient.

Table 25. Sorenson's coefficients of parasite community similarity and number of shared parasite species in common (in parentheses) in *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* for all parasite species combined for all Great Lakes.

Species	***Coregonus artedi***	***Coregonus clupeaformis***	***Coregonus hoyi***	***Prosopium cylindraceum***
Coregonus artedi	-	0.58 (21)	0.68 (20)	0.57 (17)
Coregonus clupeaformis	0.58 (21)	-	0.63 (20)	0.69 (22)
Coregonus hoyi	0.68 (20)	0.63 (20)	-	0.75 (19)
Prosopium cylindraceum	0.57 (17)	0.69 (22)	0.75 (19)	-

DISCUSSION

Our analysis of the existing literature and the inclusion of additional unpublished data document a diverse helminth community in Great Lakes coregonines that varies among the Great Lakes and coregonine species. The simple detection of a parasite does not imply disease or pathology. We would like to move our analysis in this section to the effects of parasites on each fish species, the potential effects of these parasites on human use of coregonines, and a comparison of our Great Lakes coregonine helminth community with other coregonine helminth communities worldwide.

Coregonine Parasites and Their Likely Pathogenicity

Several mastigophorans, ciliophorans, myxozoans, digenetic trematodes, cestodes, monogeneans, nematodes, acanthocephalans, leeches, and copepods were reported to cause pathology to Great Lakes coregonines. However, there were no epizootics of coregonines reported in the Great Lakes due to parasites. In the following section we examine the pathology of each of the parasite taxonomic groups to Great Lakes coregonines.

Mastigophorans, Ciliophorans, Myxozoans

Mastigophorans, ciliophorans, and myxozoans were found infrequently in or on coregonines in the Great Lakes, with only five genera (*Cryptobia*, *Epistylis*, *Trichodina*, *Chloromyxum*, and *Henneguya*) reported. We do not know if coregonines were poor hosts for these parasites or if individuals of these fish species were not critically examined for them. Lawler (1970) commented on the paucity of single-celled parasites and myxozoans infecting North American coregonines. Similarly, Bauer (1970) reported only three species of myxozoans in his review of the parasites of coregonines in several Russian lakes, and two of these included the same genus (*Chloromyxum*) and the same species (*Henneguya zschokkei*), as found in our review.

Coregonus clupeaformis infected with *Epistylis* sp. on the skin had mild hemorrhages at the base of the fins (Loch and Faisal 2011). Also, Loch and Faisal (2011) reported that *C. clupeaformis* from Lake Michigan infected with *Trichodina* sp. on the skin had focal echymotic hemorrhage on the ventrum. Richardson (1938), Davis

(1947), and Hoffman and Lom (1967) reported that *Epistylis* sp. and *Trichodina* sp. can cause a variety of fish pathologies, including gill destruction and hemorrhaging in heavy infestations. *Cryptobia salmositica* was reported in Mountain Whitefish (*Prosopium williamsoni*) in the American Northwest (Woo 1987). In other non-coregonines, pathogenic effects with this group of parasites were found as Kuperman et al. (2002) documented Tilapia (*Tilapia* sp.) infected with the external flagellate *Cryptobia branchialis* were anorexic and swam close to the water's surface, with some infested fish dying from thrombus formation.

Myxozoans such as *Chloromyxum* sp. and *Henneguya zschokkei* were considered protozoans in the past, but parasitologists moved them to the phylum Cnidaria (corals, jellyfish, sea anemones) based on similarities of their molecular analyses and the presence of cnidocytes known as polar capsules. Although the species of *Chloromyxum* infecting *Coregonus artedi* from Lake Superior is unknown, Mitchell et al. (1980) demonstrated that plasmodia of *Chloromyxum trijugum*, when attached to the epithelial cells by pseudopod projections, caused various degrees of breakdown in the mucosal layer of gall bladders in centrarchid fishes.

Boil disease is a term used for the infection of fish muscles by several species of myxozoans, whose presence results in the formation of large protruding visible cysts. When the spores mature and the cysts rupture, a milky-white fluid containing spores is released. *Henneguya zschokkei* can cause boil disease in the muscles of *Coregonus* spp. (Reichenbach-Klinke 1973). These open sores can lead to secondary infections from opportunistic pathogens, in particular bacteria. Furthermore, Feist (2008) reported that when the cysts of *H. zschokkei* are numerous in the somatic muscles of *Coregonus* spp., they result in poor fillet quality, which reduces the market value of the fish. *Henneguya* spp. may cause weight loss, extensive damage to fish, and mortalities (Reichenbach-Klinke and Elkan 1965; Reichenbach-Klinke 1973). Infected fish are not aesthetically pleasing but can be eaten by humans because this parasite does not infect them. We are not aware of boil disease being reported in coregonines from the Great Lakes.

Digenetic Trematodes

Adult digenetic trematodes are infrequent parasites of coregonines in the Great Lakes, with only *Crepidostomum farionis* and *Phyllodistomum coregoni* found in the gall bladder, ureter, and intestine. Unless intensity is $\geq$50 worms (Dechtiar and Christie 1988; Dechtiar and Lawrie 1988; Dechtiar et al. 1988), it is believed these parasites do not cause any major pathology to coregonines. One reason adult trematodes are infrequent parasites of coregonines is that the deep-water habitat of coregonines does not expose them to intermediate hosts of digenetic trematodes. Therefore, coregonines might not eat or infrequently eat organisms that serve as intermediate hosts for trematodes. Similarly, Bauer (1970) reported only two species of adult trematodes in Russian coregonines. One species was the same genus (*Phyllodistomum*), and the other species was the same species (*C. farionis*), as found in our review.

Larval trematodes (metacercariae) are more common and numerous than adult trematodes in coregonines from the Great Lakes. However, they might not be seen by the casual observer because of their small size and where they are usually found. The presence of trematode metacercariae in coregonines indicates one or more periods of their life cycles in the Great Lakes are in close association with mollusc intermediate hosts, usually snails. In doing so, the cercariae leave the mollusc, penetrate coregonines, move to the infection site in the fish and develop into metacercariae. Generally, larval and age-0 coregonines of *Coregonus clupeaformis and Prosopium cylindraceum* live close to shore (Hart 1931a; Freeberg et al. 1990) in proximity to molluscs, allowing infection by digenetic trematodes by being exposed to emerging cercariae.

Of the five species of larval trematodes (*Clinostomum marginatum*, *Diplostomum flexicaudum*, *D. spathaceum*, *Tylodelphys* sp., *Ichthyocotylurus erraticus*) found in coregonines, the genera *Diplostomum* and *Ichthyocotylurus* deserve some comments. Some authors consider *D. flexicaudum* a synonym of *D. spathaceum*. *Diplostomum spathaceum* infected the eye lens of *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium* *cylindraceum* in all Great Lakes except Lake Erie. Bauer et al. (1959) believed that *Diplostomum* sp. caused the deaths of several fish, including the Powan (*C. clupeoides*) and Common or European Whitefish (*C. lavaretus*). Lawler (1970) reported that pond-reared *C. lavaretus* infected with *Diplostomum* sp. resulted in blindness, dystrophy, growth retardation, and mortalities of 80% in infected fish. Significant mortalities have been documented in other non-coregonines as Numann (1972) found that *D. spathaceum* was the causative agent of a mass mortality of European Perch (*Perca fluviatilis*). Furthermore, Shariff et al. (1980) reported that *Diplostomum* spp. might cause lens discoloration, blindness, and emaciation of fish. Metacercariae of *Diplostomum* may live for several months in the eyes and lenses of fish and accumulate over time. Some Least Cisco (*C. sardinella*) in the western Arctic had up to 7,000 larvae of *D. baeri bucculentum* in their eyes (Stewart and Bernier 1999). Information about the vision of these infected fish was not provided.

Metacercariae of *Ichthyocotylurus erraticus* occur primarily as tiny cysts in the hearts of coregonines and salmonines. A total of 11 *Coregonus clupeaformis* from Lake Erie were infected with *I. erraticus*, with a mean intensity of 941.2 metacercariae per heart and a maximum intensity of 1,903 (PMM, unpublished data). Harrod and Griffiths (2005) commented that Pollan or Arctic Cisco (*C. autumnalis*) survival was affected by the combination of reduced blood circulation due to infection of *I. erraticus* and possible low lake oxygen concentration. Petrushevski (1958) found that 80-100% of Siberian coregonines were infected with an intensity of 400 or more *I. erraticus* and suggested these trematodes could cause serious deterioration of fish, but Petrushevski did not provide details. Petrushevski and Shulman (1961) reported that coregonine hearts infected with *Ichthyocotylurus* sp. showed noted reductions in condition, but further details were not provided. Vankara and Chikkam (2013) found pathological changes associated with *Ichthyocotylurus* metacercariae infecting the heart, which might have reduced the cardiac efficiency of *C. lavaretus*. Metacercariae of *I. erraticus* were reported in the hearts of Least Cisco, Broad Whitefish (*C. nasus*), and *C. clupeaformis* in the western Arctic (Stewart and Bernier 1999). Bauer (1970) reported only one larval trematode (*I. erraticus*) in Russian coregonines.

Monogeneans

Adult monogeneans are usually less than 1 cm in length, and they are seldom observed infesting fish. The term infested used here follows the parasitological definition of occurring on the outer surface or gills. Monogeneans were reported infrequently in coregonines from the Great Lakes, with only *Discocotyle sagittata* and *Tetronchus variabilis* being found. *Discocotyle sagittata* is a common and characteristic parasite of coregonines and salmonines from the Great Lakes. It is considered a pathogen for adult coregonines and, more particularly, for young fish from Lake Huron (Dechtiar et al. 1988). *Discocotyle sagittata* causes serious gill damage due to its attachment and feeding resulting in increased mucus production, epithelial hyperplasia, loss of lamellar structure, clubbing of gill filaments, hemorrhage, and increases in secondary infections (Roberts 1978; Williams and Jones 1994). Although the specific pathology of *T. variabilis* toward coregonines is not known, Razmashkin and Kashkovskii (1977) reported that *T. alaskensis* caused gill necrosis, provided portals of entry for secondary bacterial infections, and caused mortality of *Coregonus* spp. at intensities of 1,500 to 2,000 worms per fish in Russia.

DeGiusti (1965) reported monogeneans in the family Octocotylidae on the gills of *Coregonus hoyi* from Lake Michigan (Table 9). Bychowsky (1961) listed the monogenean family Octocotylidae that included several genera, including *Octobothrium*. Price (1943) indicated that *Octobothrium* is a synonym of *Discocotyle*, and implied *Octobothrium sagittata* is a synonym of *Discocotyle sagittata*. Therefore, we suspect that the monogeneans infesting *C. hoyi* from Lake Michigan found by DeGiusti (1965) were *D. sagittata*.

Cestodes

Most adult cestodes are white segmented ribbon-like worms, and they vary in length. They are common parasites occurring in the digestive tract of coregonines from the Great Lakes, with a total of 14 cestode species reported.

Faisal et al. (2011a) discussed *Bothriocephalus* sp. infecting *Coregonus clupeaformis* from Lakes Huron and Michigan but, in their Table III, data for multiple *Bothriocephalus* were presented. Therefore, we are not sure if data were presented for one or more species. Cross (1938) found that cestodes, primarily *Proteocephalus exiguus*, were the most common parasites by percentage in *C. artedi* from four Wisconsin lakes. Bauer (1970) reported a total of seven cestode species in Russian coregonines.

Dechtiar and Lawrie (1988) reported that *Proteocephalus longicollis* (= *P. laruei*), *Eubothrium salvelini*, *Cyathocephalus truncatus*, and plerocercoids of *Triaenophorus crassus* might cause diseases in Lake Superior coregonines. Furthermore, the adult cestodes that might cause diseases in Lake Ontario coregonines were *Proteocephalus* spp. in *Coregonus clupeaformis* and *C. artedi*, and *Cyathocephalus truncatus* in *Coregonus clupeaformis* (see Dechtiar and Christie 1988). Although we did not find support for the above statements in these articles, we surmise the comments are based on the results of other studies. Individuals of *Proteocephalus* spp. are common parasites of coregonines and can occur in the hundreds. Individuals of *Proteocephalus laruei* and *P. exiguus* may be responsible for mortality of young-of-the-year and yearling coregonines (Numann 1972). Adults of *Proteocephalus* can grow to more than 15 cm in length (PMM, personal observation, 2003).

Hanzelova and Scholz (1999) reviewed the taxonomy of *Proteocephalus* tapeworms of North America coregonines and salmonines and considered *Proteocephalus pusillus*, *P. exiguus*, *P. laruei*, *P. obtundus* (nomen nudum), *P. arcticus*, *P. wickliffi*, *P. parallacticus*, *P. californicus*, *P. salmonidicola*, and *P. primaverus* as junior synonyms of *P. longicollis*. Therefore, the reports of *P. exiguus*, *P. laruei*, and *P. wickliffi* infecting Great Lakes coregonines should be changed to *P. longicollis*. However, the synonyms of *P. longicollis* (*exiguus*, *laruei*, *wickliffi*) were considered separate species in articles published by several respected parasitologists before the review of Hanzelova and Scholz (1999). The only other report of *P. wickliffi* infecting a fish is that of Meyer (1954), who found it in *Coregonus clupeaformis* from Maine. We assume these earlier parasitologists used a variety of valid characteristics to separate these species. Furthermore, Olds (2012) identified cestodes in *C. clupeaformis*, *C. hoyi*, and *P. cylindraceum* as *P. exiguus*.

Cyathocephalus truncatus is a common parasite of coregonines throughout its distribution. It was first reported in North America by Linton (1898), infecting *Coregonus clupeaformis* from Lake Superior, and it commonly infects coregonines from across the Great Lakes. Adults can be up to 4 cm in length, have a bell-shaped scolex, and are found usually in the pyloric caecae. A few individuals of *Cyathocephalus truncatus* caused severe inflammation and rupture of the gut wall of coregonines and salmonines, leading to death of the host (Vik 1954, 1958). In large numbers, *C. truncatus* may obstruct the intestinal lumen and damage the walls (Lawler 1970).

Eubothrium crassum infrequently infected only *Coregonus artedi* from Lakes Superior and Huron while *E. salvelini* commonly infected *C. artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* from one or more of the Great Lakes, except Lake Ontario. Individuals of *E. salvelini* may reach lengths of 20 cm (PMM, personal observation, 1988). Smith and Margolis (1970) reported that *E. salvelini* may cause pathology of fish. Boyce (1979) found that *E. salvelini* had a deleterious effect on growth, survival, and swimming performance of Sockeye Salmon (*Oncorhynchus nerka*), which is in Salmonidae.

Of the larval cestodes reported in Great Lakes coregonines, species in the genera *Diphyllobothrium* and *Triaenophorus* deserve some comments. Individuals of *Diphyllobothrium* have two sucking grooves (bothria) on their anterior end called a scolex, they are long-lived, and they can accumulate as fish mature. Plerocercoids of *Diphyllobothrium ditremum*, *D. laruei*, *D. oblongatum*, and *Diphyllobothrium* spp. infected *Coregonus artedi*, *C. clupeaformis*, and *C. hoyi* from the Great Lakes. *Diphyllobothrium* infections may reduce fish growth, are pathogenic, and can be a direct cause of death (Duguid and Sheppard 1944; Hoffman and Dunbar 1961; Vik 1965; Dechtiar and Christie 1988).

Individuals of *Triaenophorus* have four small hooks on the scolex, occur in cysts of various shapes and sizes, and can reach a few centimeters in length in fish. Plerocercoids of *Triaenophorus crassus* were found commonly in *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* from the Great Lakes. These plerocercoids can cause considerable damage as they move through the stomach and intestinal walls to the viscera and muscle. The *Triaenophorus* sp. cysts in fish are white in color and can lower the value of the flesh. Miller (1952) suggested that *T. crassus* can cause reduced growth in *C. clupeaformis*. Furthermore, Miller (1952) reported that coregonine products from Canada infected with *T. crassus* were rejected by U.S. markets. Davydov (1981) reported that plerocercoids of *T. crassus* moving in *Coregonus* sp. caused muscle tissue to be reduced to a homogenous mass. Stewart and Bernier (1999) found *T. crassus* in the meat of *C. clupeaformis*; fish markets paid less for infected fish than uninfected fish since the larvae had to be removed. The occurrence of plerocercoids in the flesh of coregonines makes their presence aesthetically objectionable (Reichenbach-Klinke 1973), but there is no human health issue if fish are fully cooked. In other non-coregonines, the adults of *T. crassus* mature in the intestine of Northern Pike (*Esox lucius)* and Muskellunge (*E. masquinongy*). Several studies, including Miller (1945a, b) and Lawler (1970), were conducted on a variety of topics involving *T. crassus* in Canada.

Nematodes

Adult nematodes are worms that are usually transparent or white in color, unsegmented, and long and thin that vary in length, and are found usually in the digestive tract. Adults of *Pseudocapillaria salvelini*, *Sterliadochona ephemeridarum*, and *Spinitectus gracilis* were infrequent parasites of coregonines from the Great Lakes. Larvae or immature individuals of *Raphidascaris acus* and *Philometra* sp. are also infrequent parasites of coregonines from the Great Lakes. Individuals of *R. acus* encyst on the stomach, pyloric caeca, liver, and other viscera of several intermediate host fish species. In large numbers, larvae may cause extensive damage by forming lesions and nodules in the liver and viscera of *Coregonus clupeaformis* (see Dick and Choudhury 1995). Definitive hosts of *R. acus* are Northern Pike and other piscivorous fish. Although the species of *Philometra* found in *C. artedi*, *C. clupeaformis*, and *Prosopium cylindraceum* from the Great Lakes is unknown, Allison (1966) and Crites (1982) reported that adults of *Philometra cylindracea* occurring in the body cavity might have played a role in reduced growth and high mortality of Yellow Perch (*Perca flavescens*) (the normal host of *Philometra cylindracea*) in Lake Erie.

Adults of *Cystidicola farionis* occur in the swimbladder after traveling through the pneumatic duct of physostomous fish. These adults are 50 mm in length or larger and are usually translucent or white in color. *Cystidicola farionis* is the most common nematode parasite of coregonines from the Great Lakes because amphipods are common food items of coregonids, and larval *C. farionis* is a parasite of amphipods. Female worms produce eggs that eventually reach the water and are ingested by a variety of crustacean intermediate hosts, such as the amphipods *Gammarus fasciatus*, *Hyalella azteca*, *Diporeia* spp., and opossum shrimp (*Mysis diluviana*) (see Smith and Lankester 1979). In crustaceans, juvenile worms develop and become infective to fish. When infected crustaceans are eaten by a suitable fish, the larvae are freed and move to the swimbladder where they mature and produce eggs. Warren (1952) found 72% of 200 *Coregonus artedi* examined from Lake Superior infected with *Cystidicola farionis*, which he called *C. stigmatura*. It has been suggested that in other non-coregonines such as larger adult Lake Trout (*Salvelinus namaycush*) that do not feed on infected crustaceans, heavy infections occur by consuming smaller fish that had eaten infected crustaceans with infective juvenile worms in their digestive tracts. *Cystidicola farionis* infecting the swimbladder of *Coregonus artedi* caused inflammation, lesions, enlargement and atrophy of the epithelium, and the presence of histiocytes and granular cells (Willers et al. 1991). Faisal et al. (2010) reported that swimbladders of *C. clupeaformis* infected with large numbers of *Cystidicola farionis* had thickened walls with deteriorated linings. In other non-coregonines, Black (1984) found swimbladder lesions in Lake Trout and suggested they may have been caused by *C. stigmatura*.

Why *Cystidicola farionis* was the only nematode found in *Coregonus hoyi* from the Great Lakes is unknown. Nematodes are not common in coregonines compared to some other parasite groups in coregonines from the Great Lakes. Also, Cross (1938) did not report nematodes infecting *C. artedi* in four Wisconsin lakes, although he found nematodes commonly infecting several other non-coregonine fish species in these lakes. On the other hand, Lawler (1970) reported that nematodes made up a common group of parasites in coregonines from North America. However, some of the species listed are synonyms, and some species do not mature in coregonine fishes. Lawler did not indicate if some of these parasites are infrequent, so this list should be treated with caution.

Black (1983) reported that since 1925 *Cystidicola stigmatura* was apparently absent from coregonines in the Great Lakes. Therefore, the records of *C. stigmatura* in coregonines from the Great Lakes may be erroneous since *Salvelinus* spp. are the only known host species of *C. stigmatura* in North America (Black 1983). Furthermore, we surmise that Black (1983) believed that all reports of *C. stigmatura* in coregonines from the Great Lakes should be *C. farionis*.

Acanthocephalans

Allison et al. (1977) reported that coregonines and many other fish species in the Great Lakes are commonly infected with acanthocephalans, primarily in the genera *Echinorhynchus* and *Neoechinorhynchus*. They attach in the pyloric caecae and to the intestinal wall by embedding their anterior end, called the proboscis, which has hooks on it. Individuals of the genus *Echinorhynchus* have an elongate proboscis, and adults vary in length from approximately 4 mm to more than 20 mm. *Echinorhynchus salmonis* is one of the most common intestinal helminth species, if not the most common, in coregonines and salmonines from the Great Lakes. *Echinorhynchus salmonis* is known to cause damage to the mucosa of the posterior portion of the intestine in *Coregonus artedi*, resulting in inflammation and interference with digestion and absorption (Dechtiar and Christie 1988). Bauer and Nikolskaya (1957) reported that *C. lavaretus ludoga* infected with *E. salmonis* exhibited acute inflammation of the intestinal wall, resulting in reduced growth. Lawler (1970) reported that, in small coregonines such as *C. albula*, even a small number of *E. salmonis* can produce hyperaemia of the intestine. Furthermore, he reported that as intensities became high, the proboscides of *E. salmonis* caused marked changes in intestinal tissues and muscle layers that resulted in fish producing a copious amount of mucus and, in some infections, perforation of the intestinal wall. Watson and Dick (1979) found that *E. salmonis* was most common in *C. clupeaformis* from southern Indian Lake, Manitoba, Canada, in late autumn when the amphipod intermediate host was a prominent food item, which demonstrates the importance of the dynamics of the host-intermediate host-parasite relationships to parasite intensities.

Individuals of the genus *Neoechinorhynchus* have a small globular proboscis, and, in general, adults vary in length from approximately 1 mm to 15 mm, depending on the species. *Neoechinorhynchus tumidus* was the most common species of the genus found in *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* from the Great Lakes. Taraschewski (1989) found tissue inflammation associated with the attachment site of *N. rutili* infecting salmonines. In other non-coregonines, Amin and Heckmann (1992) reported that *N. idahoensis* caused limited host response with epithelial damage and hemorrhaging at the area of proboscis attachment in the Bridgelip Sucker (*Catostomus columbianus*). Additionally, the lumen of the host intestine was obstructed by the worms whose posterior ends caused localized inflammation of the intestinal epithelial cells. Cross (1934) reported that the numbers of *Neoechinorhynchus* sp. and the cestode *Proteocephalus longicollis* (= *P. exiguus*) in *Coregonus artedi* showed an inverse relationship in numbers to each other; he believed that nonspecific immunity limits either *Neoechinorhynchus* sp. or *P. exiguus*. Although some authors cited this study as a case of nonspecific immunity between two intestinal helminth species, individuals of these two helminth species occupy different sites in the intestine. Also, we are not aware of any laboratory studies that supported the nonspecific immunity of these specific helminth species, as suggested by Cross (1934).

Leeches

Parasitic leeches are blood-sucking invertebrates that are segmented, have a sucker at each end of their bodies, and usually attach to the surface of the fish or buccal cavity. Only two species of leeches, *Piscicola milneri* and *P. punctata*, were reported in coregonines from the Great Lakes, and they infested only *Coregonus clupeaformis* from Lake Michigan. Given the general deep-water and offshore habitats of coregonines, the infrequency of leeches on coregonines is not surprising. Individuals of *Piscicola* are approximately 3 cm in length. Depending on the size and number of leeches, they can take a large amount of blood that weakens fish and forms a wound that might become infected with bacteria or fungi. Heavy infestations of leeches may cause extensive inflammation, muscle-tissue necrosis, edema, and buccal ulcerations at the attachment sites (Faisal at al. 2011b; Schulz et al. 2011).

Copepods

There are more than 1,000 species of ectoparasitic and endoparasitic copepods. The bodies of adults are highly modified with various antennae and appendages used for attachment. Many species produce egg sacs. Copepods can affect the health and value of infested fish. In some infections, the wounds that copepods form at the site of attachment promote secondary bacterial and fungal infections that may kill fish. *Achtheres pimelodi*, *Achtheres* sp., *Argulus* sp., *Ergasilus caeruleus*, *E. nerkae*, and *Ergasilus* sp. are infrequent parasites of coregonines from the Great Lakes. Larval stages and adults of *Achtheres* may kill fish by severely damaging gills, causing hyperplasia, and increasing respiration rates, which might contribute to summer fish kills during periods of high temperatures and low oxygen concentrations (Warren 1981; Stepanova and Vjuskova 1985; Shahady et al. 2007). *Argulus coregoni* infests the Common or European Whitefish in central Europe (Reichenbach-Klinke 1973).

In heavy infestations, *Ergasilus* spp. might cause mechanical damage when attached to gills, fins, and other areas producing hemorrhaging and epithelial hyperplasia (Kabata 1970; Dechtiar and Lawrie 1988). Kozikowska (1975) reported that, in heavy infections of whitefish, *Ergasilus sieboldi* attaches not only to gill filaments but also to fins. *Ergasilus sieboldi* feeds on gill epithelial cells and, to a greater extent, on blood (Einszporn 1965a, b). Infection of the Peled Whitefish (*Coregonus peled*) with *E. sieboldi* was associated with reduced weight, growth, and condition factor and increased water content (Abrosov and Bauer 1959). Lawler (1970) reported that *E. sieboldi* damaged the tissues of the gills, which disrupted respiration and caused a general deterioration of the fish. *Ergasilus sieboldi* was documented to infect many species of fish in several areas of the world, including *Coregonus* spp. in Russia (Lester and Roubal 1995).

Individuals of the genus *Salmincola* have a circumpolar distribution and the species commonly infects coregonines. Adults attach to fish using a large, circular anchor called a bulla, which may be difficult to completely detach. Three species of *Salmincola* were found on coregonines from the Great Lakes. *Salmincola corpulentus* was common on *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum*. *Salmincola extensus* infested *C. artedi*, *C. clupeaformis*, and *C. hoyi*. *Salmincola thymalli* was only reported in *C. hoyi* and *P. cylindraceum*. *Salmincola* sp. was reported on coregonines in 11 studies from the Great Lakes. Dechtiar and Lawrie (1988) reported that species of both *Salmincola* and *Ergasilus* produce mechanical damage due to the attachment mechanisms so that hemorrhage and epithelial hyperplasia occur in heavy infections of coregonines. These parasites are of the highest epizootilogical importance because of the pathology they cause (Kabata 1970).

In general, when the intensities of parasites increase in or on coregonines and other fish species and the pathology they cause becomes worse, death of more heavily infected fish may occur, particularly young fish. Death could be caused either directly from heavy infections or indirectly through the loss of host vitality and secondary infections. To date, however, we are not familiar with any epizootics of coregonines from the Great Lakes directly attributable to parasites.

Coregonine Parasites of Possible Public Health Concern

None of the mastigophorans, ciliophorans, myxozoans, adult trematodes, cestodes, monogeneans, nematodes, acanthocephalans, leeches, and copepods found on or in coregonines from the Great Lakes area are believed to be very harmful to humans. There are two reports dated 1833 and 1907 of metacercariae of *Diplostomum spathaceum* infecting the eye lens of humans without any further details provided (Ashton et al. 1969). It is not known if other species of *Diplostomum*, *Ichthyocotylurus erraticus*, or other species of *Ichthyocotylurus* can infect humans. Also, since the eyes (*Diplostomum* infection site) and viscera (*I. erraticus* infection site) of coregonines are not usually eaten, metacercariae of these species are not acquired by humans. *Diplostomum* spp. and *Ichthyocotylurus* spp. use piscivorous birds as definitive hosts.

Of the larval cestodes with human health implications found in Great Lakes coregonines, the genus *Diphyllobothrium* deserves comments. Plerocercoids (approximately 1 cm long or larger) of *Diphyllobothrium* can be found unencysted or encysted coiled up in the musculature, in the viscera, outside the stomach wall, and on the walls of the body cavity. They can be seen as white masses in uncooked fish, but, when the flesh is cooked, some worms may not be noticed. Endotherms become infected by eating raw or poorly cooked fish infected with plerocercoids. *Diphyllobothrium ditremum* and *D. oblongatum* obtain maturity in piscivorous birds, and *D. laruei* reaches maturity in dogs and cats. *Diphyllobothrium* spp. were reported in Great Lakes coregonines in several studies. *Diphyllobothrium latum*, which was reported to infect humans in the upper Great Lakes region some time ago (Nickerson 1906; Vergeer 1928; Porter 1978), has not been reported in coregonines from the Great Lakes area. Plerocercoids of *Diphyllobothrium* can be killed by thorough cooking or freezing the muscle to -2° C. It is not known if smoking of the fish kills the plerocercoids of *Diphyllobothrium*. Scholz et al. (2009) updated information about the genus *Diphyllobothrium*, including species diversity, distribution, epidemiology, and disease distribution.

The effect of parasites on the value of coregonines might be greater than their effect on human health. Parasites can reduce the value of fish to commercial fisheries by damaging the skin, infecting the meat, or spoiling the condition or flavor of the flesh. People will not buy or eat fish with visible evidence of infection, even though most parasites will not infect people when the fish is cooked. These infected fish are often wasted or fed to domestic animals in some areas of the world. Raw fish that may harbor parasites, including *Diphyllobothrium*, is used as dog food for working dogs in the northern U.S. and Canada. Fish parasite larvae were documented to develop into adults in dogs; such infections seldom kill dogs but reduce their energy levels. Dogs can be treated regularly for parasites by their owners.

Coregonine Species and Their Parasites

Most studies of the parasites of coregonines in certain areas of the Great Lakes involve specific individuals (e.g., A.O. Dechtiar, M. Faisal, T.P. Loch, P.M. Muzzall, and their respective colleagues) associated with a few academic institutions or state/province fishery agencies (e.g., the U.S. Geological Survey's Great Lakes Science Center). The lack of parasitological studies of coregonines throughout the Great Lakes leaves fisheries managers generally uninformed about potential coregonine parasites in the lakes and the role of these parasites in affecting population dynamics and the health of coregonines (Brenden et al. 2010a). Furthermore, many of the studies were not initiated by some pressing or continuous issue involving coregonine biology, parasites, or pathology, except for the special issues of the Journal of Great Lakes Research on the health of Lake Whitefish (Brenden et al. 2010b). Brenden et al. (2010a) specifically pointed out the need for expanded sampling and targeted survey designs to understand the role of pathogens in *Coregonus clupeaformis* population dynamics. The small number of parasitological studies of coregonines from the Great Lakes is not surprising since there are few fish parasitologists employed by fishery agencies and academic institutions. Furthermore, there is a lack of funding to support parasitological and epidemiological studies of fish unless epizootics are observed (Holey et al. 1998; Riley et al. 2008).

The total number of reported parasite species was highest in *Coregonus clupeaformis* (38) and *C. artedi* (35) from the Great Lakes. Individuals of *C. clupeaformis* were examined from all Great Lakes and Lake St. Clair, with most parasitological studies conducted in Lake Huron followed by Lake Michigan. Individuals of *C. artedi* were examined from all Great Lakes, the St. Marys River, and Lake St. Clair. Most studies of *C. artedi* occurred in Lake Superior followed by Lakes Huron and Michigan. Many more individuals of *C. clupeaformis* followed by *C. artedi* and *C. hoyi* were examined for parasites than individuals of the other coregonine species from the Great Lakes (Table 2).

Although more individuals of *Coregonus hoyi* were examined than *Prosopium cylindraceum*, the same number of parasite species (26 each) was reported in these two species from the Great Lakes. Most parasitological studies of *C. hoyi* occurred in Lake Michigan followed by Lakes Superior and Huron. No individuals of *C. hoyi* were examined for parasites in Lake Erie, and only four fish were examined for parasites in Lake Ontario.

Most individuals of *P. cylindraceum* were examined for parasites from Lake Huron followed by Lakes Superior and Michigan. Only one study was published about the parasites of *P. cylindraceum* from both Lake Michigan and the St. Marys River. Individuals of *P. cylindraceum* were not examined for parasites in Lakes Erie and Ontario.

The number of parasite species found in each of *Coregonus kiyi*, *C. nigripinnis*, *C. reighardi*, *C. zenithicus*, and *Prosopium coulteri* from the Great Lakes was low. Only two parasite species were reported in *C. kiyi* from Lakes Superior and Michigan, two species from Lake Huron, and three species from Lake Ontario. Only 76 individuals of *C. kiyi* were examined for parasites in Lakes Superior, Huron, Michigan, and Ontario. No individuals were examined from Lake Erie as *C. kiyi* was not known to inhabit that lake (Eshenroder et al. 2016). Three parasite species were reported in *C. nigripinnis* from Lakes Huron and Michigan, with only 26 individuals examined for parasites based on reported studies. Individuals of *C. nigripinnis* have not been examined for parasites from Lake Superior, and they were not known to inhabit Lakes Erie and Ontario (Eshenroder et al. 2016). The last published articles about the parasites of *C. kiyi* and *C. nigripinnis* were in 1942. The number of parasite species reported in *C. reighardi* is low—three species infected it from Lake Ontario, and one species infested it from Lake Huron. Only three parasite species were reported in more than 25 individuals of *C. zenithicus* from Lake Superior. *Coregonus zenithicus* has not been examined for parasites in the other Great Lakes because it is found currently only in Lake Superior (Table 2). A total of 35 individuals of *P. coulteri* was examined for parasites from Lake Superior, with only one species found, likely because this species exists only in Lake Superior. Only one species was found in *C. prognathus* examined from Lake Michigan when it was considered a valid species.

Although fewer parasite species were reported in *Coregonus alpenae*, *C. johannae*, *C. kiyi*, *C. nigripinnis*, *C. reighardi*, *C. zenithicus*, and *Prosopium coulteri* compared to *C. artedi*, *C. clupeaformis*, *C. hoyi*, and *P. cylindraceum* from the Great Lakes, this does not mean they have fewer parasites. This information reflects that few parasitological studies were conducted on these species, and fewer individuals of them were examined in total. Possible reasons for the infrequency and lack of parasitological studies of *C. alpenae*, *C. johannae*, *C. kiyi*, *C. nigripinnis*, *C. reighardi*, *C. zenithicus,* and *P. coulteri* are

1. Some species rarely or never occurred in one or more of the Great Lakes
2. All of these species, except *P. coulteri*, were extirpated early in some lakes (Eshenroder et al. 2016)
3. Individuals of these fish species are not that common in one or more of the lakes
4. Some species are difficult to identify

Only 12 studies (LaRue 1911, 1914; Pearse 1924; Vergeer 1928, 1942; Skinker 1930, 1931; Pritchard 1931; Klick 1946; Bangham 1955; Swanson and Pratt 1977; Dextrase 1987) reported parasites infecting these fish species, with the most recent report more than 30 years old. For the coregonine species that have had few individuals examined for parasites, extensive collections archived at the University of Michigan Museum of Zoology can be examined to obtain more information about their parasites.

There are many examples of a parasite genus or species that infected a coregonine species only once or twice in one or more Great Lakes. Some parasitologists call these accidental parasites. This term can have at least two meanings, as suggested by Bush et al. (2001), because the parasite is infrequent in its occurrence and does not mature in the host of interest or the parasite is rare in its occurrence in the host relative to other species in the parasite community and does reach maturity. There has been discussion beyond the scope of this document on why the term accidental parasite should not be used, and infrequent parasite is a better term to use. Infrequent parasites may also occur in an accidental or dead-end host. Generally, this type of host does not allow transmission of the parasite to the definitive host, thereby preventing the parasite from completing its development and maturity. In addition, infrequent parasites establish themselves in hosts they do not parasitize normally.

There are several infrequent parasites reported for coregonines from the Great Lakes, including

1. *Coregonus artedi*: *Clinostomum marginatum*, *Eubothrium crassum*, *Proteocephalus ambloplitis*, rhyncobothrid plerocercoid, *Sterliadochona ephemeridarum*, *Neoechinorhynchus crassus*, *N. cylindratus*
2. *Coregonus clupeaformis*: *Schistocephalus* sp., *Philometra* sp., *Raphidascaris acus*, *Pomphorhynchus bulbocolli*, unidentified glochidium
3. *Coregonus hoyi*: Bothriocephalid plerocercoids, *Echinorhynchus lateralis*, *E. leidyi*, *Achtheres* sp., *Salmincola thymalli*
4. *Prosopium cylindraceum*: *Pseudocapillaria salvelini*, *Spinitectus gracilis*, *Philometra* sp., *Pomphorhynchus bulbocolli*, *Ergasilus nerkae*

Possible reasons for the occurrence of infrequent parasites in coregonines include

1. Parasites were acquired when an intermediate host was eaten that is not normally in the coregonine's diet
2. Common and infrequent parasites used the same intermediate host eaten by the coregonine
3. Some parasites were poor colonizers in certain fish species
4. The host occurred infrequently in the habitat where the parasite occurred
5. The normal definitive host did not associate frequently with coregonines
6. Parasites of a species were not normally distributed in the host population
7. Some parasite species were seasonal in their occurrence, and coregonines only occasionally came into contact with them
8. A tissue/organ looked different, so the investigator examined only that fish and found a parasite
9. Coregonines moved seasonally into tributaries and came into contact with infrequent parasites and their hosts

Some parasite genera and species were reported in coregonines from the Great Lakes in early studies, and since then they have not been reported. For example, *Eubothrium crassum* was reported in *Coregonus artedi* from Lakes Superior and Huron in three studies published before 1956; *Proteocephalus wickliffi* infected only *C. artedi* from Lake Erie in 1939 or before; bothriocephalid plerocercoids were reported in coregonines before 1932; and plerocercoids of *Diphyllobothrium ditremum*, *D. laruei*, and *D. oblongatum* were found in coregonines in 1969 or before. It is interesting that all of these examples involved cestodes. Possible reasons for the inconsistent identification of some parasites in coregonines are

1. Investigators believed they could identify plerocercoids of *Diphyllobothrium* to species in 1969 or earlier, but, after 1969, investigators did not attempt to identify or could not identify plerocercoids to species
2. Misidentifications occurred
3. Sites where plerocercoids infected coregonines were not examined by some investigators
4. Only a few coregonines were examined from Lake Erie after 1939
5. The low number of coregonines sampled did not provide a sample size large enough to detect infrequent parasites

We found the following general six relationships between coregonine species and their parasite species in the Great Lakes

1. More individuals of *Coregonus artedi* and *C. clupeaformis* are examined for parasites than other coregonine species
2. More parasite species are found as the number of parasitological studies, the number of each coregonine species, and the number of Great Lakes examined are increased
3. The presence or absence of a coregonine species in a Great Lake plays a role in the number of parasite species found
4. Cestodes and acanthocephalans are common parasites of coregonines
5. Most parasitological studies are 30+ years old, with few studies conducted after 2000
6. Most areas of the Great Lakes have no information about parasites in coregonines

Sparse information was generated about parasites of age-0 and age-1 coregonines from the Great Lakes. Hart (1931a) reported that one young *Coregonus clupeaformis* had individuals of *Proteocephalus* sp. in its stomach, and a glochidium was found on a fry of *C. clupeaformis* from Lake Huron. Four young *C. clupeaformis* examined by Dechtiar (1972a) from Lake Erie were infected with *Diplostomum flexicaudum*, *Echinorhynchus salmonis*, *Neoechinorhynchus tumidus*, and *Achtheres pimelodi*. We examined age-0 and age-1 coregonines and found *Proteocephalus* sp. in *C. artedi* from Lake Michigan; *Proteocephalus* sp., *E. salmonis*, and *Salmincola* sp. in *C. artedi* from Lake Superior; *Crepidostomum farionis*, *Bothriocephalus* sp., *Cyathocephalus truncatus*, *Proteocephalus* sp., *Cystidicola* sp., *E. salmonis*, *N. tumidus*, *Neoechinorhynchus* sp., and *Salmincola* sp. in *C. clupeaformis* from Lake Superior; *Proteocephalus* sp. in *C. clupeaformis* from Lake Michigan; *Neoechinorhynchus* sp. in *C. clupeaformis* from Lake St. Clair; and *Bothriocephalus* sp., *Proteocephalus* sp., *Cystidicola* sp., and *E. lateralis* in *C. hoyi* from Lake Superior (PMM, unpublished data). The hearts of young *C. clupeaformis* from Lake Erie were infected with *Ichthyocotylurus erraticus* (PMM, unpublished data). Available evidence indicates that Great Lakes coregonines acquire parasites and develop a parasite community at a young age, but more information is needed to confirm this observation. The effects on survival and abundance of this early acquisition of a parasite community on coregonines are also unknown at this time but should be examined to understand the role of parasites in recruitment of Great Lakes coregonines.

Individuals of *Coregonus artedi*, *C. clupeaformis*, and *Prosopium cylindraceum* were introduced and established in many locations across North America (Morris et al. 1974; Whitworth 1996; Power and Ryckman 1998; WDFW 2011; Montana FWP 2012). However, we have not found any publications about the parasites of transplanted coregonines in North America and, therefore, cannot make any comparisons about the parasite faunas of endemic and transplanted coregonines. However, Lawler (1970) presented Russian data on this topic involving *C. lavaretus ladoga*, *C. baeri ladoga*, and *C. albula ladogensis* that he assembled from information in Petrushevski (1958). Although a time frame was not mentioned, Lawler (1970) reported individuals of all subspecies had fewer parasite species in their new environment compared to individuals in their original environment.

Parasite Host Specificity

The presence of parasite species in hosts is determined by many factors, including the level of host specificity of the parasites, the habitat occupied by the hosts, and the ecological conditions that influence the possibility of infection directly or by eating a variety of intermediate and paratenic hosts. Some parasite species infect and mature in only a single host fish species or other species of the same family, exhibiting high host specificity; they are considered specialists. Other parasites are generalists that infect and mature in many host species in many families and exhibit low host specificity. Host specificity reflects the historical evolutionary associations with its host(s) along with the resources needed and used by their parasites.

In general, the parasites of coregonines from the Great Lakes can be divided into two groups. The first group is made up of those parasites specific (specialists) to coregonines and other Salmonidae species. These parasite specialists are found in seven taxonomic groups

1. Myxozoa: *Henneguya zschokkei*
2. Digenea: Adult: *Phyllodistomum coregoni*
   Larval/Immature: *Ichthyocotylurus erraticus*
3. Monogenea: *Discocotyle sagittata*, *Tetraonchus variabilis*
4. Cestoda: Adult: *Eubothrium salvelini*, *Proteocephalus longicollis*
   Larval: *Diphyllobothrium ditremum*, *D. laruei*
5. Nematoda: Adult: *Pseudocapillaria salvelini*, *Cystidicola farionis*
6. Acanthocephala: *Echinorhynchus leidyi*, *Neoechinorhynchus tumidus*
7. Copepoda: *Salmincola corpulentus*, *S. extensus*, *S. thymalli*

In other non-coregonines, Wilson (1908) reported that *Salmincola extensus* also infested Northern Pike. The acanthocephalan species were reported as specialists, although they were reported in a few other fish species, because it is not known if gravid females were found in these fish. Bauer (1970) reported that the parasite faunas of coregonines in Russia consisted of several dozen species, about 30 of which were specific to coregonines and salmonines.

The second category of coregonine parasite species involves generalists, which are not Salmonidae specific. They also occur and might mature in a variety of fish species in other families. This group involves four taxonomic groups

1. Digenea: Adult: *Crepidostomum farionis*
   Larval/Immature: *Diplostomum spathaceum*
2. Cestoda: Adult: *Cyathocephalus truncatus*
3. Acanthocephala: *Echinorhynchus lateralis*, *E. salmonis*
4. Copepoda: *Ergasilus caeruleus*, *E. nerkae*

Therefore, the parasite faunas of *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* from the Great Lakes are made up of both specialist and generalist parasites.

Coregonine Diet and Acquiring Parasites

The diets of *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* differ depending on the life-cycle stage being studied, due likely to the habitat used by each species throughout its life history. However, these four coregonines feed on a variety of similar food items, including cladocerans, copepods, amphipods, *Diporeia* spp., *Mysis diluviana*, aquatic insect larvae (i.e., caddisflies, mayflies, chironomids), molluscs, dreissenid mussels (*Dreissena polymorpha*, *D. bugensis*), small fish, and fish eggs (Scott and Crossman 1973; Pothoven and Madenjian 2008; Claramunt et al. 2010; Madenjian et al. 2010; Pothoven and Madenjian 2013). Most of these food items serve as intermediate hosts for a variety of parasite species.

Information about the life cycles of parasites and their intermediate hosts infecting coregonines from the Great Lakes is shown in Table 26. Some species of *Cryptobia* are transmitted to fish by leeches, and these same species, as well as others, can be transmitted directly to fish. *Epistylis* sp., *Trichodina* sp., monogeneans, leeches, and copepods have direct life cycles and *Raphidascaris acus* might have a direct life cycle. Coregonines become infected with myxozoans by eating infected aquatic oligochaetes or by penetration directly by free-swimming life stages. All digenean species found use a mollusc, usually snails, in their life cycles as the first intermediate host. Larval digeneans infect fish when cercariae leave the mollusc, directly penetrate the fish, and develop into metacercariae. Coregonines become infected with adult digeneans by eating a variety of aquatic insects such as larvae and adults of Ephemopterans and other invertebrates. Of the cestodes, *Cyathocephalus truncatus* uses amphipods and opossum shrimp as intermediate hosts. Coregonines become infected with all of the remaining adult and larval/immature cestodes by eating infected copepods. *Pseudocapillaria salvelini* is believed to have a direct life cycle or an indirect life cycle using aquatic oligochaetes as intermediate hosts. *Cystidicola farionis* and *Pomphorhynchus bulbocolli* use amphipods as intermediate hosts. *Sterliadochona ephemeridarum* and *Spinitectus gracilis* use Ephemopterans and other invertebrates as intermediate hosts. *Philometra* sp. and *Raphidascaris acus* use a variety of invertebrates (Dipterans, dragonfly and caddisfly larvae, cladocerans) as intermediate hosts. *Acanthocephalus dirus* uses isopods, species of *Echinorhynchus* use amphipods, and species of *Neoechinorhynchus* use copepods or ostracods as intermediate hosts. *Camallanus oxycephalus* also uses copepods. *Dichelyne cotylophora* and *C. oxycephalus* might also use prey fish as intermediate hosts. It is not known how many parasite species infecting coregonines from the Great Lakes use paratenic hosts in their life cycles, and the importance of paratenic hosts and post-cyclical transmission in coregonines is currently unknown. A paratenic host is an animal that a parasite occurs in. However, the parasite does not undergo any development necessary to infect the next organism in its life cycle. A paratenic host is often a bridge from the intermediate to the definitive host. Post-cyclical transmission occurs when individuals of a helminth species attached in the intestine of one animal are eaten by another one, such as a predator, and these worms attach and survive in the predator.

Table 26. Life cycles of parasites of coregonines from the Great Lakes and how they acquire these parasites. Helminths with an * are autogenic, and those without an * are allogenic.

Life Cycle and Means of Infection	Parasite Group	Parasite
Direct life cycle	Mastigophorans, ciliophorans	*Cryptobia* sp. (some species are transmitted by leeches), *Epistylis* sp., *Trichodina* sp.
	Monogeneans	*Discocotyle sagittata*, *Tetraonchus variabilis*, Octocotylidae
	Nematodes	*Pseudocapillaria salvelini**, *Raphidascaris acus**
	Leeches	*Piscicola milneri*, *Piscicola punctata*, unidentified leech

Life Cycle and Means of Infection	Parasite Group	Parasite
	Copepods	*Achtheres pimelodi*, *Achtheres* sp., *Argulu*s sp., *Ergasilus caeruleus*, *Ergasilus nerkae*, *Ergasilus* sp., *Salmincola corpulentus*, *Salmincola extensus*, *Salmincola thymalli*, *Salmincola* sp.
	Mollusca	Unidentified glochidium
Indirect life cycle with stages that directly penetrate fish	Myxozoans	*Chloromyxum* sp.*, *Henneguya* sp.*, *Henneguya zschokkei**, unidentified myxozoa*
	Larval/immature digeneans	*Clinostomum marginatum*, *Diplostomum flexicaudum*, *Diplostomum spathaceum*, *Diplostomum* sp., *Ichthyocotylurus erraticus*, *Ichthyocotylurus* sp., *Tylodelphys* sp.
Eating infected amphipods and opossum shrimp	Adult cestodes	*Cyathocephalus truncatus**
	Adult nematodes	*Cystidicola farionis**, *Cystidicola stigmatura**, *Cystidicola* sp.*, *Raphidascaris acus**
	Acanthocephalans	*Echinorhynchus lateralis**, *Echinorhynchus leidyi**, *Echinorhynchus salmonis**, *Echinorhynchus* sp.*, *Pomphorhynchus bulbocolli**
Eating infected copepods	Adult cestodes	*Bothriocephalus* sp.*, *Eubothrium crassum**, *Eubothrium salvelini**, *Proteocephalus longicollis**, Bothriocephalidae gen. sp.*
	Larval cestodes	Bothriocephalid plerocercoids, *Diphyllobothrium ditremu*m, *Diphyllobothrium laruei*, *Diphyllobothrium oblongatum*, *Diphyllobothrium* sp., *Eubothrium* sp.*, *Proteocephalus ambloplitis**, *Proteocephalus* sp.*, *Triaenophorus crassus**, *Triaenophorus nodulosus**, *Triaenophorus* sp.*, rhyncobothrid cestode*, *Schistocephalus* sp.
	Larval nematodes	*Camallanus oxycephalus**, *Philometra* sp.*
Eating infected ephemopterans and other insect larvae	Digeneans	*Crepidostomum farionis**, *Crepidostomum* sp.*, *Phyllodistomum coregoni**, *Phyllodistomum* sp.*
	Nematodes	*Sterliadochona ephemeridarum**, *Sterliadochona* sp.*, *Spinitectus gracilis**
Eating aquatic oligochaetes	Nematode	*Pseudocapillaria salvelini**
Eating dipteran and caddisfly larvae, cladocerans	Nematode	*Raphidascaris acus**
Eating infected isopods	Acanthocephalan	*Acanthocephalus dirus**
Eating infected ostracods	Acanthocephalans	*Neoechinorhynchus crassus**, *Neoechinorhynchus cylindratus**, *Neoechinorhynchus rutili**, *Neoechinorhynchus salmonis**, *Neoechinorhynchus tumidus**, *Neoechinorhynchus* sp.*
Eating infected prey/forage fish	Larval/immature nematodes	*Camallanus oxycephalus**, *Dichelyne cotylophora**
Unknown life cycle	Unidentified digeneans*	Unknown

With the above coregonine diet-parasite information in mind, coregonines become infected with at least 35 parasite species by eating infected intermediate or paratenic hosts. These parasite species include *Chloromyxum* sp., *Henneguya zschokkei*, *Crepidostomum farionis*, *Phyllodistomum coregoni*, *Bothriocephalus* sp., *Cyathocephalus truncatus*, *Eubothrium crassum*, *E. salvelini*, *Proteocephalus longicollis*, bothriocephalid plerocercoids, *Diphyllobothrium ditremum*, *D. laruei*, *D. oblongatum*, *P. ambloplitis*, *Schistocephalus* sp., *Triaenophorus crassus*, *T. nodulosus*, *Pseudocapillaria salvelini*, *Camallanus oxycephalus*, *Cystidicola farionis*, *Dichelyne cotylophora*, *Sterliadochona ephemeridarum*, *Spinitectus gracilis*, *Philometra* sp., *Raphidascaris acus*, *Acanthocephalus dirus*, *Echinorhynchus lateralis*, *E. leidyi*, *E. salmonis*, *Neoechinorhynchus crassus*, *N. cylindratus*, *N. rutili*, *N. salmonis*, *N. tumidus*, and *Pomphorhynchus bulbocolli*. Furthermore, the first two major parasite groups by percentage occurring in *Coregonus clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* from the Great Lakes were acanthocephalans and cestodes; for *C. artedi* the first two major parasite groups were cestodes and acanthocephalans.

Coregonine Species Parasite Communities among the Great Lakes

The parasite community of a fish species is composed of the (1) parasites specific to that species, or more commonly, a higher phylogenetic grouping of fish; (2) parasites whose specificity is determined by an intermediate stage in their life cycle; and (3) parasites that exhibit little host specificity. Fish are not only infected by parasites specific to them but also by species secondarily acquired from prey. These latter parasite species will vary according to the environment inhabited by the specific fish species and the other fish species present. The largest number of parasite species making up the community from the Great Lakes (number of species and location in parentheses) for the four main coregonine species are *Coregonus artedi* (24, Lake Superior), *C. clupeaformis* (29, Lake Huron), *C. hoyi* (15, Lake Superior), and *Prosopium cylindraceum* (20, Lake Huron). Most parasite species found in *C. artedi* from each Great Lake were cestodes followed by acanthocephalans from Lake Superior. Most species found in *C. clupeaformis* from each Great Lakes were cestodes followed by acanthocephalans and digeneans from Lake Superior. Most parasite species found in *C. hoyi* from Lakes Superior, Huron, and Michigan were cestodes followed by acanthocephalans. The number of parasite species in all of the major groups in *P. cylindraceum* was similar for Lakes Superior and Huron. Four species each of digeneans, cestodes, acanthocephalans, and copepods were reported in *P. cylindraceum* from Lake Huron. Most parasite species in *C. artedi*, *C. clupeaformis*, *C. hoyi*, and *P. cylindraceum* were reported from Lakes Superior and Huron because, in general, most individuals of these species and most parasitological studies were examined and conducted in these two lakes.

The highest ***CCs*** values for the parasite communities for each species (and pairwise lakes) were *Coregonus artedi* (0.64, Lakes Huron and Ontario), *C. clupeaformis* (0.69, Lakes Superior and Ontario), *C. hoyi* (0.62, Lakes Superior and Michigan), and *Prosopium cylindraceum* (0.59, Lakes Superior and Huron) (Tables 5, 8, 11). The parasite communities of each coregonine species from Lakes Superior, Huron, Michigan, and Ontario were involved in these highest coefficients because most individuals of these species were examined from these lakes. Sample size plays a role in increasing the number of parasite species found and, therefore, increasing the number of parasite species shared. Other reasons why Lakes Superior, Huron, Michigan, and Ontario had the highest parasite similarity coefficients are likely because coregonine habitat and food habits are similar in these lakes. However, the highest ***CCs*** values did not exceed 0.69, indicating these parasite communities are not strongly shared among these lakes.

Parasite Communities among Coregonine Species and Other Salmonine Species

There are some general similarities among the parasite groups of coregonines and salmonines from the Great Lakes. Acanthocephalans, cestodes, and nematodes are more common parasites of Coho Salmon (*Oncorhynchus kisutch*), Rainbow Trout (steelhead) (*O. mykiss*), Chinook Salmon (*O. tshawytscha*), and Lake Trout from the Great Lakes than single-celled parasites, myxozoans, monogeneans, leeches, molluscs, and copepods (except on Lake Trout) that are generally absent or infrequently infect these fish. This trend is similar to what we found for coregonine species and what we expected based on their similar habitat use. The digeneans can be found in both groups depending on the fish species.

The worldwide parasitic fauna of the genus *Prosopium* differs from members of the genus *Coregonus* in several classes of parasites, including trematodes and nematodes. Lawler (1970) reported that these differences support the separation of coregonines into the genera *Coregonus* and *Prosopium*. However, information summarized in our document indicates the parasite faunas of *Coregonus* and *Prosopium* are similar, suggesting that parasite faunas are not a useful characteristic for separation of these two fish genera in the Great Lakes. The biological significance of the dissimilarity in number and percentage of mastigophorans and ciliophorans and larval/immature cestodes in the four main coregonine species from the Great Lakes is unknown if it exists. The presence of *Triaenophorus nodulosus*, *Pomphorhynchus bulbocolli*, and *Ergasilus nerkae* in *Prosopium cylindraceum* and not in *Coregonus* spp. in the Great Lakes is not of any biological significance because *T. nodulosus* was reported in at least 14 other fish species, *Pomphorhynchus bulbocolli* was reported in at least 13 other fish species, and *E. nerkae* was reported in at least 9 other fish species from the Great Lakes. Individuals of *Tetraonchus variabilis* are host specific to *Prosopium cylindraceum* and *P. williamsoni*, except for one report of it infesting Brook Trout (*Salvelinus fontinalis*) in Labrador, Canada (Hicks and Threlfall 1973).

Parasite Communities and Geographical Distribution of *Coregonus* and *Prosopium* in North America

The geographical distribution of *C. clupeaformis* includes the Atlantic, Arctic, and Pacific basins in most of Canada and Alaska to northern New England, the Great Lakes region, and central Minnesota. *Coregonus clupeaformis* was also introduced into Montana, Idaho, and Washington (Page and Burr 2011). *Coregonus artedi* occurs only in North America where it is distributed throughout the northern U.S. and Canada, specifically the St. Lawrence Seaway and the Great Lakes, the upper Mississippi drainage to the Northwest Territories, and Alberta (Page and Burr 2011). *Coregonus hoyi* is endemic to the Great Lakes. Individuals of *Prosopium cylindraceum* have a broad distribution in North America, occurring in Alaska to New England, including the Great Lakes (Page and Burr 2011).

Since parasitological studies were conducted on *Coregonus artedi*, *C. clupeaformis*, and *Prosopium cylindraceum* in some areas in Canada, comments can be made on the metazoan communities and distribution of some of their parasite species in relationship to coregonine distribution. Moving east to west in northern North America, parasitological surveys in the provinces and territories of Canada are Labrador (Chinniah and Threlfall 1978), Quebec and Ontario (Dechtiar 1972a, b), Manitoba (Watson and Dick 1979; Dick and Rosen 1981), Saskatchewan (Pietrock and Hursky 2011), Alberta (Leong and Holmes 1981; Goater et al. 2005), British Columbia (Arai and Mudry 1983), Yukon Territory (Arthur et al. 1976), and Northwest and Nunavut Territories (Stewart and Bernier 1999). There are no extensive surveys examining coregonines for parasites in the U.S. outside of the Great Lakes proper because inland populations are relatively rare outside of the Great Lakes in small and scattered waters or are introduced populations well outside their native range.

We calculated ***CCs*** values to determine how similar the metazoan communities (helminths, copepods, leeches, molluscs) were for each of *Coregonus artedi*, *C. clupeaformis*, and *Prosopium cylindraceum* from the Great Lakes and various locations in some Canadian provinces. We excluded single-celled parasites and myxozoans from these analyses because we believe many authors did not make a concerted effort to examine coregonines for single-celled parasites and myxozoans or they were not involved in the study objectives. Second, larval *Diphyllobothrium* sp. and *Ichthyocotylurus* sp. that occurred in some locations used in our analysis were not identified to species, but we considered these genera to be common species shared by each of one or more of our coregonine species. Third, we are aware that parasitological studies in the Great Lakes are more numerous and might represent different aquatic environments than studies conducted in the Canadian provinces. Last, the absence of a parasite species from a coregonine species does not necessarily mean the parasite is absent from that location because host-species collections varied by coregonine species.

The metazoan communities of *Coregonus artedi* from the Canadian provinces of Ontario (outside the Great Lakes), Manitoba, and Alberta were dissimilar from the community of *C. artedi* from the Great Lakes. The ***CCs*** values for the metazoan communities of *C. artedi* from the Great Lakes and Ontario, Manitoba, and Alberta varied slightly from 0.40 to 0.43 (Table 27). The lowest ***CCs*** value involved one study that examined 446 individuals, and the highest ***CCs*** values involved two studies that examined 892 individuals. The number of metazoan species shared for each Canadian location and the Great Lakes was the same: 10 species. *Ichthyocotylurus erraticus*, *Discocotyle sagittata*, *Cyathocephalus truncatus*, *Proteocephalus longicollis*, *Diphyllobothrium* sp., *Triaenophorus crassus*, and *Echinorhynchus salmonis* infected *C. artedi* in all four locations, and *Crepidostomum farionis*, *Cystidicola farionis*, and *Salmincola extensus* occurred in two provinces and the Great Lakes.

Table 27. Sorenson's coefficients of metazoan community similarity and number of shared parasite species (in parentheses) for *Coregonus artedi*, *C. clupeaformis*, and *Prosopium cylindraceum* from the Great Lakes and various Canadian provinces. Dashes indicate comparisons could not be made because metazoan data were not generated at that location. Studies (author/year) and number of individuals examined (in parentheses) are identified in the footnotes.

	Canadian Province						
Species	**Labrador**	**Ontario**	**Manitoba**	**Saskatchewan**	**Alberta**	**British Columbia**	**Yukon Territory**
Coregonus artedi	-	0.43[a] (10)	0.40[b] (10)	-	0.43[c] (10)	-	-
Coregonus clupeaformis	0.47[d] (12)	0.61[e] (17)	0.57[f] (15)	0.54[g] (14)	0.53[h] (14)	0.36[i] (8)	0.54[d] 54[j] (13)
Prosopium cylindraceum	0.38[k] (7)	0.43[l] (8)	-	-	-	-	0.56[m] (11)

[a]Bangham 1941 (16); Dechtiar 1972b (52).
[b]Watson and Dick 1979 (446).
[c]Leong and Holmes 1981 (757); Goater et al. 2005 (135).
[d]Hicks and Threlfall 1973 (27); Chinniah and Threllfall 1978 (102).
[e]Bangham 1940 (10); Bangham and Venard 1946 (17); Dechtiar 1972b (15); Dechtiar et al. 1989 (48).
[f]Watson and Dick 1979 (570).
[g]Pietrock and Hursky 2011 (162).
[h]Mudry and Anderson 1977 (3); Leong and Holmes 1981 (836); Goater et al. 2005 (135).
[i]Arai and Mudry 1983 (86).
[j]Arthur et al. 1976 (93).
[k]Hicks and Threlfall 1973 (30; Chinniah and Threlfall 1978 (1).
[l]Bangham 1941 (10); Dechtiar et al. 1989 (43); Bangham and Venard 1946 (8).
[m]Arthur et al. 1976 (57).

The metazoan communities of *Coregonus clupeaformis* from the Great Lakes and the Canadian provinces were similar. The ***CCs*** values ranged from a low of 0.36 in British Columbia to a high of 0.61 in Ontario, and 5 values were greater than 0.5 (Table 27). The highest value involving Ontario included 4 studies and 90 individuals, and the lowest value involved 1 study and 86 individuals. The number of species shared in these pairwise comparisons ranged from 8 to 17. *Proteocephalus longicollis* occurred in *C. clupeaformis* in all 8 locations; *Crepidostomum farionis*, *Discocotyle sagittata*, and *Diphyllobothrium* sp. occurred in 6 provinces and the Great Lakes; *Cyathocephalus truncatus*, *Triaenophorus crassus*, *Cystidicola farionis*, and *Salmincola extensus* occurred in 5 provinces and the Great Lakes; and *Diplostomum spathaceum*, *Ichthyocotylurus erraticus*, and *S. corpulentus* occurred in 4 provinces and the Great Lakes.

The metazoan communities of *Prosopium cylindraceum* in the Canadian provinces was not similar to communities in the Great Lakes. The ***CCs*** values ranged from a low of 0.38 in Labrador to a high of 0.56 in the Yukon Territory (Table 27). The number of species shared ranged from 7 to 11. The lowest and highest values involved 2 studies and 31 fish and 1 study and 57 fish, respectively. *Diplostomum spathaceum* and *Tetraonchus variabilis* were shared by *P. cylindraceum* in all 4 locations; *Crepidostomum farionis*, *Discocotyle sagittata*, *Eubothrium salvelini*, and *Salmincola thymalli* occurred in 2 provinces and the Great Lakes. Morgan et al. (2018), using genetic analyses, demonstrated a phylogenetic division between eastern and western groups of *P. cylindraceum*, indicative of origins from 2 separate refugias generally supporting the differences in the metazoan communities of *P. cylindraceum* from the Great Lakes compared to various Canadian provinces.

The parasite communities of *Prosopium cylindraceum* from the Great Lakes and *P. williamsoni* from the Province of British Columbia were not similar. The ***CCs*** values for the metazoan communities of *P. cylindraceum* from the Great Lakes and *P. williamsoni* from British Columbia were 0.36. In British Columbia, 298 individuals of *P. williamsoni* were examined from lake and stream systems (specifics not provided) by Arai and Mudry (1983). *Crepidostomum farionis*, *Diplostomum* sp., *Ichthyocotylurus* sp., *Tetraonchus variabilis*, *Eubothrium salvelini*, *Cystidicola farionis*, *Pomphorhynchus bulbocolli*, and *Salmincola thymalli* were shared by *P. cylindraceum* and *P. williamsoni*. Individuals of *P. williamsoni* occurred throughout western North America in both Canada and the U.S., the upper Missouri River area, and in Nevada and Utah (Page and Burr 2011). The low similarity in parasite communities involving *P. cylindraceum* from the Great Lakes and *P. williamsoni* in British Columbia was due to large differences in habitats where individuals of these 2 species were collected. If most, if not all, of the *P. williamsoni* were collected from streams by Arai and Mudry (1983), we assume its diet was different from that of *P. cylindraceum* from the Great Lakes. The low ***CCs*** values again demonstrate the importance of habitats and diet in determining metazoan communities. The highest ***CCs*** values for each of *Coregonus artedi*, *C. clupeaformis*, and *C. hoyi* among the Great Lakes pairwise analyses were higher than all of the coefficients involving each of *C. artedi* and *C. clupeaformis* and the Canadian provinces' coefficients. Generally, the ***CCs*** values indicate the metazoan communities of these three coregonine species among the Great Lakes are more similar to one another than to the metazoan communities of these coregonine species from the Great Lakes and the Canadian provinces.

Although similarity coefficients in all of the analyses never exceeded 0.75, the parasite communities of *Coregonus artedi*, *C. clupeaformis*, *C. artedi*, and *Prosopium cylindraceum* were somewhat homogenous in the Great Lakes because several parasite species were shared by these fish species. Seven parasite species were shared by *C. artedi* from the Great Lakes and three Canadian provinces. For *C. clupeaformis,* one species was shared in the Great Lakes and seven provinces, three species occurred in the Great Lakes and six provinces, and four species occurred in the Great Lakes and five provinces. For *P. cylindraceum*, two species were shared in the Great Lakes and three provinces. Parasite species found in *C. artedi*, *C. clupeaformis*, and *P. cylindraceum* in the Great Lakes and in Labrador, Alberta, British Columbia, and Yukon Territory were *Crepidostomum farionis*, *Phyllodistomum coregoni*, *Diplostomum spathaceum*, *Ichthyocotylurus erraticus*, *Discocotyle sagittata*, *Cyathocephalus truncatus*, *Proteocephalus longicollis*, *Diphyllobothrium* sp., *Triaenophorus crassus*, *Cystidicola farionis*, *Echinorhynchus salmonis*, *Pomphorhynchus bulbocolli*, *Salmincola corpulentus*, and *S.*

extensus. Therefore, these parasite species have broad geographical distributions in northern North America. Both species specialists and generalists comprise these parasite species.

Parasites with direct life cycles (monogeneans and copepods) infecting *Coregonus artedi*, *C. clupeaformis*, and *Prosopium cylindraceum* expand their distribution as their hosts expand their geographic distributions. Parasite species with indirect life cycles (digeneans, cestodes, many nematodes, acanthocephalans) are tied to one or more intermediate hosts in their life cycles, as explained earlier in this document. The geographical distribution of intermediate hosts plays a key role in the distribution of parasites and is a primary requisite for the establishment and occurrence of parasite populations. In the presence of well-established intermediate hosts, the distribution of the fish definitive hosts, particularly those in which propagation of the parasite species can be attained, become the most critical factors determining their ultimate geographical range. The use of paratenic hosts also plays a role in the expansion of the geographical distribution of parasites. Based upon our evaluation of literature for this report, closely related species of fish (coregonines and salmonines) using the same habitats and prey bases often harbor the same or similar species of parasites. Thus, parasites such as *Discocotyle sagittata* likely move with both coregonines and salmonines.

At least 14 parasites species in seven groups infecting coregonines from the Great Lakes have also been reported in coregonines in Russia (Bauer 1970; Fagerholm and Valtonen 1980) (Table 28). Furthermore, we believe there are more of these species since we are not aware of all of the Russian studies. Coregonines examined for parasites in Russia included Arctic Cisco, Vendance (*Coregonus albula*), Valek or Konek (*C. cylindraceus*), *C. lavaretus*, Muksun (*C. muksun*), *C. nasus, C. peled,* and *C. sardinella*. Parasites found in both the Great Lakes and Russian studies include

1. Myxozoans: *Henneguya zschokkei*
2. Trematodes: Adult: *Crepidostomum farionis*
   Larval: *Ichthyocotylurus erraticus*
3. Monogeneans: *Tetraonchus variabilis* (= *Tetraonchus cylindraceum*)
4. Cestodes: Adult: *Cyathocephalus truncatus*, *Eubothrium crassum*, *Proteocephalus longicollis*
   Larval: *Diphyllobothrium ditremum, Triaenophorus crassus*
5. Nematodes: Adult: *Cystidicola farionis*
6. Acanthocephalans: *Echinorhynchus salmonis, Neoechinorhynchus tumidus*
7. Copepods: *Salmincola extensus, Salmincola extumescens*

Table 28. Partial list of parasite species found in coregonines from the Great Lakes, Finland, and Russia based on published literature.

Parasite	Great Lakes	Finland	Russia
Myxosporans			
Henneguya zschokkei	Present	Not reported	Present
Adult trematodes			
Crepidostomum farionis	Present	Not reported	Present
Larval trematodes			
Ichthyocotylurus erraticus	Present	Present	Present

Parasite	Great Lakes	Finland	Russia
Monogeneans			
Discocotyle sagittata	Present	Present	Not reported
Tetraonchus variabilis (= *Tetraonchus cylindraceum*)	Present	Not reported	Present
Adult cestodes			
Cyathocephalus truncatus	Present	Not reported	Present
Eubothrium crassum	Present	Not reported	Present
Proteocephalus longicollis (= *Proteocephalus exiguus*)	Present	Present	Present
Larval cestodes			
Diphyllobothrium ditremum	Present	Present	Present
Triaenophorus crassus	Present	Present	Present
Adult nematodes			
Cystidicola farionis	Present	Present	Present
*Pseudocapillari*a *salvelini*	Present	Present	Not reported
Larval nematodes			
Raphidascaris acus	Present	Present	Not reported
Acanthocephalans			
Echinorhynchus salmonis	Present	Not reported	Present
Neoechinorhynchus rutili	Present	Present	Not reported
Neoechinorhynchus tumidus	Present	Not reported	Present
Copepods			
Salmincola corpulentus	Present	Not reported	Present
Salmincola extensus	Present	Present	Present

At least nine parasite species in six groups infecting Great Lakes coregonines have been found also in coregonines in Finland. Coregonines examined for parasites in Finland include *Coregonus acronius, C. albula, C. lavaretus,* Valaan Whitefish (*C. widegreni*), and *Coregonus* sp. Parasites identified to species and found in coregonines from the Great Lakes and Finland (Rahkonen and Valtonen 1987; Rintamaki and Valtonen 1988; Valtonen et al. 1988; Pulkkinen et al. 1999; Pulkkinen and Valtonen 1998, 1999; Karvonen and Valtonen 1988) are

1.	Trematodes:	Larval: *Ichthyocotylurus erraticus*
2.	Monogeneans:	*Discocotyle sagittata*
3.	Cestodes:	Adult: *Proteocephalus longicollis*
		Larval: *Diphyllobothrium ditremum*, *Triaenophorus crassus*
4.	Nematodes:	Adult: *Cystidicola farionis*, *Pseudocapillaria salvelini*, *Raphidascaris acus*
5.	Acanthocephalans:	*Neoechinorhyncus rutili*
6.	Copepods:	*Salmincola extensus*

There are at least 18 parasite species infecting coregonines from the Great Lakes that are also found in coregonines from Finland and Russia. Therefore, these parasite species have broad geographical distributions. Additionally, there are many parasites found in coregonines from Russia, Finland, and other European locations not found in coregonines from the Great Lakes. However, there is commonality across the globe in coregonine parasites within our limited global literature review. We recommend that additional reviews be done on European and Asian literature to see what additional findings could be applicable to coregonine parasites from the Great Lakes.

CONCLUSIONS

The parasite faunas of coregonines from the Great Lakes and their connecting waters consisted of at least 53 species. Of these, about 15 species were specific to both coregonines and salmonines, with the rest of the parasite species infecting fish species from other families. Most parasitological studies were conducted on *Coregonus artedi and C. clupeaformis* followed by *C. hoyi* and then *Prosopium cylindraceum*. More parasite species were reported in coregonines from Lakes Superior and Huron followed by Lake Michigan. The most numerous parasite species were from the following 8 parasite groups

1. Myxozoans: *Henneguya zschokkei*
2. Trematodes: Adult: *Phyllodistomum coregoni*
   Larval: *Ichthyocotylurus erraticus*
3. Cestodes: Adult: *Proteocephalus longicollis*, *Diphyllobothrium* sp.
   Larval: *Triaenophorus* sp.
4. Monogeneans: *Discocotyle sagittata*
5. Nematodes: *Cystidicola farionis*
6. Acanthocephalans: *Echinorhynchus salmoni*, *Neoechinorhynchus tumidus*
7. Leeches: *Piscicola milneri*, *P. punctata*
8. Copepods: *Salmincola corpulentus*

Species of adult trematodes, monogeneans, leeches, and glochidia infrequently infected coregonines from the Great Lakes, and aspidobothreans were not reported in this fish group. Furthermore, the nematode species, except *Cystidicola farionis*, occurred in low numbers in Great Lakes coregonines. Similarities in parasite faunas, parasite richness, and coefficients of similarities indicated that *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* in the Great Lakes ate similar food items that served as intermediate hosts (primarily invertebrates) for acquiring similar helminth species and other parasites with direct and indirect life cycles. Most parasite species found in coregonines were autogenic, completing their life cycles in fish. Although there were some parasites that negatively affected the health of coregonines, we are not aware of epizootics of coregonines in the Great Lakes from parasites. Great Lakes coregonines carry few or no parasites that can be transmitted to humans.

The parasite communities of *Coregonus artedi*, *C. clupeaformis*, *C. hoyi*, and *Prosopium cylindraceum* were more similar to one another in the Great Lakes than the parasite communities of these four coregonines and their respective Canadian provinces. Sorenson's Coefficient of Similarity for the parasite communities among the Great Lakes coregonines varied by species: *C. artedi* (0.24-0.64), *C. clupeaformis* (0.31-0.69), *C. hoyi* (0.14-0.62), and *P. cylindraceum* (0.17-0.59). The two highest similarity coefficients for parasite communities for all data combined from all Great Lakes between coregonine species pairs involved *C. hoyi* and *P. cylindraceum* (0.75) and *C. clupeaformis* and *P. cylindraceum* (0.69). Most coefficients for the metazoan communities for each of *C. artedi*, *C. clupeaformis*, and *P. cylindraceum* from the Great Lakes and Canadian provinces were lower than the coefficients for these coregonine species among the Great Lakes. In general, the coefficients between coregonine species from all the data combined from all the Great Lakes were highest compared to all other coefficients. All these coefficients were above 0.50 because these coregonine species comparisons had the highest number of shared parasite species. We attribute the differences to a larger Great Lakes sample size from more parasitological studies, a broader range of habitats sampled for these species in the Great Lakes, and the diet and habitat similarity of the Great Lakes coregonines that allow for the acquisition of similar or the same parasite species with indirect and direct life cycles.

Given the broad ecological changes in the Great Lakes resulting from the invasion and now broad distribution of dreissenid mussels, additional parasitological studies are needed on coregonines to see how these ecosystem changes are reflected in helminth loads, which will also reflect niche changes for this important group of fish. The most recent information regarding the parasites of *Coregonus artedi*, *C. clupeaformis*, and *C. hoyi* is from unpublished studies (Table 24) and French et al. (2005) for *Prosopium cylindraceum*. Most studies of parasites in coregonines from the Great Lakes are relatively old (published before 2000). Given the large declines in recent Lake Whitefish recruitment in Lakes Michigan and Huron, as documented in Madenjian et al. (2019) and Riley et al. (2020), respectively, and the overall lack of information about the effects of parasitism on young coregonines, we recommend that more parasitological studies be done on all ages of coregonines, particularly age-0 and age-1 fish, to determine if parasites are involved in these Lake Whitefish population changes. The detection of parasites and their correct identification could also assist in identifying stocks of Great Lakes coregonines and inform investigators about likely habitat and niche changes. Finally, knowing the present parasite faunas of Great Lakes coregonines will help investigators identify new exotic parasites in the Great Lakes along with their time of arrival and potential distribution dynamics.

It is our view that this synopsis is a starting place for future studies of Great Lakes coregonine parasites and, eventually, their pathogens. A complete survey and listing of coregonine parasites and pathogens along with mapping their occurrences in relationship to abiotic and biotic variables in the Great Lakes are the next recommended steps. A holistic and integrative approach to research should be undertaken to study Great Lakes coregonine parasites, and this approach should involve parasitologists, fish health specialists, ichthyologists, and fishery biologists.

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