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Review

Canadian freshwater mussels and their host associations

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Abstract

Freshwater mussels (order Unionida) are one of the world's most imperiled taxonomic groups of animals. The two families that occur in Canada (Margaritiferidae, Unionidae) produce parasitic larvae (glochidia) that generally rely on attachment to a suitable host fish to facilitate metamorphosis into the juvenile phase. This review synthesizes the current knowledge on the hosts of all 55 species of freshwater mussels in Canada, compiled from 265 citations, 71 of which were newly identified by this review. As of October 2023, evidence for 850 mussel–host associations have been documented, though a relatively small proportion of the evidence was collected in Canada. The winged floater and the lake floater currently have no known hosts, with 14 other species having only a single associated evidence type. This review provides an updated library of current knowledge on hosts of Canadian unionoids, discusses notable trends, and outlines outstanding knowledge gaps to be addressed in future studies. Considering many of the host associations were not studied in Canadian waters, knowledge gaps remain regarding relevant ecological and climatic context in Canada.

Key words: unionoid, freshwater mussel, glochidia, parasites, fishes, host

Introduction

Freshwater mussels in the order Unionida are globally distributed and comprise 6 extant families and approximately 1020 species (Graf and Cummings 2025). North America is a hotspot for freshwater mussel diversity, supporting approximately 307 native species from 2 families: Unionidae and Margaritiferidae, which collectively comprise the superfamily Unionoidea (Graf and Cummings 2025). Canada's borders contain 55 of these species of freshwater mussels (common and scientific names are listed in Table 1 in accordance with Harris et al. (2023)), which will henceforth be referred to as *unionoid mussels* or *unionoids*.

Unionoids are filter-feeding organisms and play important ecological roles in freshwater systems (Vaughn 2018; Zieritz et al. 2022). A single unionoid mussel is capable of filtering between 1–5 L of water per hour (Kryger and Riisgard 1988), feeding on tiny organisms, bacteria, and detritus. At a population scale, unionoids often have the capacity to filter the entire volume of a lake over the course of several days (Ogilvie and Mitchell 1995; Vanderploeg et al. 2011), releasing nutrients back into the water column or sediments in bioavailable forms (Nedeau et al. 2000). Their collective filter-feeding efforts can substantially increase water clarity by removing phytoplankton and other particles that contribute to turbidity (Kasprzak 1986; Kryger and Riisgard 1988; Vaughn and Hakenkamp 2001). Furthermore, the movements of adult unionoids (crawling) simultaneously provide oxygen to sediments and free up nutrients that become available in the water column (Vaughn and Hakenkamp 2001). The shells of both live and dead unionoids add to the topographical complexity of freshwater basins, providing habitat and shelter for benthic invertebrates and epizoic organisms (e.g., hydropsychid caddisflies, chironomid larvae, algae; Sephton et al. 1980; Beckett et al. 1996; Vaughn and Hakenkamp 2001).

Unionoids are one of the world's most imperiled taxonomic groups of animals and are facing ongoing decline in both range and abundance (Williams et al. 1993; Haag and Williams 2014; Ries et al. 2016; Lopes-Lima et al. 2017, 2018; Hornbach et al. 2018; Böhm et al. 2021; Nakamura et al. 2023). In Canada, 38% of native unionoid mussels have been categorized as at-risk (MacLennan-Nobrega et al. 2024) including one extirpated species, the dwarf wedgemussel (*Prolasmidonta heterodon*; Morris 2021). Numerous threats are contributing to their decline: degradation of water quality due to anthropogenic activities (Cope et al. 2021; Goldsmith et al. 2021), fouling and competition from invasive dreissenid mussels (family Dreissenidae; Hebert et al. 1989; Schloesser and Nalepa 1996), habitat fragmentation caused by damming (Watters 1996; Tiemann et al. 2007, 2016), predation by invasive species such as the round goby (*Neogobius melanostomus*; Clark et al. 2022), and reduced or limited prevalence of larval hosts (Strayer 2008; McNichols et al. 2011; Hornbach et al. 2018; Lopes-Lima et al. 2018).

Part of what contributes to the vulnerability of unionoid mussels to these threats is their unique lifecycle. They are a long-lived group with lifespans ranging from 6 to 100+ years (Ziuganov et al. 2000; McMahon and Bogan 2001; Haag 2012) and generally only reach sexual maturity at 1–12 years old

Table 1. List of the 55 mussel species (Mollusca: Bivalvia, order Unionida) found in Canada.

Family	Subfamily	Tribe	Common name	Scientific name
Margaritiferidae (Henderson, 1929)				
	Margaritiferinae		Western pearlshell	*Margaritifera falcata* (A. Gould, 1850)
			Eastern pearlshell	*Margaritifera margaritifera* (Linnaeus, 1758)
Unionidae (Rafinesque, 1820)				
	Gonideinae			
		Gonideini	Rocky mountain ridged mussel	*Gonidea angulata* (Lea, 1838)
	Ambleminae			
		Amblemini	Threeridge	*Amblema plicata* (Say, 1817)
		Lampsilini	Black sandshell	*Ligumia recta* (Lamarck, 1819)
			Deertoe	*Truncilla truncata* Rafinesque, 1820
			Eastern lampmussel	*Lampsilis radiata* (Gmelin, 1791)
			Eastern pondmussel	*Sagittunio nasutus* (Say, 1817)
			Fatmucket	*Lampsilis siliquoidea* (Barnes, 1823)
			Fawnsfoot	*Truncilla donaciformis* (I. Lea, 1827)
			Fragile papershell	*Potamilus fragilis* (Rafinesque, 1820)
			Hickorynut	*Obovaria olivaria* (Rafinesque, 1820)
			Kidneyshell	*Ptychobranchus fasciolaris* (Rafinesque, 1820)
			Lilliput	*Toxolasma parvum* (Barnes, 1823)
			Mucket	*Ortmanniana ligamentina* (Lamarck, 1819)
			Northern riffleshell	*Epioblasma rangiana* (I. Lea, 1838)
			Pink heelsplitter	*Potamilus alatus* (Say, 1817)
			Plain pocketbook	*Lampsilis cardium* (Rafinesque, 1820)
			Rainbow	*Cambarunio iris* (I. Lea, 1829)
			Rayed bean	*Paetulunio fabalis* (I. Lea, 1831)
			Round hickorynut	*Obovaria subrotunda* (Rafinesque, 1820)
			Snuffbox	*Epioblasma triquetra* (Rafinesque, 1820)
			Threehorn wartyback	*Obliquaria reflexa* (Rafinesque, 1820)
			Tidewater mucket	*Atlanticoncha ochracea* (Say, 1817)
			Wavyrayed lampmussel	*Lampsilis fasciola* (Rafinesque, 1820)
			Yellow lampmussel	*Lampsilis cariosa* (Say, 1817)
		Pleurobemini	Eastern elliptio	*Elliptio complanata* (Lightfoot, 1786)
			Elephantear	*Elliptio crassidens* (Lamarck, 1819)
			Round pigtoe	*Pleurobema sintoxia* (Rafinesque, 1820)
			Spike	*Eurynia dilatata* (Rafinesque, 1820)
			Wabash pigtoe	*Fusconaia flava* (Rafinesque, 1820)
		Quadrulini	Mapleleaf	*Quadrula quadrula* (Rafinesque, 1820)
			Pimpleback	*Pustulosa pustulosa* (I. Lea, 1831)
			Purple wartyback	*Cyclonaias tuberculata* (Rafinesque, 1820)
	Unioninae			
		Anodontini	Alewife floater	*Utterbackiana implicata* (Say, 1829)
			Brook floater	*Alasmidonta varicosa* (Lamarck, 1819)
			Creek heelsplitter	*Lasmigona compressa* (I. Lea, 1829)
			Creeper	*Strophitus undulatus* (Say, 1817)
			Cylindrical papershell	*Anodontoides ferussacianus* (I. Lea, 1834)
			Dwarf wedgemussel	*Prolasmidonta heterodon* (I. Lea, 1829)
			Eastern floater	*Pyganodon cataracta* (Say, 1817)
			Elktoe	*Alasmidonta marginata* (Say, 1818)
			Flutedshell	*Lasmigona costata* (Rafinesque, 1820)
			Giant floater	*Pyganodon grandis* (Say, 1829)
			Lake floater	*Pyganodon lacustris* (I. Lea, 1857)

Table 1. (*concluded*).

Family	Subfamily	Tribe	Common name	Scientific name
		Anodontini	Newfoundland floater	*Pyganodon fragilis* (Lamarck, 1819)
			Oregon floater	*Anodonta oregonensis* (I. Lea, 1838)
			Paper pondshell	*Utterbackia imbecillis* (Say, 1829)
			Salamander mussel	*Simpsonaias ambigua* (Say, 1825)
			Slippershell mussel	*Alasmidonta viridis* (Rafinesque, 1820)
			Triangle floater	*Alasmidonta undulata* (Say, 1817)
			Western floater	*Anodonta kennerlyi* (I. Lea, 1860)
			White heelsplitter	*Lasmigona complanata* (Barnes, 1823)
			Winged floater	*Anodonta nuttalliana* (I. Lea, 1838)
		Cristariini	Yukon floater	*Beringiana beringiana* (Middendorff, 1851)

Note: Names are consistent with the Freshwater Mussel Conservation Society (FMCS) 2023 checklist (Harris et al. 2023) with the exception of the dwarf wedgemussel and pimpleback which have since been updated (Neemuchwala et al. 2023; Whelan et al. 2023). List is organized alphabetically by family, subfamily, tribe (Unionidae), and common name. Shading in this table corresponds to tribe, as was done in Figs. 1 and 2.

(Haag 2012), making them relatively vulnerable to rapid environment change. All Canadian unionoids must also complete an obligate parasitic larval stage during their lifecycle, wherein females release parasitic larvae called glochidia (Cummings and Graf 2015). To reach maturity, glochidia must successfully attach to either the gills or fins of a suitable host fish (or in a rare cases, amphibians; Howard 1915; Watters and O'Dee 1997) where they obtain nutrients from the host to complete a metamorphosis and detach as juveniles (Cummings and Graf 2015). The host tissue on which glochidia can be found depends on the glochidial morphology, which can be either hooked (specialize on fin tissues) or unhooked (specialized on gill tissues; Cummings and Graf 2015). The timing and frequency of larval release and the duration of the larval stage varies by both species and environmental factors (Zale and Neves 1982). Among unionoids, there are short-term (tachytictic) brooders and long-term (bradytictic) brooders (Graf and O'Foighil 2000). Tachytictic brooders spawn in the spring, and glochidia will be released and complete their metamorphosis within the same summer; bradytictic brooders spawn in late summer through fall, brooding their glochidia over winter, and releasing them the following spring (Graf and O'Foighil 2000). It should be noted, however, that there is considerable variation in brooding patterns and that these categories may not accurately describe patterns in all unionoid species or populations (Heard 1998). Many knowledge gaps remain regarding the specific periodicity of spawning, larval release, and detachment from the host (Martel et al. 2010). There are a handful of examples where glochidia of different species have been able to metamorphose without attaching to a host (e.g., Lefevre and Curtis 1911; Dickenson and Sietman 2008), but they are the exceptions rather than the rule. After metamorphosis occurs, glochidia drop off the host fish and will have limited dispersal ability (typically <10 m per year but with considerable variation across species) for the remainder of their lifecycle (Isely 1914; Strayer 1981; Watters 1992; Williams et al. 1993; Balfour and Smock 1995; Amyot and Downing 1998; Schwalb and Pusch 2007; Haag 2012). The importance of mussel hosts is therefore two-fold: accommodating the metamorphosis from glochidium to juvenile mussel, and for long distance dispersal of offspring (including upstream dispersal in streams and rivers; Schwalb et al. 2011).

The knowledge base regarding unionoid mussels and their larval hosts is still expanding. Hewitt et al. (2019) found a correlation between the number of documented hosts for a given mussel species and the number of studies that have explored those relationships, suggesting that many relationships remain undiscovered. This may be, in part, a result of the complexity associated with documenting the unionoid lifecycle. The infection of a potential host with glochidia does not guarantee that metamorphosis will occur (Cummings and Graf 2015), so host confirmation efforts must go beyond the observation of glochidia attached to a potential host. One popular approach is to induce laboratory infestation of potential hosts with glochidia to determine whether glochidia will be sloughed off or complete their metamorphosis into juveniles. The main shortcoming with standalone laboratory experiments is that they do not always translate to natural conditions (e.g., there may be inadequate temporal or spatial mussel–host overlap). For these reasons, it is important to consider the evidence type (ET) being presented by a given study.

Here, we synthesize the current evidence on the host associations for all 55 species of freshwater mussels in Canada. This review includes a comprehensive list of all the known hosts for each species and the corresponding ET (following Freshwater Mussel Host Database 2017; Table 2). Previous studies have shown that the specificity and selectivity of mussel–host relationships can vary both interspecifically (Cummings and Graf 2015) and at the intraspecific population level (Taeubert et al. 2010; Douda et al. 2014; Modesto et al. 2018). As such, the geographical context is an important piece of information and should be provided in studies examining host use or host identifications. This review, therefore, includes the locality of mussel collection, where available, giving researchers, and managers as much context as possible for the glochidia–host associations. Hoggarth (1992) developed a set of abbreviations for the various ETs found in the literature, which was later adapted by the Illinois Natural History Survey's (INHS's) database (Freshwater Mussel Host Database 2017). This is an open access dataset that contin-

Table 2. Abbreviations and definitions for the evidence type categories used in this review, based on Hoggarth (1992) and Freshwater Mussel Host Database (2017).

Evidence type	Definition
NS: Not specified	Evidence type not provided
NI: Natural infestation	Glochidia infestation observed on fish or amphibian under natural conditions
LI: Laboratory infestation	Glochidia infestation on fish or amphibian induced under experimental conditions
LT: Laboratory transformation	Complete metamorphosis into juvenile stage observed under experimental conditions
NT: Natural transformation	Complete metamorphosis into juvenile stage observed or advanced encapsulation (e.g., internal organ development) identified on fish or amphibians under natural conditions
RC: Range correlation	Suspected larval–host association based on modeled or known range overlap
ZT: Zero transformation	Fish or amphibian determined to be an unsuitable host due to unsuccessful attachment or encapsulation

ues to expand and is (to our knowledge) the most comprehensive database for freshwater mussel hosts. The evidence-type categories used by the Freshwater Mussel Host Database were used in this review to maintain continuity with this pre-existing resource and we include an additional evidence category for studies that infer relationships through range correlations.

Materials and methods

Both peer-reviewed papers and grey literature were included in this review. A literature search was conducted by a single researcher (BRA) through the Web of Science database search engine on 5 October 2023, using Carleton University's institutional agreement. Search terms included common names of all 55 Canadian unionoid species, as well as "host", "fish", "freshwater", "fresh water", "larv*", "mussel*", "bivalve*", "unionid*", "unionoid*". No date range or language requirements were selected in the query with the intention of capturing as many relevant publications as possible. This search returned 1400 results from 7 databases, including: Web of Science Core Collection, BIOSIS Citation Index, MEDLINE, Proquest Dissertations & Theses Citation Index, Grants Index, SciELO Citation index, and KCI-Korean Journal Database. Additionally, Ellipsaria Newsletter, Sterkiana, Triannual Unionid Reports, and Nautilus were scanned for relevant publications. Publication years ranged from 1927 to 2023. All Committee on the Status of Endangered Wildlife in Canada reports for Canadian mussels were examined and directed Google searches for each species were conducted to capture any additional grey literature resources. Citations from the Freshwater Mussel Host Database corresponding to Canadian mussels were included in the review. Finally, one additional citation (Porto-Hannes et al. 2025), published after the search date, was added to the dataset for completeness.

Publications were only included if they made primary observations of at least one mussel–host interaction. To ensure ETs were assigned in a fashion consistent with previous works, a subsample of citations from the Freshwater Mussel Host Database was used as a training set. Furthermore, ETs (Table 2) were assigned independently by three researchers (BRA, SES, and KLI) and compared to check for consensus. A conservative approach was taken regarding assignment of the ET "zero transformation" to avoid ruling out any potential relationships that occur at low frequencies. Wherever possible, location data were recorded at the finest resolution provided. For studies that used laboratory infestation, the location field in our dataset corresponded to the site from which mussels were collected. In the case of naturally infested hosts (i.e., potential hosts found infested in a natural setting), location corresponds to the site of host collection. Common and scientific names of fishes used in this manuscript follow Page et al. (2023).

A Pearson's product-moment correlation was conducted to determine whether there was a correlation between the number of studies looking at host use by a given mussel species and the number of hosts identified for that species (i.e., total publications vs. total hosts). Both variables were log transformed to avoid violating the test assumptions of normality and heteroscedasticity.

Results

The literature scan yielded a total of 265 publications that presented primary evidence of mussel–host relationships. Of these, 194 had already been included in the Freshwater Mussel Host Database while the remaining 71 publications were newly identified. ETs were assigned to each of the mussel–host relationships detected within these 71 newly identified publications. Across all 55 species of freshwater mussels in Canada, 850 mussel–host interactions have been documented as of the date of the literature searches.

There are two species that remain without a single known or suspected host (Fig. S1). The first is the winged floater (*Anodonta nuttalliana*). The taxonomic classification of this species is controversial due to its extreme morphological similarity to the California floater (*Anodonta californiensis*), and is considered by some to be the same species (Chong et al. 2008; Mock et al. 2010). Although no hosts have been identified for the winged floater, several have been identified for the California floater (Table 3; note that the Haley et al. (2007) study did not distinguish between the winged floater and the California floater). The second species without any known hosts is the lake floater (*Pyganodon lacustris*), a species that was re-discovered in Canadian waters in July 2018 (Morris et al. 2020).

For the Pearson's product moment correlation test, a strong positive correlation ($r = 0.64$, df $= 53$, $p < 0.001$) was found between the number of studies of host use by a given

Table 3. Host information for the California floater, *Anodonta californiensis*.

Host species	Host common name	Evidence type	Reference	INHS
Gambusia affinis	Western mosquitofish	LT	d'Eliscu (1972)	Y
Rhinichthys osculus	Speckled dace	NI, LT	O'Brien et al. (2013)	Y
Rhinichthys cataractae	Longnose dace	LT	O'Brien et al. (2013)	Y
Cottus marginatus	Margined sculpin	LT	O'Brien et al. (2013)	Y
Mylocheilus caurinus	Peamouth chub	NI	O'Brien et al. (2013)	Y
Richardsonius balteatus	Redside shiner	NI	O'Brien et al. (2013)	Y
Ptychocheilus oregonensis	Northern pikeminnow	NI	O'Brien et al. (2013)	Y
Catostomus sp.	N/A	NI	O'Brien et al. (2013)	Y
Cottus sp.	N/A	NI	O'Brien et al. (2013)	Y
Lepomis cyanellus	Green sunfish	NI, LT	Haley et al. (2007)	N
Mylopharodon concephalus	Hardhead	NI, LT	Haley et al. (2007)	N
Cottus pitensis	Pit sculpin	NI, LT	Haley et al. (2007)	N
Ptychocheilus grandis	Sacramento pikeminnow	NI, LT	Haley et al. (2007)	N
Hysterocarpus traski	Tule perch	NI, LT	Haley et al. (2007)	N

Note: Evidence type uses the abbreviations outlined in Table 2. INHS refers to the Freshwater Mussel Host Database published by the Illinois Natural History Survey; Y indicates that the relationship was already included in their database, N indicates literature identified by this review. LT, laboratory transformation; NI, natural infestation.

mussel species and the number of identified hosts for that species, which is consistent with the findings of Hewitt et al. (2019).

Of the 265 publications included in this review, locality information of the study areas was provided in 205. Most of these studies (151) were conducted in the United States, with Canada as the location for the second highest number (30). The remainder were Europe-based studies, all of which examined host relationships of the eastern pearlshell (*Margaritifera margaritifera*; Fig. S2). Across all 55 species, 23 have 5 or fewer publications providing information on potential hosts (Fig. 1).

Laboratory transformation was the most frequent ET assigned to the larval–host interactions, with 1064 instances occurring across all 265 studies. Laboratory transformations were more than three times more common than the second most frequent ET, natural infestation (317 instances). The remainder of the ETs occurred between 28 and 317 times, with natural transformation and range correlation occurring the least (28 and 43, respectively; see Fig. S3). No cases of zero transformation (ZT) were found in the newly identified publications, though a total of 73 instances occurred overall. When looking at the distribution of ETs for each mussel species, it is apparent that many lack compelling evidence for host associations (Fig. 1). Three mussel species have a single ET; in the case of the Newfoundland floater (*Pyganodon fragilis*), the only suspected hosts come from range correlations. The Yukon floater (*Beringiana beringiana*) has only three host associations, all of which came from natural infestations which does not inherently imply that transformation is possible on any suspected hosts. The evidence base for the purple wartyback (*Cyclonaias tuberculata*) is exclusively lab transformations, which is relatively weak evidence of host relationships because laboratory transformation does not necessitate that either infestation or transformation can occur naturally. Only 13 species have natural transformation as part of their evidence base, 9 of which only have a single mussel–host association established via natural transformation.

To determine which hosts may support the highest diversity of mussels, the interactions between mussels and hosts that occur within Canada were plotted in a grid-style matrix (Fig. 2). The largemouth bass (*Micropterus nigricans*) hosts the highest diversity in Canada (25 mussel species). Of the 22 hosts supporting 10 or more mussel species, 13 are common gamefish belonging to Centrarchidae (sunfishes; 8), Ictaluridae (North American catfishes; 1), Percidae (perches and darters; 3), and Sciaenidae (drums and croakers; 1). In total, sunfishes are involved in 150 mussel–host interactions, minnows (Leuciscidae) in 129, and perches and darters in 109. It should also be noted that the non-native round goby (*Neogobius melanostomus*) is tied for the third highest number of possible associations for hosts that occur in Canada.

Of host species that are native to Canada, the mottled sculpin (*Cottus bairdii*) is the host species that supports the highest diversity of mussels (eight species based on known interactions) that have been designated at-risk either at the federal (by the Species at Risk Act; SARA) or provincial level (Fig. 2). Perches and darters are responsible for the highest number of mussel–host interactions for both provincially listed (48 interactions) and SARA-listed (43 interactions) unionoids, with centrarchids and leuciscids closely following (Fig. 2). It should be noted that the relative number of associations of both sculpins (Cottidae) and salmonids (Salmonidae) is proportionally larger when considering only the subset of mussel species designated as at-risk (provincially or federally). For 20 of Canada's unionoid species, no Canadian study recorded evidence of host relationships and a further 17 species have only a single host association identified by a Canadian study. The unionoids with the most suspected associations with hosts that occur in Canada that have been identified to date are the flutedshell (54) and the creek heelsplitter (48).

There are two species of non-native fishes that were investigated in Canada that may serve as potential hosts for

Fig. 1. Pie charts showing the split of evidence types for each species of Canadian unionoid (exceptions are the winged floater and the lake floater, which have no known hosts). Numbers around the perimeter indicate the unique host species within a given evidence type (note that there may be multiple evidence types associated with a single host species; see Fig. 2 for complete list of Canadian hosts). Numbers in the center indicate the total number of studies that provide evidence for host relationships for that species. Unionoid species classified as at-risk either federally or provincially have been identified with an asterisk and/or dagger, respectively. Evidence types: laboratory infestation (LI), laboratory transformation (LT), natural infestation (NI), natural transformation (NT), range correlation (RC), zero transformation (ZT), and not specified (NS). Detailed description of evidence types can be found in Table 2.

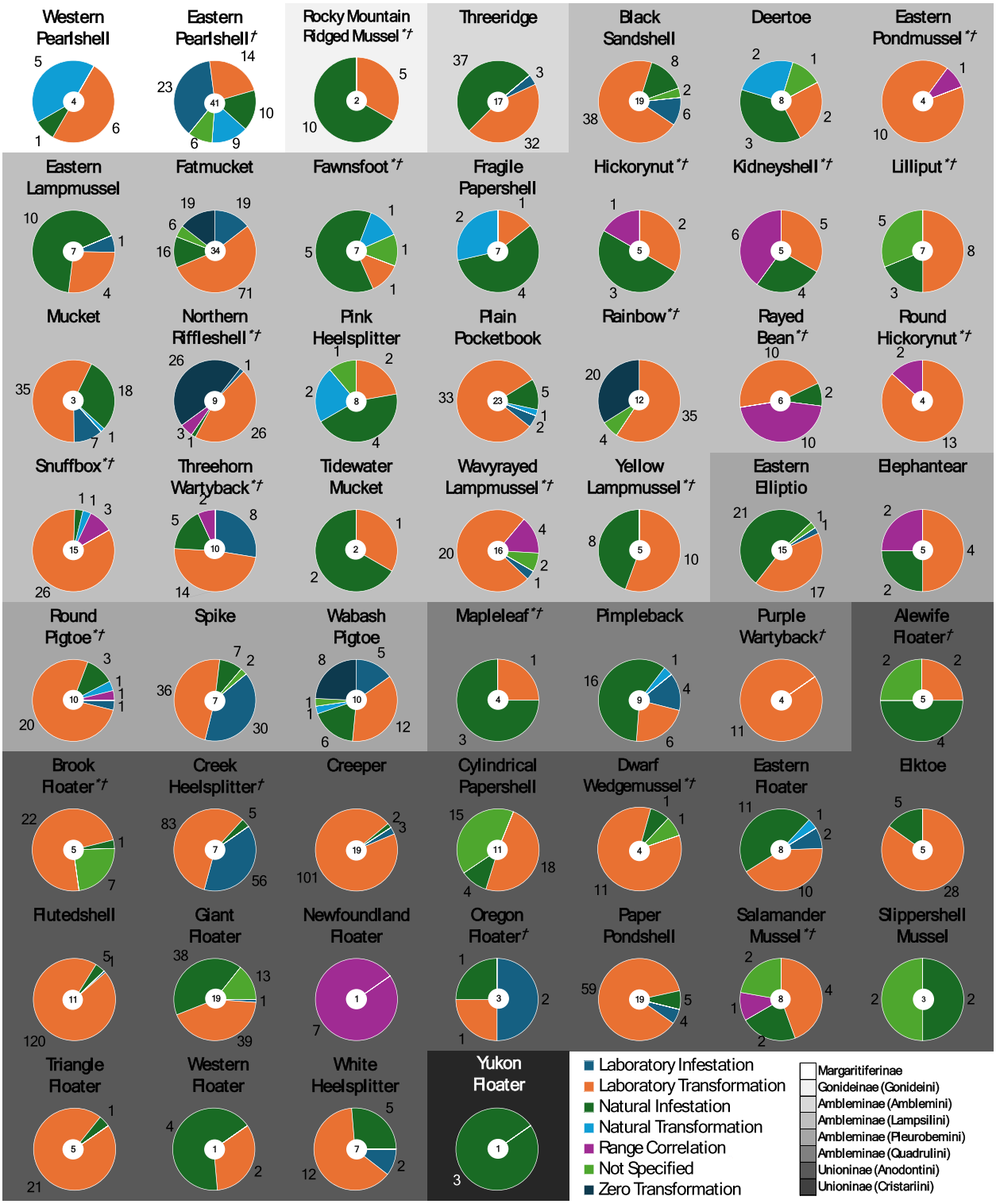


Fig. 2. Interaction matrix of Canadian unionoids and Canadian hosts (included only hosts currently found in Canada resolved to species level). Black squares indicate a known or suspected relationship. Fishes are sorted from top to bottom with highest number of interactions at the top. Taxonomic classifications are indicated by the colour codes to the left of each species. Mussels are sorted alphabetically by family, subfamily, tribe (in parentheses), and then common name. Unionoid species classified as at-risk either federally or provincially have been identified with an asterisk and/or dagger, respectively. Mussel–host interactions that have been studied in Canada were indicated with a maple leaf icon on the black squares.

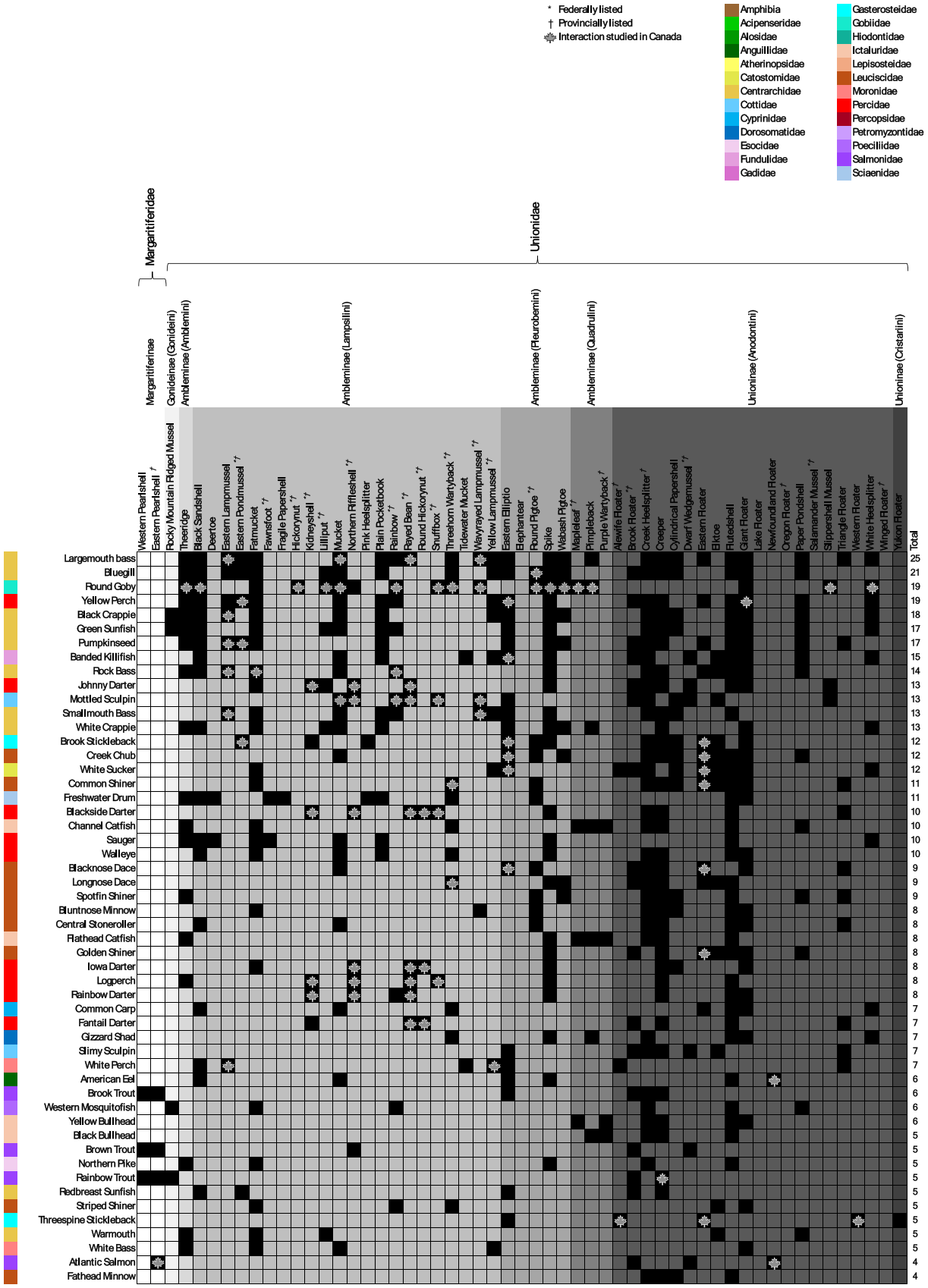
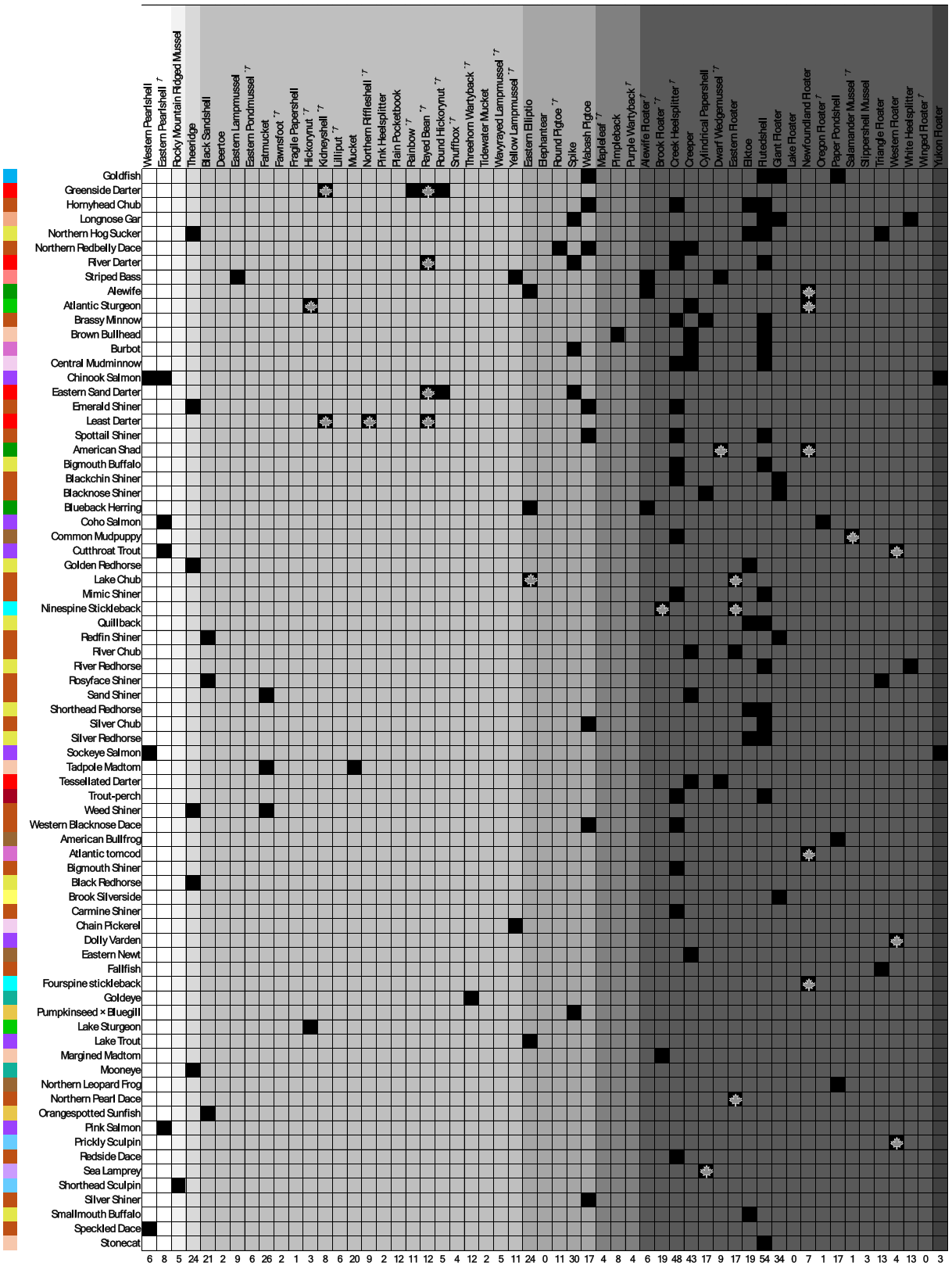


Fig. 2. (*concluded*).



Canadian unionoids: the sea lamprey (*Petromyzon marinus*; Wilson and Ronald 1967), and the round goby (*Neogobius melanostomus*; Tremblay 2012). Sea lamprey were found naturally infested by the glochidia of the cylindrical papershell (*Anodontoides ferussacianus*) in Lake Huron and several tributaries near Manitoulin Island, although metamorphosis

was not confirmed (Wilson and Ronald 1967). Three of five unionoid species artificially infested (the snuffbox, the rainbow, and the mucket) on the round goby successfully metamorphosed, albeit at lower rates than their respective native hosts (Tremblay 2012; Tremblay et al. 2016). Furthermore, several other unionoids were found to have naturally infested the round goby in the Grand River and the East Sydenham River, though this is not necessarily beneficial if transformation rates are exceedingly low (Tremblay et al. 2016). Several publications included in this review from the United States (Lefevre and Curtis 1910, 1912; Watters and O'Dee 1997; Barnhart and Baird 2000; Rogers-Lowery and Dimock 2006; Watters 1998; Martin 2018) and Europe (Salonen et al. 2016) also included information relevant to unionoid use of non-native hosts.

Discussion

Our findings underline a significant lack of knowledge for many of Canada's mussel–host relationships. This was highlighted by the outcome of Pearson's product moment correlation which yielded a strong positive relationship between the number of publications and number of known hosts. This result was consistent with Hewitt et al. (2019) and implies that until the curve levels off, new studies exploring unionoid–host relationships will continue to uncover new mussel–host relationships. Of the 55 unionoids in Canada, 23 had 5 or fewer publications related to potential hosts, with the most glaring examples being the pair of mussels with no known hosts: the lake floater and the winged floater. This may be partially a result of these two species being extremely difficult to distinguish morphologically from closely related species (Jespen et al. 2010; Morris et al. 2020). In the case of the winged floater, some potentially valuable host information is available (Table 2) but it is unclear whether hosts of the California floater are also viable for the winged floater due to unresolved taxonomy (Jespen et al. 2010). In either case, further research is needed to identify hosts for these two species.

Some interesting trends were revealed when looking at which host families accommodate the largest portion of mussel–host relationships in Canada. Percoids, centrarchids, and leuciscids constitute the majority of hosts for Canadian unionoids, with other host families supporting markedly fewer interactions (Fig. S4). This is consistent with Strayer (2008), who plotted the number of known relationships within a given fish family against the number of species belonging to that family, further facilitating comparison of families by their host suitability. Strayer (2008) suggested that host families that spend more time in shallow water closely associated with the sediments (e.g., Percidae, Centrarchidae, and Cottidae) are more likely to interact with mussels than families that tend to reside in open water or cooler, deeper water (e.g., Clupeidae, Salmonidae). We speculate that there may also be some bias toward testing more common, easily accessible, or ecologically interesting species (e.g., nonnatives) as potential hosts, and that rare or cryptic species such as burbot (*Lota lota*) or redhorses (*Moxostoma* spp.) may be underrepresented in the literature.

One important consideration is that not all hosts are equal in quality when it comes to facilitating metamorphosis of glochidia (Strayer 2008). Under natural conditions, several factors may affect reproductive success, including variation in female fecundity (Haag and Staton 2003) and spatiotemporal overlap between mussels and their hosts (Watters 1992). Host quality may also vary by individual host immunity (Rogers-Lowery and Dimock 2003; Dodd et al. 2005) or by region (Rogers et al. 2001), although this is not true in all cases (see Caldwell et al. 2016). In their study investigating host quality of the northern riffleshell and wavyrayed lampmussel, McNichols et al. (2011) identified higher metamorphosis rates on primary hosts compared to less suitable marginal hosts. A large sample size is, therefore, required to detect relationships between unionoids and their marginal hosts, and larger yet to confidently rule out any potential relationships. Nevertheless, reporting on the rate of infestation, metamorphosis, and sloughing (rejection) of glochidia is exceedingly useful in this context as it provides insight on which species may be primary versus marginal hosts for a given mussel or region. Of the 71 publications that were newly identified in this review, no relationships were assigned "zero transformation" due to small (e.g., Zale and Neves 1982; Hauswald 2010) or undisclosed (e.g., Ehlo 2014) sample sizes (i.e., number of fish tested). We feel that assigning ZT in such cases could be misleading given the low metamorphosis rates witnessed on some marginal hosts that may not have been captured by studies with smaller sample sizes. We suggest that readers consider sample size and geographical context in cases where it was assigned in the Freshwater Mussel Host Database (2017) (e.g., O'Dee and Watters 2000; Wilke et al. 2021).

Contrary to Hoggarth (1992) and the Freshwater Mussel Host Database (2017), we elected to include range correlation as an ET in this review. Range correlations occurred as an ET for 13 unionoid species, 12 of which each had additional supporting ETs (Fig. 1). In the case of the Newfoundland floater, the only available evidence comes from range correlations with potential host fish (Cyr et al. 2012). While range correlations are admittedly weak evidence of a relationship given they do not provide any evidence of either infestation or transformation, we elected to incorporate them as evidence as a means of guiding future research by providing a useful starting point for field and lab studies to further investigate these potential linkages.

One commonality across many of the laboratory experiments wherein fish were artificially infested with glochidia is that fish and mussels used were often collected from separate locations (e.g., Haag and Warren Jr 1999; Boogaard et al. 2015; Wilke et al. 2021). In other cases, locality information for neither fish nor gravid mussel collection was provided (e.g., Cliff et al. 2001; Brady et al. 2004). Compatibility of unionoid glochidia with their hosts has been shown to vary intraspecifically (Taeubert et al. 2010; Douda et al. 2014; Modesto et al. 2018), and infection and transformation rates of glochidia may vary between allopatric and sympatric hosts populations (Riusech and Barnhart 2000; Rogers et al. 2001; Serb and Barnhart 2008; Caldwell et al. 2016; St. John White et al. 2017). Thus, we advise researchers looking to test host compatibility in a laboratory setting to use specimens

collected from the same vicinity as the gravid mussels wherever possible. In cases where this is not feasible, we would emphasize the importance of reporting the locality with the highest precision possible so that researchers can formulate a more informed interpretation of infestation and transformation rates for a given relationship. There are direct implications for management programs that employ captive breeding as a conservation tool, an increasingly popular method wherein fish or mussels are propagated in a controlled setting and subsequent reintroduction into the wild to bolster or re-establish populations (Rytwinski et al. 2021). Aldridge et al. (2023) cautions that this method may have long-term implications for natural mussel–host compatibility (and by extension, reproductive success) and calls for further investigation.

Natural transformation was the least occurring ET despite its value in understanding mussel–host relationships. One of the barriers to collecting this type of evidence is the lack of knowledge on unionoid phenology. For many species, the specific timing of brooding, larval release, and detachment from hosts is largely unknown (Martel et al. 2010). This makes it logistically complicated to plan and execute field studies with a high level of efficiency, especially with limited resources. We therefore wish to highlight the importance of including specific dates of gravid female collection for laboratory experiments, or observation of infested fish in natural conditions. Including this seemingly simple information in host identification studies could lead to a reduction in knowledge gaps in unionoid phenology and subsequently facilitate future work looking to gather natural transformation data.

The impacts of invasive fish species on mussel reproduction have not been well studied, but are believed to have primarily negative impacts on unionoid recruitment via several possible mechanisms (Moore et al. 2019; Moore and Clearwater 2021). One mechanism suggested after studying the impacts of the round goby on Canadian unionoids in the Laurentian Great Lakes region is that non-natives may serve as glochidial sinks, by becoming infested with unionoid glochidia but providing highly reduced metamorphosis rates in comparison with native hosts (Tremblay 2012; Tremblay et al. 2016). Low metamorphosis rates on non-natives were also observed by several other publications included in this review (Watters 1998; Salonen et al. 2016; Martin 2018; Taylor et al. 2021). On the contrary, Watters (1998) found that some non-native species may outperform native hosts in certain cases, of which there are many other examples discussed in Modesto et al. (2018) and Moore et al. (2019). Further research is needed on the short- and long-term effects of non-native species introductions on mussel–host compatibility (Modesto et al. 2018; Moore et al. 2019), and we call for further research on this topic in a Canadian-specific context given the potential for geographic variation in effects. Future studies could also focus on the noninteractions (i.e., the blank spaces in Fig. 2); more work is needed to properly interpret what these apparent "noninteractions" mean and which ones would be important candidates for further testing. For example, if there is insufficient range or preferred habitat overlap between a mussel and a potential host, it would not be a biologically relevant interaction. One potential option would be a tiering approach for the blank squares indicating the best candidate interactions for further investigation. Furthermore, ruling out unsuitable hosts could be a useful avenue to explore. In this review, we were hesitant to assign ZT due to potential geographic variation in metamorphosis rates; if there was a standardized way to rule out relationships (e.g., no geographic overlap between unionoid and "host" species, metamorphosis rates consistently falling below a certain threshold), that could provide some useful insight for management of these species.

The primary outcome of this review is that it will serve as a valuable resource to be used alongside the INHS Mussel Host Database for researchers and managers seeking information on the hosts of any of Canada's unionoid mussels. Aside from providing a complete list of all known and suspected mussel–host relationships for Canadian unionoids, it presents insight on which unionoid species are lacking any evidence (i.e., the lake floater and the winged floater) or compelling evidence (e.g., the Newfoundland floater, the purple wartyback). Furthermore, it identifies which species have the fewest publications providing evidence on potential hosts (Fig. 1) and should help in focusing research efforts on the lesser-studied species going forward.

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Data availability

Data generated or analyzed during this study have been deposited in the Dryad Digital Repository and are publicly available at https://doi.org/10.5061/dryad.nk98sf86h. Of the 265 publications in this review, 194 came from the INHS publicly available mussel host database: (Freshwater Mussel Host Database 2017) http://wwx.inhs.illinois.edu/collections/mollusk/data/freshwater-mussel-host-database.

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Competing interests

The authors declare there are no competing interests.

Supplementary material

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