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Review

Parasites and microbial infections of lamprey (order Petromyzontiformes Berg 1940): A review of existing knowledge and recent studies

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ABSTRACT

The 48 described species of parasitic and non-parasitic lamprey within the order Petromyzontiformes span much of the globe. Although the sea lamprey (*Petromyzon marinus*) is an unwanted invasive in the Laurentian Great Lakes, most lamprey species are of ecological and cultural value, and of conservation concern. Infectious diseases affect fish health, growth, reproduction, and recruitment; yet, the impact of pathogens that cause them in lamprey have not been comprehensively assessed. This review collates existing information to gain a better understanding of pathogen distribution in lamprey populations. At least 46 genera of parasites, seven genera of bacteria, two genera of fungi and oomycetes, and two viruses belonging to two families have been documented to occur in lamprey, most of which have also been identified in other fish species. Many pathogens of lamprey have not been described completely. Moreover, many details of the host-pathogen interactions in lamprey remain unknown, leaving links between pathogens and disease causation unclear. This knowledge gap is extended by the lack of studies on lamprey immune systems, nor have Koch's or Rivers' postulates for most lamprey pathogens been fulfilled. Designing future studies aimed at addressing these knowledge shortfalls will not only clarify the effects that infectious diseases have on imperiled lamprey populations, but also contribute to assessments of potential biocontrol for invasive lamprey populations in the future.

Contents

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Introduction

Infectious diseases of fish, defined here as those diseases caused primarily by viruses, bacteria, fungi, and water molds, have been associated with widescale mortality events in a multitude of wild and feral fish populations (Garver et al., 2010; Iida and Mizokami, 1996; Lumsden et al., 2007; Meyers et al., 1999) that can lead to observable population level effects (Benjamin and Bence, 2003; Faisal et al., 2012; Holey et al., 1998). Similarly, infectious diseases are substantial impediments to hatchery-based fishery conservation efforts globally (Faisal et al., 2013; Maitland, 1995; Smith et al., 2009). Among the fish-pathogenic microbes causing these diseases, some have an exceptionally wide host-range (e.g., *Flavobacterium columnare*, causative agent of columnaris disease; Viral Hemorrhagic Septicemia Virus, etiological agent of viral hemorrhagic septicemia; Kim and Faisal, 2010; Loch and Faisal, 2017), whereas others are species specific (e.g., the Alloherpesviruses; Hanson et al., 2016). However, a common characteristic of infectious diseases of fish is their dependency on a multitude of factors relating to the host, the pathogen, and their environment(s) (Snieszko, 1973).

Micro- (e.g., myxozoa, protozoa) and macro-parasites (e.g., helminths, crustaceans, leeches) can also negatively affect fish health, but, in the absence of other stressors, infrequently lead directly to mortality. Nevertheless, parasite infestations can affect fish nutritional status (Barber, 2007; Chin et al., 2004), reproductive success (Bangham, 1927; Esch and Huffines, 1973; Gillilland and Muzzall, 2004; Moore, 1926), and even risk of predation (Ruehle and Poulin, 2020). There is also evidence that some parasite infestations can predispose hosts to infectious disease (Jacobson et al., 2003; Pylkkö et al., 2006; Sitjà-Bobadilla, 2008; Sitjà-Bobadilla et al., 2006), as well as exacerbate the negative health effects of co-occurring pathogenic microbes (Louhi et al., 2015; Xu et al., 2009).

Despite continued advances in understanding the infectious diseases and parasites that afflict teleosts, knowledge of these health risks in cyclostomes (i.e., jawless fishes) has not kept pace. Of the > 40 described lamprey species in three families (i.e., Geotriidae and Mordaciidae of the Southern Hemisphere; Petromyzontidae of the Northern Hemisphere; Maitland et al., 2015; Nardi et al., 2020; Potter et al., 2015; Tutman et al., 2017), only ~15 have been reported as harboring infectious agents and/or parasites in scientific literature, dating back to Moore (1898). Since then, Appy and Anderson (1981) reviewed and reported on multiple taxa of parasites, bacteria, and fungi that were detected in multiple lamprey species, and additional compilations of lamprey pathogen and parasites have also been conducted for specific regions (e.g., Sobecka et al., 2009) or species (e.g., Jackson et al., 2019). However, much remains unknown about the parasites and microbial infections of lamprey, and the relatively low number of reports relative to teleosts is notable.

In this context, it is certainly possible that the distinct phylogeny (Maitland et al., 2015; Potter et al., 2015) and unique and varied life history characteristics of lamprey convey a degree of refractivity to some commonly studied infectious microbes and parasites. Some lampreys are anadromous (e.g., sea lamprey, *Petromyzon marinus*, in their native range, Pacific lamprey, *Entosphenus tridentatus*, European river lamprey, *Lampetra fluviatilis*), and their complex life cycle involves a dramatic metamorphosis from freshwater resident larvae (ammocoetes) in close contact with the sediment to free-swimming parasites in seawater. Other species (e.g., silver lamprey, *Ichthyomyzon unicuspis*) or populations (e.g., invasive sea lamprey in the Laurentian Great Lakes) remain in freshwater lakes or rivers during their parasitic phase (Docker and Potter, 2019; Hume et al., 2020). These life stages also exhibit very different feeding modes that may impact their exposure to infectious microbes or parasites. Most larvae form burrows in fine sediments and filter feed on diatoms and other freshwater particulates. In contrast, metamorphosed parasitic lamprey feed at the top of the trophic structure and consume blood and/or flesh from a broad variety of fish hosts (e.g., sea lamprey feed upon at least 50 different host species, Renaud and Cochran, 2019) and have even been reported to occasionally occur as parasites on marine mammals (Renaud and Cochran, 2019). Some freshwater resident (brook) lamprey do not employ a parasitic stage and enter final sexual maturation soon after metamorphosis (Docker and Potter, 2019). Lamprey typically do not feed during metamorphosis (Youson, 1980) nor during pre-spawning migration and spawning (Moser et al., 2015), and die soon after spawning in freshwater (i.e., are semelparous). Hence, lamprey potentially are exposed to a broader range of pathogens than other aquatic species as they encounter microbes in freshwater sediments and water column as larvae, feed directly on body fluids and tissues of hosts in marine or freshwater environments, and rely on endogenous reserves and change habitat use during metamorphosis and sexual maturation.

Table 1
Parasites recorded in Great Lakes basin (lake watershed: M: Michigan; S: Superior; H: Huron; O: Ontario) sea lamprey (*Petromyzon marinus*), with information on parasite life stage (L: larvae; I: immature; A: adult), lamprey life stage (P: post-metamorphosis; A: non-specified adult; F: actively feeding adult; S: upstream migrant or spawning adult), host tissue origin, prevalence (total number of fish examined in parentheses) and intensity. NR: Not Reported.

Parasite Taxon	Parasite Life stage	Lamprey Life stage	Watershed	Tissue	Prevalence	Intensity	Reference
Protozoa, Myxozoa, and Microsporidia							
Trichodina spp.	NR	F	M	Gills	1.3% (76)	NR	Guilford, 1954
	NR	A	O	Gills	2.5% (79)	NR	MSU-AAHL Records, 2005–2019
Ichthyophthirius multifilis	NR	F	NR	Skin	NR	NR	McLain, 1952
Trematodes (Phylum Platyhelminthes, Class Trematoda)							
Diplostomum sp.	L	A	H	NR	7.7% (13)	NR	Bangham, 1955
Diplostomum huronense	L	F,S	H	Eyes	23.6% (284)	1–11	Wilson and Ronald, 1967
Plagioporus lepomis	A	S	H	Intestine	0.4% (284)	1	Wilson and Ronald, 1967
Cestodes (Phylum Platyhelminthes, Class Cestoda)							
Proteocephalus sp.	I	A	H	GI tract	61.5% (13)	NR	Bangham, 1955
	I,A	F,S	H	Intestines	0.7% (715)	1–2	Wilson and Ronald, 1967
Proteocephalus longicollis (syn. *P. laruei/P. exiguus*)	I	A	H	NR	15.4% (13)	NR	Bangham, 1955
	I	A	M	NR	46% (76)	1–49	Guilford, 1954
Triaenophorus crassus	L	A	H	NR	15.4% (13)	NR	Bangham, 1955
	NR	A	H,M	Skin, Intestine	NR	NR	Lawler and Scott, 1954
	I	F,S	H	GI tract	0.6% (501)	1–2	McLain, 1952
	A	S	H	Intestines	1.1% (284)	1–2	Wilson and Ronald, 1967
	I	A	M	NR	2.6% (76)	1	Guilford, 1954
	L	S	H	GI tract	1.0% (100)	1	Applegate, 1950
Abothrium sp.	I	A	M	NR	2.6% (76)	1	Guilford, 1954
	I	S	H	Unknown	1.0% (100)	1	Applegate, 1950
Unidentified sp.	I	S	H	Unknown	1.0% (100)	1	Applegate, 1950
	NR	A	O	Small intestine	2.2% (93)	1	MSU-AAHL Records, 2005–2019
Nematodes (Phylum Nemathelminthes, Class Nematoda)							
Camallanus spp.	A	P,F,S	H	Liver, Outer intestinal wall, Gonads, Body cavity wall	3.8% (367)	NR	McLain, 1952
Truttaedacnitis stelmioides	I,A	F,S	H	Gonads, Liver, Intestinal walls, Gills	1.8% (715)	1–108	Wilson and Ronald, 1967
Cystidicola stigmatura	L	A	M	NR	1.3% (76)	1	Guilford, 1954
Unidentified sp.	L	S	H	Intestinal wall	0.4%	NR	Applegate, 1950
Acanthocephalans (Phylum Acanthocephala)							
Echinorhynchus salmonis/coregoni	I	A	H	Intestinal tract	7.7% (13)	NR	Bangham, 1955
	A	F,S	H	Digestive tract	8.0% (501)	1–15	McLain, 1952
	I,A	F,S	H	Intestinal walls, Gills	8.3% (715)	1–15	Wilson and Ronald, 1967
	A	S	H	NR	17.0% (100)	1–3	Applegate, 1950
	NR	A	M	NR	9.2% (76)	<4	Guilford, 1954
Echinorhynchus leidyi	A	S	H	Digestive tract	NR	NR	McLain, 1952
	NR	A	M	NR	5.3% (76)	1	Guilford, 1954
Neoechinorhynchus cylindratus	NR	A	M	NR	1.3% (76)	1	Guilford, 1954
Crustaceans (Phylum Arthropoda, Subphylum: Crustacea)							
Ergasilus caeruleus	I	F,S	H	Gill pouches	15.0% (715)	1–33	Wilson and Ronald, 1967
Ergasilus megaceros	I	A	H	Nasal fossae	1.8% (56)	9	Muzzall and Hudson, 2004
Mollusks (Phylum Mollusca)							
Anodontoides ferussacianus	I	F,S	H	Gill pouches	4.9% (715)	1–9	Wilson and Ronald, 1967
Annelids (Phylum Annelida, Class Clitellata)							
Piscicola milneri	A	S	M	Body	NR	NR	Applegate, 1950

The lack of research funding and availability of specimens to study lamprey diseases could also be a primary factor behind a similar lack of information on lamprey disease incidence. Lamprey are unique anatomically and physiologically (Docker et al., 2015), leading to challenges in studying the diseases that affect them. Moreover, >10 lamprey species (IUCN, 2020) are considered threatened or endangered, which hinders the study of their diseases that often requires lethal sampling techniques. In contrast, sea lamprey have expanded outside their natural range and are considered a nuisance species in the Great Lakes (Renaud, 2011). Their occupation of the Great Lakes and its tributaries may result in exposure to a broader suite of infectious agents and parasites than sea lamprey encounter in their native range. In both situations, a better understanding of the health and diseases of lampreys is needed for conservation of native lampreys, and potentially, for control of sea lamprey in the Great Lakes.

To provide natural resource agencies, fish health experts, and researchers a reference to support ongoing lamprey population management, we reviewed published accounts of lamprey pathogens and parasites from around the world. Given that parasites and microbes vary by region, we begin by addressing the parasites and microbial infections that have been detected in invasive sea lamprey populations within the Laurentian Great Lakes of North America (native range North-East Atlantic Ocean and European watersheds, Hume et al., 2021). Next, we summarized pathogen detections of sea lamprey in their native range. Finally, we assembled data on pathogens and parasites reported in other lamprey species, including those that are native to the Great Lakes. Based on the available information in the reviewed reports, the affected lamprey life stages are denoted as follows throughout the text and tables: a) larval (i.e., ammocoetes); b) metamorphosizing (i.e., actively undergoing one of the stages of metamorphosis); c) post-metamorphosis juvenile; d) actively feeding; e) spawning (refers to any point in time from the start of upstream migration through the act of spawning); f) post-spawning; and g) non-specified adult.

Pathogens and parasites of sea lamprey in the Great Lakes basin

The Great Lakes basin is home to >170 fish species (Roth et al. 2013), many of which have been intentionally or accidentally introduced. One of the most notorious nonindigenous invasive Great Lakes fish species is the sea lamprey, which led in part to substantial declines in lake trout (*Salvelinus namaycush*) and various *Coregonus* spp. since its invasion into the basin (Christie and Goddard, 2003; Renaud, 2011). As such, sea lamprey have been the target of an array of control measures, such as chemical lampricides, physical and electromechanical barriers, and trapping (Christie and Goddard, 2003; Hume et al., 2020; Miehls et al., 2021; Renaud, 2011), as well as chemosterilization (Twohey et al., 2003). To reduce the risk of inadvertently translocating fish pathogens along with released sterilized males, the Great Lakes Fishery Commission (GLFC) initiated a health surveillance program to track the infection status of sterilized lamprey prior to their translocation. The following sections summarize the health surveillance results that were conducted at the Michigan State University – Aquatic Animal Health Laboratory (MSU-AAHL) from 2005 to 2017, and diagnostic submissions to the MSU-AAHL resulting from disease and/or mortality events. Given the interest in controlling/eradicating sea lamprey from the Great Lakes, several reports on the pathogens and parasites of sea lamprey have been published and are also summarized here.

Protozoa, myxozoa, and microsporidia

Protozoans, myxozoans and microsporidia infect a wide range of aquatic hosts and display great variation in life cycles. Many protozoans have a free-living reproductive stage, as well as a fish-associated trophont or encysted stage. Microsporidia are obligate intracellular parasites that, in fish, typically have a simple life cycle involving merogony and sporogony. Many myxozoans undergo a more complex life cycle involving two hosts (Woo, 2006). Despite the array of protozoa, myxozoa, and microsporidia that parasitize Great Lakes fishes (Faisal et al., 2013; Hoffman, 1999; Muzzall and Whelan, 2011; Phelps et al., 2015), published reports of these parasites affecting Great Lakes sea lamprey are rare. A *Trichodina* sp. was observed in the gills of 1/12 actively feeding sea lamprey (0/65 upstream migrants) from Lake Michigan (Guilford, 1954; Table 1); however, no gross signs of disease were associated with this parasite. Although the collection location was not reported, McLain (1952) reported infection by *Ichthyophthirius multifilis*, causative agent of whitespot disease (i.e., "Ich"), in actively feeding Great Lakes sea lamprey housed in aquaria that was severe and led to mortality in the affected population. Of note, Miller (2009) examined 269 sea lamprey from Lake Ontario for microsporidian parasites of the genus *Heterosporis*, causative agent of heterosporosis, but did not detect the parasite.

During MSU-AAHL sea lamprey health surveillance and diagnostic efforts (2005–2019), skin and gill biopsies were examined via light microscopy from a total of 551 sea lamprey (n = 90 larvae, 461 adults) collected from the Covert Creek (Lake Ontario watershed; n = 9), Hammond Bay (Lake Huron; n = 9), Chequamegon Bay (Lake Superior; n = 10); Blind River (Lake Huron watershed; n = 22), Bridgeland Creek (Lake Huron watershed; n = 12), Sault Ste. Marie (Lake Superior/Lake Huron watershed; n = 60) and from both the Humber River and Duffins Creek (Lake Ontario watershed; n = 429). The only micro-parasite observed was a *Trichodina* sp. on the gills of two fish, one from Duffin's Creek (2005) and one from the Humber River (2010; Table 1). These findings are also in agreement with those of McLain (1952), who did not find any external parasites in >600 sea lamprey that were examined from the Lake Huron watershed. It is noteworthy that, to our knowledge, the rarely reported, skin-associated protozoa in sea lamprey have been limited to the post-metamorphosis life stages. As suggested for European river lamprey, it is possible that living imbedded within the substrate renders larval sea lamprey relatively inaccessible to protozoan ectoparasites (Sobecka et al., 2010).

Between 2016 and 2017, MSU-AAHL personnel also examined muscle tissue from 316 adult sea lamprey (n = 11 from Chequamegon Bay, Wisconsin, Lake Superior; n = 22 from the Blind River, Ontario, Canada, Lake Huron; n = 283 from Humber River and Duffins Creek, Ontario, Canada, Lake Ontario) for *Heterosporis* sp. and did not detect this parasite.

Trematodes

Digenean trematodes have complex and indirect life cycles that use at least one intermediate invertebrate host (e.g., molluscs) and one or more vertebrate species as final hosts. Most trematodes that utilize fish as final hosts induce little to no appreciable harm to their host under natural (i.e., wild) conditions (Hoffman, 1999) and most commonly reside within the gastrointestinal tract. However, larval trematodes can cause mechanical damage to the tissues through which they migrate and localize and, in substantial numbers, can elicit mortality (Hoffman, 1956; Hoffman and Hundley, 1957; Pracheil and Muzzall, 2010).

Published reports of trematode infections in Great Lakes sea lamprey are rare. Bangham (1955) identified an encysted larval *Diplostomum* sp. in one fish collected from the South Bay, Lake Huron (Table 1). Wilson and Ronald (1967) identified larval *Diplostomum huronense* in the eyes of 67 (23.6%) stream-caught (upstream migrant or spawning) lamprey and nine (2.1%) lake-caught (actively feeding) lamprey collected on and around Manitoulin Island in Lake Huron (Table 1). Although the authors did not report any gross changes associated with these infections, high intensities of *D. huronense* have been linked to mortality events in wild juvenile cyprinids in other localities (Ieshko and Lebedeva, 2007) and other *Diplostomum* spp. have been linked to mortality in other fishes (Brassard et al., 1982; Lester, 1977). *Diplostomum* spp., most commonly known as eye flukes, induce cataract formation in other fish species, which has been linked to impaired skin pigmentation in affected fish and a subsequent reduction in the ability to avoid predation by final bird hosts (i.e., gulls of the family Laridae; Karvonen, 2012). Of note, some *Diplostomum* spp. reportedly colonize their fish hosts through the skin rather than via ingestion (Sobecka et al 2009), meaning lamprey trophic status may not affect susceptibility to infection. Wilson and Ronald (1967) also identified an adult gravid *Plagioporus lepomis* (most commonly found in centrarchids) in the intestine of one stream-caught (upstream migrant or spawning) sea lamprey (Table 1). Although the authors did not speculate as to how this lamprey became infected, it is possible this intact adult acquired the parasite through inadvertent ingestion of the parasite metacercariae. The relative sparsity of reports of trematodes in Great Lakes sea lamprey may be due to fewer studies that have focused on sea lamprey compared to other fish species; however it is also plausible that sea lamprey are either rarely exposed to trematodes (due to diet and/or feeding and life history strategies), or are incompatible intermediate or final hosts for these parasites, a supposition which would require further study.

Cestodes

The class Cestoda contains many human pathogenic and zoonotic tapeworm species, including those transmitted through consumption of infected fish tissues (Raether and Hänel, 2003; Scholz and Kuchta, 2016). In addition, there are a multitude of cestodes that harm aquatic species, such as the Asian fish tapeworm (*Bothriocephalus acheilognathi*), which has been linked to fish mortality (Scholz et al., 2012) and been introduced in the Great Lakes (Boonthai et al., 2017; Marcogliese, 2008). Fish species serving as final hosts commonly become infected via ingestion of invertebrates harboring larvae (e.g., procercoid, plerocercoid), thereby leading to colonization of the gastrointestinal tract and relatively little overt tissue damage (Hoffman, 1999). However, tissue damage is common in fish serving as intermediate tapeworm hosts, particularly as the larval plerocercoid migrates through and localizes within visceral organs (Hoffman, 1999).

Thus far, the range of cestodes reported from Great Lakes sea lamprey remain relatively limited (Table 1). Applegate (1950) identified 1 larval *Triaenophorus crassus*, a tapeworm that has a three-host life cycle typically involving a copepod, an intermediate fish host (e.g., a salmonid or coregonid), and ultimately, an esocid final host (Miller, 1952), in the gastrointestinal tract of a single spawning lamprey from the Ocqueoc River Falls and Carp Creek (Lake Huron watershed). McLain (1952) examined 257 sexually mature upstream migrants, 215 downstream migrants (post-metamorphosis), and 29 actively feeding (i.e., parasitic) sea lamprey from the Lake Huron watershed. The author identified *Triaenophorus crassus* in one upstream migrant (0.3% prevalence) and two actively feeding (6.9%) sea lamprey; one was associated with overt tissue damage in the form of "a small cyst-like" growth. Guilford (1954) also reported immature *T. crassus* in sea lamprey (non-specified adult) collected from the Lake Michigan watershed. The same parasite was identified as encysted larvae in the digestive tract of sea lamprey from Lake Huron (non-specified adult; Bangham, 1955), and its adult form was reportedly found in the gastrointestinal tract of three stream-caught (upstream migrant or spawning) sea lamprey from Manitoulin Island, Lake Huron (Wilson and Ronald, 1967). Lawler and Scott (1954) reported *T. crassus* in the intestines of sea lamprey (non-specified adults) from both Lake Huron and Lake Michigan. Although *T. crassus* has been occasionally implicated in mortality events involving other fish species (Bauer and Solomatova, 1984), it seems unlikely that this tapeworm poses serious health threats to Great Lakes sea lamprey.

Another group of cestodes that have been detected in Great Lakes sea lamprey belong to the genus *Proteocephalus* (Table 1), which is widely prevalent in other Great Lakes fish species (Muzzall and Whelan, 2011) and able to cause overt disease under some conditions (Gillilland and Muzzall, 2004; Hunter, 1928). *Proteocephalus longicollis* (syn. *P. exiguus, P. laruei;* Hanzelová and Scholz, 1999; Scholz et al., 2007) parasitizes coregonids and salmonids (Hoffman, 1999), and was detected in the gastrointestinal tracts of Lake Michigan sea lamprey (non-specified adult; average intensity of 7.2 worms per fish) with no gross pathology (Guilford, 1954). Bangham (1955) identified *P. longicollis* in sea lamprey (non-specified adult) from Lake Huron (South Bay and North Channel) and likewise an immature *Proteocephalus* sp. in the digestive tract (Table 1). Wilson and Ronald (1967) also reported mature and immature *Proteocephalus* sp. in the intestines of both stream- and lake-caught sea lamprey (upstream migrant or spawning, and actively feeding, respectively) from the Lake Huron watershed. Given that *P. longicollis* also parasitizes fish hosts that are heavily targeted by Great Lakes sea lamprey (e.g., coregonids and salmonids), sea lamprey may represent an accidental host (i.e., one not normally associated with a given parasite and that may prevent the parasite from completing its life cycle). An *Abothrium* sp. has also been detected in sea lamprey collected from both the Lake Michigan (non-specified adult) and Lake Huron (spawning adult) watersheds (Applegate, 1950; Guilford, 1954), as well as multiple unidentified cestodes (Table 1). Interestingly, all reports of cestodes infecting Great Lakes sea lamprey have been during the adult life stages (Table 1), possibly suggesting that trophic status (e.g., filter-feeding versus parasitism) and/or habitat and other behaviors affect infection status. The reported location of these cestodes exclusively within sea lamprey gastrointestinal tracts may suggest the former.

Nematodes

Nematodes, commonly known as round worms, are among the most abundant metazoan organisms in aquatic environments (Seesao et al., 2017). Of the ~23,000 species belonging to >2,000 nematode genera described thus far, approximately 1/3 are estimated to parasitize freshwater and marine vertebrates (Anderson, 2000), including a multitude of fishes within the Great Lakes basin (Faisal et al., 2010; Muzzall, 1999, 1995). Parasitic nematodes use invertebrates (e.g., copepods, nymphs) as a first intermediate host. This invertebrate host is consumed by fish (either the second or final host) and the nematode develops into an adult in the gastrointestinal tract of the final host (e.g., piscivorous fish, birds, and/or mammals; Hoffman, 1999). Some larval nematodes (i.e., larval migrans) can induce significant damage in the body cavity and visceral organs of hosts, whereas adult nematodes in the gastrointestinal tracts are generally associated with less, but not negligible, overt pathology.

McLain (1952) reported a *Camallanus* sp. in 2% of examined newly transformed sea lamprey, <1% of sexually mature upstream migrants, and 10% of actively feeding sea lamprey, all of which were collected from the Lake Huron watershed (Table 1). The presence of these parasites, which were all female, was frequently associated with either tumor-like growths within the body cavity and gonads, or with vacuolation and/or enlargement of the liver (McLain, 1952). The author went on to suggest that the damage caused by the presence of the parasite could induce sea lamprey mortality and hypothesized that the lamprey likely became parasitized while inhabiting larval beds. In this context, it is noteworthy that McLain's finding of a *Camallanus* sp. in post-metamorphosed sea lamprey is the sole report of a helminth in this life stage (Table 1) within the Great Lakes. Infection by *Camallanus* sp. in other fish species has been linked to suppressed male sexual display rates and reduced mate selection by females (McMinn, 1990), as well as significant liver damage (Shirsat and More, 2018), abdominal swelling, anorexia, intestinal damage, anemia, emaciation, and death (Menezes et al., 2006; Stumpp, 1975).

Multiple cysts, each containing 1–8 juvenile to mature *Truttaedacnitis stelmioides* (syn. *Cucullanus stelmioides*), were discovered in the gonads, liver, and intestinal walls of sea lamprey collected from Lake Huron (spawning, and actively feeding adults; Wilson and Ronald, 1967). Mature worms were rarely found in the gills. Although the prevalence of this parasite was low overall, it was higher (i.e., 2.8%) in lake-caught (feeding) individuals than in stream-caught (spawning) individuals (i.e., 0.4%; Table 1). Despite this low prevalence, the *T. stelmioides* load was high in one fish where 98 worms were detected in the gonads and 10 in the intestine. The authors noted that this individual was likely sterile as a result of parasite-induced damage to the gonads (Wilson and Ronald, 1967). Interestingly, this nematode has also been reported in the liver and intestine of American brook lamprey (*Lethenteron appendix*), a species that is non-trophic as an adult, in Ontario (Pybus et al., 1978b; Renaud, 2011). Hatched *T. stelmioides* larvae are believed to be consumed via filter feeding and remain in the intestine through the summer, migrating via the bile duct to the liver, residing there for up to four years, and migrating back to the intestine when the host metamorphoses (Pybus et al., 1978a). *Truttaedacnitis stelmioides* infection can result in biliary tree changes (e.g., duct dilation, epithelial proliferation, fibrosis), likely due to mechanical obstruction by the parasites (Eng and Youson, 1992).

Another nematode detected in Great Lakes sea lamprey is *Cystidicola stigmatura*, which is well-known for infesting the swim bladders of Great Lakes coregonids and salmonids (Black and Lankester, 1980; Faisal et al., 2010). Only one larval *C. stigmatura* was detected in examined mature (non-specified adult) sea lamprey (Guilford, 1954), possibly suggesting the sea lamprey is an accidental host for this parasite.

Acanthocephalans

Acanthocephalans, commonly referred to as spiny-headed worms, are obligatory endoparasites widely found throughout aquatic and terrestrial systems (Kennedy, 2006). Adult acanthocephalans inhabit the gastrointestinal tract of vertebrate hosts, where nutrient uptake and sexual reproduction take place. Expelled eggs are consumed by a suitable arthropod intermediate host, where the acanthella larvae hatch and develop into the cystacanth stage, which is infective to the definitive vertebrate host that consumes the infected arthropod (Kennedy, 2006). Post-cycle transmission can also occur when definitive hosts harboring adult worms are ingested, thereby leading to intestinal colonization of the predator (McCormick and Nickol, 2004). Although mortality events due to acanthocephalan infestations are uncommon, such infestations can lead to substantial damage to host gastrointestinal tracts (Nickol, 2006) and have been implicated in contributing to wild disease events (e.g., Chinook salmon, *Oncorhynchus tshawytscha*, mortality in Lake Michigan in the late 1980's and early 1990's, Holey et al., 1998).

Echinorhynchus salmonis (syn. *E. coregoni*) is found in salmonids and coregonids around the world (Amin, 1985; Amin and Redlin, 1980; McLain, 1952), including those inhabiting the Great Lakes (Faisal et al., 2011a; Muzzall and Whelan, 2011). Likewise, *E. salmonis* has been detected in Great Lakes sea lamprey multiple times (Applegate, 1950; Bangham, 1955; Guilford, 1954; McLain 1952; Wilson and Ronald, 1967; Table 1). Of the adult sea lamprey examined from the Lake Huron watershed by Applegate (1950; n = 69 from the Ocqueoc River Falls, n = 31 from Carp Creek), *E. salmonis* (syn. *E. coregoni*) was detected in the digestive tracts of 17 individuals (9 males, 8 females; spawning adults). McLain (1952) found intestinal adult acanthocephalans (primarily *E. salmonis* but also *E. leidyi*) to be the most common parasite in the >500 sea lamprey examined from the Lake Huron watershed and noted that all infestations occurred in either sexually mature upstream migrants or actively feeding lake-caught lamprey. The author went on to suggest that no individual lamprey harbored a substantial enough parasite load to be considered harmful and hypothesized that *E. salmonis* colonization likely occurred as a result of accidental amphipod ingestion rather than direct transfer from a salmonid fish host. *Echinorhynchus salmonis* and *E. leidyi* were also identified by Guilford (1954) in mature (non-specified adult) sea lamprey from the Lake Michigan watershed (Table 1). One sea lamprey (non-specified adult) collected from Lake Huron in 1955 was found to contain *E. salmonis* (see Bangham, 1955). Wilson and Ronald (1967) identified *E. salmonis* imbedded in the intestinal wall and gills of adult Lake Huron sea lamprey (13.0% of stream-caught, spawning; 5.1% of lake-caught, feeding lamprey).

One other acanthocephalan species has been reported from Great Lakes sea lamprey: *Neoechinorhynchus cylindratus* (Guilford, 1954; non-specified adult; Table 1), a parasite of many species of centrarchids in North America (Adel-Meguid et al., 1995; Ward, 1940). Similar to the findings for cestodes, all reports of acanthocephalans in Great Lakes sea lamprey have been in the adult stages of this fish (Table 1).

Crustaceans

Most of the approximately 2000 described parasitic arthropod species of fish belong to the subclass Copepoda, some of which lead to skin and muscle damage and compromise host survival (Lester and Hayward, 2006). The life cycles of parasitic crustaceans are as diverse as the group itself, with some species, such as the sea lice (*Lepeophtheirus* spp. and *Caligus* spp.), going through both free swimming, non-parasitic stages as well as parasitic stages. Others, such as *Argulus* spp., hatch directly from eggs laid on inert objects into parasitic stages (Burka et al., 2012; Lester and Hayward, 2006). In addition to direct tissue damage caused by parasite attachment and feeding (Lester and Hayward, 2006), multiple crustacean parasites of fishes have been implicated in transmitting viral fish pathogens to affected hosts (Burka et al., 2012; Hadfield and Smit, 2019).

Reports of copepods parasitizing Great Lakes sea lamprey have been rare, and are currently limited to *Ergasilus* spp., a genus that parasitizes a wide range of freshwater fishes (Tedla and Fernando, 1969). Wilson and Ronald (1967) identified *E. caeruleus* in the gill pouches of adult sea lamprey collected from the Lake Huron watershed at a prevalence of 22.5% in stream captured (spawning) lamprey and 10% in lake specimens (actively feeding; Table 1). Muzzall and Hudson (2004) identified *E. megaceros* in the nasal fossae of one non-specified adult female sea lamprey examined from the Cheboygan River, Michigan. No associated pathological changes were noted in either report.

Mollusks

Freshwater mussels have a complex life cycle, which involves a parasitic larval (glochidium) stage in some species. Mature glochidia are released from the female's brood pouch, and must attach to the fins or gills of an appropriate fish host species for further development to occur (Coker et al., 1921). Interestingly, Wilson and Ronald (1967) identified *Anodontoides ferussacianus* in the gill pouches of n = 34 (12%) stream-caught (spawning) and n = 1 (0.2%) lake-caught (feeding) sea lamprey from the Lake Huron watershed (Table 1). The glochidia were clamped tightly to the epithelial covering of the gill filaments and some had produced an adventitious cyst. *Anodontoides ferussacianus,* found in much of north-central United States and southern Canada, does not require a specific fish host species but rather releases glochidia in a mucus strand that indiscriminately entangles potential hosts (Sowards et al., 2016).

Annelids

Applegate (1950) identified one adult *Piscicola milneri* leech on a spawning sea lamprey from Carp Creek (Lake Huron watershed). The same author noted that additional leeches were observed on

Table 2
Incidence of fungal and oomycete infections in lamprey (S: silver lamprey (*Ichthyomyzon unicuspis*); M: sea lamprey (*Petromyzon marinus*); P: Pacific lamprey (*Entosphenus tridentatus*); A: Arctic lamprey (*Lethenteron camtschaticum*); K: Far Eastern brook lamprey (*Lethenteron reissneri*)), with information on lamprey life stage (L: larvae; M: metamorphosizing juvenile; P: post-metamorphosis; A: non-specified adult; F: actively feeding adult; S: upstream migrant or spawning adult), watershed from which fish were collected (M: Lake Michigan; H: Lake Huron; S: Lake Superior), tissue location, and prevalence (total number of fish examined in parentheses). NR: not reported. NI: not identified.

Lamprey Species	Lamprey Life stage	Watershed	Tissue	Pathogen	Prevalence	Reference
M	F	H	NR	*Saprolegnia parasitica*	NR	McLain, 1952
M	P	M	NR	NI	NR	Parker and Lennon, 1956
M	M	Ford River, MA	Tail	NI	1.5% (263)	Simard et al., 2017
M	S	H	NR	NI	NR	Wilson and Ronald, 1967
P	P	Idaho, Washington, Oregon	NR	NI	1.2% (20,000)	Jackson et al., 2019
A	L	Captive reared	NR	*Saprolegnia ferax*	NR	Zhang et al., 2019
P	M	Columbia River, Washington	Head, tail	NI	3–60% (1,422)	Mueller et al., 2006
K	NR	Seomjin River, South Korea		*Saprolegnia parasitica*		Kim et al., 2013
S	A	Peshtigo River, M	Head, mouth	*Saprolegnia* sp.	12.5% (8)	MSU-AAHL Records, 2009
M	A	H	Caudal fin	*Saprolegnia* sp.	33.3% (3)	MSU-AAHL Records, 2014
M	A	Bridgeland Creek, H	Skin	*Saprolegnia* sp.	50.0% (12)	MSU-AAHL Records, 2014
			Teeth	*Scopulariopsis* sp.	100.0% (3)	
M	A	Chequamegon Bay, S	Skin, gills, mouth	*Saprolegnia* sp.	100.0% (10)	MSU-AAHL Records, 2016
M	A	Blind River, H	Skin	*Saprolegnia* sp.	75.0% (12)	MSU-AAHL Records, 2016
M	A	H	Skin	*Saprolegnia* sp.	12.5% (8)	MSU-AAHL Records, 2017
M	A		Fin, eye, skin, mouth	*Saprolegnia* sp.	100.0% (6)	MSU-AAHL Records, 2019

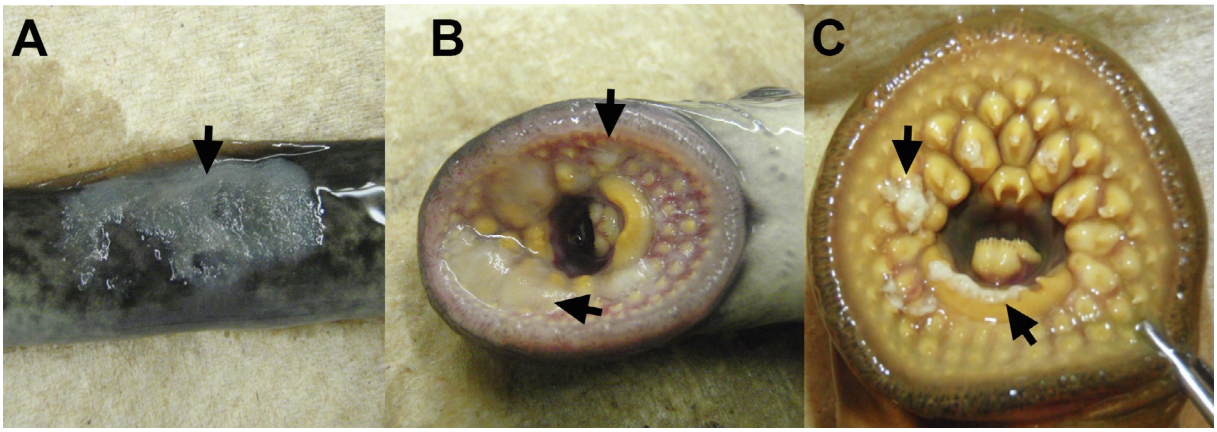

Fig. 1. A. Grossly visible whitish masses (arrow) of *Saprolegnia* sp. (Oomycota) hyphae on the skin of a sea lamprey collected from Chequamegon Bay (Lake Superior watershed). B. Grossly visible whitish masses (arrows) of *Saprolegnia* sp. (Oomycota) hyphae associated with the oral disk and teeth of a sea lamprey collected from Chequamegon Bay (Lake Superior watershed). C. Grossly visible whitish masses (arrows) associated with the ulcerating teeth of a post-spawn sea lamprey collected from Bridgeland Creek (Lake Huron watershed). The fungus, *Scopulariopsis* sp., was isolated and identified from these masses, as well as from the underlying tissues.

other sea lamprey; however, the number and species were not reported.

Infections caused by fungi and oomycetes

Diseases caused by true fungi (at least nine phyla) and water molds (oomycetes; Phylum *Oomycota*) are widespread in fishes inhabiting the Great Lakes (Records of the MSU-AAHL), and most are considered secondary to a range of primary insults, including stress, immunosuppression, suboptimal environmental conditions, and/or other infections (Bruno et al., 2011). In this context, most published reports of fungi and oomycete infections in Great Lakes sea lamprey have been documented in individuals held in aquaria under artificial conditions. For example, McLain (1952) reported infections with the oomycete, *Saprolegnia parasitica,* in aquarium-held, actively feeding sea lamprey collected from the Lake Huron watershed (Table 2). Likewise, Parker and Lennon (1956) noted multiple mortality events in parasitic phase Great Lakes sea lamprey maintained in aquaria, during which "fungi" were observed; however, other than noting a *Saprolegnia* sp. (oomycete) was involved in one event, further identification of these organisms and the presence of any other underlying infections were not reported (Table 2). Fungal infections (causative organism unknown) have been reported in juvenile metamorphosing sea lamprey that were tagged with passive internal transponder (PIT) tags and held in aquaria (Simard et al., 2017), although the role these infections play in the mortality of tagged fish remains unclear (Table 2). Unidentified fungi have also been detected in stream caught, spawning sea lamprey collected from the Lake Huron watershed, as reported by Wilson and Ronald (1967; Table 2).

Infections caused by fungi and water molds have also been detected more recently during Great Lakes sea lamprey health surveillance studies at the MSU-AAHL (adults; Table 2). Although most infections were attributed to *Saprolegnia* spp. (Table 2; Fig. 1A, B), in one case, a true fungus was recovered from whitish to greyish masses that were tightly adhered to ulcerating sea lamprey teeth (Fig. 1C; Table 2). PCR and gene sequence analyses of both the recovered fungal isolate and the affected tissues collected directly from the teeth revealed that the fungus belonged to the genus *Scopulariopsis* (family *Microascaceae;* manuscript in preparation), a genus that is associated with opportunistic infections in an array of host species, including humans (Park et al., 2020).

Bacterial infections

A multitude of enzootic and emerging fish-pathogenic bacteria cause disease outbreaks in both wild and hatchery-reared Great

Table 3

Bacteria isolated from lamprey (A: Arctic lamprey (*Lethenteron camtschaticum*); P: Pacific lamprey (*Entosphenus tridentatus*); U: Ukrainian brook lamprey (*Eudontomyzon mariae*); E: European brook lamprey (*Lampetra planeri*); R: European river lamprey (*Lampetra fluviatilis*); W: western brook lamprey (*Lampetra richardsoni*); B: American brook lamprey (*Lethenteron appendix*); G: pouched lamprey (*Geotria australis*); C: Caspian lamprey (*Caspiomyzon wagneri*); N: northern brook lamprey (*Ichthyomyzon fossor*); S: silver lamprey (*Ichthyomyzon unicuspis*); T: chestnut lamprey (*Ichthyomyzon castaneus*); V: western river lamprey (*Lampetra ayresii*); and M: sea lamprey (*Petromyzon marinus*)), with information on lamprey life stage (L: larvae; A: non-specified adult; F: actively feeding adult; S: upstream migrant or spawning adult), location and prevalence (total number of fish examined in parentheses). NR: Not Reported. Und.: Undetermined (see footnote).

Bacterium	Lamprey Species	Lamprey Life stage	Watershed	Tissue	Prevalence	Reference
Aeromonas salmonicida	M	A	Lake Ontario	Kidney	2.5% (118)	Faisal et al., 2007
	M	A	Lake Ontario	Kidney	1.2% (343)	Diamanka et al., 2014
	M	A	Lake Huron	Kidney	16.7% (6)	MSU-AAHL Records, 2019
	T	F	Manistee River	NR	66.7% (12)	Hall, 1963
	P	A	Idaho, Washington, Oregon	Kidney, liver, and/or heart	11.7% (794)	Jackson et al., 2019
	P	L	Columbia River	NR	40.7% (27)	Jolley and Lujan, 2019
	G	S	Southland, New Zealand	NR	4.3% (188)	Brosnahan et al., 2019
Motile *Aeromonas* sp.	M	A	Lake Huron			Wilson, 1967
	M	L,A	Lake Ontario	Kidney	NR	MSU-AAHL Records, 2005
	M	A	Lake Ontario	Kidney	14.9% (67)	MSU-AAHL Records, 2006
	M	A	Lake Ontario	Kidney	18.0% (50)	MSU-AAHL Records, 2007
	M	A	Lake Ontario	Kidney, Liver	20.3–23.7% (59)	MSU-AAHL Records, 2008
	M	A	Lake Ontario	Kidney	25.0% (48)	MSU-AAHL Records, 2010
	M	A	Lake Ontario	Kidney	13.3% (30)	MSU-AAHL Records, 2011
	M	A	Lake Huron	Skin	100% (3)	MSU-AAHL Records, 2014
	M	A	Lake Superior	Kidney	54.5% (11)	MSU-AAHL Records, 2016
	M	A	Lake Huron	Kidney	33.3% (12)	MSU-AAHL Records, 2016
	M	A	Lake Huron	Kidney	20.0% (10)	MSU-AAHL Records, 2017
	M	A	Lake Huron	Kidney	50.0% (6)	MSU-AAHL Records, 2019
	B	NR	Lake Huron	NR	NR	Ronald and Wilson, 1968
	B,M	L	Lake Huron and Lake Superior	NR	NR	McDermott, 1968
	G	S	Warren River, Australia	Kidney, Gills	75% (4)	Hilliard et al., 1979
	G	S	Southland, New Zealand	NR	NR	Brosnahan et al., 2019
	S	S	Lake Huron	Kidney	33.3% (3)	MSU-AAHL Records, 2008
	S	A	Lake Michigan	Kidney	41.7–50.0% (12)	MSU-AAHL Records, 2009
	S	A	Lake Huron	Kidney	21.4% (14)	MSU-AAHL Records, 2010
	P	NR	NR	Kidney	40.0% (5)	MSU-AAHL Records, 2005
	P	L	Clackamas River	NR	NR	Jolley and Lujan, 2019
Flavobacterium psychrophilum	M	A	Lake Ontario	Skin	1.7% (118)	Elsayed et al., 2006
	M	A	Lake Ontario	Kidney	3.3% (30)	MSU-AAHL Records, 2011
Flavobacterium columnare	M	A	Lake Huron	Kidney, Mouth, Skin	16.7% (6)	MSU-AAHL Records, 2019
Flavobacterium sp.	M	A,L	Lake Ontario	NR	NR	Loch et al., 2013
	M		Lake Ontario	Kidney	3.3% (60)	MSU-AAHL Records, 2010
	M		Lake Ontario	Kidney	6.7% (30)	MSU-AAHL Records, 2011
	M		Lake Huron	Kidney	NR	MSU-AAHL Records, 2014
	M		Lake Superior	Kidney	NR	MSU-AAHL Records, 2016
	M		Lake Huron	Kidney	NR	MSU-AAHL Records, 2016
	M		Lake Huron	Kidney	NR	MSU-AAHL Records, 2017
	M		Lake Huron	Kidney, Mouth	50.0% (6)	MSU-AAHL Records, 2019
	N	NR	Lake Huron	Kidney	6.3% (16)	Loch et al., 2013

(*continued on next page*)

Table 3 (*continued*)

Bacterium	Lamprey Species	Lamprey Life stage	Watershed	Tissue	Prevalence	Reference
	S	A	Lake Huron	Kidney	33.% (3)	MSU-AAHL Records, 2008
	S	A	Lake Michigan	Kidney	12.5% (8)	MSU-AAHL Records, 2009
Chryseobacterium sp.	M	NR	Lake Ontario	Fins	NR	Loch et al., 2013
	M	A	NR	Kidney, Teeth	16.7% (12)	MSU-AAHL Records, 2014
Pseudomonas fluorescens	G	S	Warren River, Australia	Liver	50.0% (4)	Hilliard et al., 1979
	P	L	Eagle Creek	NR	NR	Jolley and Lujan, 2019
Pseudomonas sp.	M	A	Lake Huron			Wilson, 1967
Shewanella sp.	M	A	Lake Ontario	Kidney	10.8% (37)	MSU-AAHL Records, 2006
	M	A	Lake Ontario	Kidney	3.3% (30)	MSU-AAHL Records, 2007
	M	A	Lake Ontario	Kidney	16.7% (30)	MSU-AAHL Records, 2010
	M	A	Lake Superior	Kidney	9.1% (11)	MSU-AAHL Records, 2016
	M	A	Lake Huron	Kidney	8.3% (12)	MSU-AAHL Records, 2016
	M	A	Lake Huron	Kidney	10.0% (10)	MSU-AAHL Records, 2017
	N	*Und.	Lake Huron	Kidney	4.5% (22)	MSU-AAHL Records, 2009
	S	A	Lake Michigan	Kidney	41.7% (12)	MSU-AAHL Records, 2009
	S	A	Lake Huron	Kidney	33.3% (3)	MSU-AAHL Records, 2008
	S	A	Lake Huron	Kidney	28.6% (14)	MSU-AAHL Records, 2010
Renibacterium salmoninarum	M	S	Lake Ontario	Kidney, Blood	0–66% (143)	Eissa et al., 2006
	M	A	Lake Ontario	Kidney	10.0% (30)	MSU-AAHL Records, 2006
	M	A	Lake Ontario	Kidney	21.9% (64)	MSU-AAHL Records, 2010
	P	A	Washington	Kidney	0.7% (794)	Jackson et al., 2019
	V	A	Puget Sound, Washington	Kidney, Gut	57.6%, 78.8% (33)	Rhodes et al., 2011
Carnobacterium sp.	G	S	Southland, New Zealand	NR	NR	Brosnahan et al., 2019

*Fish lengths ranged from 10.6 to 13.3 cm (cm).

Lakes fishes (Faisal et al., 2011b; Holey et al., 1998; Loch and Faisal, 2015). Likewise, several bacteria have been linked to infections, and occasionally overt disease, in Great Lakes sea lamprey. Among the earliest of such reports were those of Wilson (1967; unspecified adults) and McDermott (1968; larvae), both of whom detected multiple motile *Aeromonas* spp. (family *Aeromonadaceae*) in sea lamprey collected from Lakes Huron and Superior tributaries. Although the species detected by both authors are unclear given ongoing and substantial taxonomic changes within *Aeromonadaceae*, the *Aeromonas* isolates recovered by McDermott (1968) clearly were pathogenic to sea lamprey, as evidenced by: a) their isolation from the blood of captive larval sea lamprey showing severe diffuse hemorrhage and anal bleeding; and b) the same disease signs and rapid mortality in experimentally exposed larval sea lamprey. More recently, motile *Aeromonas* spp. were detected in larval and adult sea lamprey collected from the Lake Superior, Huron and Ontario watersheds (2005–2019; MSU-AAHL Records; Table 3). Although most infections were detected in the kidney tissues, motile *Aeromonas* spp. were also occasionally recovered from the liver and external lesions (Table 3). A range of grossly appreciable external signs of disease were observed in sea lamprey infected with motile *Aeromonas* spp., including varying degrees of skin and/or fin erosion and ulceration; ocular hemorrhage with or without corneal opacity; exophthalmia; rare hemorrhage of the fins and/or oral disk; and rarely, a co-occurrence of *Saprolegnia* spp. The most commonly observed internal sign of disease in fish infected with motile *Aeromonas* was hemorrhagic enteritis, whereas liver mottling and congestion of the reproductive tissues and kidneys occurred less frequently. It should be noted, however, that although many of these disease signs overlap with those that are reported in other fish species infected with motile *Aeromonas* spp., it is impossible to solely ascribe them to *Aeromonas* spp. infections.

Another member of *Aeromonadaceae* that has been recovered from Great Lakes sea lamprey on several occasions is *Aeromonas salmonicida*, causative agent of furunculosis and one of the most damaging bacterial fish pathogens globally (Gudmundsdottir and Bjornsdottir, 2017). This non-motile, Gram-negative bacterium was first reported in three diseased mature sea lamprey collected from Duffins Creek and Humber River (Lake Ontario watershed) in eastern Ontario, Canada (Faisal et al., 2007; Table 3). Importantly, this study provided evidence that *A. salmonicida* was not only capable of causing systemic infections in sea lamprey, but also clinical furunculosis due to the bacterium's association with furuncle-like lesions and skin ulcerations in infected hosts. Systemic *A. salmonicida* infections were again detected in sea lamprey collected from Duffins Creek and Humber River during surveillance from 2005 to 2011 (Diamanka et al., 2014; Table 3). Although the recovered *A. salmonicida* isolates varied genetically and phenotypically, all proved to be highly virulent to rainbow trout in experimental challenges (Diamanka et al., 2014). Most recently, systemic *A. salmonicida* infections were detected in a moribund mature sea lamprey submitted to the MSU-AAHL in the summer of 2019 (Table 3). Of note, this same fish was suffering from a mixed systemic infection comprised of motile *Aeromonas* spp. and *Flavobacterium columnare* (see below). Collectively, these studies confirm that *A. salmonicida* is not only capable of causing systemic infections in sea lamprey, but also generating overt disease in some individuals. What remains to be clarified, however, is whether *A. salmonicida* can cause mortality in sea lamprey, including in larval stages, and whether infected sea lamprey can serve as competent vectors for this pathogen.

Another group of Gram-negative bacteria that contains several devastating pathogens of fish is the family *Flavobacteriaceae* (Bernardet and Nakagawa, 2006), among the most notorious of which is *Flavobacterium psychrophilum*, causative agent of Bacterial Coldwater Disease and Rainbow Trout Fry Syndrome (reviewed in Loch and Faisal, 2017). This bacterium was recovered from sea lamprey that were collected from Duffins Creek (5/58, 3.5% prevalence; Table 3), which presented shallow skin ulcerations, severe fin erosion, and a white film covering the nares (Elsayed et al., 2006). Of note, *F. psychrophilum* was not detected amongst sea lamprey (n = 60) collected from the Humber River (Elsayed et al., 2006).

Another *Flavobacterium* species with an exceptionally wide host range and of global significance for fish health is *F. columnare*, etiological agent of columnaris disease (reviewed in Loch and Faisal, 2017). It has been suggested that *F. columnare* is capable of infecting and causing subsequent disease in nearly all freshwater fish species (Starliper and Schill, 2011), and recent investigations in the MSU-AAHL revealed that sea lamprey appear to be no exception. In the summer of 2019, *F. columnare* was recovered from the kidneys of a sea lamprey that was also co-infected with *A. salmonicida* and motile *Aeromonas* spp. (Table 3).

In addition to *F. psychrophilum* and *F. columnare*, several other *Flavobacterium* spp. have been recovered from the kidneys of systemically infected adult and larval sea lamprey collected from Duffins Creek and Covert Creek (Lake Ontario water shed; Loch et al., 2013). However, the detected *Flavobacterium* spp. were either only recently described, or are phylogenetically distinct from all known *Flavobacterium* spp. (Loch et al., 2013), making determination of their effects on sea lamprey health unclear at this time. Similarly, multiple species of the genus *Chryseobacterium* (family *Flavobacteriaceae*) have been recovered from the eroding fins of Great Lakes sea lamprey (Loch et al., 2013).

Several other infections caused by Gram-negative bacteria have also been detected in Great Lakes sea lamprey, including *Pseudomonas* sp. (Wilson, 1967; family *Pseudomonadaceae*) and *Shewanella* sp. (family *Alteromonadaceae;* Records of the MSU-AAHL; Table 3). *Shewanella* sp. isolates were recovered from adult sea lamprey collected on seven different occasions from 2006 to 2017 (Humber River and Duffins Creek, Lake Ontario watershed; Chequanegon Bay and Blind River, Lake Superior watershed; Table 3). Clinical findings in affected fish ranged from grossly normal to varying degrees of exophthalmia, hemorrhagic enteritis, hepatic mottling, and/or petechial hemorrhage of the testes.

Compared to infections caused by Gram-negative bacteria, published reports of Gram-positive bacteria infecting Great Lakes sea lamprey are less frequent. Eissa et al. (2006) isolated *Renibacterium salmoninarum*, causative agent of Bacterial Kidney Disease, at a prevalence ranging from 2% to 16% in adult sea lamprey collected from Duffins Creek and Humber River (Table 3). However, when kidney tissues were tested using a semi-quantitative enzyme-linked immunosorbent assay (Q-ELISA) and nested PCR, infection prevalence was much higher, likely resulting from the higher diagnostic sensitivity of these tests (Eissa et al., 2006). Since then, *R. salmoninarum* has been detected in sea lamprey from Duffins Creek (2006, 2010) and Humber River (2010) via Q-ELISA (Table 3; Records of the MSU-AAHL). An additional 322 adult sea lamprey were tested for *R. salmoninarum* via Q-ELISA from 2006 to 2017 and no *R. salmoninarum* was detected (Records of the MSU-AAHL).

Viral infections

There is little information regarding viruses that infect sea lamprey, whether in their native range or in the Great Lakes. From 2005 to 2020, 878 Great Lakes sea lamprey were collected from the Lake Ontario, Huron, Superior, and Michigan watersheds and analyzed for the presence of viruses via tissue culture at the MSU-AAHL, and no individuals were found to harbor active virus infections. It is important to note, however, that cell lines derived from sea lamprey are currently unavailable, potentially impeding detection of lamprey-specific viruses.

To date, the only virus that has been reported in Great Lakes sea lamprey is the *Piscine novirhabdovirus* (historically known as the Viral Hemorrhagic Septicemia Virus, VHSV; Order *Mononegavirales*; genus *Novirhabdovirus*). In 2008, following routine surveillance of sea lamprey collected from multiple sites in Michigan, VHSV IVb was isolated and its identity confirmed (Great Lakes Fishery Commission, 2009; lamprey life stage not reported; Table 4). In a subsequent laboratory challenge experiment, Coffee et al. (2017) noted evidence of virus replication in spawning phase sea lamprey intra-coelomically injected with VHSV IVb, as determined by a significant increase in viral loads in tissues from experimentally challenged sea lamprey. However, infected sea lamprey developed very mild microscopic lesions, and no fish died, suggesting that VHSV likely leads to subclinical infections in sea lamprey (Coffee et al., 2017).

Pathogens and parasites of sea lamprey beyond the Laurentian Great Lakes

Although sea lamprey populations outside of the Laurentian Great Lakes may also be susceptible to multiple microbial infections and parasites, there are far fewer published reports to that

Table 4
Viruses isolated from lamprey (R: European river lamprey (*Lampetra fluviatilis*); and M: sea lamprey (*Petromyzon marinus*)), with information on lamprey life stage (S: upstream migrant or spawning adult), location and prevalence (total number of fish examined in parentheses). NR: Not Reported. Viral Hemorrhagic Septicemia Virus genotype denoted in parentheses.

Virus	Lamprey Species	Lamprey Life stage	Watershed	Tissue	Prevalence	Reference
Viral Hemorrhagic Septicemia Virus (II)	R	S	Lestijoki and Kalajoki rivers, Finland	Kidney, Liver, Heart, Brain	1.9% (262*)	Gadd et al., 2010
Viral Hemorrhagic Septicemia Virus (IVb)	M	NR	Lake Huron	Kidney	NR	Great Lakes Fishery Commission, 2009
Infectious Pancreatic Necrosis Virus	R	NR	Loch Awe, Scotland	NR	0.9% (115)	Munro et al., 1976

*Pools of up to 10 fish/pool. A total of 2621 fish were tested.

Table 5
Parasites recorded in sea lamprey (*Petromyzon marinus*), from outside the Great Lakes Basin (tropic stage marine environments), with information on lamprey life stage (P: post-metamorphosis; D: post-spawning adult; A: non-specified adult), parasite life stage (L: larvae; I: immature; A: adult), host tissue origin, prevalence (total number of fish examined in parentheses) and intensity. NR: Not Reported.

Parasite Taxon	Parasite Life stage	Lamprey Life stage	Location	Tissue	Prevalence	Intensity	Reference
Nematodes (Phylum Nemathelminthes, Class Nematoda)							
Anisakis simplex	L	S,D	Ulla and Tea Rivers, Spain	Flesh, Gonad, Kidney, Liver, Gut, Visceral cavity	56.3% (64)	1–10	Bao et al., 2013
	L	P	Dordogne and Garonne Rivers, France	Gonad	1.7% (115)	1	Gérard et al., 2015
Hysterothylacium aduncum			Barents Sea				‡Polyansky, 1955
Annelids (Phylum Annelida, Class Clitellata)							
Piscicola zebra	A	NR	Nova Scotia, Canada	Lips	NR	NR	Moore, 1898

‡ per Sobecka et al., 2009.

Table 6
Parasites recorded in Great Lakes basin (lake watershed: M: Michigan; S: Superior; H: Huron; O: Ontario) lamprey (N: northern brook lamprey (*Ichthyomyzon fossor*), and B: American brook lamprey (*Lethenteron appendix*)), with information on lamprey life stage (A: non-specified adult), parasite life stage (L: larvae; I: immature; A: adult), host tissue origin, prevalence (total number of fish examined in parentheses) and intensity. NR: Not Reported. Und.: Undetermined (see footnote).

Parasite Taxon	Parasite Life stage	Lamprey Species	Lamprey Life stage	Watershed	Tissue	Prevalence	Intensity	Reference
Protozoa, Myxozoa, and Microsporidia								
Trichodina spp.	NR	N	**Und.	H	Gills	12.5% (16)	NR	MSU-AAHL Records, 2008
	NR	N	***Und.	H	Gills	40% (20)	NR	MSU-AAHL Records, 2009
Nematodes (Phylum Nemathelminthes, Class Nematoda)								
Truttaedacnitis stelmioides	A,L	B		Ontario, Canada	Intestine, Liver	91.3% (378)	1–31	Pybus et al., 1978b
Acanthocephalans (Phylum Acanthocephala)								
Unidentified sp.*	A	B	A	M,H	Hindgut	100% (2)	2–3	Cochran, 2008

*General description matching that of *Echinorhynchus salmonis* (Cochran, 2008). **Fish lengths ranged from 10.6 to 14.7 cm. ***Fish lengths ranged from 10.6 to 13.3 cm.

end (Table 5). Among these are two reports documenting sea lamprey from Europe infected with *Anisakis simplex* (Table 5), a nematode of particular note due to the significant human health risk this parasite also poses (Pravettoni et al., 2012). *Anisakis simplex* has a complex life cycle, whereby adults embed in the gastrointestinal mucosa of infected marine mammals and eggs are expelled in the feces (Pravettoni et al., 2012). First stage larvae form in the free-floating eggs, molt into second stage larvae and are consumed by crustaceans, in which they molt into and remain in the L3 stage, at which point they are infectious to fish who consume them (Pravettoni et al., 2012). Following consumption of the infected fish by a marine mammal, the life cycle is completed as the larva develops into an adult worm (Pravettoni et al., 2012). Human infection resulting from consuming raw or undercooked parasitized fish (Audicana and Kennedy, 2008; Pravettoni et al., 2012), has led to gastrointestinal disease, as well as immunological, allergic-type and hypersensitivity reactions (Audicana and Kennedy, 2008; Pravettoni et al., 2012).

Bao et al. (2013) examined 64 sea lamprey (n = 50 upstream migrants; n = 14 post-spawn) captured in Galician rivers (NW Spain; Table 5). *Anisakis simplex* was identified in the sea lamprey using a combination of tissue digestion, stereomicroscopy and molecular analysis. The parasites were located in the muscle, gonads, kidneys, liver, and body cavity of some upstream migrants, but predominantly in the muscle and visceral cavities of post-spawning fish (Bao et al., 2013). During their marine trophic phase, sea lamprey have been noted to co-occur with and occasionally feed upon marine mammals (Nichols and Tscherter, 2011), representing a possible infection route. Bao et al. (2013) concluded that sea lamprey likely represent a paratenic host (i.e., an alternative intermediate host in which the parasite can exist, but where no parasite development occurs) for *A. simplex*, a matter of note given that sea lamprey are considered a delicacy in some cultures (Docker et al., 2015). *Anisakis simplex* was also identified from post-metamorphic sea lamprey collected from three French rivers and the northeast Atlantic coastal waters over a one-year period (Gérard et al., 2015).

Another nematode, *Hysterothylacium aduncum,* was identified from sea lamprey in the Barents Sea (Polyansky, 1955). *Hysterothylacium aduncum* has a similar life cycle to *A. simplex* with the exception of the final host being a fish rather than a marine mammal (Klimpel and Rückert, 2005). Although humans can become exposed to *H. aduncum* through the consumption of raw or undercooked fish, its role in human infection remains highly debated (Cavallero et al., 2020).

There is a single report of an annelid leech (*Piscicola zebra*) found on the lips of sea lamprey from Nova Scotia, Canada (Moore 1898; Table 5).

Pathogens and parasites of lamprey species native to the Great Lakes basin

Four lamprey species are native to the Great Lakes basin of North America: the northern brook lamprey (*Ichthyomyzon fossor*), silver lamprey, American brook lamprey, and chestnut lamprey (*Ichthyomyzon castaneus;* Renaud, 2011; Maitland et al., 2015). Adult northern brook and American brook lamprey are non-trophic, whereas silver and chestnut lamprey have parasitic adult stages (non-specific blood feeders on a range of freshwater fishes; Renaud and Cochran, 2019; Renaud, 2011). As is the case for sea lamprey within their native range, very little is known about the microbial infections and parasites that occur in these Great Lakes natives. In fact, we are aware of only one published report of a parasite and four reports of bacterial diseases, collectively, in these species (Tables 3, 6).

American brook lamprey

Cochran (2008) detected an acanthocephalan in the hindgut of two “giant” American brook lamprey (one from the Lake Michigan watershed, and one from Lake Huron; Table 6) that resembled *E. salmonis*, but unfortunately could not be definitively identified to the species level.

Pybus et al. (1978a, 1978b) identified high intensities (>90%) of the nematode *Truttaedacnitis stelmioides* in American brook lamprey larvae and adults collected from the Lakes Erie and Ontario watersheds (Table 6). The authors suggested that the parasite larvae were ingested directly by the lamprey ammocoetes after which, the parasite life cycle appears to be closely tied with that of the lamprey, as the *T. stelmioides* moulted in the liver and migrated to the lamprey intestine to mature as the lamprey underwent metamorphosis. While brook lamprey are non-tropic as adults and have a non-functioning intestine, Pybus et al. (1978b) recovered eggs shed from adult lamprey, indicating the potential for parasite transmission despite the supposed closure of the lamprey intestine soon after transformation.

McDermott (1968) reported the isolation of an *Aeromonas* sp. from the blood of dead and moribund American brook lamprey ammocoetes being held in captivity at the University of Guelph after being collected from the Lake Huron and Lake Superior watersheds (Table 3). Diseased fish had diffuse hemorrhage throughout their bodies. The isolated *Aeromonas* sp. was experimentally injected subcutaneously into American brook lamprey, and resulted in mortality and gross disease signs within 48 h that were consistent with the initial disease event. Ronald and Wilson (1968) also detected an *Aeromonas* sp. from American brook lamprey (Table 3), but further detail was not provided.

In 2009, 93 American brook lamprey (Lake Superior watershed; fish length 2.1–17.2 cm) were examined by the MSU-AAHL with no signs of disease, microbial infections, or parasites detected.

Chestnut lamprey

Hall (1963) reported that actively feeding chestnut lamprey from the Manistee River, Michigan, which were being held for use in experimental monitoring, repeatedly suffered from furunculosis outbreaks, which in some cases led to ≤75% mortality. However, no information on bacterial isolation and/or identity confirmation as *A. salmonicida* was given.

Silver lamprey

From 2008 to 2010, a total of 32 adult silver lamprey (Lakes Huron and Michigan watersheds) were examined by MSU-AAHL personnel. Bacteriological analyses of kidney tissues yielded a *Flavobacterium* sp. from two silver lamprey (one in 2008, one in 2009; Table 3). *Shewanella* spp. were recovered from multiple silver lamprey, and motile *Aeromonas* spp. were recovered on four separate occasions (Table 3). The only abnormal gross finding from the silver lamprey infected with motile *Aeromonas* spp. was ovarian congestion in a single fish. No parasites were detected in these fish.

Northern brook lamprey

From 2008 to 2010, 64 northern brook lamprey (Lake Huron watershed; fish lengths 10.0–14.7 cm) were examined by MSU-AAHL personnel. On two separate occasions (2008 and 2009), a *Trichodina* sp. was observed from the gills of northern brook lamprey at varying prevalence and intensities (Table 6). Bacteriological analyses of kidney tissues yielded a *Flavobacterium* sp. from a single northern brook lamprey in 2008 (Loch et al., 2013; Table 3). However, the only abnormal gross finding in the northern brook lamprey was severe congestion of the ovaries. Likewise, *Shewanella* spp. were recovered from a single northern brook lamprey (Table 3).

Pathogens and parasites of other lamprey species beyond the Laurentian Great Lakes

For other species outside of the Great Lakes, much of the published literature on parasites and microbial infections come from Pacific lamprey on the west coast of the United States, Arctic lamprey (*Lethenteron camtschaticum*) in Japan, pouched lamprey (*Geotria australis*) from Australia, and European river lamprey (Tables 3, 4, 7). Of note, adult Arctic, pouched, and European lamprey are believed to primarily feed upon the flesh of their host, whereas Pacific lamprey are often considered flesh – blood feeders (Renaud and Cochran, 2019).

Protozoa, myxozoa and microsporidia

Using ultrastructural analyses, Mori et al. (2000) reported frequent parasitism of Arctic lamprey in Japan with myxosporean trophozoites that were found in the kidneys (Table 7). Although species identification was not possible due to a lack of mature spores, infection was observed in 10/13 non-specified adults and 2/3 ammocoetes obtained from three separate rivers. Interestingly, immune cell presence seemed to directly correlate with trophozoite load (i.e., areas with more parasites contained more immune cells, while immune cells were rare when trophozoites were few or absent), suggesting a local immune response against the infection.

There are two reports of parasitic ciliates occurring in various lamprey species as well (Table 7). Jolley and Lujan (2019) examined a total of 164 larval (2009, 2012, 2013) and 27 adult (2014) Pacific lamprey from the Clackamas River subbasin in Washington state and detected *Trichodina* spp. at low intensities and prevalence in the gills of the larvae. Honma et al. (1982) identified a *Urceolaria* sp. ciliate while performing scanning electron microscopy as part of a larger histological study on metamorphosizing juvenile Arctic lamprey, whereby the ciliates were attached to the oral mucosa of a lamprey collected from the Ishikawa River, Japan. Areas of mucosal swelling were evident where parasites had detached.

Trematodes

Zekhnov (1958) reported a number of larval trematodes from the Ukrainian brook lamprey (*Eudontomyzon mariae*) and European brook lamprey (*Lampetra planeri*) in eastern Europe (Table 7). These included *Metorchis* sp., *Apophallus* sp., *Paratormopsolus siluri*, *Diplostomum spathaceum*, *D. petromyzontis fluviatilis*, *Neodiplostomulum hughesi*, *Tetracotyle* sp., as well as a number of unidentified Acanthocolpidae metacercaria, some of which come from known or likely zoonotic genera (Mordvinov et al., 2012; Palmieri and Heckmann, 1976; Shin et al., 2006). Sweeting (1976) reported on the life cycle of *Diplostomum* sp. metacercariae originally collected from the brains of European river lamprey. Various *Diplostomum* spp. were also noted from European river lamprey by Dogel and Petruševkij (1933), Gecevičute (1974), and Shulman (1950, 1957), and from European brook lamprey by Gintovt (1969; Table 7). Shulman (1950, 1957) also identified adult *Sphaerostoma bramae* in the intestines of European river lamprey from the Neva River, Russia (Table 7). Beverley-Burton and Margolis (1982) identified a novel species of *Ophioxenos*, designated *O. lampetrae,* in the intes-

Table 7

Parasites recorded in other lamprey species (A: Arctic lamprey (*Lethenteron camtschaticum*); P: Pacific lamprey (*Entosphenus tridentatus*); U: Ukrainian brook lamprey (*Eudontomyzon mariae*); E: European brook lamprey (*Lampetra planeri*); R: European river lamprey (*Lampetra fluviatilis*); W: western brook lamprey (*Lampetra richardsoni*); B: American brook lamprey (*Lethenteron appendix*); G: pouched lamprey (*Geotria australis*); C: Caspian lamprey (*Caspiomyzon wagneri*); S: silver lamprey (*Ichthyomyzon unicuspis*)) outside the Great Lakes basin, with information on lamprey life stage (L: larvae; M: metamorphosizing juvenile; A: non-specified adult; F: actively feeding adult; S: upstream migrant or spawning adult), parasite life stage (L: larvae; I: immature; A: adult), host tissue origin, prevalence (total number of fish examined in parentheses) and intensity. NR: Not Reported.

Parasite Taxon	Parasite Life stage	Lamprey Species	Lamprey Life stage	Location	Tissue	Prevalence	Intensity	Reference
Protozoa, Myxozoa, and Microsporidia								
Myxosporean sp.	I	A	L,A	Agano, Ebetsu, and Makomanai Rivers, Japan	Kidney	75.0% (16)	Numerous	Mori et al., 2000
Trichodina sp.	NR	P	L	Clackamas River subbasin	Gills	1.8% (164)	Low	Jolley and Lujan, 2019
Urceolaria sp.	NR	A	M	Ishikawa River, Japan	Oral mucosa	NR	NR	Honma et al., 1982
Trematodes (Phylum Platyhelminthes, Class Trematoda)								
*Various spp.	NR	U,E		Eastern Europe	NR	NR	NR	Zekhnov, 1958
Diplostomum sp.	I	R		River Ure, Yorkshire	Brain, Spinal cord	100% (40)	2–51	‡Sweeting, 1976
		E						‡Dogel and Petruševkij, 1933 ‡Gecevičute, 1974 ‡Shulman, 1950, 1957 ‡Gintovt, 1969
Sphaerostoma bramae	A	R		Neva River	Intestine	3.3% (30)		‡Shulman, 1950, 1957
Ophioxenos lampetrae	I,A	W	M	British Columbia	Intestine	53.8% (13)	1–17	Beverley-Burton and Margolis, 1982
Brachyphallus crenatus	A	A	A	Ishikari River, Japan	NR	3.0% (33)	1	Katahira et al., 2014
	A	A		White Sea, Baltic Sea	Intestine	47.6% (21)		+Shulman and Shulman-Albova, 1953
Lecithaster gibbosus	A	A	A	Ishikari River, Japan	NR	3.0% (33)	1	Katahira et al., 2014
	A	A		White Sea, Baltic Sea	Intestine	23.8% (21)		+Shulman and Shulman-Albova, 1953
Unidentified sp.	I	P	L	California	NR	14.2% (56)	NR	Jackson et al., 2019
	I	W,P	A	Ritner Creek, Oregon	Pericardium, liver, kidney	NR	NR	Law, 1975
Nanophyetus salmincola	I	W,P	A	Oak Creek, Oregon	Gills, fins	100% (33)	4–50	Gebhardt et al., 1966
Cestodes (Phylum Platyhelminthes, Class Cestoda)								
Pelichnobothrium sp.	L	G	S	Donnelly River, Australia	Anterior intestine	54.8% (42)	2–11	Lethbridge et al., 1983
Hepatoxylon trichiurid	L	G	S	Donnelly River, Australia	Body cavity	11.9% (42) **	1–2	Lethbridge et al., 1983
Nybelinia surmenicola	L	A	A	Ishikari River, Japan	NR	30.3% (33)	1–8	Katahira et al., 2014
Nybelinia sp.	L	A		Amur River, USSR	Mesentery			+Shulman, 1957
Tetraphyllidean cestode	L	A	A	Ishikari River, Japan	NR	57.6% (33)	1–15	Katahira et al., 2014
Pseudophyllidea	I	A		White Sea, USSR	Intestine	9.5% (21)		+Shulman and Shulman-Albova, 1953; +Shulman, 1957
Eubothrium crassum	I/A	A,R		Lake Ladoga, Dvina River, Baltic Sea, White Sea, USSR	Intestine			+Jääskeläinen, 1921 +Shulman, 1950, 1957; +Gecevičute, 1974
Bothriocephalus sp.	L	R		Lake Ladoga, Russia	Mesentery			+Jääskeläinen, 1921
Triaenophorus crassus	L	A		Great Slave Lake, Canada	Body cavity	12.5% (112)		+Buchwald and Nursall, 1969
Triaenophorus nodulosus	L	R		Lake Ladoga, Russia	Body cavity			+Jääskeläinen, 1921
Diphyllobothrium sp.	L	R		Lake Ladoga, RussiaBaltic Sea	Body cavity, gut wall, kidneys			+Jääskeläinen, 1921 +Gecevičute, 1974
Phyllobothrium sp.	I	P	F	Lake Lakelse, British Columbia	Intestine	55.6% (9)	NR	Bangham and Adams, 1954

Table 7 (*continued*)

Parasite Taxon	Parasite Life stage	Lamprey Species	Lamprey Life stage	Location	Tissue	Prevalence	Intensity	Reference
Proteocephalus percae	I/A	R		Lake Ladoga, Russia	Intestine			[+]Jääskeläinen, 1921
Proteocephalus sp.	I/A	R		Neva Delta, Dvina River, USSR	Intestine			[+]Dogel and Petruševkij, 1933; [+]Shulman, 1950.
Ligula intestinalis	L	E		NR	Body cavity			[+]Sprehn, 1960; [+]Reichenbach-Klinke and Elkan, 1965
Nematodes (Phylum Nemathelminthes, Class Nematoda)								
Anisakis simplex	L	R	S	Lake Dabie, Poland	Intestine	2.68% (40)	1	Sobecka et al., 2010
Anisakis sp.	L	A		Shite Sea, Amur River	Mesentery	5% (21)	1	[+]Shulman and Shulman-Albova, 1953; [+]Shulman, 1957
Hysterothylacium aduncum	L,I	A		White Sea, Amur River	Intestine			[+]Shulman and Shulman-Albova, 1953
Phocanema decipiens	L	A		White Sea, Amur River	Mesentery, flesh	9.5% (21)	1	[‡]Shulman and Shulman-Albova, 1953
Truttaedacnitis truttae (syn. *Cucullanus truttae*)	A	E		River Stensan, Sweden	Abdominal cavity			[‡]Moravec, 1976; [‡]Moravec and Malmqvist, 1977
Gordius aquaticus	L	E R U		USSR, Europe	Intestine, Liver, Kidney	88–94% 67%		[+]Villot, 1881; [+]Linstow, 1898; [+]Dorier, 1926, 1930; [+]Zekhnov, 1956; [+]Malmqvist and Moravec, 1978 [‡]Moravec and Malmqvist, 1977 [+]Zekhnov, 1956
Truttaedacnitis stelmioides	A,L	R			Intestine, Liver, Gonads			[”]Shulman, 1950; [”]Shulman 1957; [”]Gecevičute, 1974
	A,L	E			Intestine, Liver, Gonads			[+]Vessichelli, 1910; [+]Loman, 1912; [++]Yorke and Maplestone, 1926; [+]Tornquist, 1931; [+]Zekhnov, 1956, 1958; [+]Shulman, 1957; [+]Yamaguti, 1961; [+]Moravec, 1976; [+]Moravec and Malmqvist, 1977; [+]Malmquist, 1978; [+]Moravec, 1979
Cystidicola farionis	I	R			Intestine			[+]Hardisty and Potter, 1971
Eustrongylides sp.	L	P	F	Lake Lakelse, British Columbia, Canada	NR	33.3% (9)	NR	Bangham and Adams, 1954
Acanthocephalans (Phylum Acanthocephala)								
Bolbosoma sp.	I	A	A	Ishikari River, Japan	NR	6.1% (33)	1	Katahira et al., 2014
Metaechinorhynchus salmonis	A	R		Lake Ladoga, USSR	Intestine			[+]Jääskeläinen, 1921; [+]Sprehn, 1960
Corynosoma semerme	I I	R A		Lake Ladoga, White Sea, USSR	Body cavity Body cavity			[+]Jääskeläinen, 1921; [+]Shulman, 1950, 1957 [+]Shulman and Shulman-Albova, 1953; [+]Petrochenko, 1956
Corynosoma strumosum	I	R		Kama River, Lake Ladoga, USSR	Body cavity			[+]Jääskeläinen, 1921
		C		Caspian Sea, USSR		100%		[+]Zakhuatin, 1936; [+]Zekhnov, 1958
Echinorhynchus sp.	A	C		Caspian Sea, USSR	Intestine	91% (319)		[+]Zekhnov, 1958
Crustaceans (Phylum Arthropoda, Subphylum: Crustacea)								
Argulus foliaceus	A	E		Finland	External			[+]Gadd, 1904
Argulus appendiculosus	NR	S	NR	Wisconsin River	Branchial region	NR	NR	Cochran et al., 1992
Ergasilus sieboldin	A	R		Kursiu Marios Lagoon, Baltic Sea, USSR	Gills			[+]Getsevichyute, 1974
Mollusks (Phylum Mollusca)								
Unionidae glochidia	I	C		Kuma River, White Sea	Gills			[+]Zakhuatin, 1936

[*] *Metorchis* sp., *Apophallus* sp., *Paratormopsolus siluri*, *Diplostomum apathaceum*, D. *petromyzontis fluviatilis*, *Neodiplostomulum hughesi*, *Tetracotyle* sp., and unidentified Acanthocolpidae metacercaria. [**] Lethbridge et al., 1983 reported the additional finding of "rare" degenerate H. trichiurid in lamprey collected at the Pemberton Weir. [+] per Appy and Anderson, 1981; [‡] per Sobecka et al., 2009; [”] per Pybus et al., 1978b

tine of western brook lamprey (*Lampetra richardsoni*) metamorphosizing ammocoetes in British Columbia (Table 7). These parasites were found as gravid amphistomes, representing the first record of a digenean utilizing a petromyzontid as its definitive host (Beverley-Burton and Margolis, 1982).

More recently, Katahira et al. (2014) identified two species of digeneans (*Brachyphallus crenatus* and *Lecithaster gibbosus*) in one non-specified adult Arctic lamprey each, collected from the Ishikari River (Japan) in 2010 and 2012 (Table 7). Although these parasites are typically found in marine fishes of the North Pacific, the presence of gravid worms in Arctic lamprey suggest that they can serve as a definitive host for these parasites. Shulman and Shulman-Albova (1953) also identified *B. crenatus* and *Lecithaster gibbosus* in the intestines of Arctic lamprey collected from the White and Baltic Seas (Table 7).

In North America, Jackson et al. (2019) gathered data from regional fish health laboratories (i.e., the Idaho Fish Health Center, Lower Columbia River Fish Health Center, Oregon Department of Fish and Wildlife, Northwest Fisheries Science Center, and Olympia Fish Health Center) on pathogen presence in Pacific lamprey from histopathological assessments, and reported the presence of trematode metacercariae in larvae from California (Table 7). However, there were no external parasites identified in any of the 518 examined adults. Law (1975) described a novel monorchiid digenean found as metacercaria in non-specified adult western brook and Pacific lamprey collected from Ritner Creek, Oregon. An earlier report from those same two lamprey species (Gebhardt et al., 1966) identified *Nanophyetus salmincola* metacercaria on the gills and fins of the lamprey (Table 7). The identification of this species is particularly relevant as it is known to transmit *Neorickettsia helmintheca,* the causative agent of "salmon poisoning", a severe disease in dogs that consume raw fish, and also poses a risk to human health where it can cause non-specific gastrointestinal distress (Appy and Anderson, 1981).

Collectively, the aforementioned reports rarely noted gross pathological changes in lamprey infected with trematodes; however, Law (1975) reported rapid mass hemorrhage across the body (within 15 min) following experimental exposure of brook lamprey to trematode cercariae.

Nematodes

There have been a handful of reports of parasitic nematodes in lamprey outside of the Laurentian Great Lakes (Table 7). Sobecka et al. (2010) identified a single L3 *Anisakis simplex* larva in a spawning adult European river lamprey collected from Lake Dabie in Poland (Table 7). An *Anisakis* sp. was also identified from Arctic lamprey in the White Sea and Amur River (Shulman, 1957; Shulman and Shulman-Albova, 1953; Table 7). Shulman and Shulman-Albova (1953) also identified *Hysterothylacium aduncum* and *Phocanema decipiens* in Arctic lamprey from the Amur River and White Sea (Table 7).

Moravec and Malmqvist (1977) reported adult *Truttaedacnitis truttae (*syn. *Cucullanus truttae*) in the abdominal cavity of European brook lamprey collected from the River Stensan in Sweden (Table 7). Malmqvist and Moravec (1978) also identified *Gordius aquaticus* larvae in both European brook lamprey and European river lamprey (Table 7). Also found in European river lamprey were *Truttaedacnitis stelmioides* (Gecevičute, 1974; Shulman, 1957, 1950) and *Cystidicola farionis* (Hardisty and Potter, 1971; Table 7).

In North America, Bangham and Adams (1954) identified a *Eustrongylides* sp. in actively feeding Pacific lamprey from Lakelse Lake, British Columbia, Canada (Table 7). *Eustrongylides* nematodes are zoonotic parasites known to cause gastritis and intestinal perforation in humans following the consumption of raw or undercooked fish (Eberhard et al., 1989; Wittner et al., 1989).

Cestodes

At least 13 cestode genera have been identified from lamprey outside of the Laurentian Great Lakes (Table 7). Lethbridge et al. (1983) observed larval cestodes in 28 of 159 spawning phase pouched lamprey collected from the Donnelly River (Australia), which were identified as *Pelichnobothrium* sp. and *Hepatoxylon trichiuri*. However, none of the recovered parasites were living or intact, suggesting to the authors that these cestodes likely do not survive when lamprey transition from marine to fresh water.

Katahira et al. (2014) identified plerocercoids belonging to two cestode taxa (*Nybelinia surmenicola* and a tetraphyllidean) in non-specified adult Arctic lamprey (Table 7) collected from the Ishikari River in Japan. Although Arctic lamprey likely serve as a dead-end host for these cestodes, they could be transmitted to definitive host blue (*Prionace glauca*) and salmon (*Lamna ditropis*) sharks via predation. Several other species of cestodes were also identified from Arctic lamprey, including a *Nybelinia* sp. (Shulman, 1957), Pseudophyllidea larva (Shulman and Shulman-Albova, 1953), and *Eubothrium crassum* (Table 7). *Eubothrium crassum* has also been identified from European river lamprey (Gecevičute, 1974; Jääskeläinen, 1921; Shulman 1950, 1957; Table 7).

Jääskeläinen (1921) identified multiple species of cestodes from European river lamprey in Lake Ladoga, including *Bothriocephalus* sp., *Triaenophorus nodulosus, Diphyllobothrium* sp., and *Proteocephalus percae* (Table 7). *Diphyllobothrium* sp. were also found in European river lamprey collected from the Baltic Sea (Gecevičute, 1974). *Proteocephalus* sp. were found in the same species by Dogel and Petruševkij (1933) and Shulman (1950; Table 7). *Ligula intestinalis* were found in brook lamprey by Sprehn (1960) and Reichenbach-Klinke and Elkan (1965; Table 7).

Acanthocephalans

Other than those reported from sea lamprey, there are only a few reports of acanthocephalans in lamprey (Table 7). Katahira et al. (2014) identified post-cystacanths of a *Bolbosoma* sp. in non-specified adult Arctic lamprey collected from the Ishikari River (Japan) in 2010 and 2012 (Table 7). Although it is unlikely that the Artic lamprey are a preferred host for this parasite, which is known to most commonly infect marine mammals (Costa et al., 2000), they may serve as an additional source of transmission to piscivorous marine mammals. Jääskeläinen (1921) and Sprehn (1960) identified *Echinorhynchus salmonis* (syn. *Metechinorhynchus salmonis*) from European river lamprey (Table 7). Two species of *Corynosoma* (found as adults in seals and piscivorous sea birds; Appy and Anderson, 1981) have also been identified in lamprey: *C. semerme* from European river lamprey (Jääskeläinen, 1921; Shulman 1950, 1957) and Arctic lamprey (Petrochenko, 1956; Shulman and Shulman-Albova, 1953) and *C. strumosum* from European river lamprey (Jääskeläinen, 1921) and Caspian lamprey (*Caspiomyzon wagneri*; Zakhuatin, 1936; Zekhnov, 1958; Table 7).

Crustaceans

There are at least three reports of crustaceans on lamprey outside of the Laurentian Great Lakes (Table 7). Gadd (1904) identified adult *Argulus foliaceus* on the external surfaces of brook lamprey in Finland, and Gecevičute (1974) identified adult *Ergasilus sieboldi* on the gills of European river lamprey in Kursiu Marios Lagoon and the Baltic Sea (Table 7). The only other published report of these parasites affecting lamprey that we are aware of is that of Cochran et al. (1992), who identified *Argulus appendiculosus* attached to silver lamprey collected from the Wisconsin River in Sauk County, Wisconsin (USA; Table 7). Of note, however, this same parasite was also detected on common carp (*Cyprinus carpio*) and shorthead redhorse (*Moxostoma macrolepidotum*) collected from the same site and that were housed in the same laboratory enclosure.

Mollusks

We are aware of a single report of mollusks from lamprey outside of the Laurentian Great Lakes (Table 7). Zakhuatin (1936) identified Unionidae glochidia on the gills of Caspian lamprey in the Kuma River and White Sea (Russia).

Infections caused by fungi and oomycetes

During the process of visually examining 20,000 juvenile (post-metamorphosis) Pacific lamprey for signs of disease without further laboratory analyses over a four-year period, Jackson et al. (2019) observed a low prevalence of signs consistent with fungal/water mold infections (Table 2). Further, Mueller et al. (2006) reported the death of juvenile (metamorphosizing), captive Pacific lamprey following insertion of passive integrated transponder (PIT) tags from an unidentified, white-colored fungus. However, it was noted that when water temperature decreased, mortality rates decreased from 60% to <3%.

In an effort to better understand host pathogen interactions between oomycetes and lamprey, Zhang et al. (2019) used transcriptomic analyses to examine alterations in gene expression following experimental exposure of larval Arctic lamprey to *Saprolegnia ferax*. In so doing, they identified a number of genes involved in pathogen recognition, inflammation, phagocytosis, lysosomal degradation, soluble humoral effectors, and lymphocyte development that were upregulated following *Saprolegnia* infection. Kim et al. (2013) identified *Saprolegnia parasitica* from infected wild Far Eastern brook lamprey (*Lethenteron reissneri*).

Bacterial infections

There have been a few reports of bacteriological screening and experimentation in Pacific lamprey (Table 3). Bell and Traxler (1986) experimentally exposed spawning stage Pacific lamprey to *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease in salmon and trout. Interestingly, despite being injected with up to 1.3x10^6 cfu of the bacterium, none of the 12 challenged lamprey were positive for the bacterium via kidney culture, Gram stain and Immunofluorescence Antibody Test (IFAT) at the end of the study, nor did any lamprey mortality occur. As a result, the authors concluded that adult Pacific lamprey, unlike the sea lamprey, may not be susceptible to *R. salmoninarum*, and thus were unlikely to serve as carriers of the pathogen.

Rhodes et al. (2011) tested non-specified adult western river lamprey (*Lampetra ayresii*) from Puget Sound (Washington state, USA) and found *R. salmoninarum* via fluorescent antibody testing (Table 3). As the authors linked river lamprey density to increased odds of Chinook salmon infection, these lamprey may serve a vector or reservoir role in *R. salmoninarum* transmission. Jackson et al. (2019) reported that 275 larval Pacific lamprey that were screened for bacterial infections by several regional fish health laboratories were negative; however, in contrast to the findings of Bell and Traxler (1986), a low percentage of adults did test positive for *Renibacterium salmoninarum* using ELISA (Table 3). The six positive adults were in a collection of 30 from an abatement pond receiving hatchery effluent from Chinook salmon that showed clinical signs of BKD. *Renibacterium salmoninarum* was also detected in 3/5 additional Pacific lamprey using fluorescence microscopy (Jackson et al., 2019).

Aeromonas salmonicida has been detected in Pacific lamprey from Oregon and Washington (USA, non-specified adults, Jackson et al., 2019; larvae, Jolley and Lujan, 2019). Jackson et al. (2019) detected *A. salmonicida* at a prevalence ranging from 0% to 69% in dead adult Pacific lamprey lots submitted for screening (n = 320 specimens). Incidence was higher in dead specimens received from lamprey holding operations (59 of 140, 42.1%) than for dead specimens collected in the wild (33 of 180, 18.3%). In contrast, grab samples of live lamprey from culture operations had no incidence of this bacterium and only 1 of 39 live specimens collected at Willamette Falls (Oregon, USA) was positive for this pathogen (2.6%). None of the 275 larvae examined by Jackson et al. (2019) were positive for *A. salmonicida*. In an attempt to clarify the effects of *A. salmonicida* infections in larval Pacific lamprey, 148 larvae (average weight 0.2 g) were experimentally challenged with the bacterium, leading to infrequent mortality and a lack of detectable infections in fish that succumbed to death, as well as the survivors. Jolley and Lujan (2019) examined adult Pacific lamprey from the Clackamas River sub-basin in Oregon (USA), revealing *A. salmonicida* infections (Table 3). Collectively, these studies suggest that in some cases, *A. salmonicida* infections can lead to systemic disease and mortality in Pacific lamprey.

In the Southern Hemisphere, Brosnahan et al. (2019) identified an atypical *A. salmonicida* in spawning phase pouched lamprey presenting with areas of abnormal reddening (Table 3). A small number of individuals were positive for *A. salmonicida* by PCR, yet negative by bacterial culture. This finding, combined with histopathological evaluations, made unclear the role that this bacterium played in the overt disease signs that were observed. It is noteworthy, however, that *A. salmonicida* can enter a “viable but non-culturable” state and still contribute to disease (Cipriano and Bullock, 2001).

A range of other bacterial infections have been reported in lamprey. For example, Brosnahan et al. (2019) isolated motile *Aeromonas* and *Carnobacterium* spp. from pouched lamprey (Table 3). Pacific lamprey larvae from the Clackamas River sub-basin, Oregon, reportedly had bacterial infections due to *Vibrio vulnificus, Ochrobactrum anthropi, A. hydrophila, Salmonella enterica* serovar Pullorum, *Pseudomonas aeruginosa, P. fluorescens, Hafnia alvei, Pantoea* spp., and *Enterobacter cloacae* detected from heart tissues (Jolley and Lujan, 2019). These isolations occurred in spite of the fact that the fish were apparently healthy upon gross examination.

Hilliard et al. (1979) isolated *Aeromonas hydrophila* and *P. fluorescens* from the internal organs of diseased pouched lamprey (Table 3). Fish were captured after recently entering fresh water in southwestern Australia (i.e., upstream migrants). Diseased animals exhibited generalized pallor and petechial hemorrhage around the branchial region, around the eyes, the lateral surfaces of the trunk, and the dorsal and caudal fins. Terminal fish often had hemorrhage and edema obscuring the eyes and significant mucus production. Internally, hemorrhage was observed in the subcutaneous fat, musculature, kidney, and gills. Although mortality reached 95% (n = 124/130), only four individuals were examined for bacterial infection. *Pseudomonas fluorescens* was isolated from a single liver and *A. hydrophila* was isolated from the kidney of one individual and the gills of three individuals. Following bacterial isolation, surviving animals were treated with chlortetracycline and within four days had recovered from all visible signs of disease.

Viral infections

The earliest report of an aquatic virus in a lamprey came from Scotland by Munro et al. (1976; Table 4). During a survey to determine prevalence of Infectious Pancreatic Necrosis Virus (IPNV) in Loch Awe, a total of 115 European river lamprey were caught and divided into 16 pools by size and collection location for IPNV screening using the rainbow trout gonad-2 (RTG-2) cell line. A single pool was determined to be positive for IPNV following either persistent CPE over three passages, neutralization by IPNV-specific antiserum, or plaque reduction neutralization test. Although the source of infection was undetermined, Munro et al. (1976) suggested the possibility of direct ingestion of the virus from trout farm effluent water, among others.

The remaining references to virus screening in lamprey focus primarily on viruses that are also of substantial significance to sal-

Table 8
Summary of the number of parasite and pathogen genera (number of separate reports in parentheses) that have been documented in various lamprey species (Tables 1–7).

Lamprey species	Number of genera										
	Protozoa, Myxozoa, and Microsporidia	Trematodes	Cestodes	Nematodes	Acanthocephalans	Crustaceans	Mollusks	Annelids	Fungi and Oomycetes	Bacteria	Viruses
American brook				1 (1)	1 (1)					0 (2)	
Arctic	2 (2)	2 (4)	5 (9)	3 (4)	2 (3)				1 (1)		
Caspian					2 (3)		1 (1)				
Chestnut										1 (1)	
European brook		6 (2)	1 (2)	2 (20)		1 (1)					
European river		2 (5)	5 (9)	3 (6)	2 (6)	1 (1)					2 (2)
Far Eastern									1 (1)		
Northern brook	1 (2)									2 (2)	
Pacific	1 (1)	1 (3)	1 (1)	1 (1)					0 (2)	3 (6)	
Pouched			2 (2)							3 (5)	
Sea (Great Lakes)	2 (3)	2 (3)	3 (14)	3 (4)	2 (8)	1 (2)	1 (1)	1 (1)	2 (10)	6 (39)	1 (1)
Sea (non-Great Lakes)				2 (3)				1 (1)	0 (1)		
Silver						1 (1)			1 (1)	3 (8)	
Ukrainian brook		6 (1)		1 (1)							
Western brook		2 (3)									
Western river										1 (1)	
Total	3 (8)	14 (21)	13 (37)	9 (40)	5 (21)	2 (5)	2 (2)	1 (2)	2 (16)	6 (64)	2 (3)

monid health, including VHSV and the *Salmonid novirhabdovirus* historically known as Infectious Hematopoietic Necrosis Virus (IHNV). There were two studies that presented a substantial volume of results with no evidence of such viruses in wild lamprey. Jackson et al. (2019) reported that 518 adult and 275 larval Pacific lamprey tested negative for IPNV, IHNV, and VHSV on epithelioma papulosum cyprini (EPC) and Chinook salmon embryo (CHSE-214) cell lines. Jolley and Lujan (2019) examined a total of 164 larval (2009, 2012, 2013) and 27 adult (2014) Pacific lamprey from the Clackamas River sub-basin in Washington state. All fish tested negative for viruses via cell culture screening on EPC and CHSE cell lines.

To more directly test the ability of VHSV (genotype IVa) and IHNV (U and M subgroups) to infect, replicate, and cause disease in Pacific lamprey, Kurath et al. (2013) challenged larval Pacific lamprey with both viruses under controlled laboratory conditions. Similar to the VHSV IVb study in adult Great Lakes sea lamprey, little to no mortality occurred despite being exposed to $2x10^3$ to $2x10^6$ plaque forming units (PFU) per mL (immersion) and 10^4 PFU/fish (intraperitoneal injection). Moreover, and in contrast to the sea lamprey study, there was no evidence of viral replication within the exposed lamprey larvae throughout the study, thereby suggesting that Pacific lamprey larvae are relatively refractile to VHSV IVa and IHNV-U and -M infection.

The only other report of viral infections in lamprey that we are aware of is that of Gadd et al. (2010), who sampled wild, healthy, spawning European river lamprey in Finland over a 10-year period and isolated VHSV genotype II from several samples (Table 4). These isolates were then used to challenge rainbow trout fry, yet induced no mortality. Likewise, no overt signs of disease were reported in infected lamprey.

Concluding remarks

Despite serving as an "evolutionary link" that bridges invertebrates and vertebrates (Heimberg et al., 2010), as well as their importance ecologically, culturally (Close et al., 2002), and in some habitats, as destructive invasive aquatic pests, little is truly known about the physiology, pathology, and parasitic and microbial infections that affect lamprey of the order Petromyzontiformes. The studies reviewed and summarized herein document at least 46 genera of parasites, seven genera of bacteria, two genera of fungi and oomycetes, and two viruses belonging to two families that are capable of infecting at least 15 lamprey species, yet many were identified only to the genus level, and very few of these studies definitively linked the presence of parasitic and microbial infections with a disease status in the lamprey host. Even fewer studies have attempted to fulfill Koch's or Rivers' postulates and, in most instances, the modes of infection and transmission pathways are incompletely understood.

Among the lamprey species from which microbial infections and/or parasites have been documented (n = 15; Table 8), it is noteworthy that ~77% of the reports come from only four species (i.e., Arctic, European brook, European river, and sea lamprey). It is clear that among the major groups of parasites that were detected in these four species, reports of nematodes (n = 37) and cestodes (n = 34) were the most frequent (Table 8). Conspicuously absent from all reported lamprey parasite fauna are monogeneans, which is a group of common fish parasites globally (Buchmann and Bresciani, 2006). In terms of bacterial infections in lamprey, it is evident that reports are substantially more numerous in Great Lakes sea lamprey (n = 39; Table 8) when compared to those in their native range (n = 0 within this review), as well as when compared to other lamprey species (Table 8). Whether this relates to their presence in a non-native environment and/or a potentially a heightened susceptibility to infection, to more frequent bacteriological analyses due to the various sea lamprey control efforts, and/or a multitude of other factors remains unknown. Table 8 also reveals how little we truly know about the presence of many parasites and microbial infections in many of these lamprey (i.e., parasites, fungi/oomycetes, bacteria, and viruses were not reported in 3/15, 10/15, 7/15, and 13/15 species, respectively). Carrying this forward and to the best of our knowledge, this means that there are no reports of parasites or microbial infections in 33 of the 48 described lamprey species. From that observation, it is tempting to speculate on an inherent refractivity of Petromyzontiformes to a variety of parasites and pathogens; however, until more lamprey health studies focus on these taxa, such a hypothesis cannot begin to be explored.

What is perhaps most notable when evaluating parasite and pathogen reports by lamprey life stage is that more than 80% of the reports (where life stage was included) came from lamprey in an active feeding stage or later (Tables 1–7), whereas only ten reports in total originated in larval lamprey (11%). This could suggest that lamprey feeding behavior, susceptibility to infection, and/or habitat associated with these life stages have important implications for infection status, but could also be a result of a greater number of adult lamprey having been examined to date. Clearly, further studies to this end are warranted.

In the face of such knowledge gaps and coupled with the incomplete understanding of the lamprey immune system, which includes an adaptive immune response that is vastly different from that of jawed vertebrates (Docker et al., 2015; Kishishita and Nagawa, 2013), it is nearly impossible to determine how lamprey defend themselves against infections, nor how diseases could imperil lamprey populations or affect their reproductive success. Moreover, until more consistent and comprehensive surveillance studies are undertaken, it is difficult to assess whether infrequent reports of parasites and pathogens in lamprey are due to a biological or evolutionary trait of the lamprey, a component of the life cycle that may be missing in the new environment of invasive lamprey, or simply due to a "lack of looking".

This shortfall in knowledge is concerning for lamprey management. Indeed, lampricide treatments in the Great Lakes are known to have negative health effects on non-target lamprey species (Schuldt and Goold, 1980), a matter that could be exacerbated by the presence of infectious diseases in the exposed populations. Further understanding pathogen presence and disease effects (e.g., immune modulation, growth, and reproductive proficiency) in wild lamprey is critical for both lamprey conservation and control. To this end, well planned and executed general surveillance programs are needed for identifying pathogens that have the potential to negatively affect native lamprey populations, thereby allowing fishery managers to design effective strategies to ameliorate their impacts.

On the other hand, there is growing interest in the potential of biocontrol agents that target invasive sea lamprey; however, the general lack of host specificity amongst lamprey pathogens reviewed here is problematic (McColl et al., 2014). Given the lack of cell-lines derived from, and diagnostic reagents specific to lamprey, as well as a lack of funding dedicated to the development of such tools and lamprey disease research in general, it is unsurprising that researchers have yet to uncover a sea lamprey-specific pathogen (i.e., host-specific viruses most commonly require cell-lines derived from their preferred host, and sea lamprey cell-lines are currently unavailable).

In summary, this review presents a compendium of surveys and studies on the parasites and pathogens found in lamprey species around the world, and will serve as a baseline for future studies focused on improving the taxonomic resolution of these organisms and elucidating the role that specific pathogens and diseases play in the population dynamics of both native and invasive lamprey species. Clearly, a better understanding of the extent and impact of individual parasites and pathogens on lamprey, at both the individual and population levels, is needed. Filling this knowledge gap will provide much needed information for fishery management agencies and scientists as they seek to conserve and protect fish populations, including lamprey, around the globe.

CRediT authorship contribution statement

Megan A. Shavalier: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing - review & editing. **Mohamed Faisal:** Funding acquisition, Project administration, Writing - review & editing. **Mary L. Moser:** Writing - review & editing. **Thomas P. Loch:** Conceptualization, Data curation, Funding acquisition, Investigation, Project administration, Writing – original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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