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Natural Enemies of Zebra and Quagga Mussels: Predators, Parasites, and Ecological Competitors

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ABSTRACT
This article reviews the international literature on the natural enemies of *Dreissena* spp.—bivalves which internationally have strong impacts on aquatic ecosystems, industries, fisheries, and aquaculture. It represents a revised edition of the initial treatment on this topic published over two decades ago, and as in the previous publication, it reviews the biology and ecology of organisms known to be involved in the predation (143 species), parasitism and commensalism (86 species and higher taxa), and competitive exclusion (14 species) of species in the genus *Dreissena*. Predators can at times have major impacts on dreissenid populations, but these reductions are typically only temporal and in restricted (e.g., shallow) areas within large waterbodies. A cumulative effect of a growing suite of enemies may have a constant, but overall limited, role in suppressing *Dreissena* densities—one far from any likelihood of population eradication. A diverse and abundant community of natural enemies, however, is beneficial because of its positive impact on energy flow. The introduction of dreissenids has redirected energy from the planktonic to the benthic community and predators, in particular molluscivorous fish and waterfowl, have served to redistribute this energy flow back into the pelagic environment.

KEYWORDS
Birds; *Dreissena*; Europe; fish; North America; parasites; predation

1. Introduction

The dreissenid bivalves *Dreissena polymorpha* (Pallas), the zebra mussel and *D. rostriformis bugensis* (Andrusov), the quagga mussel—two species native to the Ponto Caspian region—are considered among the most aggressive freshwater invaders due to the economic and ecological disruptions that have accompanied their spread across Europe and North America (Beekey et al. 2004; Burlakova et al. 2012; Higgins and Vander Zanden 2010; Karatayev and Burlakova 2022a; Karatayev et al. 1997, 2002a, 2007, 2015; Nalepa and Schloesser 2013; van der Velde et al. 2010). Numerous factors have been cited to explain their rapid spread and explosive population growth in invaded habitats, including life history traits, such as short generation time, high fecundity, a planktonic larval stage that facilitates dispersal, a byssate adult stage allowing dense aggregations, the ability to filter-feed on a wide range of plankton, high individual growth rates, and wide tolerance of a range of environmental conditions (Johnson and Carlton 1996; Karatayev and Burlakova 2022a; Karatayev et al. 1997, 2007, 2015). While their economic impacts typically stem from increased operating expenses resulting from their fouling of water pipes and other raw water-dependent infrastructure (Connelly et al. 2007; Nakano and Strayer 2014; O'Neill 2008; Pimentel 2005), their ecological impacts are primarily related to their effectiveness as ecosystem engineers in modifying the bottom substrates and reshaping energy and nutrient fluxes through benthic and pelagic habitats, resulting in fundamental changes in food web structures (Burlakova et al. 2023; Higgins and Vander Zanden 2010; Karatayev and Burlakova 2022a; Karatayev et al. 1997, 2002a, 2007, 2015; Mayer et al. 2002). Both economic and ecological consequences of dreissenids invasion have extremely strong impacts on fisheries and aquaculture (reviewed in Burlakova et al. 2023; Karatayev and Burlakova 2022a, 2022b).

Because of their significant impacts, there has been a concerted effort to better understand the biotic and abiotic factors that govern their population dynamics, in particular, to identify the factors that lead to their

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mortality and population control. In this regard, a recurrent question is what role do natural enemies play in controlling their population dynamics? According to the enemy release hypothesis, the relative absence of a diverse suite of native enemies (mainly predators and parasites) in newly invaded regions contributes to their rapid population growth (Gozzi et al. 2020; Jeschke and Heger 2018; MacLeod et al. 2010; Torchin et al. 2003). With time, however, native predators may adapt to become more effective at feeding on the exotic prey, either rapidly, due to phenotypic plasticity, or more slowly, *via* natural selection (Carlsson et al. 2009, 2011). Thus, the introduction and rapid spread of dreissenids throughout North America has been associated with the virtually complete escape of both *D. polymorpha* and *D. r. bugensis* from their species-specific endosymbionts (defined in this article as parasites and commensals) (Karatayev and Burlakova 2022a; Mastitsky et al. 2014; Molloy et al. 1997), and most of the predators evolutionary adapted to consume these mussels. Although the vast majority of the enemies of *Dreissena* in their Ponto Caspian native range are not present in North America, ecologically similar species do exist in the newly invaded areas, and these native predators, parasites, and ecological competitors are gaining the status as the new natural enemies of dreissenids (reviewed in Burlakova et al. 2023; Carlsson and Strayer 2009; Carlsson et al. 2011; Karatayev and Burlakova 2022a, 2022b; Molloy et al. 1997).

The first contribution synthesizing the international literature on the natural enemies, including predators (95 species), parasites and commensals (34 species), and competitors (11 species) of *Dreissena* was published over 25 years ago (Molloy et al. 1997).[1] The rate of publications on *Dreissena*, including surveys of their enemies and competitors, increased greatly in the last three decades following their discovery in North America in the late 1980s (reviewed in Karatayev and Burlakova 2022a; Nalepa and Schloesser 2013; van der Velde et al. 2010) and their parallel spread to several European countries in the late twentieth century (Karatayev and Burlakova 2022a). During the last 25 years, a large number of predators were reported to feed on dreissenids both in the Old and in the New World (reviewed in Burlakova et al. 2023; Karatayev and Burlakova 2022a), and new species-specific parasites of *D. polymorpha* were described (Molloy et al. 2005, 2012).

The present article is an updated and significantly expanded second edition of Molloy et al. (1997), summarizing the current knowledge of the diversity, impact, and geographical distribution of *Dreissena*'s enemies as well as the ecological interactions between dreissenids and their enemies. A total of 606 references are cited, including the 252 publications cited by Molloy et al. (1997) which reported on nearly 140 years of research (from 1858 to 1996).

Although this review covers available information on the enemies of *D. polymorpha* and *D. r. bugensis* that have earned this genus its international pest status, it also includes available information (albeit relatively limited due to their non-pest status) on the enemies of other *Dreissena* spp. (e.g., *D. carinata*, endemic to Lake Ohrid, Republic of North Macedonia).

Obviously, not all enemies have been studied with equal intensity. In organizing this review, subheadings were used freely to assist the reader in identifying the subject areas where information on a specific enemy was significant. As a result, subheadings differ among sections, and some potentially important issues are missing altogether due to the lack of published information. Because of space limitations, this review has attempted to be thorough, but not exhaustive in coverage, and has focused on papers containing clear and conclusive data, as opposed to anecdotal information.

Species and common names of the fishes listed in the text follow Robins et al. (1991a, 1991b).

2. Predators

2.1. Anti-predator adaptations: a cost-benefit tradeoff

Sedentary organisms are particularly vulnerable to predation and often have evolved morphological adaptations in response to predation threats. In molluscs, the shell is the main morphological defense against predators (Ponder et al. 2019), and in dreissenids and other byssate bivalves, its firm adhesion to the substrate significantly decreases their vulnerability to predation (Reimer and Tedengren 1997). The shell's strength (i.e., its crush resistance) is also a major defense. Stronger shells in zebra mussel populations from European lakes with increased predation mortality indicate that higher energy investments in shell production are evolutionarily justified (Czarnoleski et al. 2006). Both zebra and quagga mussels respond to predation risk cues by forming thicker shells (Naddafi and Rudstam 2014a), but the responsiveness of mussels to predators decreases as shells grow in

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[1] In Molloy et al. (1997), the total numbers of predators and competitors were erroneously reported as 176 and 10.

size and become less vulnerable to crushing (Czarnoleski and Muller 2013).

In addition to morphological adaptations, a wide and complex variety of behaviors (as detailed below) have been reported from experimental laboratory studies in which zebra mussels were exposed to predation risks (Coons et al. 2004; Czarnoleski and Muller 2013; Czarnoleski et al. 2011; Dzierzynska-Bialonczyk et al. 2019; Kobak 2013; Kobak and Rynska 2014; Kobak et al. 2010; Naddafi et al. 2007; Toomey et al. 2002). In the presence of predators, they are more likely to reduce their mobility and form denser aggregations (Kobak 2013; Kobak et al. 2010). In response to predation cues, zebra mussels may increase or decrease the strength of byssal attachment (Czarnoleski and Muller 2013; Czarnoleski et al. 2011; Hirsch et al. 2014). Their crawling tends to reflect a negative phototaxis, suggesting a strategy to decrease their vulnerability to predators by their seeking darkness or dimly lit refugia (Kobak 2002, 2013). Small zebra mussels often climb upwards, but light and predator scents inhibit that movement (Kobak 2013). In the presence of light mussels gape less and have lower feeding/clearance rates—suggesting a strategy to reduce both the release of disclosing metabolites, as well as potential injury to their exposed soft tissues (Kobak 2013). In the presence of crushed conspecifics, zebra mussels reduce their gaping and decrease their crawling speed resulting in traveling shorter distances (Kobak and Rynska 2014). Houghton and Janssen (2013) found that in the presence of high round goby densities, dreissenids strike a balance between lowered risk of predation by occupying sheltered habitats (under rocks and in crevices), and enhanced feeding opportunities (and likely spawning) by occupying more exposed habitats. Like other byssate mussels, zebra mussels appear to adjust these antipredator strategies in relation to the spatio-temporal variability of predation pressure during their lifespan (Antol et al. 2018; Czarnoleski and Muller 2013; Czarnoleski et al. 2010, 2011; Dzierzynska-Bialonczyk et al. 2019; Reimer and Tedengren 1997). Zebra mussels use chemosensors to assess predation risks and differentiate between species of predators, to tune their responses to the type and intensity of the alarm cues, and to recognize the immediacy of predatory attacks (Czarnoleski and Muller 2013).

Anti-predator behaviors have also been investigated in quagga mussels. In laboratory experiments comparing the predator-induced responses of zebra and quagga mussels, Naddafi and Rudstam (2013) observed that quagga mussels did not lower their clearance rates as much as zebra mussels, but that the strength of the other responses measured, e.g., increased aggregation, increased attachment strength, and increased use of refuge sites, was similar between the two species.

The energy resources invested in anti-predator morphological and behavioral responses can have negative long-term consequences for the bivalves themselves. Anti-predator adaptive strategies similar to those aforementioned in dreissenids have also been observed in marine bivalves, such as hard clams, *Mercenaria mercenaria* (Smee and Weissburg 2006) and blue mussels, *Mytilus edulis* (Reimer and Tedengren 1997). Anti-predator responses (in particular reduced gaping/feeding) in these non-dreissenid bivalves, although potentially enhancing their short-term survival, have been documented to also be costly, with growth and reproductive output potentially diminished when the exposure to predation is prolonged (Large et al. 2012; Nakaoka 2000). Similarly, Naddafi and Rudstam (2014c) found that predator-induced increases in shell thickness in zebra and quagga mussels observed in laboratory tests were negatively correlated with their growth rates. In their study of European lakes, where zebra mussels had been gradually replaced by quagga mussels, Balogh et al. (2019, 2022) reported that in contrast to quagga mussels, zebra mussels exhibited two better developed anti-predator strategies—more crush-resistant shells and stronger byssal attachment, but at the cost of their lower weight increments per unit length and lower glycogen content throughout their entire size range. Balogh et al. (2019) concluded that the comparatively faster growth rate they observed in quagga mussels was likely enabled by their weaker development of the aforementioned anti-predation strategies and may have promoted their competitive success over zebra mussels.

2.2. Fish

Of the 77 fish species recorded as consuming dreissenids, 42 were field-documented as preying only on attached mussels, 22 on both life stages, and 13 feeding exclusively on planktonic larvae (Tables 1 and 2). These numbers include the 46 species listed by Molloy et al. (1997), of which 23 prey on attached mussels only, 15 prey on both planktonic and attached mussels, and 8 were observed to feed on planktonic mussels only (Tables 1 and 2).

2.2.1. Fish predation on planktonic dreissenid mussels

Relatively little research had been conducted on the predation of planktonic dreissenids by fish (primarily

Table 1. Fish documented in field studies in Europe (E) and North America (NA) as predators of planktonic *Dreissena.*

Species[a]	Common names[b]	Family	Where predation observed	References
Abramis bjoerkna (=Blicca bjoerkna)	Silver bream, white bream	Cyprinidae	E	Voronchuck et al. 1983
Abramis brama	Bream	Cyprinidae	E	Belyaev et al. 1970
Alburnus alburnus	Bleak	Cyprinidae	E	Voronchuck et al. 1983; Wilkońska and Strelnikova 2000
Alosa aestivalis	Blueback herring	Clupeidae	NA	Limburg and Ahrend 1994
Alosa pseudoharengus	Alewife	Clupeidae	NA	Creque and Czesny 2012; Eppehimer et al. 2019; Mills et al. 1995; Withers et al. 2015
Alosa sapidissima	American shad	Clupeidae	NA	Nack et al. 2015
Atherina boyeri	Sand smelt	Atherinidae	E	Chrisafi et al. 2007
Chondrostoma nasus	Nase	Cyprinidae	E	Mogilchenko 1986
Coregonus hoyi	Bloater	Salmonidae	NA	Eppehimer et al. 2019
Dorosoma cepedianum	Gizzard shad	Clupeidae	NA	Mills et al. 1995
Leuciscus idus	Ide, orfe	Cyprinidae	E	Mogilchenko 1986
Lota lota	Barbot	Gadidae	NA	George et al. 2013
Morone americana	White perch	Percichthyidae	NA	Limburg and Ahrend 1994; Limburg et al. 1997
Morone saxatilis	Striped bass	Percichthyidae	NA	Limburg et al. 1997
Notropis hudsonius	Spottail shiner	Cyprinidae	NA	Creque and Czesny 2012
Osmerus eperlanus	European smelt, sea smelt	Osmeridae	E	Wiktor 1958
Osmerus mordax	Rainbow smelt	Osmeridae	NA	Mills et al. 1995
Perca fluviatilis	Eurasian perch, European perch	Percidae	E	Wiktor 1958
Perca flavescens	Yellow perch	Percidae	NA	Creque and Czesny 2012; Marin Jarrin et al. 2015; Withers et al. 2015
Rutilus rutilus	Roach	Cyprinidae	E	Belyaev et al. 1970; Mogilchenko 1986; Wiktor 1958; Wilkońska and Strelnikova 2000; Zhdanova and Gusynskaya 1985
Scardinius erythrophthalmus	Rudd	Cyprinidae	E	Voronchuck et al. 1983; Wilkońska and Strelnikova 2000
Stizostedion lucioperca (=Lucioperca lucioperca)	Zander, pikeperch	Percidae	E	Draulans and Wouters 1988; Wiktor 1958

[a] Standard scientific names follow Robins et al. (1991a, 1991b); names in parentheses are synonyms which appear in the corresponding references.
[b] Common names used in the accompanying references.

Table 2. Fish documented in field studies in Europe (E) or North America (NA) as predators of attached (i.e., juvenile and adult) *Dreissena.*

Species[a]	Common names[b]	Family	Where predation observed	References
Abramis bjoerkna (=Blicca bjoerkna)	Silver bream, white bream	Cyprinidae	E	Draulans and Wouters 1988; Filuk and Zmudzinski 1965; Gerasimov 2015; Karatayev et al. 1994; Kogan 1970; Mikheev 1963, 1977; Nagelkerke and Sibbing 1996; Nikitenko and Shcherbina 2016; Pliszka 1953; Prejs 1976; Shcherbina and Buckler 2006; Specziár et al. 1997; Zhokhov 2001
Abramis brama	Bream, common bream	Cyprinidae	E	Budzynska et al. 1956; Draulans and Wouters 1988; Filuk and Zmudzinski 1965; Gerasimov 2015; Gontya 1971; Mikheev 1963, 1977; Hartmann 1982; Karatayev et al. 1994; Martyniak et al. 1987; Nagelkerke and Sibbing 1996; Severenchuk and Kaftannikova 1983; Shcherbina and Buckler 2006; Specziár et al. 1997; Zheltenkova 1955; Zhokhov 2001
Acipenser brevirostrum	Shortnose sturgeon	Acipenseridae	NA	Gaygusuz et al. 2007; Bain, M. B., pers. comm.
Acipenser fulvescens	Lake sturgeon	Acipenseridae	NA	Bruestle et al. 2019; French 1993
Acipenser gueldenstaedti	Russian sturgeon	Acipenseridae	E	Yablonskaya 1985
Acipenser ruthenus	Sterlet	Acipenseridae	E	Karatayev et al. 1994; Egereva 1971; Mikheev 1977
Alburnus alburnus (=Alburnus lucidus)	Bleak	Cyprinidae	E	Sebestyén 1937
Ambloplites rupestris	Rock bass	Centrarchidae	NA	Watzin et al. 2008
Ameiurus nebulosus (=Ictalurus nebulosus)	Brown bullhead	Ictaluridae	NA	French 1993
Anguilla anguilla	European eel	Anguillidae	E	Biro 1974; de Nie 1982; Kublitskas 1959
Aplodinotus grunniens	Freshwater drum, drum	Sciaenidae	NA	Bartsch et al. 2005; French 1993; French and Bur 1993; Magoulick and Lewis 2002; Morrison et al. 1997; Shields and Beckman 2015; Thorp et al. 1998; Watzin et al. 2008
Babka (=Neogobius) gymnotrachelus	Racer goby	Gobiidae	E	Gaygusuz et al. 2007; Smirnov 1986
Benthophilus stellatus	Stellate tadpole-goby	Gobiidae	E	Kasyanov and Klevakin 2011; Smirnov 1986
Carassius carassius	Crucian carp	Cyprinidae	E	Naberezhny et al. 1971

(*Continued*)

Table 2. Continued.

Species[a]	Common names[b]	Family	Where predation observed	References
Carassius auratus gibelio	Wild goldfish	Cyprinidae	E	Specziár et al. 1997
Carpoides carpio	River carpsucker	Catostomidae	NA	Thorp et al. 1998
Carpiodes cyprinus	Quillback carpsucker	Catostomidae	NA	Bartsch et al. 2005
Catostomus commersoni	White sucker	Catostomidae	NA	French 1993
Clupeonella cultriventris	Caspian sprat	Clupeidae	E	Sherstyuk and Severenchuk 1989
Coregonus clupeaformis	Lake whitefish	Salmonidae	NA	French 1993; Owens and Dittman 2003; Pothoven and Nalepa 2006; Pothoven et al. 2001; Lumb et al. 2007; Rennie et al. 2012
Coregonus lavaretus	Powan	Salmonidae	E	Peczalska 1961; Pliszka 1953
Coregonus macrophthalmus	Gangfisch, benthivorous whitefish	Salmonidae	E	Baer et al. 2022
Cyprinus carpio	Common carp	Cyprinidae	E and NA	Aleksenko 2004; Bartsch et al. 2005; Botnariuc et al. 1964; Marsden 1997; Mikheev 1963; Sebestyén 1937; Specziár et al. 1997; Stein et al. 1975; Thorp et al. 1998; Tucker et al. 1996
Huso huso	Beluga	Acipenseridae	E	Yablonskaya 1985
Ictiobus bubalus	Smallmouth buffalo	Catostomidae	NA	Thorp et al. 1998
Ictalurus furcatus	Blue catfish	Ictaluridae	NA	Herod et al. 1997; Magoulick and Lewis 2002
Ictalurus punctatus	Channel catfish	Ictaluridae	NA	Thorp et al. 1998
Lepomis auritus	Redbreast sunfish	Centrarchidae	NA	Boles and Lipcius 1997; Schmidt, R., pers. comm.
Lepomis gibbosus	Pumpkinseed	Centrarchidae	NA and E	Andraso 2005; Berchtold et al. 2015; Boles and Lipcius 1997; Colborne et al. 2015; Locke et al. 2014; Naddafi and Rudstam 2014c[a]; Rezsu and Specziár 2006; Spataru 1967; Watzin et al. 2008
Lepomis macrochirus	Bluegill	Centrarchidae	NA	Andraso 2005; Bartsch et al. 2005; Magoulick and Lewis 2002; Mercer et al. 1999; Thorp et al. 1998
Lepomis microlophus	Redear sunfish	Centrarchidae	NA	Magoulick and Lewis 2002
Leuciscus idus	Ide, orfe	Cyprinidae	E	Mikheev 1963, 1977; Pliszka 1953; Shcherbina and Buckler 2006; Zhokhov 2001
Leuciscus leuciscus	Dace	Cyprinidae	E	Baer et al. 2022b)
Macrhybopsis storeriana	Silver chub	Cyprinidae	NA	Kočovský 2019
Morone americana	White perch	Percichthyidae	NA	French 1993
Morone chrysops	White bass	Percichthyidae	NA	French 1993
Moxostoma sp.	Redhorse sucker	Catostomidae	NA	Bartsch et al. 2005; Thorp et al. 1998
Moxostoma valenciennesi	Greater redhorse	Catostomidae	NA	French 1993
Mylopharyngodon piceus	Black carp, black amur, Chinese roach	Cyprinidae	E and NA	Evtushenko et al. 1994; Konradt and Mukhammedova 1974; Krepis et al. 1981; Nebolsina et al. 1991; Poulton et al. 2019
Neogobius fluviatilis	Monkey goby	Gobiidae	E	Smirnov 1986; Yablonskaya 1985
Neogobius kessleri	Bighead goby	Gobiidae	E	Gavlena 1977; Yablonskaya 1985
Neogobius melanostomus	Round goby	Gobiidae	E and NA	Bunnell et al. 2015; Campbell et al. 2009; Camp et al. 1999; Djuricich and Janssen 2001; Jude et al. 1995; Kuhns and Berg 1999; Lederer et al. 2006, 2008; Miano et al. 2021; Muzzall et al. 1995; Naddafi and Rudstam 2014b, 2014c[a]; Rakauskas et al. 2008; Ray and Corkum 1997; Rybczyk et al. 2020; Shemonaev and Kirilenko 2009; Smirnov 1986; Turschak and Bootsma 2015; Yablonskaya 1985
Perca flavescens	Yellow perch	Percidae	NA	French 1993; Morrison et al. 1997; Watzin et al. 2008
Perca fluviatilis	Eurasian perch, European perch	Percidae	E	Naberezhny et al. 1971; Sebestyén 1937
Percina caprodes	Logperch		NA	Burkett and Jude 2015
Platichthys flesus (=*Pleuronectes flesus*)	European flounder, flounder	Pleuronectidae	E	Filuk and Zmudzinski 1965
Proterorhinus marmoratus (=*Priolepis marmoratus*)	Tubenose goby	Gobiidae	E	Yablonskaya 1985
Pylodictis olivaris	Flathead catfish	Ictaluridae	NA	Bartsch et al. 2005; Thorp et al. 1998
Rhodeus sericeus	Bitterling	Cyprinidae	E	Naberezhny et al. 1971
Rutilus rubilio	Adriatic roach	Cyprinidae	E	Daoulas and Economidis 1984
Rutilus rutilus	Roach	Cyprinidae	E	Aleksenko 2004; Baer et al. 2022; Balkuvienė and Pernaravičiūtė 1994; Dmitrenko 1967; Draulans and Wouters 1988; Filuk and Zmudzinski 1965; Gerasimov 2015; Grigorash 1963; Karatayev et al. 1994; Kharchenko 1975; Kodukhova and Karabanov 2017; Mikheev 1963; Nagelkerke and Sibbing 1996; Nikitenko and Shcherbina 2016; Olszewski 1978; Pliszka 1953; Pirozhnikov 1971; Prejs 1976; Rask 1989; Specziár et al. 1997; Shcherbina and Buckler 2006; Stanczykowska 1987; Zheltenkova 1949; Zhokhov 2001

(*Continued*)

Table 2. Continued.

Species[a]	Common names[b]	Family	Where predation observed	References
Stizostedion vitreum	Walleye	Percidae	NA	French 1993
Tinca tinca	Tench	Cyprinidae	E	Baer et al. 2022; Pliszka 1953; Severenchuk and Kaftannikova 1983
Vimba elongata	No common name	Cyprinidae	E	Ritterbusch-Nauwerck 1991
Vimba vimba	Vimba	Cyprinidae	E	Aleksenko 2004; Kublitskas 1959; Okgerman et al. 2013
Fish that consume dreissenids only occasionally				
Acipenser sturio	European Atlantic sturgeon	Acipenseridae	NA	Ferreira-Rodriguez et al. 2016
Gymnocephalus cernua	Ruffe	Percidae	E	Baer et al. 2022b
Esox lucius	Northern pike	Esocidae	E	Millane et al. 2012
Notropis hudsonius	Spottail shiner	Cyprinidae	NA	Creque and Czesny 2012; Turschak and Bootsma 2015
Prosopium cylindraceum	Round whitefish	Salmonidae	NA	Turschak and Bootsma 2015
Salmo trutta	Brown trout	Salmonidae	E	Millane et al. 2012
Salvelinus profundus	Deep-water Arctic charr	Salmonidae	E	Baer et al. 2022b
Salvelinus umbla	Normal Arctic charr	Salmonidae	E	Baer et al. 2022b
Squalius cephalus	Chub	Cyprinidae	E	Baer et al. 2022b

[a]Standard scientific names follow Robins et al. (1991a, 1991b); names in parentheses are synonyms which appear in the accompanying references.
[b]Common names used in the corresponding references.

fry), and their impact on dreissenid populations is generally unknown. This literature review indicates that 11 European and 11 North American fish species have been field-documented as containing planktonic *Dreissena* larvae in their alimentary tracts. These fishes include several families: Atherinidae (one species); Cyprinidae (eight species), Clupeidae (four species), Gadidae (one species), Osmeridae (two species), Percidae (three species), Percichthyidae (two species), and Salmonidae (one species) (Table 1). Predation on larval dreissenids by fish is likely far more common than these few records indicate. Published reports frequently use the term "veliger" to characterize the larval stage of *Dreissena* observed. The mussel's initial larval stage, the trochophore, is also likely a prey item for fish, but this has not been specifically reported.

During the summer, *Dreissena* veligers often comprise up to 73% of total zooplankton density and up to 40% of the zooplankton biomass and production (Bowen et al. 2018; David et al. 2009; Karatayev et al. 2010; Kornobis 1977; Lazareva et al. 2016; Lvova et al. 1994; Mitrakhovich and Karatayev 1986; Wiktor 1958; Withers et al. 2015). In Europe, fish predation on dreissenid larvae has not been extensively quantified but is considered to be high, for example, in the eutrophic inland waters of the Netherlands which contain dense fish stocks (van der Velde et al. 1994). In a Russian reservoir, Grigorash (1963) reported 20–40 veligers in roach (*Rutilus rutilus*) fry during July. Wiktor (1958), who observed up to 65 *D. polymorpha* larvae in one fry, reported that predation on *Dreissena* larvae in the Lagoon of Szczecin (Poland) by hatchlings of several fish species was typically brief (2–4 weeks) and involved primarily fry >12 mm in length. In studies in Poland, *Dreissena* veligers were recorded in unidentified 10–16 mm fry (Kornobis 1977), and in Russia in 12–16 mm roach (Spanowskaya 1963). In the Dnieprodzershinskoe Reservoir (Ukraine), larval *Dreissena* represented 63 and 37% of the biomass ingested, respectively, by fry of roach (*R. rutilus*) and bream (*Abramis brama*) (Belyaev et al. 1970). In the Khodorovskoe region of the Kanewskoe Reservoir (Ukraine), veligers were a regular component in the diet of fry of the silver bream (*Abramis bjoerkna*), rudd (*Scardinius erythrophthalmus*), and bleak (*Alburnus alburnus*) (Voronchuck et al. 1983). Chrisafi et al. (2007), analyzing stomach contents from 240 specimens collected monthly in Trichonis Lake (Greece), found that larvae of *D. polymorpha* were the dominant prey for *Atherina boyeri*.

In North America, Limburg and Ahrend (1994) reported that in the Hudson River (USA) dreissenid veligers were present in 44.2% of the feeding white perch (*Morone americana*) fry between 3.1 and 6.6 mm standard length. The heaviest predation of veligers occurred in the 3.5–4.4 mm size class. Of the 23 white perch analyzed, 70 and 17% contained one and four veligers, respectively (Limburg et al. 1997), as well as one blueback herring (*Alosa aestivalis*) with a single veliger. In the latter study, the authors found that zebra mussel larvae in the Hudson River were most commonly consumed by the smallest larval size class (<5 mm) of striped bass and white perch. In Lake Ontario, Mills et al. (1995) observed planktivory of dreissenid veligers by young-of-the-year and adults of both alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), but they concluded that consumption was not sufficient to substantially reduce veliger densities in nearshore waters. Likewise, Stanczykowska (1987) concluded that fish fry (species not identified) consume only small amounts of larval *D. polymorpha* and that this predation does not have major effects on mussel populations.

More data on fish predation has become available in the last few decades. In Lake Ontario, veliger biomass increased between 2008 and 2014, and represented up to 39% of total zooplankton biomass in May–October (Bowen et al. 2018). In contrast, zooplankton biomass declined markedly in the deep Great Lakes colonized by dreissenids (reviewed in Karatayev and Burlakova 2022b). As a result, fish learned to prey on the abundant veligers when other more preferred food items are rare. In southeastern Lake Michigan in 2010 and 2011 dreissenid veligers comprised 69–100% of yellow perch and up to 38% of alewife diets, complementing early-feeding larvae with a relatively abundant prey source that may partially offset the apparent low consumption of other prey (Withers et al. 2015). In western Lake Erie, dreissenid veligers comprised 20% of larval yellow perch diet, indicating that dreissenid mussels may influence larval yellow perch foraging, growth, and survival (Marin Jarrin et al. 2015). In Hudson River *D. polymorpha* veligers made up over 68% of *Alosa sapidissima* diet by individual counts and 25% by dry weight (Nack et al. 2015). The importance of veligers as a diet item, however, greatly depends on larval fish–veliger temporal and spatial (both in-depth and local distribution) overlap, yearly shifts in veliger abundance, as well as their digestibility, nutritional quality, and the fate of veliger production incorporated into the food web—all questions in need of further study.

2.2.2. Fish predation on attached (byssate) dreissenid mussels

Consumption of dreissenids attached to the substrate has been recorded for at least 64 fish species (13 families), including 31 species (10 families) in North America and 37 species (10 families) in Europe (Table 2). Only four species—the common carp (*Cyprinus carpio*), pumpkinseed (*Lepomis gibbosus*), black carp (*Mylopharyngodon piceus*), and round goby (*Neogobius melanostomus*)—have been field-documented as predators on both continents. Some of these references, however, contain records of only occasional findings of a few dreissenids in the guts of fish species. For example, in a four year study summarizing food consumption by eels (*Anguilla anguilla*) in Lake Balaton (Hungary), the percentage of prey items in the gut that were bivalves (including *Dreissena*) averaged 0.4%, with a maximum of 5.6% (Biro 1974). Nine other species of fish (*Acipenser sturio*, *Gymnocephalus cernua*, *Esox lucius*, *Notropis hudsonius*, *Prosopium cylindraceum*, *Salmo trutta*, *Salvelinus profundus*, *Salvelinus umbla*, and *Squalius cephalus*) were reported feeding on *Dreissena* at very limited rates (Table 2). Dreissenids occurred in their diets very sparsely, seasonally, and in some cases, mussels could possibly have been consumed as incidental by-catch.

In Europe, Cyprinidae are the most common dreissenid predators, especially roach, and to a lesser degree, carp, silver bream, and common bream (Table 2). Among all fish species, roach is clearly the most dominant, widely reported, and aggressive predator of *Dreissena* in European waters. In North America, round gobies are the most commonly reported predators of dreissenids, although freshwater drum (*Aplodinotus grunniens*: Sciaenidae), common carp (*Cyprinus carpio*), and pumpkinseed (*Lepomis gibbosus*) are also well documented (Table 2).

2.2.3. Factors affecting fish predation

Some of the biotic and abiotic factors affecting fish predation rates on dreissenids are discussed below. This list, however, is far from complete because population-wise fish consumption of dreissenids is not well understood and is difficult to assess accurately. For example, the same fish species, such as common bream (*Abramis brama*), has been noted to feed on *Dreissena* at different intensities in various waterbodies. Dreissenids are rarely eaten by common bream in Russia's Kuibyshev Reservoir basin (Egereva 1971) but are common dietary items in both the Moldovan Kuchurgansky Liman (Gontya 1971) and in the Ukrainian Kanevskoe Reservoir (Severenchuk and Kaftannikova 1983). Similarly, their consumption by round gobies varies both seasonally and with depth (French and Jude 2001; Schaeffer et al. 2005; Walsh et al. 2007) and differs substantially depending on the time of day, habitat, and region, suggesting a capacity to adapt to locally abundant food sources (Kornis et al. 2012). In lakes Huron and Ontario round gobies prey on dreissenids in shallow water (27–46 m) and on native invertebrates at greater depths (Schaeffer et al. 2005; Walsh et al. 2007).

2.2.3.1. Fish size. Fish have a clearly marked threshold body size above which they begin to feed on dreissenids (Table 3), which often relates to morphological changes in their pharynx. The presence of molariform pharyngeal teeth is the key characteristic shared by benthivorous fishes that are

Table 3. Relationship between predation on attached (i.e., juvenile and adult) *Dreissena* and fish length and/or age in field populations.

Species[a]	Fish length and/or age when start feeding on *Dreissena*	Location	References
Abramis bjoerkna (=Blicca bjoerkna)	>70 mm	Mikolajskie Lake, Poland	Prejs 1976
	>105 mm (2+ years)	Rybinsk Reservoir, Russia	Zhokhov 2001
Abramis brama	18% of ≥4-year old (<1% of diet)	Goplo Lake, Poland	Budzynska et al. 1956
	>370 mm	Pierzchaly Reservoir, Poland	Martyniak et al. 1987
	≥315 mm long	Rybinsk Reservoir, Russia	Zhokhov 2001
Aplodinotus grunniens	Mainly >250 mm but consumption increases with fish length: dreissenids present in 16% of 200–249 mm long fishes; 250–374 mm individuals feed mainly on dreissenids; >375 mm fish feed almost exclusively on dreissenids (97–99% of the total dry weight of food ingested). The smallest ind. capable of crushing dreissenid shells is 265 mm.	Lake Erie, USA	French and Bur 1993
	>250 mm	Lake Erie, USA	Morrison et al. 1997
	>200 mm; ~50% of large fish consumed mussels.	Lake Dardanelle, USA	Magoulick and Lewis 2002
Coregonus clupeaformis	73–149 mm (age-0 fish) mainly consume large-bodied cladoceran zooplankton; ≤350 mm feed on soft-bodied macroinvertebrates and a few molluscs; >350 mm mainly eat molluscs, particularly *D. r. bugensis*	Lake Huron, USA	Pothoven and Nalepa 2006
Cyprinus carpio	No conclusive evidence that 381–666 mm fish consumed more dreissenids than 299–373 mm	Mississippi River, USA	Tucker et al. 1996
Ictalurus furcatus	22% of 25–50 cm feed on dreissenids	Ohio River, USA	Herod et al. 1997
Leuciscus idus	≥220 mm	Rybinsk Reservoir, Russia	Zhokhov 2001
Mylopharyngodon piceus	Age 2	Tsimlyanskoe Reservoir, Russia	Mukhammedova et al. 1989
Neogobius melanostomus	47–65 mm fish feed on dreissenids and of soft-bodied invertebrates; in 80–90 mm dreissenids comprise up to 82% of diet >100 mm can feed almost exclusively on dreissenids.	Great Lakes, USA	Jude et al. 1995
	Age 2+ diet was dominated by zebra mussels (75% by weight)	Curonian Lagoon, Lithuania	Rakauskas et al. 2008
Perca flavescens	>150 mm	Lake Erie, USA	Morrison et al. 1997
Rutilus rubilio	<159 mm fish feed on plant and animal food, the largest ones mainly consuming dreissenids	Lake Trichonis, Greece	Daoulas and Economidis 1984
Rutilus rutilus	≥100 mm 7% of *Dreissena* in guts of 200 mm roach, 72% in 250 mm, and 99% in 300 mm roach	Dnieper-Bug estuary region, Ukraine	Aleksenko 2004
	57% of 4-year old and 100% of ≥8-year-old roach had dreissenids in their guts (54–97% of the gut contents)	Goplo Lake, Poland	Budzynska et al. 1956
	140–160 mm	Lake Harsz, Poland	Budzynska et al. 1956
	140–160 mm	Goplo Lake, Poland	Pliszka 1953
	140–160 mm	Mikolajskie Lake, Poland	Prejs 1976
	180–320 mm roach feed almost exclusively on dreissenids	Lake Harsz, Poland	Pliszka 1953
	>160 mm feed on molluscs (95% dreissenids)	Mikolajskie Lake, Poland	Prejs 1976
	<160 mm rarely fed on dreissenids; <180 mm fed on plants; 160–179 mm had 6% dreissenids in diet, 230–240 mm—75%, >280 mm—95%	Lake Sniardwy, Poland	Prejs et al. 1990
	Start feeding at >150 mm; feed almost exclusively when >200 mm	Uchinskoe Reservoir, Russia	Spanowskaya 1963
	160–179 mm roach had 6% dreissenids in the diet; 280–350 mm had 97%	Lakes in Poland	Stanczykowska 1987
	>140 mm long (at 2+ years)	Rybinsk Reservoir, Russia	Zhokhov 2001

[a] Standard scientific names following Robins et al. (1991a, 1991b); names in parentheses are synonyms which appear in the accompanying references.

effective predators of molluscs, including dreissenids (French 1993, 1997). The roach, the most aggressive European predator of dreissenids, does not begin to prey on them until its teeth become well developed (at fish lengths of ca. 140–160 mm) (French 1993). The crushing power of the pharyngeal teeth of the roach is exceptional, thus, allowing them to ingest relatively large dreissenids (Nagelkerke and Sibbing 1996). Round gobies also have robust molariform teeth capable of crushing dreissenids (Ghedotti et al. 1995), but sometimes swallow intact specimens (Andraso et al. 2011; Ray and Corkum 1997). Ontogenetic changes in the pharyngeal morphology of round gobies at ca. 60 mm of length may contribute to their diet shift to dreissenids. The pharyngeal teeth of gobies <50 mm are small, narrow, and papilliform, consistent with a diet based on soft-bodied prey, whereas in larger individuals (~80 mm) they develop into the molariform teeth typical for molluscivorous fish (Andraso et al. 2011). Dreissenids comprise up to 82% of the diet of round gobies that are 80–90 mm in total length, while larger (>100 mm) round gobies can feed almost exclusively on dreissenids (Jude et al. 1995). The pharyngeal morphology of round gobies can also change depending on the prevalent food: gobies preying mostly on dreissenid mussels have wider and more robust lower pharyngeal teeth than those from dreissenid-free locations, where crustaceans are their main prey (Andraso et al. 2017). The molariform pharyngeal teeth of the common carp are adapted to move upward to crush and grind mollusc shells against a chewing pad located on the pharyngeal roof; European studies suggest that the common carp prefers more thin-shelled molluscs than dreissenids (Ivlev 1961; Stein et al. 1975). Tucker et al. (1996) provided evidence of the effectiveness of the common carp's molariform pharyngeal teeth and chewing pads concluding that all dreissenids consumed are crushed, regardless of the size of the carp or the dreissenid.

In efficient predators, form and function complement each other. In the closed position, the angle of the pharyngeal teeth of the cyprinid *Vimba elongata* (~44°) is almost identical to that of the valves of *D. polymorpha* (~45°), suggesting that this species is particularly well adapted for crushing the shells of dreissenids (Ritterbusch-Nauwerck 1991). Among the cyprinids, oral gape, pharyngeal slit, and chewing cavity are particularly well matched in size in roach, i.e., any large mussel that can reach the chewing cavity can be crushed. In contrast, although the oral gape of the common bream is large, its ability to crush large mussels in the pharyngeal region is limited, and large individuals are often rejected (Nagelkerke and Sibbing 1996).

In addition to the nonindigenous species like the common carp and the round goby, molariform pharyngeal teeth are only present in a limited number of native fishes in North America, including freshwater drum (*A. grunniens*), redear sunfish (*Lepomis microlophus*), pumpkinseed (*L. gibbosus*), copper redhorse (*Moxostoma hubbsi*), and river redhorse (*Moxostoma carinatum*) (French 1993). Predation of dreissenids by freshwater drum commences at a length where they first become able to crush shells (ca. 250–265 mm) and increases with the total length of drum; while 70% of the dreissenid shells in drum stomachs are shattered, no apparent damage was reported to the digestive tracts from these fragments (French and Bur 1993). The diet of lake whitefish in Lake Michigan changes with growth from cladoceran zooplankton to soft-bodied macroinvertebrates, and large (>350 mm) fish mainly consume molluscs, particularly *D. r. bugensis* (Pothoven and Nalepa 2006) (Table 3). In contrast, lake whitefish from Lake Champlain, invaded only by *D. polymorpha*, did not show a dietary shift toward dreissenid mussels, but instead fed primarily on fish eggs, *Mysis diluviana*, gastropods, and sphaeriids, resulting in higher fish condition and energy density compared with those of lakes Michigan, Huron, and Ontario after the dreissenid invasion (Herbst et al. 2013).

Since well-developed molariform pharyngeal teeth are clearly the key characteristic of highly effective molluscivores, fishes lacking these structures, although capable of preying on bivalves, will likely only be minor consumers of dreissenids. Ictalurids (e.g., the channel catfish, *Ictalurus punctatus*) and most centrarchids have cardiform pharyngeal teeth which are not adapted for crushing shells; these fish swallow the bivalves whole (Herod et al. 1997) and are likely to prey on dreissenids only when their preferred prey items are scarce (French 1993; McMahon 1991). The presence or absence of molariform pharyngeal teeth can also affect the rate of net energy intake by fish. Due to the lack of shell-crushing organs, blue catfish (*Ictalurus furcatus*) spend little time processing zebra mussel prey and ingest large amounts of low-energy food per unit time (dreissenids with their shells). Conversely, freshwater drum and redear sunfish spend more time processing their prey (i.e., crushing the shells), and thus, obtain less but higher-energy food (only the flesh) (Magoulick and Lewis 2002). Eels are known to be mollusc predators and have occasionally been reported preying on dreissenids (Table 2); since they lack well-developed pharyngeal teeth, the shells instead are crushed by their powerful jaws (French 1993).

2.2.3.2. Habitat overlap. Obviously, in order for predation to occur at all, the foraging habitats of a benthivorous fish must overlap areas of dreissenid presence. Pumpkinseed prefers vegetated or otherwise sheltered littoral areas in rivers and lakes, which are also suitable habitat for dreissenids. Microhabitats are also important; although common carp is known dreissenid predator, in Skadar Lake (Montenegro), dreissenids avoid intensive carp predation by attaching to large objects in the sediments (usually gravel or other shells); in addition, they are scarce in areas of

Table 4. Seasonal changes in fish predation on attached (i.e., juvenile and adult) *Dreissena*: a reflection of preferred prey seasonal scarcity?

Species	Food spectrum and when feed on *Dreissena*	Location	References
Abramis brama	Food spectrum was very wide with chironomid larvae as preferred prey year long; *Dreissena* was the most important mollusc in the diet and was eaten primarily May through September	Pierzchaly Reservoir, Poland	Martyniak et al. 1987
Anguilla anguilla	Exhibit stronger preference for fish; bivalves like *Dreissena* contributed significantly to the diet in September and October	Tjeukemeer, Netherlands	de Nie 1982
Aplodinotus grunniens	250–374 mm drum feed at reef sites predominately on dipterans in May and dreissenids in July and September, whereas in locations with silt or sand shifted from dreissenids in July to small fish in September	Lake Erie, USA	French and Bur 1993
	The lowest dreissenid predation was in October (of studied May, July and October)	Lake Erie, USA	Morrison et al. 1997
Cyprinus carpio	Dreissenid predation was higher in summer months (in this July-January study)	Kuibyshev Reservoir, Russia	Mikheev 1963
	Dreissenids were observed in stomachs in summer and December	Lake Michigan, USA	Marsden 1997
Ictalurus furcatus	Feed on abundant zebra mussels during summer and shifted to shad *Dorosoma* spp. during winter	Lake Dardanelle, USA	Magoulick and Lewis 2002
Neogobius melanostomus	*Dreissena* spp. and *Bythotrephes longimanus* dominated the diet in the summer	Lake Huron, USA	Pothoven and Madenjian 2013
	Large gobies consumed relatively high proportions of dreissenids in all seasons; small gobies mostly feed on dreissenids in spring and autumn	Lake Michigan, USA	Bunnell et al. 2015
Perca flavescens	The highest dreissenid predation was in May (stomachs examined in May, July and October)	Lake Erie, USA	Morrison et al. 1997
Rutilus rubilio	Older fish consumed molluscs (dreissenids and gastropods) all year long in large quantities; small and medium fish consumed molluscs only from October to February.	Lake Trichonis, Greece	Daoulas and Economidis 1984
Rutilus rutilus	Dreissenids are the main food in July when the growth rates are high	Goplo Lake, Poland	Budzynska et al. 1956
	Feed on dreissenids primarily in autumn and winter	Firth of Szczecin, Poland	Wiktor 1969

soft sediment, where carps forage most frequently (Stein et al. 1975). Although the European eel is a relatively minor *Dreissena* predator, dreissenids are a more common prey item in eel stomachs in samples from open-waters than from littoral areas (Biro 1974).

In addition to dreissenids, *Neogobius melanostomus* feeds on zooplankton (as juveniles), benthic invertebrates, small fishes, and the eggs and larvae of large fishes. They exhibit a high feeding plasticity predominantly preying on molluscs, which are abundant in lentic (seas and lakes) habitats, but switching to non-mollusc benthic invertebrates in lotic habitats (streams) where molluscs are often less abundant (reviewed in Kornis et al. 2012).

2.2.3.3. Preferred prey items. Fish predation rates on dreissenids are likely related to the availability of preferred prey items throughout the year in any given habitat; in general, intensive consumption of bivalves seems highest when other more profitable food items become scarce. Even for fishes widely known to actively feed on molluscs (e.g., roach, freshwater drum), dreissenids are often the dominant prey item during certain seasons only, most often in summer (Table 4). In laboratory trials with rams-horn snails (*Helisoma anceps*) and dreissenids, redear sunfish (200–222 mm long) strongly preferred the snails, a more bioenergetically profitable prey due to their higher proportion of digestible tissue in comparison with dreissenids of similar size. Thus, in habitats where gastropods are abundant, the redear sunfish may not rely heavily on dreissenids (French and Morgan 1995). In Lake Dardanelle (USA) the blue catfish shows a distinct seasonal prey shift: during the summer, it chiefly feeds on the abundant but low-energy zebra mussels, whereas in the winter it feeds on shad (*Dorosoma* spp.). This change has been attributed to the fact that while shad is energetically more profitable, at the higher summer water temperatures it is harder to locate, pursue, capture, and ingest, whereas in winter it suffers temperature-dependent stress and mortality, thus, making it an easier and more profitable food item (Magoulick and Lewis 2002). In southwestern Lake Ontario, round goby guts contain mostly *Dreissena* spp. and *Mysis relicta*, but the proportions of the latter, a higher-energy prey, increase with depth, suggesting that round gobies may switch from dreissenids to more profitable prey when it is available (Walsh et al. 2007).

The bioenergetic profitability, and thus, the feeding preferences, are likely also related to the ease of removing a prey item from the substrate. The difficulty of breaking the dreissenid's byssus may represent a formidable obstacle for many fish species. Dreissenids and other molluscs are relatively large, shelled prey that must often be handled individually by their predators. Mussels must be detached from the substratum, positioned properly in the buccal cavity, transported to the pharynx, and finally swallowed whole or crushed by pharyngeal teeth (Prejs et al. 1990). In cyprinids, the feeding efficiency is largely determined by the time needed to handle the mussels, rather than by the energy required for specific feeding actions like detaching or crushing them (Nagelkerke and Sibbing 1996). In a laboratory study of cyprinid species, the highest individual feeding efficiency values were achieved by large white bream and roach, while common bream performed poorly, suggesting that for the latter feeding on dreissenids was possibly only of marginal profitability (Nagelkerke and Sibbing 1996). In experimental conditions, smaller *D. polymorpha* were consumed more frequently by round gobies than larger individuals because more effort was required to remove larger mussels than smaller mussels. This conclusion is supported by the fact that nearly all *D. polymorpha* on rock tops in a location invaded by the round goby were larger than the size range preferred by gobies, in contrast to a goby-free location, where most of the mussels on rock tops were within the size range preferred by round gobies (Djuricich and Janssen 2001).

It should be noted that ingestion of dreissenids by fish may also be unintentional. Marsden (1997) noted that even though dreissenids were found in the stomachs of common carp, the microhabitats created by dreissenid colonies in the study area were richly inhabited by crustaceans and snails which may actually have been the primary goal of the foraging carp. In Lake Balaton, however, the common carp was found to be strongly selective in choosing dreissenids as prey (Specziár et al. 1997).

2.2.3.4. Dreissenid mussel density. Marsden (1997) reported that, in southwestern Lake Michigan, predation on dreissenids by the common carp was greatest at the site with the highest dreissenid densities, suggesting that dreissenid consumption is proportional to their availability. Likewise, *Dreissena* abundance can be a determinant of habitat use by round gobies because they frequently consume dreissenid mussels and are commonly found in habitats with high mussel densities (Coulter et al. 2015; Johnson et al. 2005b; Kornis et al. 2012; Walsh et al. 2007). Higher densities of dreissenids, however, may not always result in increased predation by fishes. Sterlet and bream actively fed on dreissenids when they first colonized the Kuibyshev Reservoir (Russia), but after mussel densities rose, predation declined, probably because isolated mussels are easier to remove from the substrate than those included in compact, high-density mussel beds (Egereva 1971).

2.2.3.5. Dreissenid mussel size. As aforementioned, predation tends to be size-selective, and thus, also has the potential to restructure the size-frequency of the prey population, resulting in important community and ecosystem-level consequences (Strayer et al. 2019). Round gobies, for example, prefer foraging on smaller *D. polymorpha* (see above; Andraso et al. 2011; Djuricich and Janssen 2001; Ghedotti et al. 1995; Naddafi and Rudstam 2014b, 2014c; Ray and Corkum 1997) (Table 5). Fish lacking the molariform pharyngeal teeth required for crushing the shells of large mussels are generally limited to small ones. Fish mouth size is also an important trait limiting the consumption of larger dreissenids and other prey (Prejs et al. 1990). Consequently, fish generally exhibit prey size preferences and select molluscs in proportions that do not match their abundance and accessibility in the habitat. For example, roach ≥120 mm long in Lake Sniardwy (Poland) ingested 11–17 mm mussels, but none of the 5–8 mm mussels that were most abundant in the habitat surveyed (Prejs et al. 1990). Data based on laboratory and field studies suggest that dreissenids ca. >15 mm are generally less vulnerable to fish predation, except by large roaches which can crush the shells of large mussels (Table 5). Tucker et al. (1996) reported that, at their study site in the Mississippi River, larger common carp tended to prey on larger dreissenids (up to 42.5 mm) (Table 5). In Kuibyshev Reservoir (Russia) ide typically consume 8–17 mm zebra mussels (Mikheev 1977), whereas in the Upper Volga Basin, the same fish feeds on 10–30 mm quagga mussels (Shcherbina and Buckler 2006).

2.2.4. Impact of fish on dreissenid populations

Relatively few quantitative studies on the impact of fish predation on dreissenid populations have been conducted (Table 6). Soon after the discovery of *Dreissena* in North America in the late 1980s, McMahon (1991) proposed that fishes would be the most active predators of attached *D. polymorpha*, and this has been borne out in several studies (Bartsch et al. 2005; Eggleton et al. 2004; Watzin et al. 2008). A negative relationship between *D. polymorpha* and roach densities and biomass has also been observed in Sweden, indicating that fish predation might be a strong regulating factor of dreissenid populations (Naddafi et al. 2010). Several surveys from North America showed declines in quagga mussel densities

Table 5. Size of *Dreissena* consumed by fish.

Species[a]	*Dreissena* length	Where predation observed	References
Abramis bjoerkna (=Blicca bjoerkna)	2–14 mm	Kuibyshev Reservoir, Russia	Mikheev 1977
	Largest dreissenids ingested by 128–246 mm fish were, respectively, 4.1 and 9.7 mm in width	Lab study, the Netherlands	Nagelkerke and Sibbing 1996
	4–14 mm	Upper Volga Basin, Russia	Shcherbina and Buckler 2006
Abramis brama	6–8 mm (max 13 mm)	Kuibyshev Reservoir, Russia	Mikheev 1977
	2–10 mm	Upper Volga Basin, Russia	Shcherbina and Buckler 2006
	Largest dreissenids ingested by 155–298 mm fish were, respectively, 3.0 and 7.0 mm in width	Lab study, Netherlands	Nagelkerke and Sibbing 1996
Acipenser ruthenus	2–6 mm (max 15 mm)	Kuibyshev Reservoir, Russia	Mikheev 1977
Aplodinotus grunniens	Maximum 21.4 mm	Lake Erie, USA	French and Love 1995
	Drum <350 mm total length selected 4–6 mm dreissenids; larger fish were less selective, consuming sizes in proportion to availability	Lake Erie, USA	Morrison et al. 1997
Cyprinus carpio	1–6 mm (young carp)	Kuibyshev Reservoir, Russia	Mikheev 1963
	Large carp (~54 cm) fed on large dreissenids (28 mm)	Dnieper-Bug estuary region, Ukraine	Aleksenko 2004
	Large carp (299–666 mm) fed on 1.5 to 42.5 mm dreissenids (average 11.8 mm)	Mississippi River, USA	Tucker et al. 1996
Cyprinus carpio, Moxostoma sp., *Aplodinotus grunniens*, and possibly other species	>12 mm (enclosure experiments in low-density mussel populations)	Mississippi River, USA	Thorp et al. 1998
Ictalurus furcatus	25–50 cm fish fed on dreissenids 3–15 mm (preference for 3–7 mm)	Ohio River, USA	Herod et al. 1997
Ictiobus bubalus, Ictalurus punctatus, Aplodinotus grunniens, Carpoides carpio, Pylodictis olivaris, and possibly other species	Enclosure experiments in high-density mussel populations did not provide evidence of size-selective predation	Ohio River, USA	Thorp et al. 1998
Lepomis microlophus	7 mm long juvenile fish consumed dreissenids <3 mm long; 180–260 mm long adults fed on dreissenids up to 20 mm	Lab study, USA	French and Morgan 1995
Lepomis gibosus	140–185 mm fish consume 5–13 mm long *D. polymorpha*	Lab study, USA	Naddafi and Rudstam 2014c
Leuciscus idus	8–15 mm (max 17 mm)	Kuibyshev Reservoir, Russia	Mikheev 1977
	10–30 mm	Upper Volga Basin, Russia	Shcherbina and Buckler 2006
Neogobius melanostomus	60–100 mm gobies consumed 4.5–12.5 mm dreissenids	Lab study, USA	Ghedotti et al. 1995
	55–103 mm gobies ate dreissenids <10.0 mm long; 85–103 mm gobies ate 10.0–12.9 mm dreissenids, but preferred smaller sizes	Lab study, Canada	Ray and Corkum 1997
	Gobies 94–135 mm ate 5–13 mm *D. polymorpha*	Lab study, USA	Naddafi and Rudstam 2014c
	0.5–14.3 mm (mean 3.4 mm)	Saginaw Bay of Lake Huron, USA	Foley et al. 2017
Perca flavescens	<200 mm fish consumed dreissenids <6 mm larger fish preferred 1–15 mm mussels	Lake Erie, USA	Morrison et al. 1997
Rutilus rutilus	6–18 mm (max 19 mm)	Kuibyshev Reservoir, Russia	Mikheev 1977
	180–209 mm and ≥210 mm roach preferred 10–11 mm and 11–17 mm dreissenids, respectively.	Lake Sniardwy, Poland	Prejs et al. 1990
	5–20 mm	Upper Volga Basin, Russia	Shcherbina and Buckler 2006
	Largest dreissenids ingested by fish from 146 to 235 mm were, respectively, 5.4 and 10.3 mm in width	Lab study, Netherlands	Nagelkerke and Sibbing 1996
	Up to 24 mm	Dnieper-Bug estuary region, Ukraine	Aleksenko 2004

[a] Standard scientific names following Robins et al. (1991a, 1991b); names in parentheses are synonyms which appear in the accompanying references.

caused by the round goby (Lederer et al. 2006, 2008; Rudstam and Gandino 2020). Some studies in Russia indicate that high percentages (up to over 80%) of dreissenid production can be consumed by fish, with the greatest impact on mussels <15 mm long (Lvova 1977). In the North Caspian Sea, ~90% of dreissenid annual production (130,000 tons) is consumed by fish (Yablonskaya 1985).

Other studies, however, have provided evidence that few fish species are important as predators, and that dreissenid densities will not be regulated unless predator fish abundance increases significantly (Boles and

Table 6. Impact of fish predation on *Dreissena* populations.

Species	Notes	Where predation observed	References
Aplodinotus grunniens	Long-term suppression of dreissenid populations by freshwater drum not likely; drum >250 mm long can consume large numbers of dreissenids, but represented only 19% of population; most efficient predators, drum >350 mm long, were not common.	Lake Erie, USA	French and Bur 1993
Aplodinotus grunniens (and possibly other fish)	Predation affected *D. r. bugensis* (particularly <10 mm long) but not *D. polymorpha* abundance.	Lake Erie, USA	Mitchell et al. 2000
Aplodinotus grunniens, Ictalurus furcatus, Lepomis microlophus (and possibly other fish)	Densities of large (>5 mm) zebra mussels were significantly lower in in predator exposure treatments than in predator exclosure treatments during 2 years of trials	Lake Dardanelle, USA	Magoulick and Lewis 2002
Cyprinus carpio, Moxostoma sp., *Aplodinotus grunniens* (and possibly other fish)	Fish-exclusion cages had an overall significantly higher densities and biomass of dreissenids than fish-accessible cages	Mississippi River, USA	Thorp et al. 1998
Ictiobus bubalus, Ictalurus punctatus, Aplodinotus grunniens, Carpoides carpio, Pylodictis olivaris, and possibly other species	Fish-exclusion cages had an overall significantly higher densities and biomass of dreissenids than fish-accessible cages	Ohio River, USA	Thorp et al. 1998
Lepomis auritus, Lepomis gibbosus and possibly other fish species	14% reduction of dreissenids likely due to predation (two weeks open cage field studies in summer); current levels of finfish unlikely to limit dreissenid populations	Hudson River, USA	Boles and Lipcius 1997
Mylopharyngodon piceus	4-year-old fish consumed 1.4 kg/day of *Dreissena* in experimental ponds and 1.8 kg/day in hatcheries	Artificial fish rearing areas, Moldavia	Krepis et al. 1981
Neogobius melanostomus	Preference for small dreissenids has the potential to alter the size structure of dreissenid populations in specific locales	Lab study, Canada	Ray and Corkum 1997
	During 2001–2004 densities of *D. r. bugensis* decreased 94% in the nearshore rocky zone	Easter basin of Lake Erie, USA	Barton et al. 2005
	Increase in goby abundance was associated with the decline of dreissenids biomass from 344–524 to 34–73 g shell-on dry weight/m^2 from 2009–2011 to 2016–2018	Onondaga Lake, USA	Rudstam and Gandino 2020
	Have little (if any) lake-wide effect at the scale of deep Great Lakes	Great Lakes, USA	Bunnell et al. 2005; Foley et al. 2017; Johnson et al. 2005b; Karatayev et al. 2022a
Rutilus rutilus	Benthophagous fish (mainly roach) eat 80% of the annual production of <15 mm dreissenids	Uchinskoe Reservoir, Russia	Lvova 1977
Rutilus rutilus, Anguilla anguilla, and others	Fish consumed $1–2 \times 10^{12}$J of lake annual dreissenid production (total $41–102 \times 10^{12}$J)	Lake IJsselmeer, the Netherlands	Smit et al. 1993
Species not mentioned	130×10^6 kg of dreissenids (ca. 90% of the annual production) are eaten by fish yearly	Caspian Sea, Russia	Yablonskaya 1985

Lipcius 1997; Mitchell et al. 2000; Thorp et al. 1998) (Table 6). In North America, long-term suppression of *Dreissena* populations by freshwater drums has not been considered likely (French and Bur 1993; Mitchell et al. 2000), possibly due to the fact that the drum's preference for mussels ≤21 mm long lessens their impact in reducing dreissenid populations (French and Love 1995). Enclosure studies in the Mississippi and Ohio Rivers and Lake Dardanelle (USA) suggested that although fish can reduce numbers of dreissenids, current levels of fish predation seemed insufficient to regulate their densities because of the large reproductive capacity of the remaining individuals (Bartsch et al. 2005; Magoulick and Lewis 2002; Thorp et al. 1998). Predation, however, could potentially suppress initial zebra mussel colonization and recolonization of adult zebra mussels following temperature-dependent mortality (Magoulick and Lewis 2002). Studies in the Hudson River (Boles and Lipcius 1997) recorded a 14% reduction in dreissenids within two weeks due likely to fish predation; the authors noted, however, that the presence of experimental cages may have increased predation rates by attracting fish and concluded that dreissenid populations in the Hudson River will not be regulated by the local predator guild (including finfish) unless predator abundances increase significantly. Unfortunately, many studies that examine the diet of fish species do not include a quantitative assessment of the impact of predation on dreissenids populations.

Even though large round gobies prefer small dreissenids, they are generally not regarded to be effective enough to significantly impact dreissenid populations systemwide (Ray and Corkum 1997). Intensive size-selective predation of small dreissenids by round gobies was hypothesized to have occurred in Lake Erie in 2002 (i.e., 3–12 mm dreissenids were absent in the samples analyzed), resulting in a decline of overall mussel population density, but not in population biomass which actually increased from previous years due to an increase in the average size of adult mussels that apparently escaped the round goby predation (Patterson et al. 2005). Moreover, small mussels were present later in 2009–2012 at most of the sites sampled, suggesting that the predation impact observed in 2002 was a transient event (Karatayev et al. 2014). As expected, using mass balance dietary simulations and stomach content data, Campbell et al. (2009) observed that amphipods and chironomids were the preferred prey of small round gobies (<11.2 cm), whereas larger individuals showed a strong preference for dreissenids. According to Bunnell et al. (2005) and Johnson et al. (2005b), however, round gobies in Lake Erie consume a relatively small fraction of dreissenids, whose densities are mostly limited by hypoxia (Karatayev et al. 2018a). In reviewing the literature, Burlakova et al. (2014) pointed out that the predation of gobies on *Dreissena* is spatially heterogeneous (Ruetz et al. 2012) depending on the substratum and water clarity/visibility (Diggins et al. 2002). Due to the preference of round gobies for smaller dreissenids, there will always be mussels surviving predation—either very large mussels or small mussels protected in refuges (between larger zebra mussels, on the underside of rocks, in crevices, etc.). Hence, the impact of round gobies is very variable, and they are unlikely to totally remove dreissenids from a habitat (Djuricich and Janssen 2001). Finally, the consumption rates may not be high enough to effect dreissenid populations on a system-wide scale (Johnson et al. 2005b; Kornis et al. 2012; Pennuto et al. 2012).

Another important factor for the magnitude of round goby impacts on *Dreissena* in lakes can be lake morphometry, as dreissenids are available for round goby only at shallow to intermediate depths (<60 m) (Karatayev et al. 2022a). Although declines in quagga mussel densities caused by round gobies in shallow areas/lakes, lake basins, or bays have been reported (Barton et al. 2005; Karatayev et al. 2022b; Lederer et al. 2006, 2008; Naddafi and Rudstam 2014b; Rudstam and Gandino 2020), at the scale of deep Great Lakes, gobies have little lake-wide effects (Bunnell et al. 2005; Foley et al. 2017; Johnson et al. 2005b; Karatayev and Burlakova 2022b; Karatayev et al. 2022a). For example, in Lake Ontario, which hosts large round goby populations, between 2008 and 2018 there were no declines in dreissenid densities, despite the frequent drops at <90 m in mussels around 5–10 mm, and even up to 15 mm (which is the size-range that gobies consume most actively, Table 5) (Karatayev et al. 2022a). In Lake Michigan, although *Dreissena* populations declined between 2010 and 2015 at depths <90 m (Mehler et al. 2020; Nalepa et al. 2020), factors other than round goby predation (e.g., food limitation) were likely involved (Karatayev et al. 2022a). Moreover, this decline appeared to be a temporary event as the most recent survey in 2021 recorded a substantial increase in quagga mussel densities both lake-wide and at the shallowest (<30 m) zone where small (<5 mm) mussels were most abundant (87%), suggesting a negligible predation impact (Burlakova and Karatayev 2023). Thus, although in shallow areas/lakes dreissenid populations can temporarily decline due to recruitment bottlenecks resulting from round goby predation on small mussels, if a large portion of the lake is deep, mussels inhabiting these areas will continue to reproduce and compensate for the losses.

To summarize, in shallow lakes large populations of predators can likely affect dreissenid densities but cannot eliminate them due to the large reproductive potential of the prey. If the density of predators or level of consumption is insufficient, or large areas of the waterbody colonized by dreissenids are not available to the predators, there will be no lake-wide effects on dreissenid populations. Most importantly, to validate these conclusions (which are based primarily on indirect evidence), more studies are needed that not only include an examination of the diet of the fish but also a quantitative assessment of the impact of predation on dreissenids populations.

2.2.5. Predation by fish: effect on fish populations

When dreissenids colonize new habitats, they can quickly become a major component of the diet of molluscivorous fishes. This has been reported repeatedly in Eurasia and North America. In general, the effect of dreissenids on the fishes varies depending on the feeding mode of the consumer, the morphology of the waterbody invaded, the time elapsed since mussel invasion, co-evolutionary history, and *Dreissena* species, and is different in Europe and North America (Higgins and Vander Zanden 2010; Karatayev and Burlakova 2022a, 2022b; Karatayev et al. 1997, 2002a, 2015; Molloy et al. 1997; Strayer et al. 2004). Pelagic species can be negatively affected as a result of lower phytoplankton abundance and associated decreases in zooplankton, competition with benthic species, and higher larval fish predation due to increased water transparency (Francis et al. 1996; Higgins and Vander Zanden 2010; Lozano et al. 2001; Strayer et al. 2004). Benthivorous fishes are usually affected positively, even those that do not feed on dreissenids, due to the increased biomass of invertebrates associated with the mussel beds (Karatayev and Burlakova 1992, 1995, 2022a; Karatayev et al. 1997, 2002a; Lyakhnovich et al. 1988; Molloy et al. 1997; Strayer et al. 2004). Indirect negative impacts on benthivorous fishes due to declines of important prey items, such as *Diporeia* and sphaeriids, were also well documented, particularly in the Laurentian Great Lakes (Dermott and Kerec 1997; Hoyle et al. 1999; Lozano et al. 2001; Nalepa et al. 2009a; Pothoven et al. 2001).

2.2.5.1. Effects on European fishes. In Europe, the introduction of zebra mussels is often associated with increases in fish productivity and commercial catches (Karatayev and Burlakova 1995, 2022a; Lyagina and Spanowskaya 1963; Lyakhnovich et al. 1988; Poddubny 1966; reviewed in Karatayev et al. 1994; Molloy et al. 1997). A vivid example is the roach (*Rutilus rutilus*), the most prominent consumer of dreissenids, that after *Dreissena*´s introduction exhibited much higher individual growth rates, larger body size, and higher lipid content (Lyagina and Spanowskaya 1963; Poddubny 1966; Zheltenkova 1949). One of the best documented Eurasian examples of diet shift is the effect on fish populations following the introduction of *D. polymorpha* in the Rybinsk Reservoir in Russia (Gerasimov 2007, 2015). Following *D. polymorpha*'s introduction in the reservoir during 1960–1965, roaches started to feed on *Dreissena* in all parts of the reservoir, and by 1967 it consumed *D. polymorpha* in the entire waterbody, including the central part and its river reaches. As a result, the population of roaches in the Rybinsk Reservoir formed two ecological groups: the coastal group, with a mixed food spectrum, and the floodplain-bottom or migratory group, feeding mainly on dreissenids. This diet-related pressure likely drives the differentiation of two morphotypes. Roach-consuming *Dreissena* significantly increased their growth rates, and the biomass of roaches caught by fishermen doubled (reviewed in Gerasimov 2007).

A similar phenomenon was also observed in Lake Pleshcheyevo (Russia): since the introduction of *D. polymorpha*, a new "mollusc-eating" roach morphotype emerged, characterized by massive pharyngeal teeth, higher growth rates, larger maximum size, and a longer lifespan (Kodukhova and Karabanov 2017). In addition to roach, bream and silver bream became active *D. polymorpha* feeders in the reservoir. These latter two fish species, however, are less efficient than roach in feeding on *Dreissena*, because they can only handle smaller mussels (10–14 mm, as opposed to roach: 20 mm) (Shcherbina and Buckler 2006).

Due primarily to *Dreissena* consumption, 4.1×10^5 kg of black carp (*Mylopharyngodon piceus*) were reported to be harvested annually from the Russian Tsimlyanskoe Reservoir (Miroshnichenko 1990). Likewise, the rapid rate of growth of common carp in Lake Balaton was attributed in part to consuming dreissenids (Specziár et al. 1997).

2.2.5.2. Effects on North American fishes. In North America, predation on dreissenid mussels has been documented for many commercially important native fishes (Tables 1 and 2). In Oneida Lake (USA), dreissenid mussels are a substantial component of the diets of large lake sturgeon, a species of conservation concern (Jackson et al. 2020), although high dreissenid densities can reduce juvenile sturgeon foraging (McCabe et al. 2006). Dreissenids comprise a major part of the diet of the endangered silver chub (*Macrhybopsis storeriana*), having largely replaced formerly abundant local molluscs (Kočovský 2019). A similar shift from a pre-invasion diet of other benthic littoral invertebrates to zebra mussels was recorded for several species of true sunfish *Lepomis* (Colborne et al. 2015; Magoulick and Lewis 2002; Mercer et al. 1999; Molloy et al. 1997). In addition, after the dreissenid invasion, many other nearshore invertebrates that benefited from dreissenid-mediated benthification became the primary forage of nearly all nearshore fish species (Turschak and Bootsma 2015). After Lake Erie was invaded by dreissenids, benthic resources were estimated to support 75–95% of the potential fish production (Johannsson et al. 2000). In Lake Ida (USA) 90% of fish species increased the use of littoral carbon (from 43 to 67%) after zebra mussels established there (Morrison et al. 2021). Yellow perch can exploit the new prey associated with zebra mussel colonies, although it may require slightly more effort than foraging on isolated individuals in loose sediments (Cobb and Watzin 2002). The growth rate of yellow perch in pond enclosures with *D. polymorpha* is higher than in enclosures without mussels, largely due to mussel-induced changes in the benthic structure and biota (Thayer et al. 1997). Conversely, for several fish species (e.g., ruffe, perch) the refuges provided by complex dreissenid beds can negatively affect predation success (Dieterich et al. 2004).

In some waterbodies, the effects of *D. polymorpha* on yellow perch do not occur *via* benthic pathways but through modifications of water clarity and zooplankton. Thus, after the introduction of the zebra mussel in Lake Oneida, the growth rates of young of the year yellow perch increased due to increases in the size of the zooplankton resulted from factors associated with zebra mussels (those affected by water clarity) and another that is not (low yellow perch numbers relative to historic values) (Mayer et al. 2000).

In the food webs of the North American Great Lakes *Dreissena* were initially considered as a "dead end" (reviewed in Madenjian et al. 2010) and as a major loss of energy and potential production because food resources were withdrawn from the pelagial and incorporated into benthos (Johnson et al. 2005b). Dreissenid-induced loss of primary production and oligotrophication of the Great Lakes resulted in large declines in pelagic fish, including some commercially important species, like the whitefish (*Coregonus clupeaformis*), largely due to dramatic decreases in their main food, deep-water amphipod *Diporeia* (Dermott and Kerec 1997; Lozano et al. 2001; Nalepa 2010; Nalepa et al. 2009a; Pothoven et al. 2001), likely outcompeted by dreissenids. Despite its feeding on *Dreissena*, the shift from *Diporeia* to quagga mussels resulted in the decline of whitefish condition, growth, and abundance (Hoyle et al. 2008; Lumb et al. 2007; Nalepa et al. 2009b; Owens and Dittman 2003; Pothoven et al. 2001; Rennie et al. 2009) because *Diporeia* is rich in lipids (up to 54% of *Diporeia* dry weight, Gardner et al. 1985) and provides a much better source of energy than dreissenids (Owens and Dittman 2003). The decline in *Diporeia* was also associated with a decline of alewife (*Alosa pseudoharengus*), sculpin (*Cottus cognatus*), bloater (*Coregonus hoyi*), and other fishes that are prey for larger piscivores, including salmon and trout (reviewed in Nalepa 2010). The consequences of dreissenid introductions to fisheries in other inland lakes, however, have been much less significant than those in the Great Lakes (Nienhuis et al. 2014).

The introduction in the Great Lakes of another Ponto-Caspian invader, the round goby, added a very important previously missing trophic link between dreissenids and commercially and recreationally valuable fish species (Johnson et al. 2005b; Madenjian et al. 2011). A population explosion of the invasive round goby occurred in the early 2000s in the western part of Lake Erie where their population size was estimated at 9.9 billion (Johnson et al. 2005a). These high population densities, however, were not only attributable to their preying on dreissenids, since smaller round gobies prefer a variety of benthic invertebrates, including chironomids and amphipods (Campbell et al. 2009; Dermott et al. 2012; Diggins et al. 2002; French and Jude 2001; Kornis et al. 2012; Walsh et al. 2007). Nevertheless, consumption of dreissenids by round gobies substantially increased the transfer of energy stored by dreissenids in the benthos back to the pelagial and eventually increased fish productivity, including commercially important species. The round goby is actively consumed by a number of North American fishes, including lake trout (*Salvelinus namaycush*) (Dietrich et al. 2006), burbot (*Lota lota*) (Madenjian et al. 2011), yellow perch (*Perca flavescens*) (Weber et al. 2011), whitefish (*Coregonus clupeaformis*) (Lehrer-Brey and Kornis 2014; Pothoven and Madenjian 2013), smallmouth bass (*Micropterus dolomieu*) (Crane and Einhouse 2016), lake sturgeon (*Acipenser fulvescens*) (Bruestle et al. 2019; Jacobs et al. 2017), and walleye (*Sander vitreus*) (Pothoven et al. 2017). In Lake Huron, the overall percentage of adult (>400 mm in length) lake whitefish that fed on other fishes increased from 10% in 2002–2006 to 20% in 2007–2011 when round gobies accounted for 92% of all fishes consumed by lake whitefish (Pothoven and Madenjian 2013).

Finally, dreissenids can play a significant role in the biomagnification of organic contaminants and trace elements up through the food chain as they bioaccumulate many pollutants, toxins, and heavy metals (reviewed in Binelli et al. 2015), but bioaccumulation and trophic transfer of contaminants vary among species (Evariste et al. 2018; Matthews et al. 2015; Zimmermann et al. 1997), locations (Hanari et al. 2004; Kimbrough et al. 2013), and pollutant types (Perez-Fuentetaja et al. 2015). The switch of fish consumption to dreissenids, and especially the invasion of the round goby, created a new pathway through which these contaminants can be incorporated into the food webs. Hogan et al. (2007) documented that in Lake Erie the concentrations of methyl mercury (MeHg) are lowest in the sediments, and increase progressively in dreissenids, round gobies, and smallmouth bass (e.g., concentrations in the smallmouth bass are 1000 times higher than those in the sediments). Conversely, concentrations of other pollutants (e.g., PBDEs—polybrominated diphenyl ethers) in mussels have been found to be lower than in zooplankton and amphipods (Perez-Fuentetaja et al. 2015), which may decrease the levels of these compounds in mussel-feeding fishes (Hahm et al. 2009). Further research is needed to assess the magnitude of dreissenid biomagnification and whether dreissenids are effectively more harmful in transferring contaminants than other native or introduced prey species. This topic, however, is too large to be comprehensively covered in this review.

2.3. Birds

Consumption of attached *Dreissena* has been recorded for at least 39 species, including 22 in Europe and 22 in North America (Table 7). Five species—greater scaup (*Aythya marila*), goldeneye (*Bucephala clangula*), oldsquaw (*Clangula hyemalis*), herring gull (*Larus argentatus*), and white-winged scoter (*Melanitta fusca*)—have been observed eating *Dreissena* both in Europe and North America. In Europe, the tufted duck (*Aythya fuligula*), greater scaup (*A. marila*), and pochard (*Aythya ferina*) are the primary predators in most situations, sometimes accompanied by goldeneye (*B. clangula*) and coot (*Fulica atra*) (Suter 1982a; van Eerden and de Leeuw 2010; van Eerden et al. 1997). In North America, greater scaup (*Aythya marila*), lesser scaup (*Aythya affinis*), and bufflehead (*Bucephala albeola*) have been most commonly recorded, with less frequent reports for goldeneye (Mazak et al. 1997; Petrie and Knapton 1999; Wormington and Leach 1992). A 20-year study conducted in the Lake IJsselmeer area of the Netherlands (van Eerden et al. 1997) is the most extensive investigation to date of the patterns of food exploitation by diving waterfowl feeding on dreissenids. This long-term study was conducted in parallel with a comprehensive series of experiments on the foraging behavior and energetics of diving ducks (Carbone et al. 1996; de Leeuw 1997a, 1997b, 1999; de Leeuw and van Eerden 1992).

2.3.1. Factors affecting bird predation

2.3.1.1. Dietary preferences of bird species. The proportion of a waterfowl's diet that is comprised of bottom-dwelling invertebrates, particularly molluscs, can be a useful predictor of its potential importance as a dreissenid predator. Tufted duck feed almost exclusively on benthic animals and are the most aggressive avian predators of dreissenids in Europe (Draulans 1987). In Lake IJsselmeer (The Netherlands) between 80 and 95% of the diet of adult tufted duck consists of dreissenids (de Kock and Bowmer 1993). Likewise, in the brackish lagoons of the Odra River Estuary greater scaups feed almost exclusively on zebra mussels (97% in terms of biomass) (Marchowski et al. 2015). The availability of dreissenids, however, does not always lead to intense predation; in Szczecin Firth (Poland), even though dreissenids are abundant, their consumption by tufted ducks and other waterfowl is low (Wiktor 1969). Pochard (Draulans 1987) and coot (Borowiec 1975) may preferentially consume plant material when seasonally available. The relative importance of dreissenids in the diet of waterfowl was further investigated by studies of overwintering populations in the Rhine River (Swiss-German border); tufted duck and pochard fed almost exclusively on dreissenids, while coot and goldeneye used them as main and supplementary food, respectively (Suter 1982a, 1982b). Although dietary preferences are best revealed in field studies under natural conditions, controlled feeding studies can provide useful supplementary information. Dobrowolski et al. (1996) carried out experiments showing that coot, mallard, and pochard readily ingest dreissenids, but the red-crested pochard feeds on plants only. Diving ducks do not seem to discriminate between *D. polymorpha* and *D. r. bugensis* (Mitchell et al. 2000).

A simple list of bird species observed to consume dreissenids (Table 7) can be misleading, as some of these data are based on a single literature reference and include species that are not generally molluscivorous. In contrast, the number of literature citations for a particular bird species (Table 7) is a much more reliable indicator of which species are true molluscivorous predators. The common merganser (*Mergus merganser*) and the red-breasted merganser (*M. serrator*), for example, feed chiefly on fish and were reported as ingesting dreissenids only once (Jacoby and Leuzinger 1972). Likewise, redheads (*Aythya americana*) mostly consume dreissenids attached to the stems of aquatic plants, suggesting that mussels are not their primary feeding target (Custer and Custer 1996; Petrie and Knapton 1999).

2.3.1.2. Dreissenid density. Birds prey on dreissenids because they are often very abundant, requiring low search and handling times (Draulans 1982; Kornobis 1977; Leuzinger and Schuster 1970; Suter 1982c; Wormington and Leach 1992). Regions of high dreissenid density are, thus, the preferred foraging areas for their waterfowl predators. In both European (Kornobis 1977; Leuzinger and Schuster 1970; Stanczykowska 1987; van Eerden et al. 1997) and North American (Wormington and Leach 1992) lakes, waterfowl flocks tend to concentrate in shallow areas where dreissenids are abundant. In the Plas Leblanc (a sand-pit pond in Belgium), predation by tufted duck flocks was observed to be most intense in areas of the highest dreissenid density (Draulans 1982). At the outlet of Lake Constance (Swiss-German border), overwintering waterfowl always feed first where dreissenid populations are the most dense (Suter

Table 7. Birds documented to eat *Dreissena* in the field and where predation was observed (E—Europe, NA—North America).

Species	Common name	Duck type	Where predation observed	References
Anas platyrhynchos	Mallard	Puddle duck	E	Jacoby and Leuzinger 1972; Kozulin 1995; Zuur et al. 1983
Anas rubripes	Black duck	Puddle duck	NA	Petrie and Knapton 1999
Anas strepera	Gadwall	Puddle duck	E	Jacoby and Leuzinger 1972
Aythya affinis	Lesser scaup	Diving duck	NA	Badzinski and Petrie 2006; Custer and Custer 1996; Hamilton and Ankney 1994; Hamilton et al. 1994; Mazak et al. 1997; Mitchell and Carlson 1993; Petrie and Knapton 1999; Wormington and Leach 1992
Aythya americana	Redhead	Diving duck	NA	Custer and Custer 1996; Petrie and Knapton 1999
Aythya collaris	Ring-necked duck	Diving duck	NA	Wormington and Leach 1992
Aythya ferina	Pochard, European pochard	Diving duck	E	bij de Vaate 1991; Cleven and Frenzel 1992; Géroudet 1978; Jacoby and Leuzinger 1972; Leuzinger and Schuster 1970; Pedroli 1981a; Smit et al. 1993; Suter 1982a, 1982b; Zuur et al. 1983; van Eerden and de Leeuw 2010; van Eerden et al. 1997; Wiktor 1969
Aythya fuligula	Tufted duck	Diving duck	E	Burla and Lubini-Ferlin 1976; Cleven and Frenzel 1992; de Leeuw and Renema 1997; Draulans and De Bont 1980; Géroudet 1966, 1978; Jacoby and Leuzinger 1972; Leuzinger and Schuster 1970; Olney 1963; Pedroli 1981a; Smit et al. 1993; Suter 1982a, 1982b; van Eerden and de Leeuw 2010; van Eerden et al. 1997; Zuur et al. 1983
Aythya marila	Greater scaup	Diving duck	E and NA	Badzinski and Petrie 2006; bij de Vaate 1991; Custer and Custer 1996; Géroudet 1966, 1978; Hamilton and Ankney 1994; Hamilton et al. 1994; Jacoby and Leuzinger 1972; Leuzinger and Schuster 1970; Marchowski et al. 2015; Mazak et al. 1997; Mitchell and Carlson 1993; Pedroli 1981a; Petrie and Knapton 1999; Smit et al. 1993; Suter 1982a; van Eerden and de Leeuw 2010; van Eerden et al. 1997; Wormington and Leach 1992
Aythya nyroca	Ferruginous duck, white-eye	Diving duck	E	Jacoby and Leuzinger 1972; Suter 1982a
Aythya valisineria	Canvasback	Diving duck	NA	Custer and Custer 1996
Bucephala albeola	Bufflehead	Diving duck	NA	Custer and Custer 1996; Hamilton and Ankney 1994; Hamilton et al. 1994; Mazak et al. 1997; Petrie and Knapton 1999; Wormington and Leach 1992
Bucephala clangula	Goldeneye, common goldeneye	Diving duck	E and NA	bij de Vaate 1991; Custer and Custer 1996; de Leeuw and Renema 1997; Géroudet 1966, 1978; Jacoby and Leuzinger 1972; Hamilton and Ankney 1994; Leuzinger and Schuster 1970; Smit et al. 1993; Suter 1982a, 1982b; van Eerden and de Leeuw 2010; van Eerden et al. 1997; Wormington and Leach 1992
Calidris alpina	Dunlin	Shore bird	NA	Wormington and Leach 1992
Calidris maritima	Purple sandpiper	Shore bird	NA	Wormington and Leach 1992
Charadrius vociferus	Killdeer	Shore bird	NA	Wormington and Leach 1992
Clangula hyemalis	Oldsquaw, longtailed duck	Diving duck	E and NA	Essian et al. 2016; Hamilton and Ankney 1994; Knapton R. W., pers. comm.; Suter 1982a
Cygnus olor	Mute swan	Swan	E	Jacoby and Leuzinger 1972; von Wicht 1972; Włodarczyk and Janiszewski 2014
Euphagus carolinus	Rusty blackbird	Passeriform	NA	Wormington and Leach 1992
Fulica americana	American coot	Diving rail	NA	Wormington and Leach 1992
Fulica atra	Coot, baldcoot	Diving rail	E	Borowiec 1975; de Leeuw and Renema 1997; Géroudet 1966; Jacoby and Leuzinger 1972; Königstein 1986; Kornobis 1977; Krauß 1979; Leuzinger and Schuster 1970; Piesik 1983; Smit et al. 1993; Stempniewicz 1974; Suter 1982a, 1982b; van Eerden and de Leeuw 2010; van Eerden et al. 1997; Zuur et al. 1983
Gallinula chloropus	Common gallinule, moorhen	Diving rail	E	Jacoby and Leuzinger 1972
Larus argentatus	Herring gull	Gull	E and NA	Jacoby and Leuzinger 1972; Marchowski et al. 2015; Wormington and Leach 1992
Larus canus	Common gull, mew gull	Gull	E	Jacoby and Leuzinger 1972; Marchowski et al. 2015
Larus delawarensis	Ring-billed gull	Gull	NA	Wormington and Leach 1992
Larus ridibundus	Blackheaded gull	Gull	E	Jacoby 2005
Larus spp.	Gulls	Gull	E	de Leeuw and Renema 1997; Marchowski et al. 2015
Lophodytes cucullatus	Hooded merganser	Diving bird	NA	Wormington and Leach 1992
Melanitta fusca	White-winged scoter, velvet scoter	Diving duck	E and NA	Géroudet 1966; Hamilton and Ankney 1994; Knapton R. W., pers. comm.; Wormington and Leach 1992
Melanitta nigra	Black scoter, common scoter	Diving duck	NA	Wormington and Leach 1992
Melanitta perspicillata	Surf scoter	Diving duck	NA	Essian et al. 2016; Guillemette et al. 1994; Wormington and Leach 1992

(*Continued*)

Table 7. Continued.

Species	Common name	Duck type	Where predation observed	References
Mergus merganser	Common merganser, goosander	Diving bird	E	Jacoby and Leuzinger 1972
Mergus serrator	Red-breasted merganser, sawbill	Diving bird	E	Jacoby and Leuzinger 1972
Netta rufina	Red-crested pochard, scarp duck	Diving duck	E	Jacoby and Leuzinger 1972; Leuzinger and Schuster 1970; Suter 1982a
Phalacrocorax auritus	Double-crested cormorants	Diving bird	NA	Essian et al. 2016
Podiceps ruficollis	Grebe	Diving bird	E	Jacoby and Leuzinger 1972
Somateria mollissima	Eider, common eider	Diving duck	E	Géroudet 1966, 1978; Jacoby and Leuzinger 1972; Leuzinger and Schuster 1970
Sturnus vulgaris	European starling	Passeriform	NA	Wormington and Leach 1992
Tadorna tadorna	Shelduck, common shelduck	Puddle duck	E	Jacoby and Leuzinger 1972

1982a). In the Netherlands, diving ducks concentrate in larger numbers at patches of high dreissenid density, and their overall pattern of mussel exploitation is clearly density-dependent (van Eerden et al. 1997).

Dense mussel colonies can apparently be located rather quickly by migrating waterfowl flocks. At a power plant on Lake Michigan, this behavior had unfortunate consequences when ca. 400 scaup (primarily lesser scaup) were entrained and killed as they congregated to feed on dreissenids encrusting a 4-m deep water intake structure (Mitchell and Carlson 1993). Not all birds, however, always feed in the areas of the highest mussel density within a waterbody (Stanczykowska et al. 1990), suggesting that the selection of the foraging area is not governed by prey density only. de Leeuw (1997b) suggested that the energetic cost of searching for sites with high mussel densities, in particular in areas where mussel beds are patchy, might explain the decoupling between foraging areas and mussel densities.

2.3.1.3. Depth. Predation rates by birds are obviously higher at shallower depths. Although coots are capable of diving to 7 m, they prefer to feed in areas ≤2 m deep (Borowiec 1975). Tufted ducks are very good divers with the capability of sustained foraging down to 14 m (reviewed in Werner et al. 2005), but their predation rates decline with depth (Draulans 1982), with the highest activity at 1–2 m when mussels are available (Olney 1963). Pochards also usually forage at 1–2.5 m but can dive down to 4.5–5 m (reviewed in Werner et al. 2005). Predation by tufted ducks and greater scaup declines significantly below 4 m (van Eerden et al. 1997). In the Lake IJsselmeer area (the Netherlands), both tufted duck and scaup exploit the shallow, coastal zones early in winter, but feed in deeper water, farther off-shore, in late winter (de Leeuw 1997b). The preference for foraging at shallow depths is clearly energetically advantageous since diving effort increases with depth, the energy content of mussels decreases, and feeding in deeper waters usually requires longer flight distances from the shore-based roosts (de Leeuw 1997b), but could be justified considering weaker attachment and higher mussel biomass and at these depths. Thus, on sandy substrates in Lake Constance where *D. polymorpha* is loosely attached and can easily be dislodged, diving ducks were documented to retrieve mussels from depths of up to 11 m (Werner et al. 2005).

2.3.1.4. Dreissenid size. The size of the mussels ingested can relate to many factors, including water temperature, water depth, bird species, the predator's satiation, mussel size availability, and whether mussels are actively selected (*vs.* passively and inadvertently ingested with vegetation). Many of these factors, of course, are related to energy profitability, since foraging decisions are largely governed by their effects on the energy balance of the predator and their fitness consequences (de Leeuw 1997b).

Waterfowl which actively forage on dreissenids generally appear to prefer mussels of ca. 8–20 mm (Table 8), but interspecific differences have been recorded. In lakes Erie and St. Clair, Hamilton and Ankney (1994) found that larger species of diving ducks appeared to select the largest mussels, greater scaups consumed larger mussels than did lesser scaups, and both scaup species preferred larger mussels prey than did bufflehead and common goldeneye. Nevertheless, all species took a very broad and overlapping range of dreissenids. In laboratory feeding experiments, tufted ducks and greater scaups were able to swallow all mussels ≤30 mm long, but showed a slight preference for 7–16 mm mussels; selectivity decreased with biomass consumed and increased with water temperature (de Leeuw 1999). Other laboratory trials provided

Table 8. Size of *Dreissena* consumed by birds.

Species	Common name	Length of mussels	Where predation observed	References
Aythya affinis	Lesser scaup	≤24 mm (7–15 mm most common)	Lake Erie, Canada	Mazak et al. 1997
		9.0 mm (spring), 6.5 mm (autumn) 10.9 mm (Lake Erie) 6.9 mm (Lake Ontario), 5.5 mm (Lake St. Clair)	Great Lakes, Canada	Badzinski and Petrie 2006
		Mean 12 mm at Long Point and 14 mm at Point Pelee	Lake Erie, Canada	Hamilton and Ankney 1994
		Mean 8 mm	Lake St. Clair, Canada	Hamilton and Ankney 1994
Aythya ferina	Pochard, European pochard	≤27 mm, but tended to take <15 mm, especially at depths of <2.5 m	Lake IJsselmeer area, the Netherlands	van Eerden et al. 1997
Aythya fuligula	Tufted duck	10–20 mm preferred	Lake Zurich, Switzerland	Burla and Lubini-Ferlin 1976
		11–25 mm	Waterbodies in England and Northern Ireland	Olney 1963
		Males: ≤25 mm (15–20 mm preferred) Females: ≤2.5 mm (10–17 mm preferred)	Experimental chambers	Draulans 1982
		≤30 mm (slight preference for 7–16 mm)	Experimental chambers	de Leeuw 1999
		≤27 mm (<15 mm preferred, especially at depths of <2.5 m)	Lake IJsselmeer area, the Netherlands	van Eerden et al. 1997
Aythya marila	Greater scaup	≤27 mm (10–21 mm most common)	Lake Erie, Canada	Mazak et al. 1997
		≤30 mm (slight preference for 7–16 mm)	Experimental chambers	de Leeuw 1999
		≤27 mm (preferred <15 mm, especially at depths of <2.5 m)	Lake IJsselmeer area, the Netherlands	van Eerden et al. 1997
		Mean 12 mm at Long Point	Lake Erie, Canada	Hamilton and Ankney 1994
		Mean 10 mm	Lake St. Clair, Canada	Hamilton and Ankney 1994
Bucephala albeola	Bufflehead	≤21 mm (1–9 mm most common)	Lake Erie, Canada	Mazak et al. 1997
		Mean 9 mm at Long Point and 10.5 mm at Point Pelee	Lake Erie, Canada	Hamilton and Ankney 1994
Bucephala clangula	Goldeneye	≤27 mm (preferred <15 mm, especially at depths of <2.5 m)	Lake IJsselmeer area, the Netherlands	van Eerden et al. 1997
		Mean 14 mm at Long Point and 11 mm at Point Pelee	Lake Erie, Canada	Hamilton and Ankney 1994
Clangula hyemalis	Oldsquaw	Mean 14 mm at Port Stanley	Lake Erie, Canada	Hamilton and Ankney 1994
Melanitta fusca	White-winged scoter	Mean 13.5 mm at Port Stanley	Lake Erie, Canada	Hamilton and Ankney 1994
Aythya affinis, Aythya marila, Bucephala albeola	Lesser scaup, greater scaup, bufflehead	11–21 mm (11–13 mm preferred)	Lake Erie, Canada	Hamilton et al. 1994
Aythya affinis, Aythya marila, Aythya americana, Bucephala albeola	Lesser scaup, greater scaup, bufflehead, redhead	<15 mm	Lake Erie, Canada	Petrie and Knapton 1999
Aythya affinis, Aythya marila, Bucephala albeola, Bucephala clangula	Lesser scaup, greater scaup, bufflehead, goldeneye	Mean 8–12 mm for individuals specifically foraging on dreissenids	Lake Erie and Lake St. Clair, USA/Canada	Custer and Custer 1996

evidence that pochards select mussels smaller than tufted ducks do (Draulans 1987). The size-composition of *Dreissena* from the guts of diving ducks in Lake Erie also differed, with increasingly larger mussels consumed, respectively, by bufflehead, lesser scaup, and greater scaup (Mazak et al. 1997) (Table 8). Goldeneye in the upper Rhine River also tended to select smaller mussels, presumably due to the relatively weak musculature of their gizzards (Suter 1982a). Dreissenids consumed by waterfowl while feeding on macrophytes tend to be smaller as macrophytes die back each winter and mussels attached to vegetation are <1-year old (e.g., mean of 3 mm, Custer and Custer 1996), therefore, in this case, the size of mussels retrieved from the gut may be a misleading indicator of a predator's size preferences as only small mussels were available.

Analyses of the size of the mussels consumed must obviously take into account their availability in the area. In lakes Erie and St. Clair, the average mussel sizes taken by diving ducks differ greatly among sites, but these differences matched those of the mussel sizes available at the sites studied (Badzinski and Petrie 2006; Hamilton and Ankney 1994). In Lake Erie, greater and lesser scaup favored 11–13 mm dreissenids (Hamilton et al. 1994), whereas in Lake Michigan the mean length of dreissenids consumed by scaups was 4 mm. This contrast is likely influenced by the fact that, at the time, all mussels at the Lake Michigan site were <10 mm long (Mitchell and Carlson 1993).

Size feeding preferences by diving ducks have been the subject of several analyses. Why, for example, do tufted duck prefer medium-sized mussels when larger, higher-profitability mussels are available? The calorific value of a mussel increases exponentially with shell length, but shells also thicken as mussels grow, so there probably is a tipping point where shell thickness and the amount of digestible tissue are optimal, which has been suggested to occur in medium-sized mussels (Hamilton and Ankney 1994). Further, the size and number of mussels that a diving bird can retrieve in a single dive may also play a major role. Draulans (1982) suggested that the preference for medium-sized mussels is a reflection of optimum energetic gain per dive. For example, in one dive a tufted duck can swallow a maximum of either two 16 mm mussels (total energy content ca. 400 calories) or one 21 mm mussel (ca. 275 calories). The relation of the preference for medium-sized dreissenids to energy profitability was also suggested by de Leeuw and van Eerden (1992) in their study of the tufted duck. van Eerden et al. (1997) reported that even though tufted duck, pochard, greater scaup, and goldeneye all consumed mussels ≤27 mm long, they tended to take mussels <15 mm, especially at depths of <2.5 m. They suggested that size preference was apparently operating only at depths <2.5 m because of the time constraint on the foraging ducks set by water depth. Likewise, at lower temperatures, the dive duration of tufted ducks is shorter and less time is spent selecting small mussels, with the result that larger mussels are ingested (de Leeuw et al. 1999). Diving ducks feeding in the Great Lakes, however, appear to feed on mussels of widely varying sizes, and although larger ducks consume larger mussels when available, even very small mussels are sufficiently profitable and are common in the diet (Hamilton and Ankney 1994). Finally, the size selection of mussels by birds may be impacted by kleptoparasitism. According to Marchowski and Neubauer (2019), mallards attempt to steal zebra mussels from other mallards and coots when large or intermediate-sized prey items are involved. The probability of success of a kleptoparasitic attack is lowest when the attacked bird holds small prey items, but higher if the prey is intermediate or large.

2.3.1.5. Season. High rates of bird predation have been most commonly reported between autumn and spring, when flocks are either temporarily present during their migration (Hamilton et al. 1994; Mitchell and Carlson 1993), or overwintering (bij de Vaate 1991; Cleven and Frenzel 1993; van Eerden et al. 1997). During these seasons predation on dreissenids can be enhanced by the absence of some other food items. Plants, for example, are a major food item for coots, but are less available in winter; Stempniewicz (1974) observed that in the winter dreissenids represent 93% of coot's food, but decline to 63% in summer due to their grazing on plants.

In cool climates, winter ice formation precludes predation activities and results in duck emigration (van Eerden et al. 1997). If ice formation is hindered (for example, due to the discharge of heated water by electric power stations), flocks may overwinter on site. This occurs in Lukomskoe Lake (Belarus), where large flocks of mallard regularly overwinter and consume large numbers of *Dreissena* in shallow areas (Karatayev et al. 1994; Kozulin 1995). Similarly, in an ice-free hole generated by a discharge of coolant water at Nanticoke, Lake Erie, predation by wintering waterbirds causes dramatic, but very localized, declines in the abundance of *D. polymorpha* (Mitchell et al. 2000).

2.3.2. Bird diving and feeding behavior

2.3.2.1. Diel patterns. Waterfowl predation on dreissenids can take place during both day and night. Both goldeneye and coot locate their prey visually, and thus, are only active during the day, spending, respectively, up to 10 and 16 hr/day feeding (Borowiec 1975; Suter 1982a). In contrast, tufted ducks and pochards are primarily active at night, especially in autumn and early winter when dreissenids are abundant due to recent reproduction and settlement; yet they become more active during the day to locate their prey visually when dreissenid densities decline (Suter 1982a). Werner et al. (2005) found that in October and November, diving ducks (tufted ducks and pochards) and coots are mainly active at night; as winter progresses, the birds forage increasingly during the daytime as well. This change is likely due to the fact that with decreasing food supply tactile foraging becomes less effective (Suter 1982a), forcing the birds to resort to search visually for the scarcer remaining mussels.

de Leeuw and Renema (1997) provide observations on how feeding behavior may be impacted by kleptoparasitism. They suggest that night feeding by tufted ducks that rely on tactile cues when feeding on mussels, may be partly driven by the need to avoid food stealing behavior of other birds, such as coots and gulls (*Larus* spp.). Goldeneye and coot use visual cues for feeding and are, thus, active during the day, despite the risk of food stealing. Swallowing the prey underwater (e.g., goldeneye) and social feeding in dense flocks (e.g., coots) are likely alternative tactics to avoid food stealing.

2.3.2.2. Dive duration.

Dive duration differs among species Coots prefer feeding in shallow waters, and thus, typically have a short diving time (ca. 5 sec) (Borowiec 1975). In Lake Constance (Swiss-German border), the mean time for the deeper-diving goldeneye is about 14 sec (Suter 1982a). The mean diving time of tufted ducks increases from ca. 19 sec at 2 m, to ca. 27 sec at 4–6 m depth (Draulans 1982). Dive duration can also be affected by prey density (Draulans 1982); the mean diving time of the tufted duck declines with increasing prey density (ca. 30–20 sec), but increases slightly again at the highest prey densities; this may be due to their tendency to be most size-selective at the highest dreissenid densities.

Birds that dive to consume dreissenids are physiologically well adapted for this activity (Woakes and Butler 1983). The diving energy budgets of tufted ducks and pochards have been comprehensively analyzed by Carbone et al. (1996), chiefly centering on the problem of the limited oxygen supply during breathhold, particularly in deep water.

2.3.2.3. Consumption patterns. Diving ducks typically swallow dreissenids whole and crush the shells in the gizzard. van Eerden et al. (1997) observed that diving ducks relied particularly on individual, unattached mussels, but were also able to take mussels in clumps. In laboratory trials, for tufted ducks, the food intake rates decreased with the degree of byssal thread attachment of the mussels, while intake rates of scaups were only affected when mussels grew in tightly attached clumps (de Leeuw 1999). In Lake Constance, zebra mussels attached to rocks are consumed mostly from shallow (1–3 m depth) areas, while loosely attached mussels on sand are retrieved from depths down to 11 m (Werner et al. 2005).

The details of how birds eat dreissenids have been particularly well studied in the tufted duck (de Leeuw and van Eerden 1992; de Leeuw et al. 1999; Draulans 1982; Olney 1963). Tufted ducks sieve mussels in a manner similar to how puddle ducks (*Anas* spp.) filter seeds. While at the bottom, tufted ducks collect mussels ≤16 mm in length in a water-suction-flow generated by repeated tongue movements. Kooloos et al. (1989) provided a detailed anatomical and functional analysis of this mechanism in the tufted duck. Longer mussels (maximum of 25 and 30 mm, respectively, for tufted duck females and males) are typically picked up individually. While underwater, tufted ducks generally feed on small mussels, but may pick up a large mussel before returning to the surface. Consequently, feeding observations based on birds at the surface only are likely to yield biased prey-size preferences. In laboratory trials, feeding activity was observed to consist of short feeding bouts involving several dives in quick succession to fill the esophagus with mussels, followed by longer resting periods of 5–10 min to crush mussel shells in the gizzard and digest the flesh (de Leeuw 1999). For tufted ducks, much time can be spent at the surface orienting large mussels in the bill to achieve a suitable position for swallowing them whole. In their Lake Erie study, Hamilton et al. (1994) observed bufflehead, greater scaup, and lesser scaup returning to the surface with several mussels in their bills and manipulating them one by one before swallowing them.

Feeding on mussels in open waters is apparently not the only strategy among diving birds. Kornobis (1977) has reported that coots also recover other larger bivalves like *Unio* and *Anodonta* bivalves (Unionidae), transport them to the shore, and remove the dreissenids attached to their shells.

Gulls with limited diving abilities developed two kinds of interspecific relationships with ducks—food commensalism and interspecific kleptoparasitism. Gulls steal mussels from ducks emerging with a clump of mussels or pick up lost dreissenids lying on the water surface, thus, obtaining otherwise inaccessible food (Marchowski et al. 2016). As a result, the diet of gulls in Szczecin Lagoon (Poland) changes dramatically from predominantly fish parts to almost exclusively mussels when large numbers of *Aythya* ducks arrive in November (Marchowski et al. 2016).

2.3.3. Impact of bird predation on dreissenid mussel populations

The interactions of birds and their dreissenid prey have been studied more intensively than that of any other *Dreissena* enemy. Impacts of bird predation on dreissenid populations can include a reduction in mussel density and biomass, an alteration of mussel distribution within a waterbody, and a shift in mussel size-frequency distributions.

2.3.3.1. Documented reductions in dreissenid populations. Reductions in mussel abundance can be one of the most dramatic impacts of bird predation. Birds can consume up to 30% of the annual zebra mussel production in shallow areas (Smit et al. 1993) and up to 70–97% of their biomass (Mikulski et al. 1975; Stempniewicz 1974; Werner et al. 2005). In a 20-year study, diving ducks (e.g., tufted duck, pochard, greater scaup, and goldeneye) annually reduced dreissenid biomass by 5–22% throughout the entire Lake IJsselmeer area of the Netherlands and in some shallow areas by up to over 90% (van Eerden et al. 1997). In the littoral zones of Lake Constance, overwintering waterbirds can have a severe impact on zebra mussel populations, with only 2–3% of the *D. polymorpha* biomass remaining in shallower water (Werner et al. 2005). In Goplo Lake (Poland), coots annually consume 20–70% of the yearly *Dreissena* production (Mikulski et al. 1975; Stempniewicz 1974). Intense predation by overwintering diving ducks at an ice-free site in Lake Erie (Canada) resulted in reductions of 74–93% for *D. r. bugensis* and 86–100% for *D. polymorpha*, depending on mussel length (Mitchell et al. 2000). In a Lake Erie bay, diving duck predation, in combination with reduced food resources (phytoplankton), contributed to a 67% decline in dreissenid density over a three year period (Petrie and Knapton 1999). Other studies have recorded smaller impacts (reviewed in Stanczykowska et al. 1975). In Skoszewska Cove of the Odra River Estuary (Poland) greater scaups alone consumed about 38% of the zebra mussel population (Marchowski et al. 2015).

In studies where significant declines in mussel populations have been documented, the reductions tend to be temporary, with mussel densities rebounding the next year. During their migration passage, diving ducks (bufflehead, greater scaup, and lesser scaup) foraging at Point Pelee (Lake Erie, Canada) reduced dreissenid biomass by 57% during November, which was their period of heaviest feeding; differences between study and control areas, however, had disappeared by the following spring (Hamilton et al. 1994). In a four-year study of the Rhine River at the outflow of Lake Constance (Swiss-German border), one of the highest biomasses of dreissenids recorded in Europe (up to 12 kg/m^2) was annually reduced by 97% by overwintering waterfowl flocks; immigrant mussels from adjacent areas, however, recolonized the site each spring and restored mussel biomass to previous levels (Suter 1982b). In the Seerhein River, which connects the two main basins of Lake Constance, from autumn 1988 through spring 1989 overwintering waterfowl (mainly tufted duck and pochard) reduced the dreissenid standing crop (ash-free dry weight) by 91% (i.e., from 56,400/m^2 to 5,100/m^2); however, subsequent springtime immigration of large numbers of dreissenids from deeper parts of Lake Constance, i.e., areas out of the reach of the diving ducks, combined with summertime reproduction, completely restored population densities by fall 1989 (i.e., 59,800/m^2) (Cleven and Frenzel 1993).

The above studies demonstrate that significant long-term (i.e., multi-year) reductions in mussel densities are most likely to occur only in localized areas where waterfowl overwinter (rather than just stage during their fall migrations) and mussel recruitment is limited. During 1975–1985, throughout Lake IJsselmeer, diving ducks reduced dreissenid biomass annually by 10–13% on average, but because mussel recruitment was successful throughout this period, dreissenid populations actually increased over this decade (van Eerden et al. 1997). In contrast, in nearby Lake Markermeer, years of irregular larvae fall, in combination with intense duck predation, eventually led to a collapse of the mussel population, thus, providing the clearest evidence to date that successful annual recruitment of dreissenids is a key factor in determining to what degree predation by overwintering ducks impacts mussel populations. Using data from their experimental enclosure studies in Lake Erie (Canada), Mitchell et al. (2000) also concluded that reductions in *Dreissena* densities caused by diving ducks are typically short-lived due to recolonization by small mussels migrating from refugia in the spring and settling of larval mussels during the following summer.

The extent of avian predation on dreissenid populations depends on several factors, including the predator density, depth, substrate, mussel accessibility (see discussion above), and *Dreissena* species. Considering lake morphology, waterfowl predation is likely to be more intense in shallow polymictic lakes than in deep dimictic lakes. Since zebra mussels are largely limited to the littoral zone, they are probably more vulnerable to waterfowl predation than quagga mussels which are usually more abundant in the profundal than in the littoral zones (Karatayev et al. 2021a). Conversely, the survival of quagga mussels may be hindered by their thinner, more fragile shells that are more easily crushed (Bowers et al. 2005; Casper and Johnson 2010).

Because of their depth feeding preferences, diving waterfowl can alter the distribution of dreissenid populations within a water body. The average depth of dreissenid colonies in Lake Zurich (Switzerland) increased from 4 to 5 m, due in part to predation by large populations of tufted duck and coot (Burla and Lubini-Ferlin 1976).

Waterfowl predation can also significantly affect dreissenid population size-structure due to size feeding preferences (Table 6). From autumn 1988 through spring 1989 in the Seerhein River (Germany and Switzerland) overwintering waterfowl, mainly tufted duck and pochard, completely eliminated their preferred size class (1+ cohort mussels, >5 mm) (Cleven and Frenzel 1993). Likewise, in the shallow zone of Lake Constance, almost all mussels >1 year (>5 mm) were consumed by tufted ducks, pochards, and coots in the winter of 2001/2002 (Werner et al. 2005). In Lake Neuchâtel (Switzerland), entire cohorts of dreissenids disappeared in years following heavy mussel predation (Pedroli 1977). The effect of tufted duck predation on the size composition of mussel populations is most pronounced at high prey densities; in theory, increased prey densities reduce the diving time required for tufted duck to locate dreissenids, thereby reducing the effort in prey-size selection (Draulans 1982).

2.3.4. Importance of dreissenids as food for birds and their effects on bird populations

2.3.4.1. Benefits from dreissenids as a food source. Dreissenids can be a valuable food source for waterfowl, and their consumption by migrating or overwintering birds is well documented both in Europe and in North America. In the Lake IJsselmeer area of the Netherlands, dreissenids were reported as the main food item for over 300,000 overwintering diving ducks (tufted duck, pochard, greater scaup, and goldeneye) (bij de Vaate 1991; de Leeuw 1997a). In these Dutch lakes during the winter, in terms of biomass, dreissenids can make up to over 90% of the birds' diets (van Eerden et al. 1997). The daily consumption of mussels can be extremely high, up to 2–3 times the bird's body mass (de Leeuw et al. 1999). In the brackish lagoons of the Odra River Estuary (Baltic Sea), an important resting area for greater scaup (*A. marila*) during the non-breeding season, the birds consume an average of 5400 tons of zebra mussels annually (Marchowski et al. 2015). The declining European populations of *A. marila*, thus, now depend on the non-native zebra mussels that constitute >90% of their food (in terms of biomass). Their dietary importance for coots and greater scaup in Poland (Marchowski et al. 2015; Mikulski et al. 1975), for tufted ducks in Belgium (Draulans 1982) and the British Isles (Olney 1963), and diving ducks in the Great Lakes region (Custer and Custer 1996; Hamilton et al. 1994; Mazak et al. 1997; Petrie and Knapton 1999) has been well documented.

2.3.4.2. Increases in flock sizes and overwintering. Because of their importance as a prey item, dramatic increases in flock sizes can occur following dreissenid colonization of a waterbody, as observed in France (Géroudet 1966), Switzerland (Jacoby and Leuzinger 1972; Leuzinger and Schuster 1970; Pedroli 1981b; Suter and Schifferli 1988), Germany (Hiller 1997; Ziegler 1987), and North America (Luukkonen et al. 2013; Petrie and Knapton 1999; Wormington and Leach 1992). Dreissenids are not the only molluscs in North America to attract large flocks of molluscivorous waterfowl; high densities of fingernail clams (*Sphaerium transversum*) have made the Keokuk Pool on the Mississippi River (Iowa) a favored annual migration stopover for nearly 20 million diving ducks including lesser scaup and goldeneye (Thompson 1973). Before the appearance of dreissenids in Swiss lakes, birds fed on aquatic macrophytes in the fall, and after plant die-back, they migrated to the south. Following the buildup of dreissenid densities, thousands of birds began to overwinter locally (Leuzinger and Schuster 1970). In western Lake Constance, soon after the arrival of dreissenids in the late 1960s, 45,000 tufted ducks, pochards, and coots were observed overwintering, representing a 10- to 50-fold increase over previous levels (Suter 1982a). Following the establishment of dreissenids in western Lake Constance, goldeneye began to arrive at overwintering areas earlier (Suter 1982a). The densities of *D. polymorpha* larvae in Lake Walensee (Switzerland), which were assumed to be a reflection of the densities of adult mussels present the previous winter, were found to correlate with the size of winter populations of the tufted duck, the common goldeneye, and the common coot. Between 1982 and 1990, a 9-fold increase in larval numbers resulted in a doubling in common goldeneye and a 3-fold increase in common coot and tufted duck populations. Further, these increases were much smaller than those reported for other Swiss lakes (5- to 10-fold), because the densities of *Dreissena* in Lake Walensee were still relatively low due to nutrient-poor waters and because only a small area of the lake was accessible to diving waterbirds (Marti et al. 2004). Midwinter counts of diving ducks in the Rhone River near Lake Geneva (France) increased dramatically following the arrival of dreissenids (Géroudet 1978).

Conversely, the decline of dreissenids may trigger decreases in wetland use by waterfowl. Thus, in the Inner Long Point Bay of eastern Lake Erie, colonization by zebra mussels in the early 1990s increased water clarity, which in turn favored the growth of submerged aquatic vegetation (SAV) and increased the usage of the wetland by waterfowl (Petrie and Knapton 1999). In the 2020s, however, increased eutrophication, sediment loads, and predation of the mussels by both fish and waterfowl led to a >90% decline in filter-feeding dreissenid populations. Enhanced phytoplankton densities reduced light penetration and SAV, lowering the bay's carrying capacity for waterfowl, fish, and other wildlife (Churchill et al. 2016).

2.3.4.3. Changes in the timing and routes of waterfowl migrations. The location and density of dreissenid populations cannot only affect waterfowl distribution and overwintering (see above) but also the timing and routes of their migration. The geographical range of tufted duck in England expanded due in part to the spread of dreissenids (Olney 1963). Food abundance and availability, particularly *Dreissena*, were suggested as the main factor governing lake choice by overwintering diving ducks in Switzerland (Suter 1994).

The arrival of dreissenids in North America has resulted in changes in migration routes and increases in flock sizes of diving ducks (Wormington and Leach 1992). The combined lesser and greater scaup use (i.e., waterfowl days) of Long Point Bay, one of the most important waterfowl staging areas in North America, increased 92-fold between 1986 and 1997, despite a substantial decline in the North American scaup population (Petrie and Knapton 1999). Waterfowl days for bufflehead in Long Point Bay increased 14-fold during the same period (Petrie and Knapton 1999). The number of waterfowl, including scaup, canvasback (*Aythya valisineria*), and redhead ducks (*Aythya americana*) that use Lake St. Clair (in its USA section) during their fall migrations increased from 1.1 million use-days before dreissenids arrived to 2.1 million after dreissenid establishment (Luukkonen et al. 2013). Conversely, in areas where dreissenid populations declined, diving birds show a tendency to leave overwintering areas earlier (Suter 1982c) or not return the following winter (van Eerden et al. 1997). Likewise, the establishment of dreissenids in Lake Neuchâtel (Switzerland) modified the migratory phenology of tufted ducks, pochards, and greater scaup (Pedroli 1981a).

2.3.4.4. Positive indirect effects of dreissenids on birds. In addition to the direct consumption of dreissenids, waterfowl also prey on the invertebrates facilitated by the mussels, as well as on macrophytes and bottom algae that benefit from dreissenid-enhanced water clarity. Thus, in unprotected enclosures in shallow areas of Lake Constance, the abundance of macroinvertebrates associated with *Dreissena* colonies (mostly Oligochaeta, Chironomidae, and Ephemeroptera) were significantly reduced, presumably due to waterfowl predation (Mörtl et al. 2010). The number of waterfowl, including canvasbacks, that do not directly prey on *Dreissena*, increased after the colonization of Lake St. Clair by dreissenid mussels, likely due to increased submerged aquatic macrophyte food associated with the enhanced water clarity following mussel colonization (Luukkonen et al. 2013). The bay of Lucerne (Switzerland) has become an internationally important overwintering site for the red-crested pochard (*Netta rufinadue*) due to its recolonization by stoneworts (Characeae) after the introduction of zebra mussels in the 1980s (Schwab et al. 2001). In some lakes, both *Chara* and zebra mussels are now considered keystone species that control ecosystem resilience, and careful management of these species has been suggested to be as important as the control of nutrients (Ibelings et al. 2007). Declines in dreissenid densities can diminish wetland quality and usage by reducing water transparency and the concomitant decline in submerged aquatic vegetation (Churchill et al. 2016).

While generally advantageous, reliance on dreissenids as the main prey item can involve hazards. For example, in the unusually cold winter of 1986 in Europe, dreissenid populations were severely affected, leading to the starvation deaths of thousands of diving birds which depended on this resource (Suter and van Eerden 1992).

Because of their efficient filter feeding, dreissenids can concentrate various pollutants from the water column (Binelli et al. 2015), which are subsequently transferred to mussel-eating birds. Accumulation of PCBs derived from their food was reported in tufted ducks in the Linth Canal in Switzerland (Zimmermann et al. 1997) as was the presence of organic contaminants in North American diving ducks (Mazak et al. 1997). In a European study where caged tufted ducks fed on dreissenids contaminated with cadmium and organochlorine compounds, these toxins were carried over into their eggs with teratogenic effects (de Kock and Bowmer 1993). Dreissenids can also accumulate and transfer selenium to waterfowl (Custer and Custer 2000; Schummer et al. 2010; Weegman and Weegman 2007), yet the short- and long-term impacts of this element on bird health and reproduction are unknown. These are only a few examples from the extensive literature that was not reviewed comprehensively due to limited space.

Ingestion of dreissenids by birds can also lead to infections with trematode parasites of the family Echinostomatidae, such as *Echinoparyphium recurvatum*. The role of dreissenids and waterfowl in the life cycle of these trematodes is discussed later in this review.

2.4. Crustaceans

2.4.1. Cladocerans

Their small size, patchy distribution, and slow locomotion (Karatayev and Burlakova 2022a) make dreissenid larvae an attractive and easily obtainable food for various planktonic predators. Lazareva et al. (2016) estimated that, in Rybinsk Reservoir (Russia), up to 90% of veliger production is consumed by pelagic invertebrate predators. In laboratory tests with Great Lakes zooplankton, Pichlová-Ptáčníková and Vanderploeg (2009) observed that the invasive Ponto-Caspian cladoceran *Cercopagis pengoi* feeds efficiently on *D. polymorpha* veligers, but they also noted that densities of *C. pengoi* in Lake Michigan are comparatively low and that these cladocerans are very unlikely to have a significant impact, if any, on dreissenid larvae.

2.4.2. Copepods

Laboratory experiments by Karabin (1978) in Poland suggest that the predatory copepod *Mesocyclops* may feed on planktonic larvae of *D. polymorpha*. Mogilchenko (1986) reported that in the Kanewskoe Reservoir (Ukraine) copepods feed on dreissenid veligers, but they do not actively hunt for this prey, consuming veligers when they circumstantially come into contact with them. The North American laboratory experiments of Liebig and Vanderploeg (1995) with the calanoid copepods *Diaptomus sicilis*, *Limnocalanus macrurus*, and *Epischura lacustris* indicated that both the trochophore (the initial shell-less larval stage) as well as the D-stage of *D. polymorpha* could be successfully preyed upon, but it was the trochophore that was especially vulnerable to this predation. Although consumption of trochophores by a wide variety of predators must be common in nature, these laboratory experiments apparently still remain the only record of any organism preying specifically on this dreissenid larval stage.

2.4.3. Amphipods

There is no clear evidence that the amphipod *Dikerogammarus villosus*—well-known for its aggressive, carnivorous nature—preys on dreissenids. There is a single laboratory observation of *D. villosus* feeding on the byssal threads of *D. polymorpha* when both were held in experimental containers (Platvoet et al. 2009). In contrast, extensive laboratory observations of *D. polymorpha* by Kobak et al. (2012) and Dzierzynska-Bialonczyk et al. (2019) did not report any evidence of predation by *D. villosus*. Kobak et al. (2012) did indicate, however, that when in the presence of *D. villosus*, mussels moved less and increased their byssal attachment strength—two behavioral reactions suggested to indicate inadvertent mechanical irritation of the exposed mussels' soft tissues by the amphipod's appendages. Dzierzynska-Bialonczyk et al. (2019) observed that when exposed to *D. villosus*, *D. polymorpha* reduced its gaping activity, and they suggested that the mechanical irritation to the mussel's siphons and mantle caused by the appendages of the crawling *D. villosus* was likely involved. They further noted that although it is unlikely that *D. villosus* could pose a direct predatory threat to dreissenids, if the amphipod's populations are sufficiently high, the repeated mechanical irritation and resulting reduced gaping/feeding might negatively affect *D. polymorpha*'s body condition.

2.4.4. Mysids

Mysids are a major component of estuarine and coastal zooplankton communities. In trials involving multi-prey assemblages, two native mysid species from the St. Lawrence River middle estuary, *Neomysis*

Figure 1. Blue crab *Callinectes sapidus* eating *D. polymorpha* (Credit: D. P. Molloy).

americana and *Mysis stenolepis*, exhibited high predation rates on zebra mussel veligers (Winkler et al. 2007). Another mysid, *Mysis diluviana* actively consumed veligers in Lake Michigan in summer, with up to 50% of *Mysis* stomachs examined containing dreissenid larvae (O'Malley and Bunnell 2014).

2.4.5. Crabs

Both laboratory and field data suggest that blue crabs, *Callinectes sapidus,* were responsible for a 1992 population crash of 2–3 cm long dreissenids in the Hudson River near Catskill, New York (Molloy et al. 1994). Laboratory trials confirmed that these crabs can aggressively consume such large dreissenids (Figure 1). Further supportive evidence of the blue crab predation hypothesis was gained in subsequent summers when blue crabs did not migrate into the Catskill area and no massive declines in 2–3 cm mussels occurred. Cage experiments in the Hudson River suggest that blue crabs could be more effective in reducing dreissenid abundance than either local fish or other invertebrate predators, but that mussel populations would not be regulated unless predator abundance, including blue crabs, increased significantly (Boles and Lipcius 1997). Later observations conducted in the Hudson River estuary in control areas open to predation and in exclosures inaccessible to large predators provided further evidence that blue crabs cause high mortality of zebra mussels (Carlsson et al. 2011). In Oklahoma and Texas, two invasive species, zebra mussels and Harris mud crabs (*Rhithropanopeus harrisii*) now coexist in a novel predator–prey relationship (Hallidayschult and Hambright 2018). Laboratory experiments showed that Harris mud crabs consume zebra mussels and may play an important role as a predator of dreissenids. In nature, however, the consumption may be lower: in the Odra estuary (Poland), *R. harrisii tridentatus* was found to feed mainly on detritus (61% of the gut content), while animal food (13%) contained remains of copepods, insects, fragments of the blue mussel (*Mytilus edulis*) and the zebra mussel (*D. polymorpha*) (Czerniejewski and Rybczyk 2008).

Table 9. Crayfish species documented eating *Dreissena*.

Species	Where predation observed	References
Astacus astacus	Germany	Chucholl and Chucholl 2021[a]
Astacus leptodactylus	Ukraine	Grinbart and Suprunovitch 1981
	Kazakhstan	Malinowskaya 1976
	Hungary	Sebestyén 1937
Austropotamobius pallipes	Ireland	Reynolds and Donohoe 2001[a]
Cambarus affinis	Germany	Pieplow 1938
Cambarus robustus	United States	Hazlett 1994[a]
Faxonius immunis	Germany	Chucholl and Chucholl 2021[a]
Faxonius limosus	Germany	Chucholl and Chucholl 2021[a]; Linzmaier and Jeschke 2020[a]
Orconectes limosus	Poland	Kornobis 1977; Piesik 1974[a], 1983; Szlauer 1974
	Netherlands	Smit et al. 1993
Orconectes propinquus	Canada United States	MacIsaac 1994[a]; Martin and Corkum 1994[a]; Perry et al. 1997[a]
Orconectes rusticus	United States	Green et al. 2008; Naddafi and Rudstam 2014c[a]; Perry et al. 1997, 2000
Orconectes virilis	United States	Hazlett 1994[a]; Love and Savino 1993[a]; Perry et al. 1997[a]
Pacifastacus leniusculus	Sweden Germany Sweden U.K.	Chucholl and Chucholl 2021[a]; Schreiber et al. 1998[a]; zu Ermgassen and Aldridge 2011[a]
Procambarus clarkii	Italy	Chucholl 2013; Gonçalves et al. 2016[a], 2017[a]
Procambarus virginalis	Germany	Chucholl and Chucholl 2021[a]; Linzmaier and Jeschke 2020[a]

[a] Lab observations only.

2.4.6. Crayfish

Most crayfish species are omnivorous, and mollusks are often one of their main prey items (Lodge et al. 1994; Nyström 2002). It is generally accepted that consumption of dreissenids by crayfish (Decapoda: Astacoidea) occurs widely in nature, but to date, only the following five species have been field-documented as predators: *Orconectes rusticus* in North America (Green et al. 2008; Perry et al. 1997, 2000), and four species in Europe: *Astacus leptodactylus* (Grinbart and Suprunovitch 1981; Malinowskaya 1976; Sebestyén 1937), *Cambarus affinis* (Pieplow 1938), *Orconectes limosus* (Kornobis 1977; Piesik 1974; Smit et al. 1993; Szlauer 1974), and *Procambarus clarkii* (Chucholl 2013) (Table 9). Laboratory feeding trials showed that nine other crayfish species consume dreissenids as well (Table 9). Martin and Corkum (1994) and Schreiber et al. (1998) stressed, however, that laboratory results do not necessarily accurately predict feeding habits in the wild where other prey is available and that future research needs to focus on crayfish foraging under field conditions.

2.4.6.1. Feeding preferences. Although crayfish are omnivores (Nystrom 2002), they do have feeding preferences. In laboratory trials, the rate of predation on dreissenids by *Orconectes* decreased when crayfish were concurrently offered either macrophytes (MacIsaac 1994) or trout eggs (Love and Savino 1993). Malinowskaya (1976) observed that in the Kyshunskoe Reservoir (Kazakhstan) dreissenids were a predominant food item for *Astacus leptodactylus* females, while males ate mainly vegetation. In laboratory trials, MacIsaac (1994) observed a higher predation rate in *O. propinquus* females and Piesik (1974) in *O. limosus* females; the latter author considered that the lower rate of male predation was a short-term effect related to their reproductive cycle. The laboratory trials of Perry et al. (1997) recorded no difference in the maximum size of dreissenids consumed by male and female *O. rusticus*. Laboratory trials with *O. virilis* and *Cambarus robustus* indicated that feeding on dreissenids may involve odor cues (Hazlett 1994).

2.4.6.2. Prey handling techniques and size preference. Laboratory trials provided extensive details on the handling techniques used by crayfish preying on dreissenids (MacIsaac 1994; Reynolds and Donohoe 2001; Schreiber et al. 1998). Such trials have also consistently demonstrated that crayfish prefer small dreissenids, with a positive correlation between predator and prey sizes (MacIsaac 1994; Martin and Corkum 1994; Naddafi and Rudstam 2014c; Perry et al. 1997; Piesik 1974; Reynolds and Donohoe 2001; Schreiber et al. 1998; zu Ermgassen and Aldridge 2011). Martin and Corkum (1994) observed that *O. propinquus* consumed mussels up to 17 mm in length, with a preference for mussels ≤8 mm long. MacIsaac (1994) determined that *O. propinquus* can consume small to medium-sized mussels (3–14 mm long), but preferred that 3–5 mm in length; he suggested that the high predation rates on these small mussels were related to the relative ease with which they are handled, i.e., small mussels require significantly less manipulation time (median: 68 sec) than medium-sized mussels (median: 456 sec) before they are ingested. Piesik (1974) observed that 90 mm long *O. limosus*, although capable of consuming *Dreissena* up to 12 mm long, also preferred small mussels (1–5 mm long). Schreiber et al. (1998) observed that all *Pacifastacus leniusculus* showed a clear preference for the smallest mussels offered, but also that when breaking the shell was no longer a barrier for the crayfish (as in the case when dead and crushed mussels were offered as prey), there was no size-selectivity, leading to the conclusion that dead mussels are likely more attractive than live mussels. In laboratory experiments, Reynolds and Donohoe (2001) observed that white-clawed crayfish *Austropotamobius pallipes* predominantly feed on mussels <11 mm in length, with 3–7 mm mussels consumed in the highest numbers, but when eaten mussels were not replaced, crayfish shifted to larger sizes. Larger crayfish consumed more mussels of a wider size range, but females consumed on average both 50–80% less than their male counterparts and smaller mussels than males. While in the presence of alternative prey experienced crayfish ate mussels and alternative food items in similar amounts, whereas those that had no prior experience with zebra mussels nearly always chose the alternative items first (Reynolds and Donohoe 2001).

The intensity of crayfish predation decreases with water temperature (Piesik 1974). Although *Cambarus affinis* in Germany consumes dreissenids from at least April through December (the entire period of the field study), the highest predation rates are in July and August (Pieplow 1938). Feeding rates on attached mussels are also lower compared to feeding rates on detached mussels (Schreiber et al. 1998).

2.4.6.3. Impact of crayfish predation. Information on the impact of crayfish predation on dreissenid populations in nature is very limited. Predation leading to significant declines in a European dreissenid population was reported in a non-controlled study (Piesik 1974). In caged field studies in Lake Erie, *Orconectes rusticus* had a negligible effect on *Dreissena*'s density and shell-length frequency distribution, likely due to their feeding preferences on other macroinvertebrate prey (Stewart et al. 1998). In North American stream trials, however, crayfish did reduce dreissenid recruitment and density in enclosures (Perry et al. 1997, 2000). These results suggested that relative to lakes, predation by crayfish in streams may be a more important population density regulating mechanism since mussel recruitment in streams is already constrained by water velocity and other factors (reviewed in Karatayev and Burlakova 2022a). Even at high predation pressures, it is unlikely that in streams crayfish can reduce dreissenid populations below densities that are ecologically important (Perry et al. 1997). Although zebra mussels can be important food items for predators, such as *O. rusticus* which use chemical cues, their vulnerability to predators appears to be directly related to the integrity of the mussel shell and/or their byssus threads and is less pronounced in nature (lakes) than in the laboratory, probably owing to the presence in nature of alternative prey items (Green et al. 2008). Therefore, although zebra mussels may represent a substantial food source, only local and temporary reductions of mussels may occur in the wild, and crayfish are unlikely to be able to significantly impact established zebra mussel populations.

2.4.6.4. Impact of dreissenids on crayfish. Dreissenids have been observed on the exoskeleton of *Astacus leptodactylus*, particularly older specimens which normally do not molt as frequently as juveniles, e.g., >7 cm length (Lamanova 1971). Sebestyén (1937) considered that such overgrowth has only a temporary negative effect on *Astacus leptodactylus*, but Lamanova (1971) reported chitinous sores (≤1 cm diameter) on this species, with potentially adverse effects on crayfish vision and feeding. Anwand (1996) reported that *O. limosus* neither suffered apparent damage nor benefited from dreissenid colonization, but that the mussels likely benefited from the additional substrate, enlarged activity area, and better feeding conditions. Brazner and Jensen (2000) reported observing six rusty crayfish (*O. rusticus*) colonized with *D. polymorpha* near Green Bay (Lake Michigan, USA). The mean length of attached mussel was 3.6 mm, and the number of mussels ranged from 16 to 431 per crayfish. The authors suggested that the energetic costs or physical constraints caused by the attached dreissenids might be detrimental to the infested crayfish.

2.5. Other predator groups

2.5.1. Coelenterates

Conn and Conn (1993) documented *Hydra americana* preying on *Dreissena* veligers in the St. Lawrence River (United States-Canadian border); these hydrae immobilized their prey with tentacles containing stinging nematocysts. Both attached and planktonic hydra fed on dreissenid veligers, and some were observed to have several veligers in their gastrovascular cavities (Conn and Conn 1993). Predation on dreissenid planktonic larvae by *Cordylophora* was reported from the Bay of Szczecin (Poland) (Wiktor 1969).

2.5.2. Rotifers

Veligers up to 300 µm in diameter were found comparatively often (13% of the specimens analyzed) in the stomachs of the predatory *Asplanchna herricki*, the largest pelagic rotifer species in Rybinsk Reservoir (Russia) (Lazareva 2004).

2.5.3. Annelids

Reports of leeches feeding on molluscs are rare. Consumption of juvenile dreissenids in Europe by *Glossiphonia complanata* (Hirudinea: Glossiphoniidae) (Smit et al. 1993) is the only record available. Predation on North American dreissenids is likely since *G. complanata* has been reported feeding on molluscs in Iowa, including the freshwater bivalve *Lampsilis siliquoidea* (Waffle 1963).

2.5.4. Turtles

Laboratory studies with map turtles, *Graptemys geographica*, collected from the St. Lawrence River suggest that these reptiles forage on dreissenids in nature: turtles 6–9 cm (plastron length) in size consumed mussels 4–32 mm in length. The authors noted, however, that dreissenids can be important only when more desirable prey (e.g., snails) are scarce (Serrouya et al. 1995). In contrast, Bulté and Blouin-Demers (2008) documented that in Lake Opinicon (Canada) zebra mussels constitute up to 36% of the diet of the map turtle and estimated that turtles can consume over 3000 kg of zebra mussels per year.

In addition to map turtles *G. geographica*, the stinkpot turtle *Sternotherus odoratus* was also found to prey heavily on invasive mussels in the Laurentian Great Lakes (Lindeman 2006; Patterson and Lindeman 2009). While juvenile and male map turtles fed on zebra and quagga mussels occasionally (33–44% occurrence), 100% of the adult females consumed dreissenids compared to only 20% of the adult males. The Index of relative importance (IRI) of dreissenids in adult females was 98%, compared to 1% in males (Lindeman 2006). In contrast, no differences between the sexes were found for the stinkpot turtle: dreissenids were the most prevalent food item consumed, with similar values of IRI (62 for males, 60 for females) (Patterson and Lindeman 2009). Therefore, both map and stinkpot turtles exhibited shifts toward increased molluscivory having switched to heavy consumption of invasive dreissenids.

2.5.5. Rodents

Consumption of dreissenids by the Norway rat, *Rattus norvegicus*, has been reported from Italy (Bedulli and Franchini 1978). Although muskrats, *Ondatra zibethicus*, prefer plant food, they have been observed to consume dreissenids in Germany (Reichholf 1985) and Poland (Wolk 1979). Muskrats have been documented to have a significant impact on other bivalves before dreissenid introduction: thus, in Narrow Lake (Canada) they annually consume 3% of the *Anodonta grandis simpsoniana* (Unionidae) population, which represents 31% of its annual tissue production. The authors speculate that muskrat consumption of the largest mussels (>55 mm) reduced the reproductive capacity of the mussel population (Hanson et al. 1989). After some waterbodies were invaded by dreissenids, muskrats began preying on zebra mussels attached to unionids but left the native unionids untouched and alive (Sietman et al. 2003). All live unionids from middens left by the muskrats had zebra mussel byssal threads or in some cases, live zebra mussels on their shells. The change in muskrat prey selection from native unionids to zebra mussels is probably due to the fact that the latter may be easier to open and consume than unionids (Sietman et al. 2003).

2.5.6. Other animals

Dreissenids were found in the guts of a declining Laurentian Great Lakes native species, the large mudpuppy salamander (*Necturus maculosus*), but at low frequency (2–6%), likely due to difficulties in the consumption of the hard shells (Beattie et al. 2017). To evaluate possible customers for potential zebra mussel farming in Germany, feeding experiments were carried out in The Zoological Garden in Osnabrück with mussels harvested in the Oder Lagoon (Schernewski et al. 2019). The trials showed that mongooses (*Mungos mungo*) and the oriental small-clawed otters (*Aonyx cinerea*) immediately accepted zebra mussels as food, and raccoons (*Procyon lotor*) even showed a preference for zebra mussels. Further studies are needed to confirm if otters and racoons feed on dreissenids in the wild.

2.5.7. Intraspecific predation on dreissenid larvae

The cannibalism of planktonic larvae by sessile *Dreissena* has been documented in Europe (Mikheev 1966; Shevtsova et al. 1986) and in North America (MacIsaac et al. 1991). MacIsaac et al. (1991, 1995) conducted laboratory and field studies addressing the impact of this intraspecific predation and suggested that it may be a density-dependent population regulatory mechanism. They observed that rates of clearance of veligers from the water column increased with mussel size, with maximum prey sizes likely constrained by the diameter of the inhalant siphon. They proposed that larval mortality in North America was initially substantially lower than today due to the scarcity of predatory adult mussels. The percentage of dreissenid plankton that are drawn into the mantle cavity but are rejected and survive has not been documented, although in other bivalve species (e.g., *Mytilus edulis*) conspecific larvae have been observed to emerge alive after having passed through the digestive tract of adult predators (Voskresensky 1973).

3. Endosymbionts

Seventy-five species and higher taxa of endosymbionts (commensals and parasites) have been found within the mantle cavity and/or associated with *D. polymorpha* tissue, including ciliates, trematodes, nematodes, chironomids, oligochaetes, mites, and leeches in Europe, and 21 in North America (Tables 10 and 11). All these organisms have been reported living within attached mussels. There have been no records of endosymbionts reported from planktonic larvae, but this is likely due in large part to the absence of research on this topic. While some species are highly specific and found exclusively within a particular *Dreissena* species (e.g., certain ciliates and trematodes), others have a broader range of hosts (e.g., the oligochaete *Chaetogaster limnaei* and the trematode *Echinoparyphium recurvatum*). Although some parasites and commensals use dreissenids as the only host in their life cycle, others, such as digenetic trematodes, may use them as intermediate hosts, developing into adults typically in fish or waterfowl (reviewed in Molloy et al. 1997). In addition to obligate endosymbionts, a large range of free-living benthic species are occasionally reported from dreissenid mantle cavities, including chironomid larvae (Karatayev et al. 2000a; Mastitsky and Samoilenko 2005; Ricciardi 1994), nematodes (Karatayev et al. 2000a, 2003a; Mastitsky and Gagarin 2004), and leeches (Karatayev et al. 2000a; Kuperman et al. 1994).

Reports of *Dreissena* endosymbionts vary from extremely common, recorded from virtually all European populations examined (e.g., *Conchophthirus* spp., Ciliophora), to those recorded from very few locations (e.g., haplosporidians) (Table 10). In addition, many more parasites and commensals were reported for *D. polymorpha* than for *D. r. bugensis*, and more from Europe than from North America (Tables 10 and 11). These differences, however, could be due to the actual differences in their occurrence or to sampling bias. Some species like *Conchophthirus* spp. and *Ophryoglena* spp. can be easily identified when mussels are dissected, and therefore historically they were reported from numerous waterbodies

Table 10. Endosymbionts including commensal (C) and parasitic (P) reported from attached *Dreissena polymorpha* and *D. r. bugensis* populations in Europe.

Endosymbionts	Type of symbiont	*D. polymorpha*	*D. r. bugensis*
Ciliates			
Conchophthirus acuminatus	C	Switzerland (Claparède and Lachmann 1858) Bulgaria (Raabe 1934) Poland (Dobrzanska 1958; Raabe 1934, 1956) Hungary (Raabe 1950) Denmark (Fenchel 1965) Belarus (Burlakova et al. 1998; Karatayev et al. 2000a, 2000b, 2003a, 2007; Mastitsky 2012) Russia (Laruelle et al. 1999; Pryanichnikova et al. 2011; Tyutin et al. 2013a) Ukraine (Karatayev et al. 2000a; Yuryshynets et al. 2008) Ireland (Burlakova et al. 2006a; Conn et al. 2008) Sweden (Mastitsky et al. 2008) Lithuania (Chuševė et al. 2012) France (Minguez et al. 2009, 2011, 2013) Germany (Molloy et al. unpublished data) Italy (Molloy et al. unpublished data) Greece (Molloy et al. unpublished data) The Netherlands (Molloy et al. unpublished data)	Ukraine (Karatayev et al. 2000b; Yuryshynets 2019) Russia (Pryanichnikova et al. 2011; Tyutin et al. 2013a)
Hypocomagalma dreissenae	P	Hungary (Raabe 1950) Poland (Dobrzanska 1958; Raabe 1956) Denmark (Fenchel 1965) Russia (Laruelle et al. 1999) Belarus (Laruelle et al. 1999) France (Molloy et al. unpublished data) Germany (Molloy et al. unpublished data) Greece (Molloy et al. unpublished data) Italy (Molloy et al. unpublished data) The Netherlands (Molloy et al. unpublished data) Ukraine (Molloy et al. unpublished data)	Ukraine (Molloy et al. unpublished data; Yuryshynets et al. 2003)
Sphenophrya dreissenae	P	Poland (Dobrzanska 1958) Russia (Laruelle et al. 1999) France (Minguez et al. 2009) Belarus (Molloy et al. unpublished data) Denmark (Molloy et al. unpublished data) Germany (Molloy et al. unpublished data) Italy (Molloy et al. unpublished data) The Netherlands (Molloy et al. unpublished data) Ukraine (Molloy et al. unpublished data)	Ukraine (Yuryshynets et al. 2003)
Ophryoglena hemophaga	P	Russia (Fokin et al. 2003; Molloy et al. 1996) Germany (Fokin et al. 2003) The Netherlands (Fokin et al. 2003) France (Minguez and Giambérini 2012; Minguez et al. 2009, 2013) Ireland (Burlakova et al. 2006a) Poland (Yuryshynets 2009) Lithuania (Chuševė et al. 2012) Denmark (Molloy et al. unpublished data) Switzerland (Molloy et al. unpublished data) Ukraine (Molloy et al. unpublished data)	Russia (Pryanichnikova et al. 2011; Tyutin and Scherbina 2006)
Ophryoglena sp. (small form)	P	Belarus (Karatayev et al. 2000a, 2002b, 2003a) France (Minguez et al. 2013)	
Ancistrumina limnica	C	Poland (Raabe 1956) The Netherlands (Laruelle et al. 1999) Greece (Laruelle et al. 1999) Belarus (Karatayev et al. 2000a) Ireland (Burlakova et al. 2006a) Russia (Molloy et al. unpublished data) Ukraine (Molloy et al. unpublished data)	Ukraine (Molloy et al. unpublished data; Yuryshynets 2019)
Peritrichia	C	Belarus (Molloy et al. unpublished data) Greece (Molloy et al. unpublished data) The Netherlands (Molloy et al. unpublished data) Ukraine (Molloy et al. unpublished data)	
Trematodes			
Bucephalus polymorphus	P	France (de Kinkelin et al. 1968b; Minguez and Giambérini 2012; Wallet and Lambert 1986)	Ukraine (Chernogorenko and Boshko 1992)

(*Continued*)

Table 10. Continued.

Endosymbionts	Type of symbiont	*D. polymorpha*	*D. r. bugensis*
		Poland (Baturo 1977; Kulczycka 1939; Taskinen et al. 2021)	
		Russia (Golikova 1960; Kuperman et al. 1994; Pryanichnikova et al. 2011; Tyutin et al. 2005, 2013a)	
		Ukraine (Chernogorenko and Boshko 1992; Zdun 1965)	
		Kazakhstan (Smirnova and Ibrasheva 1967)	
		Uzbekistan (Aristanov 1986, 1992)	
		Belarus (Karatayev et al. 2000a; Stunžėnas et al. 2004)	
		Croatia (Lajtner 2012; Lajtner et al. 2008)	
		Czech Republic (Ondračková et al. 2015)	
		Denmark (Molloy et al. unpublished data)	
		Germany (Molloy et al. unpublished data)	
		The Netherlands (Molloy et al. unpublished data)	
Phyllodistomum macrocotyle	P	The Netherlands (Kraak and Davids 1991)	
		Poland (Kulczycka 1939; Petkevičiūtė et al. 2015; Travina et al. 2021; Wisniewski 1957)	
		Belarus (Karatayev 1983; Karatayev et al. 2000a; Lyakhnovich et al. 1983; Petkevičiūtė et al. 2015; Stunžėnas et al. 2004; Travina et al. 2021)	
		Russia (Kuperman et al. 1994; Molloy et al. 1996; Petkevičiūtė et al. 2015; Travina et al. 2019, 2021)	
		Ukraine (Zdun 1965)	
		Kazakhstan (Smirnova and Ibrasheva 1967)	
		Spain (Peribáñez et al. 2006, 2011)	
		France (Minguez and Giambérini 2012; Minguez et al. 2013)	
		Lithuania (Petkevičiūtė et al. 2015, 2020; Travina et al. 2021)	
		Germany (Molloy et al. unpublished data)	
		Greece (Molloy et al. unpublished data)	
		Italy (Molloy et al. unpublished data)	
Echinoparyphium recurvatum	P	Russia (Ginezinskaja 1959; Kochnev 1977; Pryanichnikova et al. 2011)	
		Belarus (Mastitsky and Veres 2010)	
		Croatia (Lajtner 2012)	
Echinoparyphium echinatoides	P	Ukraine (Chernogorenko and Boshko 1992)	
		Russia (Pryanichnikova et al. 2011; Tyutin et al. (2013a)	
Echinostoma paraulum	P	Russia (Kochnev 1977)	
Echinostomatidae (unidentified)	P	Ukraine (Yuryshynets 1999, 2019)	Russia (Pryanichnikova et al. 2011)
		France (Minguez and Giambérini 2012)	Ukraine (Yuryshynets 1999, 2019)
		Belarus (Karatayev et al. 2000a)	
		Denmark (Molloy et al. unpublished data)	
		Germany (Molloy et al. unpublished data)	
		Greece (Molloy et al. unpublished data)	
		Italy (Molloy et al. unpublished data)	
		The Netherlands (Molloy et al. unpublished data)	
Leucochloridiomorpha constantiae	P	Ukraine (Chernogorenko and Boshko 1992; Molloy et al. 1997)	
Sanguinicola sp.	P	Poland (Stanczykowska 1977)	
Aspidogaster limacoides	P	Russia (Kuperman et al. 1994; Molloy et al. 1996; Nagibina and Timofeeva 1971; Pryanichnikova et al. 2011; Tyutin and Scherbina 2006; Tyutin et al. 2013a; Zhokhov 2001)	Russia (Popova and Biochino 2001)
		Croatia (Lajtner 2012)	
Aspidogaster conchicola	P	Poland (Kulczycka 1939)	
		Ukraine (Chernogorenko and Boshko 1992)	
Aspidogaster (unidentified)	P	Belarus (Karatayev et al. 2000a)	
		France (Minguez et al. 2011)	
		The Netherlands (Molloy et al. unpublished data)	
Haplosporidians			
Haplosporidium raabei	P	The Netherlands (Bowmer and van der Meer 1991; de Kock and Bowmer 1993; Molloy et al. 2012)	
		Germany (Molloy et al. unpublished data)	
		France (Molloy et al. unpublished data)	
Prokaryote bacteria			
Rickettsiales-like and/or *Chlamydiales*-like organisms	P	Greece (Molloy et al. 2001)	
		France (Minguez and Giambérini 2012; Minguez et al. 2012, 2013)	
		United States (Minguez et al. 2013)	
Nematodes			
Brevitobhlus stefanskii	C	Belarus (Mastitsky and Gagarin 2004)	
Chromadorita leuckarti	C	Belarus (Mastitsky and Gagarin 2004)	

(*Continued*)

Table 10. Continued.

Endosymbionts	Type of symbiont	*D. polymorpha*	*D. r. bugensis*
Chromadorina bioculata	C	Belarus (Karatayev et al. 2003a; Mastitsky and Gagarin 2004)	
	C	Sweden (Mastitsky et al. 2008)	
Crocodorylaimus flavomaculatus	C	Belarus (Mastitsky and Gagarin 2004)	
Dorylaimus stagnalis	C	Belarus (Mastitsky and Gagarin 2004)	
	C	Russia (Kuperman et al. 1994)	
Epitobrilus medius	C	Belarus (Mastitsky and Gagarin 2004)	
Eumonhystera pseudobulbosa	C	Belarus (Mastitsky and Gagarin 2004)	
Eumonhystera vulgaris	C	Belarus (Mastitsky and Gagarin 2004)	
Laimydorus sp.	C	Sweden (Mastitsky et al. 2008)	
Monhystera uncispiculatum	C	Belarus (Mastitsky and Gagarin 2004)	
Monhystera paludicola	C	Belarus (Mastitsky and Gagarin 2004)	
Monhystera iemani	C	Belarus (Mastitsky and Gagarin 2004)	
Monhystrella sp.	C	Belarus (Karatayev et al. 2003a)	
Mononchus truncatus	C	Belarus (Mastitsky and Gagarin 2004)	
Neoactinolaimus dzjubani	C	Belarus (Mastitsky and Gagarin 2004)	
Plectus cirratus	C	Belarus (Mastitsky and Gagarin 2004)	
Plectus palustris	C	Belarus (Mastitsky and Gagarin 2004)	
Punctodora ratzeburgensis	C	Belarus (Mastitsky and Gagarin 2004)	
Rhabdolaimus terrestris	C	Belarus (Mastitsky and Gagarin 2004)	
Semitobrilus gagarini	C	Belarus (Mastitsky and Gagarin 2004)	
Tobrilus gracilis	C	Belarus (Mastitsky and Gagarin 2004)	
Tobrilus helveticus	C	Belarus (Mastitsky and Gagarin 2004)	
Tobrilus tenuicaudatus	C	Belarus (Karatayev et al. 2003a)	
Tridentulus floreanae	C	Belarus (Karatayev et al. 2003a; Mastitsky and Gagarin 2004)	
Tripyla glomerans	C	Belarus (Mastitsky and Gagarin 2004)	
Nematoda (unidentified)	C	Russia (Kuperman et al. 1994; Pryanichnikova et al. 2011)	Russia (Tyutin et al. 2013a)
		Belarus (Karatayev et al. 2000a, 2003a)	
		Ireland (Burlakova et al. 2006a)	
		Sweden (Mastitsky et al. 2008)	
		Lithuania (Chuševė et al. 2012)	
		Poland (Krasutska 2017)	
		Czech Republic (Molloy et al. unpublished data)	
		Denmark (Molloy et al. unpublished data)	
		France (Molloy et al. unpublished data)	
		Germany (Molloy et al. unpublished data)	
		Greece (Molloy et al. unpublished data)	
		Italy (Molloy et al. unpublished data)	
		The Netherlands (Molloy et al. unpublished data)	
		Switzerland (Molloy et al. unpublished data)	
		Ukraine (Molloy et al. unpublished data)	
Oligochaetes			
Chaetogaster limnaei	P?	Ukraine (Chernogorenko and Boshko 1992)	
		Belarus (Karatayev et al. 2000a)	
		Germany (Molloy et al. unpublished data)	
Psammoryctides baebatus	C	Russia (Kuperman et al. 1994)	
P. moldavensis	C	Russia (Kuperman et al. 1994)	
		Russia (Kuperman et al. 1994)	
Oligochaeta (unidentified)	C	Belarus (Karatayev et al. 2000a)	Russia (Pryanichnikova et al. 2011; Tyutin et al. 2013a)
		Ireland (Burlakova et al. 2006a)	Ukraine (Yuryshynets 2019)
		Denmark (Molloy et al. unpublished data)	
		Ukraine (Molloy et al. unpublished data)	
Leeches			
Caspiobdella fadejewi	C	Russia (Kuperman et al. 1994)	
Helobdella stagnalis	C	Russia (Kuperman et al. 1994)	
Helobdella sp.	C	Belarus (Karatayev et al. 2000a)	Tyutin et al. 2013a
Erpobdella octoculata	C	Belarus (Karatayev et al. 2000a)	
Erpobdella sp.	C		Tyutin et al. 2013a
Chironomids			
Chironomus bathophilus	C	Russia (Kuperman et al. 1994)	Ukraine (Yuryshynets 2019)
Cryptochironomus sp.	C	Belarus (Mastitsky and Samoilenko 2005)	
Glyptotendipes gr. *gripekoveni*	C	Belarus (Mastitsky and Samoilenko 2005)	

(*Continued*)

Table 10. Continued.

Endosymbionts	Type of symbiont	*D. polymorpha*	*D. r. bugensis*
Limnochironomus gr. *nervosus*	C	Belarus (Mastitsky and Samoilenko 2005)	
Limnochironomus tritomus	C	Belarus (Mastitsky and Samoilenko 2005)	
Paratanytarsus gr. *lauterborni*	C	Belarus (Mastitsky and Samoilenko 2005)	
Polypedilum gr. *convictum*	C	Belarus (Mastitsky and Samoilenko 2005)	
Tanytarsus gr. *gregarius*	C	Belarus (Mastitsky and Samoilenko 2005)	
Corynoneura celeripes	C	Belarus (Mastitsky and Samoilenko 2005)	
Cricotopus gr. *algarum*	C	Belarus (Mastitsky and Samoilenko 2005)	
Cricotopus gr. *silvestris*	C	Belarus (Mastitsky and Samoilenko 2005)	
Cricotopus sp.	C	Belarus (Mastitsky and Samoilenko 2005)	
Eukieferiella bicolor	C	Belarus (Mastitsky and Samoilenko 2005)	
Prodiamesa sp.	C	Belarus (Mastitsky and Samoilenko 2005)	
Orthocladiinae spp.	C	Belarus (Mastitsky and Samoilenko 2005)	
Chironomidae (unidentified)	C	Belarus (Karatayev et al. 2000a)	
		Ireland (Burlakova et al. 2006a)	
		Sweden (Mastitsky et al. 2008)	
		Russia (Pryanichnikova et al. 2011)	
		Czech Republic (Molloy et al. unpublished data)	
		Denmark (Molloy et al. unpublished data)	
		Germany (Molloy et al. unpublished data)	
		Greece (Molloy et al. unpublished data)	
		Ukraine (Molloy et al. unpublished data)	
Mites			
Unionicola sp.	P?	Ukraine (Chernogorenko and Boshko 1992)	
		Russia (Kuperman et al. 1994)	Russia (Tyutin et al. 2013a)
Hydrachnidia (unidentified)	P?	Belarus (Karatayev et al. 2000a)	
		Sweden (Mastitsky et al. 2008)	

This list does not include *C. klimentinus* and *S. naumiana* found exclusively in *D. carinata* in Lake Ohrid.

Table 11. Endosymbionts reported from the attached *Dreissena polymorpha* and *D. r. bugensis* populations in North America.

Endosymbionts	Type of symbiont	*D. polymorpha*	*D. r. bugensis*
Ciliates			
Ophryoglena hemophaga	P	New York (Molloy unpublished data; Mastitsky personal communication)	
Trematodes			
Echinostomatidae (unidentified)	P	New York (Karatayev et al. 2012)	New York (Karatayev et al. 2012)
Sphaeridiotrema sp.	P	New York (Karatayev et al. 2012)	New York (Karatayev et al. 2012)
Aspidogaster conchicola	P	New York (Toews et al. 1993)	
Nematodes			
Achromadora sp.	C		California (Reid et al. 2012)
Chromadorina bioculata	C		California (Reid et al. 2012)
Dichromadora sp.	C		California (Reid et al. 2012)
Diplogaster sp.	C		California (Reid et al. 2012)
Ironus sp	C		California (Reid et al. 2012)
Mononchus sp.	C	New York (Conn et al. 1994)	
Monhystrella sp.	C		California (Reid et al. 2012)
Laimydorus sp.	C		California (Reid et al. 2012)
Plectus geophilus	C		California (Reid et al. 2012)
Rhabdolaimus sp.	C		California (Reid et al. 2012)
Seinura sp.	C		California (Reid et al. 2012)
Nematoda (unidentified)	C	New York (Conn et al. 1994; Toews et al. 1993)	New York (Conn et al. 1994)
Oligochaets			
Chaetogaster limnaei	P?	New York (Conn et al. 1994, 1996)	New York (Conn et al. 1994, 1996)
Ophidonais serpentine	C	New York (Conn et al. 1994)	
Oligochaeta (unidentified)	C	New York (Conn et al. 1994)	New York (Conn et al. 1994)
Chironomids			
Paratanytarsus sp.	C	New York (Conn et al. 1994; Ricciardi 1994)	New York (Conn et al. 1994; Ricciardi 1994)
Mites			
Hydrachnidia (unidentified)	P?	New York (Conn et al. 1994)	

(reviewed in Karatayev et al. 2000a, 2007; Molloy et al. 1997), whereas other endosymbionts, particularly microbial parasites, such as haplosporidians and prokaryote bacteria, require histological analyses, and therefore, will almost certainly be missed when only dissections are performed. The massive research efforts initiated by Molloy et al. during the 1990s, based on samples from 12 European countries and United States where almost 5800 mussels were dissected and over 3300 mussels were histologically analyzed, have greatly increased the information on *Dreissena* endosymbionts, especially those whose identification requires histological analysis (Molloy et al. unpublished data, Table 10).

3.1. Ciliates

Four species of host-specific ciliates (*Conchophthirus acuminatus*, *Hypocomagalma dreissenae*, *Sphenophrya dreissenae*, and *S. naumiana*) are known from the mantle cavity of *D. polymorpha*, and at least two ophryoglenine species (*Ophryoglena hemophaga* and an undescribed *Ophryoglena* sp.) from the digestive gland (Figure 2). The nature of the symbiotic relationships of these species with their dreissenid hosts is usually poorly known but appears to range from commensalism to parasitism (reviewed in Molloy et al. 1997). In her review of protozoans in molluscs, Bradbury (1994) noted that a healthy mollusc in a low-stress environment is usually in equilibrium with the ciliates in its mantle cavity and that typically the hosts are not seriously affected unless protist populations increase beyond control. As with ciliates in *Dreissena*, most ciliates in molluscs, in general, retain the cilia that identify them as members of the phylum, but with or without cilia, all of them possess dimorphic nuclei and an infraciliature at some point in their life history—the basic characteristics of the phylum (reviewed in Molloy et al. 1997). Ciliates occupying the mantle cavity are also present in the gill water tubes and the suprabranchial cavities, suggesting that they can exit into surrounding waters *via* the exhalant siphon and colonize other individuals (Laruelle et al. 1999).

3.1.1. Conchophthirus (Scuticociliatida: Conchophthiridae)

3.1.1.1. General description and biology. The mantle cavities of lamellibranchs are infected with *Conchophthirus* spp. worldwide, both in marine and freshwater habitats (Kirby 1941). The species *Conchophthirus acuminatus* has been reported from *D. polymorpha* and *D. r. bugensis,* while *C. klimentinus* was found exclusively in *D. carinata (=D. stankovici)* (Figures 2A,B). The most common endosymbiont of *D. polymorpha* in Europe is *C. acuminatus*, and it is typically reported to have the highest prevalence (i.e., percent of mussels with endosymbionts) and intensity (i.e., number of endosymbionts per infected mussel) of infection (Burlakova 1998; Burlakova et al. 1998; Karatayev et al. 2000a, 2007; Molloy et al. 1997). Please note that the term “infection” is used for convenience and consistency for all symbionts even if some of them are commensals.

As is typical for the Conchophthiridae, *C. acuminatus* and *C. klimentinus* are strongly laterally compressed and lie on their flattened left side (i.e., the side in contact with the substrate is not their ventral side). The body of *C. acuminatus* (ca. 50–120 μm in length, 30–60 μm wide) is slightly tapered anteriorly and rounded posteriorly (Raabe 1971). In contrast to *C. acuminatus*, the body of *C. klimentinus* is slightly rounded at both ends, has a more ovoid outline, and its left side is uniformly concave along almost its entire length; $L = 60–130\,\mu m$ (mean ca. $100\,\mu m$) and $W = 40–100\,\mu m$ (mean ca. $55\,\mu m$) (Raabe 1966, 1971).

Little is known about their biology, and conjugation has rarely been observed (Raabe 1971). They live primarily on the gills, the visceral mass, or the walls of the mantle cavity, with some species preferring specific regions (Kirby 1941). In unionids, for example, *C. anodontae* is primarily attached to the nonciliated surface of the oral palps (Kidder 1934). In *Dreissena*, *C. acuminatus* can be found in a variety of locations (Laruelle et al. 1999) but is most frequently observed on the visceral mass and gills, where they creep about using their short, dense cilia. According to Kidder (1934), all *Conchophthirus* spp. have an obligate association with bivalves and likely can tolerate only short periods outside their hosts, as during their transfer to new hosts. Karatayev et al. (2003b), however, demonstrated in laboratory trials that *C. acuminatus* can survive outside a host for up to 6 days, but most ciliates died within 48 hr.

3.1.1.2. Host specificity. Both in North America (Antipa and Small 1971; Kidder 1934) and in Europe (Raabe 1950), *Conchophthirus* spp. tend to be fairly host-specific. The *Conchophthirus* spp. occurring in North American unionids, for example, have not been reported from dreissenids on this continent (Molloy et al. 1997). Dreissenid endosymbiont *C. acuminatus*, whose range is limited to Europe, in addition to *D. polymorpha*, has been reported in *D. r. bugensis* from the Dnieper River, Ukraine (Karatayev et al. 2000b; Yuryshynets 2019), Volga River reservoirs, Russia

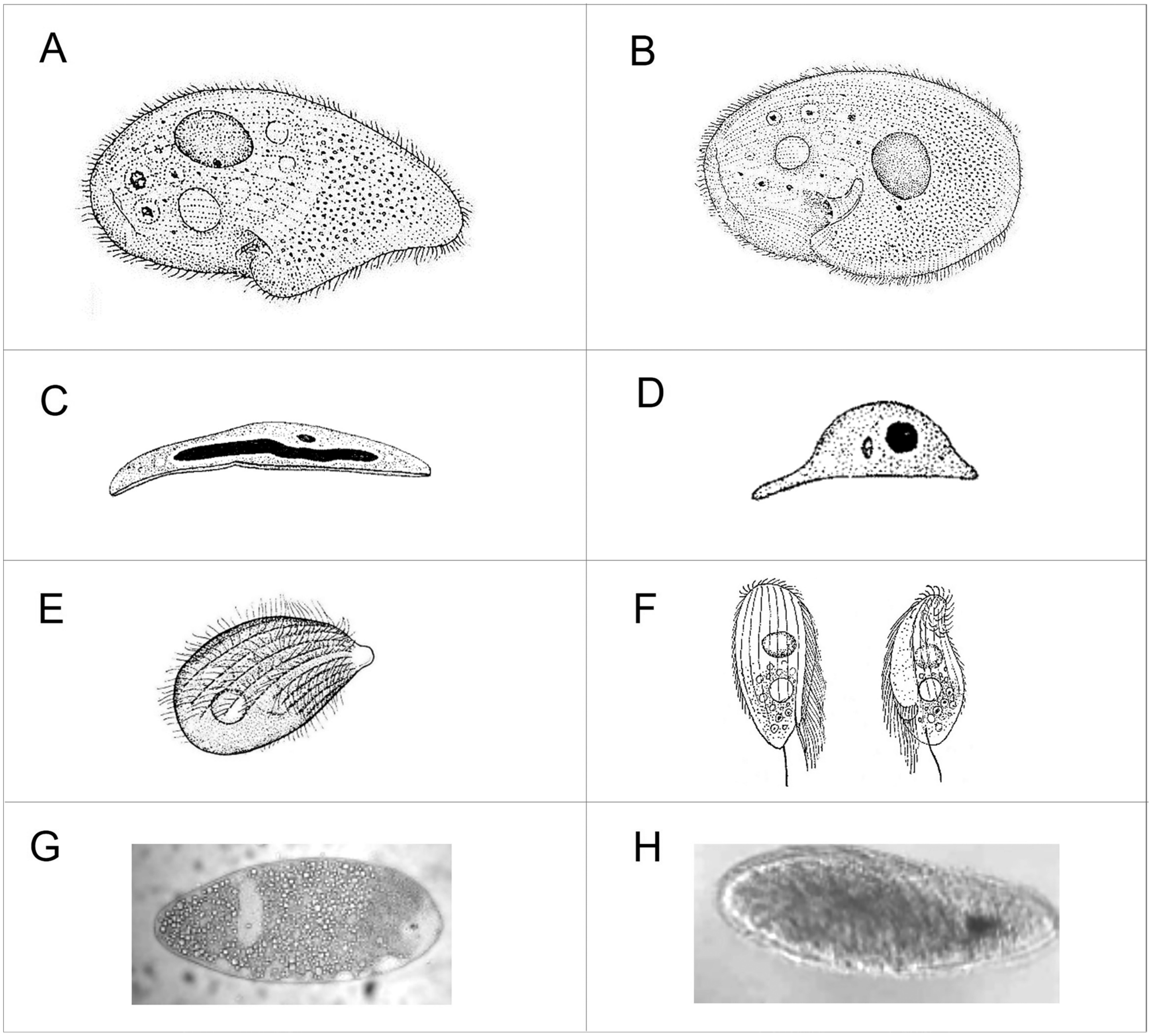

Figure 2. Ciliates from *Dreissena* spp.: A, *Conchophthirus acuminatus*; B, *Conchophthirus klimentinus* (both adapted from Raabe 1971); C, *Sphenophrya naumiana*; D, *Sphenophrya dreissenae* (both adapted from Raabe 1966); E, *Hypocomagalma dreissenae* (adapted from Fenchel 1965); F, *Ancistrumina limnica* (adapted from Raabe 1947); G, H, trophont and theront of *Ophryoglena hemophaga* (adapted from Molloy et al. 2005).

(Pryanichnikova et al. 2011; Tyutin et al. 2013a), and in *D. carinata* from Lake Ohrid, Macedonia (Molloy et al. 2010; Raabe 1966). Although in the Dnieper River and Volga reservoirs both *Dreissena* species coexist, the prevalence of infection in *D. r. bugensis* is consistently significantly lower than in *D. polymorpha*. Because in the Dnieper River, both *Dreissena* species were sampled at the same locations, Karatayev et al. (2000b) suggested that *D. r. bugensis* may not be as suitable a host as *D. polymorpha*, or possibly *D. r. bugensis* may just be an accidental host in which *C. acuminatus* cannot survive and/or reproduce. In Lake Ohrid, where only one dreissenid species is present (*D. carinata*) (Lvova and Starobogatov 1982; Molloy et al. 2010), two species of *Conchophthirus* were reported: *C. klimentinus* (endemic to this lake), and *C. acuminatus* (Molloy et al. 2010; Raabe 1966). Recent data, however, suggest that ciliates reported as *C. acuminatus* from Lake Ohrid are actually an undescribed *Conchophthirus* species (Molloy, unpublished data).

3.1.1.3. *Nature of the relationship.*

The *Conchophthirus* spp. in bivalves are generally considered commensals (reviewed in Molloy et al. 1997). No evidence exists of any detrimental effects on unionid bivalves (Antipa and Small 1971) or *D. polymorpha* (reviewed in Karatayev et al. 2007), even at the highest densities.

Fenchel (1965) reported that the ciliature near the cytostome (mouth) of *Conchophthirus* spp. was very much reduced, suggesting that these ciliates are incapable of ingesting suspended particles and that they likely feed primarily on items present on the epithelial tissues within the mantle cavity. Food vacuoles in *Conchophthirus* spp. typically contain algae, bacteria, and sloughed-off epithelial cells (Kirby 1941). Kidder (1933), for example, concluded that in the saltwater mussel, *Mytilus edulis*, *Conchophthirus mytili* was "no doubt" a commensal since its food vacuoles were filled primarily with algae. A year later, however, the same author (Kidder 1934) reported observing well-preserved unionid epithelial cells in *Conchophthirus magna,* which suggested active consumption of the host's tissues. In examining the food vacuoles of *C. curtus* from unionids, Antipa and Small (1971) found host cilia and host tissue nuclei but concluded that *C. curtus* had only consumed sloughed cells and other cellular debris. Although Laruelle et al. (1999) occasionally observed dreissenid sperm in food vacuoles of *C. acuminatus*, epithelial tissues in contact with high densities of these ciliates showed no evidence of pathology, thus, providing further evidence of this species' commensal nature. There is also a generally accepted parasitological concept that the prevalence of infection is inversely related to pathogenicity (Anderson and May 1981). Therefore, the ubiquitous high prevalence of infection in European *D. polymorpha*, which often reaches 100%, and the infection intensity that often exceeds thousands of ciliates per mussel (see below) are indirect evidence suggesting that *C. acuminatus* is commensal rather than parasitic.

3.1.1.4. Prevalence and infection intensity. High prevalence rates of *Conchophthirus* infection in *D. polymorpha* have been commonly reported, with 100% infection observed in Denmark (Fenchel 1965), Belarus (Burlakova et al. 1998), and Ukraine (Yuryshynets et al. 2008). Overall, the prevalence of infection in 37 European populations of *D. polymorpha* ranged from 75 to 100% (Karatayev et al. 2007; Tyutin et al. 2013a). In the Dnieper River (Ukraine), Karatayev et al. (2000b) recorded *C. acuminatus* in both *D. polymorpha* and *D. r. bugensis*, but the prevalence and intensity of infection were significantly lower for *D. r. bugensis*, suggesting lower susceptibility. Intensity of *C. acuminatus* infection in *D. polymorpha* correlates directly with mussel length ($r^2 = 0.83–0.92$), and when infection prevalence is 100%, it is not uncommon to find from 500 to 2000 *C. acuminatus* in the mantle cavity of a single individual (Burlakova et al. 1998; Karatayev et al. 2000b). The smallest infected mussel ever reported was 2-mm long and contained only a single *C. acuminatus*, whereas the maximum number (14,035 ciliates/mussel) was recorded in a 26.4-mm *D. polymorpha* (Karatayev et al. 2000b).

The laboratory experiments of Burlakova et al. (1998) showed that dying mussels are swiftly left by the ciliate and authors hypothesized that the dying mussels were likely a major source for the spread of *C. acuminatus* infections. These ciliates commonly leave their hosts when they are still alive, with the rate of emergence being temperature dependent and episodic, with periods of no emergence followed by periods of high emergence (up to 720 ciliates per mussel per day) (Karatayev et al. 2003b). During a 24-day experiment, the average number of *C. acuminatus* that emerged from each experimental mussel at 21 °C (207 ciliates/mussel) was significantly higher than the number that emerged at 14 °C (29 ciliates/mussel) (Karatayev et al. 2003b). Field observations also demonstrated that the presence of live mussels with high intensity of infection could also serve as a source to initiate and subsequently amplify the infection of nearby dreissenids. Similarly, Karatayev et al. (2000b) stressed that since infection intensity and prevalence were strongly correlated with mussel size, the presence of large, infected mussels was likely important to serve as a reservoir for maintaining infection in the overall population. They also suggested that mass emigration of *C. acuminatus* into surrounding waters might be synchronized to occur when new potential hosts, i.e., juvenile mussels, become abundant. In a study conducted in 2001–2002 in Drozdy Reservoir in Belarus, Karatayev et al. (2003a) recorded clear infection peaks in August, positively correlated with water temperature. In addition, the mean size of *C. acuminatus* was negatively correlated with temperature, and the timing of temperature increase was positively correlated with asexual reproduction, with a peak in cell division in April (5% of fusion pairs in the population) when water temperature increases (Karatayev et al. 2003a).

3.1.1.5. Geographical distribution. This ciliate is widespread in European *D. polymorpha* populations and is the most common of all known symbionts (Table 10). In Belarus, for example, this species was observed in all 31 *D. polymorpha* populations sampled (reviewed in Karatayev et al. 2007). It was recorded in dreissenid populations from all 16 European countries studied (Table 10).

Because *C. acuminatus* is present in virtually all European freshwater populations of *D. polymorpha* and has not been found in North America yet, Karatayev et al. (2000b) hypothesized that: (1) planktonic larvae, rather than attached *Dreissena,* invaded North America, and (2) the European waterbodies invaded by *Dreissena* where *C. acuminatus*-infestations are found were either colonized by adult mussels or, if a waterbody was colonized by planktonic larvae, it is connected to an upstream source with infested adults and the ciliates were transported as free-living individuals, since they can survive in the water-column for up to 6 days (Karatayev et al. 2003b). Ireland, being an island, is not directly connected by freshwater to any previously existing source population of *D. polymorpha*. The presence of *C. acuminatus* and other species-specific endosymbionts of *D. polymorpha* in the River Shannon system (Burlakova et al. 2006a) supports the hypothesis proposed by Pollux et al. (2003) that Ireland was colonized by adult *D. polymorpha* (infested with *C. acuminatus*). Therefore, analyses of *Dreissena* endosymbionts may help reconstruct the mechanisms of invasion of these mussels (reviewed in Karatayev et al. 2007).

Zebra mussels can live in fresh and brackish (<6‰) waters, but *C. acuminatus* may be less tolerant to salinity: in a Polish Bay, the prevalence of *C. acuminatus* was noted to decline from 100 to 0% with increasing salinity (Raabe 1956 but see Chuševė et al. 2012). In order to confirm whether *D. polymorpha* and *C. acuminatus* have different tolerance to salinity, Karatayev et al. (2007) suggested to check for the presence of *C. acuminatus* or related ciliates in other species and subspecies of *Dreissena* from their native area in the Caspian Sea and the Azov seas. Such studies may help to explain whether *D. polymorpha* and *C. acuminatus* have different origins and will shed light on their coevolutionary history.

3.1.2. *Hypocomagalma* (Rhynchodida: Ancistrocomidae)

Only one species of ancistrocomid ciliate, *Hypocomagalma dreissenae*, has been reported from *Dreissena* spp. (reviewed in Molloy et al. 1997) (Figure 2E). The body of *H. dreissenae* is almost entirely covered with cilia, elongated, banana-shaped, has reduced ciliation, and typically has a rounded posterior end (Fenchel 1965; Raabe 1966, 1970). Its dimensions ($L \times W \times H$) are 32–50 × 14–19 × 10–15 µm (Jarocki and Raabe 1932; Raabe 1970). In *Dreissena* this ciliate was most frequently observed attached to epithelial cells lining the outer gill surfaces, but also occasionally on the visceral mass, the mantle cavity epithelium, in gill water tubes, and rarely on labial palps and within the suprabranchial cavities (Laruelle et al. 1999). The mouth in all *Hypocomagalma* spp. has been functionally replaced by a suctorial tentacle (attachment knob) at the anterior end, which is inserted into the cytoplasm of the host's epithelial cell. Material from the epithelial cell passes into the ciliate through this tentacle, damaging the penetrated host cell in the process (reviewed in Molloy et al. 1997). Three dreissenid species: *D. polymorpha*, *D. r. bugensis*, and *D. carinata* have been reported as hosts of *H. dreissenae.* This ciliate species does appear to be specific to *Dreissena* and is widely distributed in Europe (Table 10). In contrast, records of *H. dreissenae* from *D. r. bugensis* exist in Ukraine only (Yuryshynets et al. 2003; Molloy et al. unpublished data). In addition, *H. dreissenae* was reported from *D. carinata* in Lake Ohrid (Molloy et al. 2010; Raabe 1966).

While prevalence rates of up to 100% have been reported (Fenchel 1965), they usually are much lower (Molloy et al. 2010; Raabe 1966). Salinity may affect their distribution: in a Polish bay, the prevalence of *H. dreissenae* has been observed to rise from 2 to 80% with increasing salinity (Raabe 1956). In bivalves, *Hypocomagalma* spp. are clearly parasitic in nature, their infections are typically of low intensity, with little pathological effect (Bradbury 1994), which is also true for *H. dreissenae* (reviewed in Laruelle et al. 1999; Molloy et al. 1997, 2010).

3.1.3. *Sphenophrya* (Rhynchodida: Sphenophryidae)

3.1.3.1. *General description and biology.*

Ciliates in the genus *Sphenophrya* spp. are parasites on bivalve gills (Bradbury 1994; Fenchel 1965). Two species, *Sphenophrya dreissenae* and *S. naumiana,* have been described from dreissenids (reviewed in Molloy et al. 1997) (Figures 2C,D). Adult *S. dreissenae* are frequently shaped like an elongate helmet (their dimensions range around 30 × 24–40 × 34 µm), slightly flattened laterally, and with one or two distinctly protruding processes on the body margin (Dobrzanska 1958; Raabe 1970). The ciliate *S. dreissenae* was frequently recorded attached to the mantle cavity epithelium and outer gill surfaces, within the gill water tubes, occasionally on the visceral mass, and rarely in the suprabranchial cavities. Depending on how *S. dreissenae* is attached to the gill epithelium, however, its shape may vary considerably; if adults attach by the "sucoir" located at their anterior end, they may be pear-shaped; if they attach by their entire inferior surface, they may appear flat or even concave (Dobrzanska 1958). In contrast, *S. naumiana* is elongate to canoe-shaped ($L \times W = 60–80 \times 12–18\,\mu m$)—a form more typical of other species in this genus (Raabe 1966, 1970). Whereas adult *S. dreissenae* lives on the gills, their immature "tomit" forms, which are produced by budding, can be found either on the gills or on the epithelium lining the mantle cavity (Dobrzanska 1958). Immature *Sphenophrya* resemble species of the suborder Ancistrocomina (e.g., *Hypocomagalma*) in the pattern of their ciliature, the shape of their bodies, and the presence of an anterior suctorial tentacle (Bradbury 1994). In *S. dreissenae*, both asexual budding and sexual reproduction (conjugation) are relatively synchronous in individual mussels (Dobrzanska 1961).

3.1.3.2. Nature of the relationship, prevalence, and infection intensity. Although *S. dreissenae* has always been considered as a parasite (Dobrzanska 1958, 1961), the histological observations of Laruelle et al. (1999) provided the first conclusive evidence of its pathology. They reported that foci of high ciliate presence frequently show tissue damage, including epithelial hyperplasia, cell hypertrophy, and extensive vacuolization.

In *Dreissena* from Lake Ohrid, Raabe (1966) reported ≤1% prevalence and low infection intensity by both *S. dreissenae* and *S. naumiana*. In contrast, Dobrzanska (1961) recorded high intensity and prevalence (up to 100%) with *S. dreissenae* in littoral areas of Polish lakes but noted marked reductions in low density mussel populations in sublittoral areas. She found that the highest intensities occurred generally in spring and autumn, and in younger dreissenids (as has been reported for *Sphenophrya* spp. in other freshwater bivalves).

3.1.3.3. Geographical distribution. So far *Sphenophrya naumiana* has been reported only from Lake Ohrid (Raabe 1966) where *D. carinata* is the only documented dreissenid species. Historically (before the 1990s), in addition to the Republic of North Macedonia (Raabe 1966), *S. dreissenae* was reported only from Poland (the type locality of *S. dreissenae*), where it is common in both flowing and standing waters (Dobrzanska 1958, 1961). Over the last few decades, *S. dreissenae* has also been reported in *D. polymorpha* in Russia (Laruelle et al. 1999), France (Minguez et al. 2009), Belarus, Denmark, Germany, Italy, and in the Netherlands (Molloy et al. unpublished data), as well as in both *D. polymorpha* and *D. r. bugensis* in Ukraine (Molloy et al. unpublished data; Yuryshynets et al. 2003). As is often the case with host records, however, genetic analyses are needed to confirm that these are truly valid records of *S. dreissenae* and not new undescribed, morphologically similar species.

3.1.4. Ophryoglena spp. (Ophryoglenida: Ophryoglenidae)

3.1.4.1. General description and biology. Ciliates in the genus *Ophryoglena* were repeatedly observed living inside the digestive gland of *D. polymorpha* (Karatayev et al. 2000a, 2002b, 2003a; Molloy et al. 1996, 2005; Zdun et al. 1994). Two morphotypes have been described: large and small. The large forms were observed primarily inside the digestive gland ducts of *D. polymorpha* and were described as the new species *Ophryoglena hemophaga* (Molloy et al. 2005). When released from the digestive gland ducts during dissection, *O. hemophaga* is nearly cylindrical and have a mean $L \times W$ of 278×77 µm (Figures 2G,H). In contrast, the small *Ophryoglena* form is found exclusively in the digestive gland tubules of *D. polymorpha* and represents an undescribed species (Molloy, unpublished data). In infected *D. polymorpha* populations, dozens of these relatively small undescribed *Ophryoglena* are often found during dissections, but *O. hemophaga* rarely exceeds 10 per host (reviewed in Molloy et al. 1997).

The ciliate *O. hemophaga* is the first ophryoglenine species recorded as a molluscan parasite, with some evidence of pathological effects on their host (Molloy et al. 1997; Zdun et al. 1994). As is typical of ciliates in the suborder Ophryoglenina, *O. hemophaga* exhibits a polymorphic life history with encystment and reproduction by palintomy (Molloy et al. 2005). The presence of a single, longitudinal tract of multiple contractile vacuoles represents *O. hemophaga*'s most unique morphological feature and distinguishes it from all other described *Ophryoglena* spp. Its life cycle includes the parasitic trophont (96–288 µm in length), an emerging protomont, the encysted tomont (50–150 µm in diameter), and the infective theront (96–131 µm in length) (Figure 3).

3.1.4.2. Prevalence and infection intensity. In the Dnieper-Bug Canal in Belarus the prevalence and intensity of infection of *D. polymorpha* with the small undescribed *Ophryoglena* sp. varied, respectively, from 11 to 62%, and from 0.9 to 24.1 ciliates/mussel (Karatayev et al. 2002a). This canal is believed to be the main route of invasion of *D. polymorpha* into

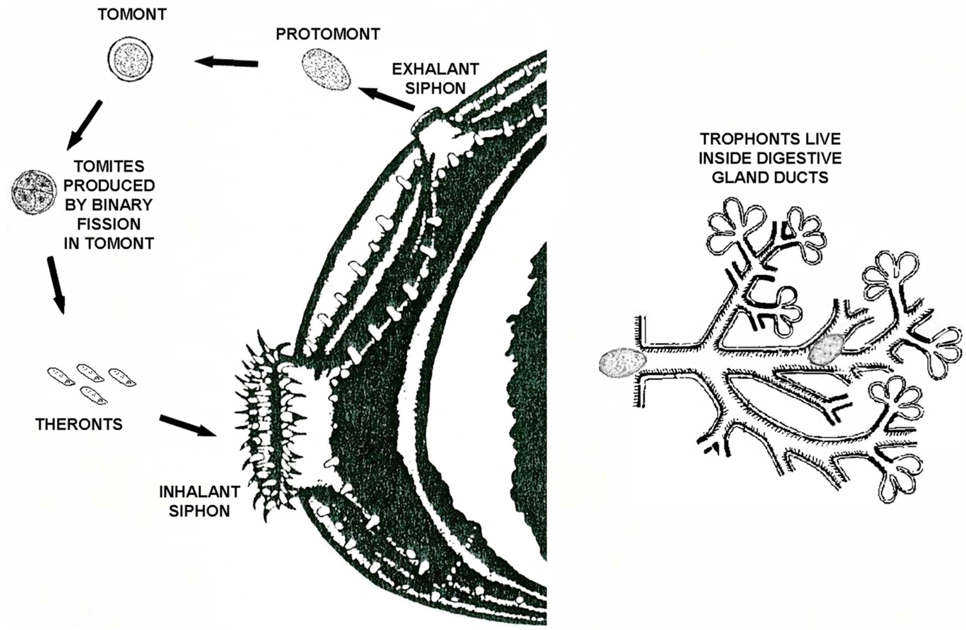

Figure 3. Hypothetical life cycle of *Ophryoglena hemophaga* (adapted from: Canella and Rocchi-Canella 1976; Morton 1993; Owen 1955; Thorp and Covich 1991). In laboratory studies (Molloy et al. 2005), (1) the presence of "trophonts" (the feeding stage) was repeatedly observed in the ducts of the digestive gland (right image); (2) well-fed trophonts were subsequently commonly found to have recently emerged as "protomonts" from infected D. polymorpha (left image), but it is unknown if they emerged *via* the exhalant siphon (as pictured) or the inhalant siphon; (3) likewise, protomont encystment into the "tomont" stage, followed by "tomite" production within the tomont, followed by the exit of these tomites from the cyst as free swimming "theronts" was also commonly observed, but it is unknown if these theronts immediately initiate reinfection by entering through the inhalant siphon (as pictured) or possibly go through another encystment-tomont-tomite-theront production cycle again outside the mussel before initiating infection again.

Western Europe and likely also a corridor for the western migration of their symbionts, including this undescribed small *Ophryoglena* sp. Moderate to high prevalence (43–100%) and low to moderate intensity (1.4 – 65.8 ciliates/mussel) of *Ophryoglena* infection were reported from the Svisloch River (Belarus) (Karatayev et al. 2003a). A high prevalence of infection (100%) of *D. polymorpha* with *O. hemophaga* was reported from the Shannon River (Ireland) (Burlakova et al. 2006a), low to high (up to 97%) *Ophryoglena* infection in the Meuse River (Minguez and Giambérini 2012), and low to moderate (17.5 – 82.5%) infection in the brackish Curonian Lagoon (Chuševė et al. 2012).

In two separate studies of seasonal dynamics of *D. polymorpha* symbionts in Belarus, Karatayev et al. (2000a, 2003a) demonstrated that both prevalence and intensity of infection with the undescribed small *Ophryoglena* sp. were negatively correlated with temperature and were considerably lower in summer as compared to winter. A similar seasonal pattern in the prevalence of *Ophryoglena* infection was observed in *D. polymorpha* in France (Minguez and Giambérini 2012).

Karatayev et al. (2002b) reported that a transinfection of *D. polymorpha* by the undescribed small *Ophryoglena* sp. was achieved in the laboratory where initially infected and uninfected mussels were kept together. In 15 days, specimens initially free from the ciliate reached a mean prevalence of 86.7% and intensity of 8.3 ciliates/mussel, which were similar to those of initially infected animals.

3.1.4.3. Geographical distribution. Infection of *Dreissena* with *Ophryoglena* has been reported in many European populations of *D. polymorpha* (Table 10). In addition, *O. hemophaga* is the only parasite specific to *Dreissena* that was also reported from North America. This ciliate was found in *D. polymorpha* from the Mohawk River (Minguez et al. 2013; Molloy, unpublished data) and Lake Erie (Mastitsky, personal communication). Toews et al. (1993) observed *Ophryoglena* inside "the shells" (i.e., mantle cavity) of living and dead *D. polymorpha* from Lake Erie. Because Toews et al. (1993), however, did not report these *Ophryoglena* from the digestive gland or any other organ, Molloy et al. (1997) suggested that they are not the same species as the one found in European *D. polymorpha* and may simply have been a free-living histophagous species.

In addition to *D. polymorpha,* observations of *Ophryoglena* spp. have also been reported from *D. r. bugensis* and *D. carinata*. Tyutin and Scherbina (2006) reported *Ophryoglena* sp. from *D. r. bugensis* in the Volga River reservoirs and mentioned that the prevalence of infection was much lower than in *D. polymorpha*. The low prevalence (ca. 1%) of infection in *D. r. bugensis* from Volga reservoirs was confirmed by Pryanichnikova et al. (2011). Therefore, compared to *D. polymorpha* where the prevalence of infection may reach 100% (see above), the prevalence of *D. r. bugensis* infection is always much lower, suggesting lower susceptibility.

An *Ophryoglena* sp. was frequently found by Raabe (1966) in the mantle cavity of *Dreissena* in Ohrid Lake. More recently, Molloy et al. (2010) found large (151–160 µm) and small (ca. 40 µm) *Ophryoglena* sp. in *D. carinata* from Lake Ohrid. It is likely that these ophryoglenids are new undescribed species (Molloy, unpublished data).

3.1.5. Ancistrumina (Scuticociliatida: Ancistridae)

The ciliate *Ancistrumina* (=*Ancistrina*) *limnica* is a non-host-specific symbiont of freshwater lamellibranchs and gastropods (Raabe 1947, 1959, 1965) (Figure 2F). Its dimensions ($L \times W$) are $35 \times 18\,\mu m$ (Raabe 1947). In *D. polymorpha, A. limnica* was recorded frequently within gill water tubes, occasionally on the outer gill epithelium, and rarely within the suprabranchial cavities (Laruelle et al. 1999). Ancistrumids typically feed on bacteria, diatoms, and other material retrieved from water currents (Kirby 1941), and thus, are not considered parasitic (Laruelle et al. 1999).

The geographic range of *A. limnica* includes European populations of *D. polymorpha* in Poland (Raabe 1956), the Netherlands and Greece (Laruelle et al. 1999), Belarus (Karatayev et al. 2000a), Ireland (Burlakova et al. 2006a), and Russia and Ukraine (Molloy et al. unpublished data) (Table 10). This species was also reported from *D. r. bugensis* in Ukraine (Yuryshynets 2019; Molloy et al. unpublished data). In Belarus, *A. limnica* was reported in the mantle cavities of *D. polymorpha* in 11 of the 17 waterbodies studied, with a prevalence around 0.3–21.6% (Karatayev et al. 2000a), but occasionally as high as 94% (Karatayev et al. 2003a). The highest intensity of infection was observed in a single mussel (299 *A. limnica* in a 25 mm long individual) from the Svisloch River, Belarus (Karatayev et al. 2000a). Both prevalence and intensity of infection were positively correlated with temperature, being considerably higher in summer and fall than in winter and spring (Karatayev et al. 2003a).

3.1.6. Peritrichia

Laruelle et al. (1999) reported ciliates in the subclass Peritrichia in the mantle cavity of European *D. polymorpha*. Although peritrichs have been previously reported from bivalve mantle cavities (Fenchel 1965), this was the first report of these commensal ciliates within dreissenids. It is likely that these ciliates were attached to the epithelium of the visceral mass and not simply free-floating. No signs of negative effects were found in the adjacent epithelium. Since peritrich populations were observed on the shells of *D. polymorpha*, these ciliates were likely carried passively by water currents into the mantle cavity where they reattached. Records of Peritrichia from European populations of *D. polymorpha* include Belarus, Greece, the Netherlands, and Ukraine; in Ukraine, they were also found in *D. r. bugensis* (Molloy et al. unpublished data) (Table 10).

3.2. Trematodes

Seven genera of trematodes have been reported as parasites of *Dreissena* spp. (Molloy et al. 1997; Stunženas et al. 2004). In their life cycles, dreissenids can serve as the first intermediate host (e.g., *Bucephalus polymorphus* and *Phyllodistomum macrocotyle*), second intermediate host (*Echinoparyphium recurvatum, Echinoparyphium paraulum,* and *Echinoparyphium echinatoides*), or the only host (*Aspidogaster* spp.). Most of these trematodes are Digenea—a subclass in which species require more than one host to complete their life cycle. While trematodes like *B. polymorphus and P. macrocotyle* have been reported in *Dreissena* exclusively from Europe (Molloy et al. 1997; Stunženas et al. 2004), nonspecific trematodes like *E. recurvatum* are also known from North American dreissenids (Karatayev et al. 2012; Toews et al. 1993). Chernogorenko and Nizovskaya (1986) suggested that trematodes exerted antagonism toward each other in their hosts (e.g., inhibition of one species by the other) and suggested that this may explain why two trematode species were rarely recorded in the same mussel; the only double infection they observed was a *Dreissena* with both *B. polymorphus* and echinostomatid cysts.

3.2.1. Bucephalus polymorphus (Digenea: Bucephalidae)

3.2.1.1. Life cycle. Three hosts are required to complete the life cycle of *Bucephalus polymorphus* (Figure 4).

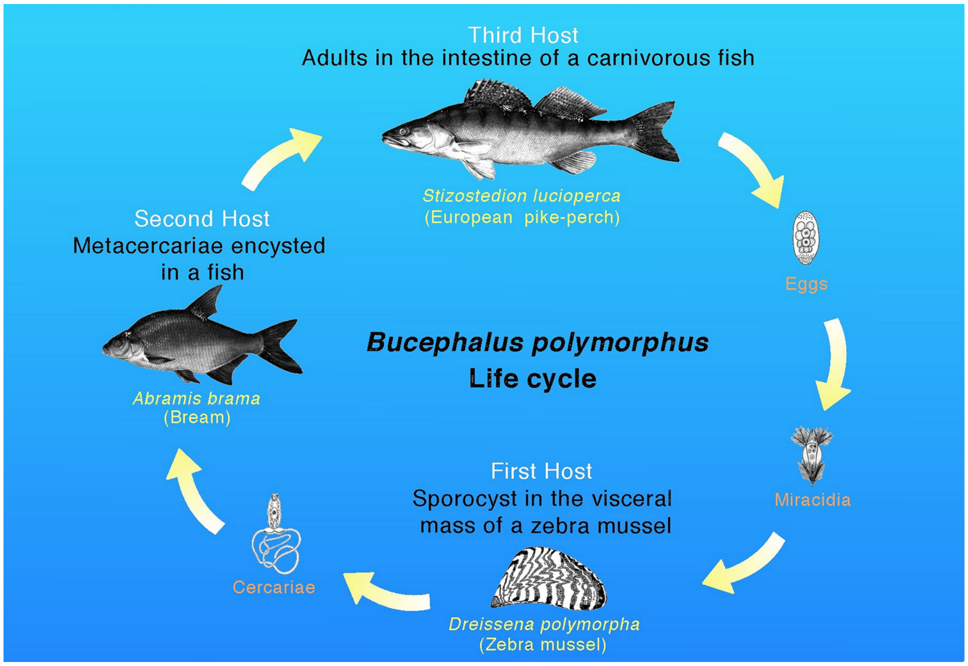

Figure 4. Life cycle of *Bucephalus polymorphus* (adapted from Molloy et al. 1997).

Infection commences in a dreissenid when the earliest larval stage, the miracidium, hatches from an egg, enters a mussel's visceral mass, and gives rise to the sporocyst stage (reviewed in Molloy et al. 1997). The sporocyst of *B. polymorphus* appears as an entanglement of branching, white tubules of knotty, irregular diameter, within which cercariae develop. Located primarily in the gonads, where they typically induce sterility, these tubules may extend out into other tissues, such as the digestive gland, the gills, the mantle epithelium lining the internal surface of the shells, and the connective tissue between the bundles of adductor muscles (Baturo 1977; de Kinkelin et al. 1968b; Laruelle et al. 2002; Molloy et al. 1996). Heavy infections can lead to host castration, with the entire gonadal space often occupied by the sporocysts (Laruelle et al. 2002; vom Scheidt 1984). Digestive gland tubules in infected *D. polymorpha*, however, are as numerous and full-bodied as in uninfected specimens (Laruelle et al. 2002; Molloy et al. 1996).

Cercariae released into the surrounding waters attach to fish fry, encyst in their tissues, and transform into metacercariae. Although specifically for *B. polymorphus* observations are lacking, European research on bucephalid species that infect other freshwater bivalves (Taskinen et al. 1994) has indicated that the infection is carried over from year to year. Thus, it is likely that once a dreissenid is infected with *B. polymorphus*, its gonads will annually produce cercariae, rather than gametes, for the rest of its life (reviewed in Molloy et al. 1997).

The cercarial release is seasonal and appears to have diurnal periodicity. Laboratory studies indicate that in a 12:12 hr light:dark cycle, the highest cercarial releases occur during darkness, whereas under a 16:8 hr light:dark cycle they peak during the first hour of illumination (Wallet et al. 1985). These patterns possibly increase the chances of contact with their fish hosts. In the Seine Basin (France), cercarial release was recorded from June through October (de Kinkelin et al. 1968b). In two lakes in the Konin region of Poland, cercarial emission occurred throughout the entire sampling period from April to November, with a peak between June and October (Baturo 1978). In the latter study, the lakes are artificially heated by waters from hydroelectric plants, which likely contributes to the longer duration of cercarial release. In the Drava River, Croatia, young cercariae are dominant in *D. polymorpha* in autumn and winter while mature cercariae are dominant in spring and summer (Lajtner et al. 2008). Cercarial release from dreissenids overlaps periods of fish hatching, thus, facilitating infection. In Goslawickie Lake (Poland), *B. polymorphus* metacercariae were found as early as April in fish fry 8–11 mm long, with prevalence in fry reaching a maximum in summer and early fall (Baturo 1978). This trematode species appears to be widely distributed in European *D. polymorpha* populations (Table 10).

Although a wide range of fish species can serve as hosts for the metacercarial stage of *B. polymorphus*, cyprinids are the most common (Baturo 1978), and also the only hosts reported to be adversely affected. In an epizootic in the Seine River Basin (France), 20 species in six families (Cyprinidae, Percidae, Esocidae, Centrarchidae, Cobitidae, and Gasterosteidae) were observed with *B. polymorphus* metacercariae, but serious pathologies and deaths were only recorded in cyprinids. The presence of encysted metacercariae in the fins, eyes, and mouths of cyprinids causes a hemorrhagic and necrotic syndrome, which is usually chronic and sometimes fatal (de Kinkelin et al. 1968a). Cyprinids in Polish lakes have metacercariae in almost all organs, but the majority are in somatic muscles, the head, and the body cavities (Baturo 1978).

Apparently, the pathological impact of *B. polymorphus* on fish cannot be predicted solely from the prevalence of dreissenid infection. The degree of pathology in cyprinids noted in the Seine Basin (de Kinkelin et al. 1968a) was not observed in cyprinids in waterbodies in southern France, even though dreissenid populations had about the same infection prevalence (Wallet and Lambert 1986).

From the extensive studies in Poland by Baturo (1978) it would appear that the severe, adverse effects on cyprinids observed in the Seine Basin (de Kinkelin et al. 1968a) are an exception. In the Polish lakes investigated by Baturo, no adverse effects were observed on cyprinids, except possibly for bleak *A. alburnus* (Baturo 1978).

The final hosts of *B. polymorphus* are predatory fish that had consumed fish infected with metacercariae. European records include northern pike (*Esox lucius*), Eurasian perch (*Perca fluviatilis*), zander (*Stizostedion lucioperca*), brown bullhead (*Ictalurus nebulosus*), burbot (*Lota lota*), and Wels catfish (*Silurus glanis*) (Baturo 1978; de Kinkelin et al. 1968b; Kvach and Mierzejewska 2011). Adult worms are located in the intestines (Dubinin 1952; de Kinkelin et al. 1968b), and prevalence and intensity rates can be high. In Goslawickie Lake (Poland), all 14 zanders sampled were infected and contained a mean of 483 adult parasites, but no evidence of pathological effects (Baturo 1978). The absence of ill effects was also noted during the Seine Basin epizootic event, where zander individuals hosted up to several thousand *B. polymorphus* adults (de Kinkelin et al. 1968b). The presence of fish species that are highly suitable as hosts for adult *B. polymorphus* may be critical for epizootic outbreaks. The explosive development of *B. polymorphus* populations in the Seine Basin during the 1960s was attributed to the recent introduction of zander (de Kinkelin et al. 1968b). Recently, infections by metacercariae of *B. polymorphus* have increased in several water systems in Europe, due to the expansion of both the first intermediate host, *D. polymorpha*, and the second intermediate hosts, gobiid fishes from the Ponto-Caspian region, which are heavily preyed upon by piscivorous fish, an essential condition for the completion of the parasite's life cycle (Kvach and Mierzejewska 2011; Ondračková et al. 2015). Although *D. polymorpha* has been present in the River Morava basin (Czech Republic) for more than 40 years, a marked increase in *B. polymorphus* abundance was observed only after the introduction of the tubenose goby (reviewed in Ondračková et al. 2015). In the Vistula drainage (Poland), the life cycle of *B. polymorphus* includes three non-indigenous organisms: *D. polymorpha*, the source of cercariae; gobiids (*Babka gymnotrachelus* and *Neogobius fluviatilis*), recent invasive fish that could play a more important role in the life cycle than the commonly occurring cyprinids as their small sizes might be favorable for parasite transmission up the food-web; and the last component of the life cycle of *B. polymorphus,* the Chinese sleeper fish (*Perccottus glenii*), which is a new accidental definitive host of this parasite (Kvach and Mierzejewska 2011).

3.2.1.2. Host specificity. Infections of *D. polymorpha* by *B. polymorphus* have been reported frequently (reviewed in Karatayev et al. 2000a; Molloy et al. 1996, 1997; Ondračková et al. 2015; Stunžėnas et al. 2004). It appears that *B. polymorphus* is specific to *D. polymorpha*, as this trematode is usually absent in *D. r. bugensis* sampled from waterbodies with infected *D. polymorpha* populations (Pryanichnikova et al. 2011; Tyutin and Scherbina 2006; Tyutin et al. 2005). According to Tyutin et al. (2013b), replacement of *D. polymorpha* by *D. r. bugensis* in the Upper Volga reservoirs led to a decrease in the parasitic load of *B. polymorphus* on their fish hosts. So far, there is only one record of the infection of *D. r. bugensis* with *B. polymorphus* (Chernogorenko and Boshko 1992).

In Lake Ohrid, *B. polymorphus* was not found in *D. carinata* (Molloy et al. 2010). In the past, *B. polymorphus* was reported from *Anodonta* and *Unio* (Unionidae) (Chernogorenko and Boshko 1992; Combes et al. 1980; Kulczycka 1939; Smirnova and Ibrasheva 1967). The accuracy of the unionid host data is doubtful, however, because the sporocysts and cercariae of *B. polymorphus* are very similar to those of the bucephalid trematode *Rhipidocotyle*. Evidence is accumulating that *B. polymorphus* is a host specific to *Dreissena* and that the "*B. polymorphus*" recorded from unionids were actually *Rhipidocotyle* spp.

(reviewed in Molloy et al. 1997; Petkevičiūtė et al. 2014). Based on a careful examination of cercarial morphology, Baturo (1977) recorded *B. polymorphus* only in *Dreissena* and in the unionid *R. campanula* (=*R. illense*). Gibson et al. (1992) concluded that the bucephalid cercariae with long filamentous furcae (typical of *B. polymorphus*) recorded in a unionid population in Finland are actually *Rhipidocotyle fennica*.

3.2.1.3. Prevalence of infection. Although widely distributed geographically, infection in dreissenid populations is not common, and the prevalence of infection can vary widely. In the most extensive field study conducted to date, very high prevalence rates (up to 73%) were recorded in *D. polymorpha* from southeastern France (Wallet and Lambert 1986). This four-year study also showed seasonal fluctuations: maximum prevalence occurred each year at the warmest water temperatures, with subsequent shedding of cercariae 1–2 months later. Prevalence rates, however, are typically low (0.4%) to moderate (28%) (Aristanov 1986; Baturo 1977; Chernogorenko and Boshko 1992; de Kinkelin et al. 1968b; Karatayev et al. 2002b; Kuperman et al. 1994; Lajtner 2012; Lajtner et al. 2008; Minguez and Giambérini 2012; Molloy et al. 1996; Smirnova and Ibrasheva 1967; Tyutin et al. 2013a).

According to Aristanov (1992), the prevalence of infection varies strongly with mussel size and season of the year. He found a strong increase in the prevalence of infection with *D. polymorpha* length, from 0.7% in mussels 5–10 mm, to 17.9% in mussels 11–16 mm, and to 51% in mussels 17–23 mm. There was also a substantial increase in prevalence from May (4.3%) to July (31.7%), and a decline in October (19.5%). In contrast, no clear seasonal patterns in the prevalence of infection were found by Minguez and Giambérini (2012). In the only record of *B. polymorphus* infection in *D. bugensis*, a prevalence of 6% was reported from Ukraine (Chernogorenko and Boshko 1992).

3.2.2. *Phyllodistomum macrocotyle* (Digenea: Gorgoderidae)

3.2.2.1. Life cycle. Historically, *Phyllodistomum* trematodes found in *D. polymorpha* were referred to as *P. dogeli*, *P. angulatum*, or *P. folium*. Recent molecular evidence (Petkevičiūtė et al. 2015, 2020), however, showed that *P. macrocotyle* is the only valid *Phyllodistomum* species documented, thus, far observed in *D. polymorpha*. Only one other host, a fish, is required for *P. macrocotyle* to complete its life cycle (Figure 5). A free-swimming miracidium which has hatched from an egg is drawn into the mantle cavity of *D. polymorpha* where it penetrates a gill demibranch by peristaltic contractions. Following its transformation into a mother sporocyst, 12–14 daughter sporocysts are produced. Each daughter sporocyst migrates out of the mother sporocyst to another location within the gills, transforms into a parent sporocyst, and gives rise to additional sporocysts which embed themselves elsewhere in the gills (Figure 6). Several such non-

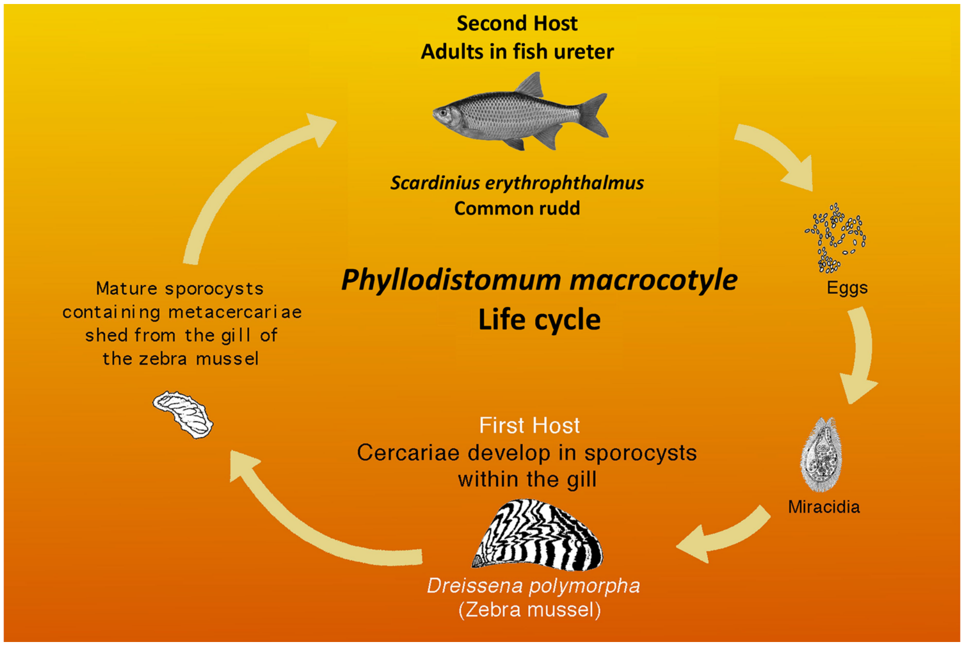

Figure 5. Life cycle of *Phyllodistomum macrocotyle* (adapted from Molloy et al. 1997 with information in Petkevičiūtė et al. 2020).

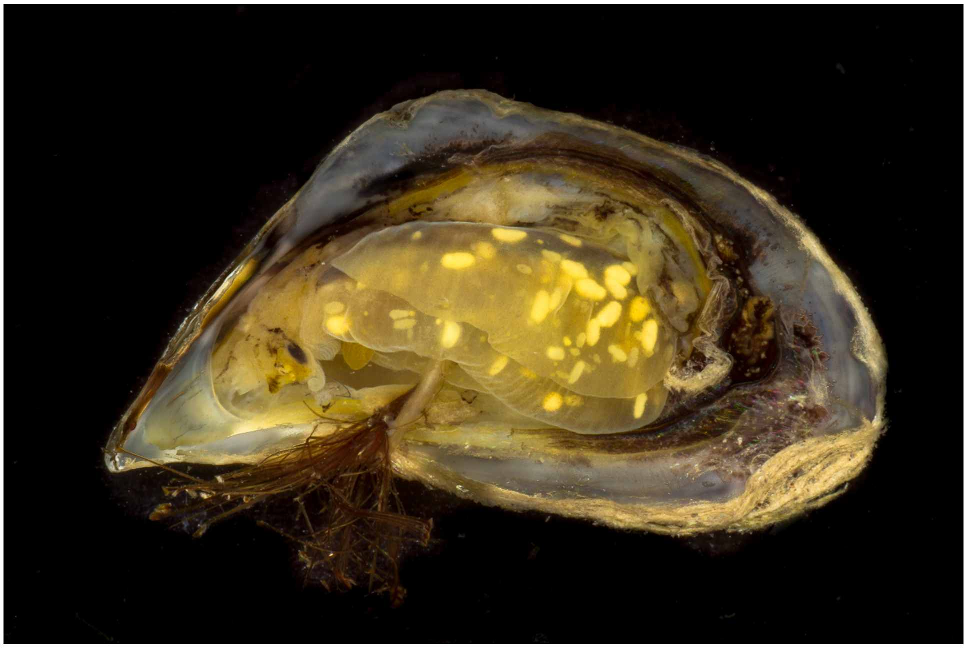

Figure 6. Sporocysts (yellow bodies) within the gills of a *Phyllodistomum* sp. in *Dreissena carinata* from Lake Ohrid, Republic of North Macedonia (Credit: D. P. Molloy).

synchronous multiplications lead to a total of ca. 200–300 yellow sporocysts between the lamellae of the four gill demibranchs (reviewed in Molloy et al. 1997). Mature free-swimming sporocysts, each containing metacercariae, are shed from the gills and float to the water surface where they are consumed by fish. Although many fish species were reported as hosts of adult *P. folium* trematodes that were presumably shed from *D. polymorpha* (Molloy et al. 1997; Pietrock et al. 1999), a recent study (Petkevičiūtė et al. 2020) showed that many of them are *P. folium* (rather than *P. macrocotyle*) shed from other bivalves (Sphaeriidae). According to Petkevičiūtė et al. (2020), *P. macrocotyle* develops into adults in the ureters of fish like rudd (*Scardinius erythrophthalmus*) and ide (*Leuciscus idus*). A detailed description of adult *P. macrocotyle* was recently produced by Petkevičiūtė et al. (2020).

In choosing an intermediate host, *P. macrocotyle* appears quite specific since they have only been reported from *D. polymorpha*. In Rybinsk and Gorky reservoirs (Russia), for example, *P. macrocotyle* parasitizes *D. polymorpha*, but not *D. r. bugensis* (Pryanichnikova et al. 2011; Tyutin et al. 2005). In Lake Ohrid, sporocysts containing metacercariae of *Phyllodistomum* sp. were observed in the gills of 7% of the dissected and 3% of the histologically examined *D. carinata* (Molloy et al. 2010).

No adverse effects on the fish hosts have been reported. *D. polymorpha* infected with *P. macrocotyle*, however, have been reported as having 30% less dry weight than uninfected mussels, presumably due to diminished feeding caused by the presence of sporocysts in the gills. Some toxicants (e.g., Cd and Pb) were also more concentrated in infected mussels, due apparently to the loss of soft tissues (Kraak and Davids 1991). Although reduced gonadal tissue has also been reported (Davids and Kraak 1993), some infected mussels are still capable of producing gametes (Molloy et al. 1996).

3.2.2.2. Prevalence and infection intensity. Infections by *P. macrocotyle* are not common in dreissenid populations, and when present, the prevalence is low to moderate (<1–33%) (Karatayev et al. 2000a; Kraak and Davids 1991; Kuperman et al. 1994; Lyakhnovich et al. 1983; Minguez et al. 2013; Molloy et al. 1996; Peribáñez et al. 2011; Smirnova and Ibrasheva 1967; Tyutin et al. 2013a; Zdun 1965). Water temperature can affect the prevalence of infection in dreissenid populations; in Lukomskoe Lake (Belarus), higher rates occur in areas where waters are artificially heated by the outflow of electricity generation plants (Karatayev 1983; Lyakhnovich et al. 1983). The prevalence of infection also tends to be higher in larger mussels: in the Volga Basin infection is restricted to mussels 23–29 mm in length (Kuperman et al. 1994). In Lukomskoe Lake (Belarus), infection is absent in mussels <8 mm long and increases steadily in mussels up to 28 mm long; intensity also increases,

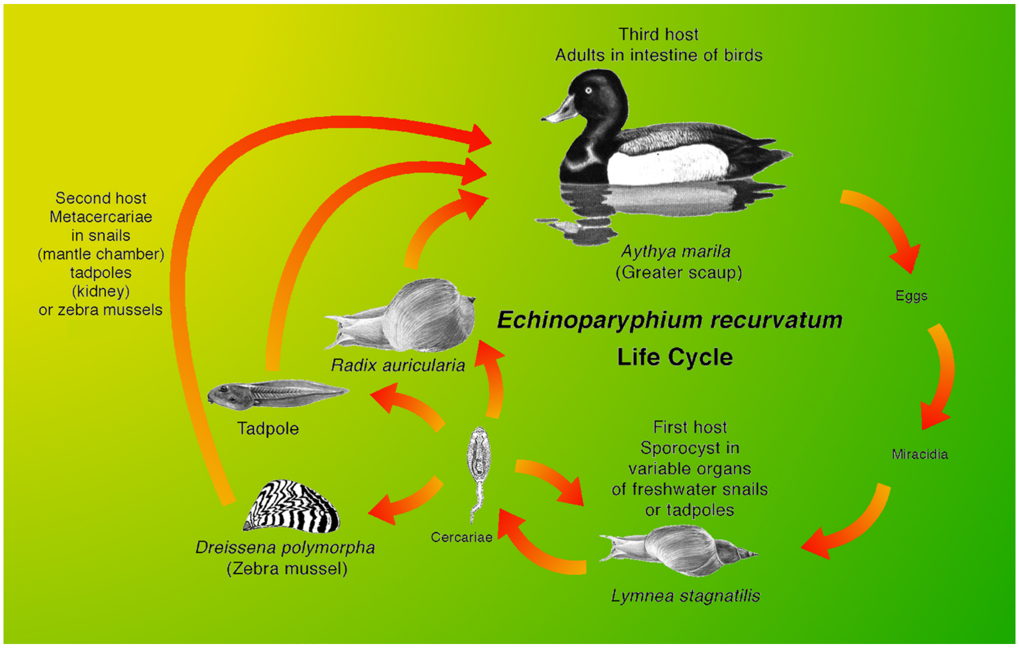

Figure 7. Life cycle of *Echinoparyphium recurvatum* (adapted from Molloy et al. 1997).

from ca. 40 to ca. 200 sporocysts/mussel as mussel length increases from 10 to 26 mm (Lyakhnovich et al. 1983). A maximum of 222 sporocysts were reported from *D. polymorpha* in the Volga Basin (Kuperman et al. 1994). In the Netherlands, infected *D. polymorpha* with all sporocyst developmental stages are present throughout the year (Kraak and Davids 1991).

The trematode species *P. macrocotyle* (including those previously identified as either *P. folium*, *P. dogieli*, or *P. angulatum*) appears to be widely distributed among European *D. polymorpha* populations (Table 10).

3.2.3. Echinoparyphium recurvatum and related species (Digenea: Echinostomatidae)

3.2.3.1. Life cycle. Three species of echinostomatids were reported from dreissenids, including *Echinoparyphium recurvatum* (Ginezinskaja 1959; Kochnev 1977; Lajtner 2012; Mastitsky and Veres 2010; Molloy et al. 1997; Pryanichnikova et al. 2011), *E. echinatoides* (Chernogorenko and Boshko 1992; Molloy et al. 1997; Pryanichnikova et al. 2011; Tyutin et al. 2013a), and *Echinostoma paraulum* (Kochnev 1977; Molloy et al. 1997). Identification of the echinostomatid species found in *Dreissena* is problematic due to the morphological similarity of *E. recurvatum* with species from the *Echinostoma revolution* complex and usually requires additional identification approaches, such as enzymatic and molecular techniques (Le et al. 2020; Saijuntha et al. 2011a, 2011b; Tkach et al. 2016). Therefore, in most publications these trematodes are not identified at the species level (e.g., Karatayev et al. 2000a, 2012; Minguez and Giambérini 2012; Yuryshynets 1999, 2019). Rearing of metacercariae to the adult stage is sometimes used for their identification. Using this technique, infected dreissenids in Russia were fed to ducklings, and the adult trematodes identified as *E. recurvatum* and *Echinostoma paraulum* (Kochnev 1977).

Three hosts are required for the completion of the life cycle of *E. recurvatum* (reviewed in Molloy et al. 1997). In contrast to other trematodes, *Dreissena* is not the first host, but rather one of several possible second intermediate hosts. Its life cycle details have been summarized by McDonald (1969) and Yamaguti (1971, 1975) (Figure 7). Miracidia hatching from eggs invade snails (sometimes tadpoles), where sporocysts and rediae develop. Free-swimming cercariae emerge from infected snails in about 32 days and form a cyst (ca. 120–165 µm in diameter) in a second host—typically an aquatic animal, such as a snail, tadpole, or *Dreissena*. These cysts containing metacercariae are double-walled, transparent, spherical, and enclosed in a very thin sheet of host connective tissue.

In dreissenids, cysts containing metacercariae found upon dissection are those loosely attached to the epithelia of either the mantle cavity, gills, or the visceral mass, indicating that many cercariae do not succeed in penetrating the epithelium to become embedded in mussel tissue. Histological examinations, however, demonstrated that some cercariae had successfully encysted internally within the kidney, gonadic tubule, gills, gonads, visceral mass epithelia, and pericardial cavity (Laruelle et al. 2002; Molloy et al. 1997, 2010).

Adults of echinostomatids are parasites of the small intestines of waterfowl (e.g., anatid ducks), and occasionally of mammals, including humans (Saijuntha et al. 2011b). These final hosts become infected by eating animals harboring the encysted metacercariae. Following the rupture of the cyst, the metacercariae mature in 8–22 days within the intestines of the consumer (reviewed in Molloy et al. 1997).

The effect of echinostomatids on *Dreissena* and other intermediate hosts is usually benign (Laruelle et al. 2002; Molloy et al. 1997, 2010). A North American laboratory trial in which *Echinoparyphium* sp. cercariae were successfully transmitted from field-collected *Physa* snails to *D. polymorpha* indicated that no damage to the host's tissues was apparent (Conn and Conn 1995). Infection of amphibian kidneys by metacercariae, however, can result in severe pathologies (Martin and Conn 1990). The trematode *E. recurvatum* is a common and occasionally fatal helminth parasite of North American waterfowl (McDonald 1969; Roscoe and Huffman 1982). Other echinostomatids could also be moderately to highly pathogenic to their definitive hosts (McDonald 1981). Since infection with this species (as well as metacercariae of other unidentified species) has been field documented in *D. polymorpha* and *D. r. bugensis* in the Lower Great Lakes region (Karatayev et al. 2012), a potential increase in echinostomatid infections in North American water birds preying on dreissenids is of concern.

3.2.3.2. Geographical distribution. In Europe, metacercariae of *E. recurvatum* were reported from *D. polymorpha* from Russia, Belarus, and Croatia; *E. echinatoides* from Ukraine and Russia, and *E. paraulum* from Russia (Table 10). In addition, unidentified metacercariae of Echinostomatidae were reported from Ukraine, France, Belarus, Denmark, Germany, Greece, Italy, the Netherlands, and the United States (Table 10). Echinostomatids were also reported from *D. r. bugensis* in Russia, Ukraine, and United States, as well as from *D. carinata* in the Republic of North Macedonia (Table 10).

3.2.3.3. Prevalence and infection intensity. Echinostomatid (*E. recurvatum, E. echinatoides*) prevalence of infection in *D. polymorpha* is usually low, from <1 to 4.7% (Chernogorenko and Boshko 1992; Ginezinskaja 1959; Pryanichnikova et al. 2011; Tyutin et al. 2013a). For unspecified Echinostomatidae species prevalence of infection has been reported as low (1–5%, Minguez and Giambérini 2012), moderate (0.3–28.5%, Karatayev et al. 2000a), and high (up to 68.9%) (Karatayev et al. 2012; Mastitsky and Vezhnovets 2002). In Lake Naroch (Belarus), the prevalence and intensity of infection for *E. recurvatum* in *D. polymorpha* varies with depth, with peak values at 2 m, as well as seasonally, being much higher in October (prevalence: 36.5%; intensity: 6.1 ± 1.2 metacercariae/mussel) than in May (prevalence: 10.3%; intensity: 2.7 ± 0.6 metacercariae/mussel), but occasionally the maximum prevalence reaches 100% with the infection intensity up to 190 metacercaria/mussel (Mastitsky and Veres 2010).

In Russia, the prevalence of infection of *D. r. bugensis* with *E. recurvatum* was 0.5%, and 2.1% with *E. echinatoides* (Pryanichnikova et al. 2011). In the Dnieper River (Ukraine) in 1996, the average prevalence of infection in *D. polymorpha* (14.8 ± 5.5%) was similar to that in *D. r. bugensis* (16.3 ± 7.9%) (authors' unpublished data). In contrast, in Oneida Lake (USA) the echinostomatid prevalence of infection in *D. polymorpha* was substantially higher (63.6%) than in *D. r. bugensis* (24.2%) (Karatayev et al. 2012). In *D. carinata* from Lake Ohrid cysts containing metacercariae of echinostomatid trematodes were observed in 47% of the dissected mussels (Molloy et al. 2010).

Prevalence of echinostomatid infection in *D. polymorpha* in a cooling water reservoir (Russia) correlated positively with temperatures within a waterbody; although unheated zones lacked infection, waters of 12.3, 16.4, and 19.0 °C had, respectively, 3.7, 7.8, and 8.5% infection (Kochnev 1977).

3.2.4. Aspidogastrea

3.2.4.1. Life cycle. In Europe, two *Aspidogaster* species are known from *D. polymorpha*, including *Aspidogaster limacoides* (Kuperman et al. 1994; Molloy et al. 1996; Nagibina and Timofeeva 1971; Popova and Biochino 2001; Tyutin et al. 2013a) and *A. conchicola* (Chernogorenko and Boshko 1992; Kulczycka 1939). There are also records of *A. limacoides* from *D. r. bugensis* (Popova and Biochino 2001). It should be mentioned that *A. conchicola* is the only European dreissenid parasite also native to North America, where it has been observed in *D. polymorpha* (Toews et al. 1993). Like other trematode parasites of *Dreissena*, these worms are quite small (the maximum size of *A. limacoides* is 1.3 × 0.9 mm) (Kuperman et al. 1994). Their shape is quite distinctive, with an oval, muscular, attachment disk on their ventral surface. In bivalve hosts, *Aspidogaster* spp. are typically found in the pericardial and renal cavities, where they feed on blood cells and hemolymph (Bakker and Davids 1973). In *D. polymorpha*, *A. limacoides* has been reported in the gonads, the pericardial cavity, and on the outer epithelium of the visceral mass (Kuperman et al. 1994; Molloy et al. 1996). Records of the encapsulation of this trematode in connective tissue within the digestive gland of *D. polymorpha* represents the first report of a host defense reaction to an aspidogastrid infection in zebra mussels (Laruelle et al. 2002).

Only a single host is needed for *Aspidogaster* spp. to complete their life cycle since eggs containing larvae infect molluscs and give rise to adult worms (Rohde 1994). In addition to *Dreissena*, *A. limacoides* has been recorded from other bivalves including Unionidae, Sphaeriidae, *Cardium*, and *Adacna* (Bakker and Davids 1973; Brian and Aldridge 2021; Nagibina and Timofeeva 1971; Pauley and Becker 1968). Vertebrates, including fish, may also become hosts by ingesting infected molluscs (Evlanov 1990; Kuperman et al. 1994; Nagibina and Timofeeva 1971; Roitman et al. 1981; Zhokhov and Kasyanov 1995; Zhokhov 2001).

3.2.4.2. Effect of infection.

The species *A. conchicola* feeds on blood cells and hemolymph (Gentner 1971). According to Huehner et al. (1989), *A. conchicola* graze on the epithelium of the freshwater mussel *Anodonta grandis* using its ventral sucker disk to disrupt the host's tissues. In *D. polymorpha,* aspidogastrids were observed to induce hemocyte hemorrhage, suggesting that blood cells may be at least part of its diet (Laruelle et al. 2002). Bakker and Davids (1973) observed no visible damage to the freshwater lamellibranchs *Unio* and *Anodonta* experimentally infected with *A. conchicola*. In contrast, Michelson (1970) examining snails infected with *A. conchicola*, noted pathological changes at the cellular level. Renal metaplasia was observed in *Anodonta* spp. (Unionidae) which were heavily infected with *A. conchicola*, but this did not represent a severe pathological condition (Pauley and Becker 1968).

The colonization of Rybinsk Reservoir by *D. polymorpha* was followed by the introduction of *A. limacoides* (discovered in 1980, Roitman et al. 1981), which infect many cyprinid fish and became the most common parasite of roach. The switch in roach to feeding on *D. polymorpha* led to a dramatic increase in its infection intensity with *A. limacoides* (Zhokhov and Kasyanov 1995; Zhokhov 2001).

3.2.4.3. Prevalence and infection intensity.

Prevalence and infection intensity in *D. polymorpha* with *A. limacoides* is always low: 0.1–7.6% (Kuperman et al. 1994; Nagibina and Timofeeva 1971; Pryanichnikova et al. 2011; Tyutin and Scherbina 2006; Tyutin et al. 2013a; Zhokhov 2001). For *A. conchicola* the values for *D. polymorpha* are similar: 0.2% (Chernogorenko and Boshko 1992), as well as those for the unidentified *Aspidogaster*: 2.7% with ≤2 worms/host (Toews et al. 1993).

3.2.4.4. Geographical distribution.

The species *A. limacoides* has been reported from *D. polymorpha* in Russia and Croatia, and *A. conchicola* from Poland, Ukraine, and North America (Table 10). In addition, *A. limacoides* has also been reported in *D. r. bugensis* in Russia (Popova and Biochino 2001). Unidentified *Aspidogaster* species were reported in *D. polymorpha* from Belarus (Karatayev et al. 2000a), France (Minguez et al. 2011), and the Netherlands (Molloy et al. unpublished data) (Table 10).

3.2.5. Other digenetic trematodes

Other digenetic trematodes were briefly mentioned in Molloy et al. (1997) as having been reported from dreissenids, including representatives of two families (Brachylaemidae and Sanguinicolidae) from Europe and one from North America (Plagiorchiidae). In dreissenids, however, these three families rarely have been observed (Molloy et al. 1997).

According to Chernogorenko (personal communication in Molloy et al. 1997), *Leucochloridiomorpha constantiae* (Digenea: Brachylaemidae) was found in dreissenids from the Dnieper Delta and Dnieper-Bug Liman (Ukraine). Their cysts (≤1 mm in diameter) contained freely moving, relatively small metacercariae. The intensity of infection ranged from 1 to 15 cysts per mussel, with a prevalence of ca. 35%. Chernogorenko and Boshko (1992) reported a *Leucochloridiomorpha* sp. in 6% of the *D. polymorpha* sampled in the Dniester River (Ukraine).

Plagiorchiid (Digenea) metacercariae were observed in 2.9% of *D. polymorpha* at Port Colborne on Lake Erie (Toews et al. 1993). The Plagiorchiidae develop into adults in the intestines, or occasionally the bile duct/gall bladder, of vertebrates, especially birds and mammals (Yamaguti 1971).

Metacercariae of Psilostomatidae (Digenea), tentatively identified as *Sphaeridiotrema* sp., were found in *D. r. bugensis* from Lake Oneida (New York, NY, USA). The prevalence of infection in mussels with these trematodes was 3%, and the infection intensity was 2 metacercariae/mussel (Karatayev et al. 2012). In

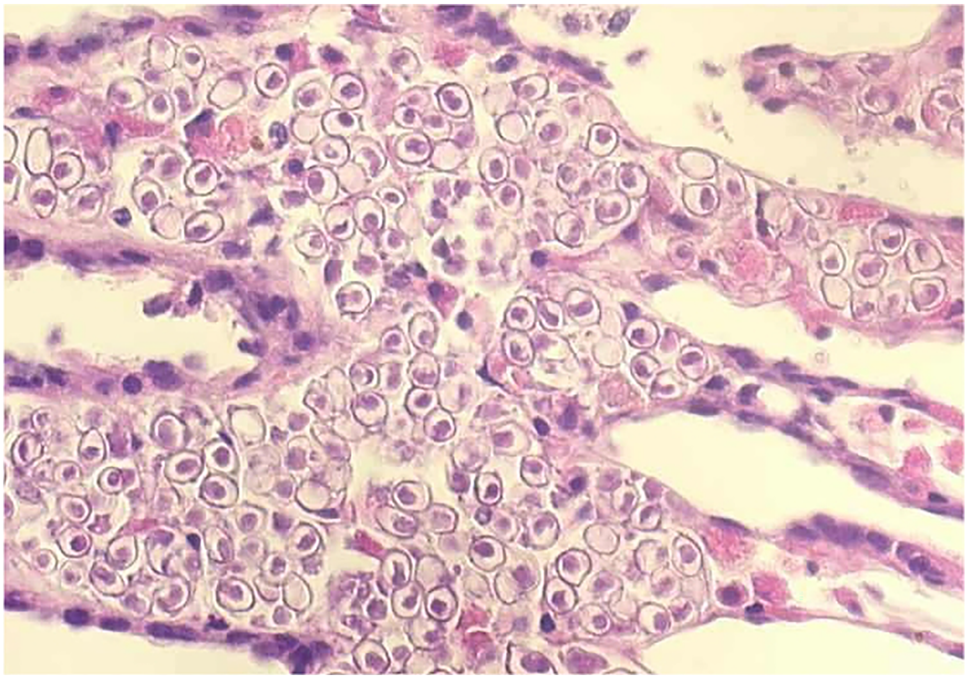

Figure 8. Histological section of advanced infection with the haplosporidian *Haplosporidium raabei* in gill of *Dreissena polymorpha* (adapted from Molloy et al. 2012).

addition, in Lake Erie Karatayev et al. (2012) reported frequent infections of dreissenids with large and small unidentified trematode metacercariae. The prevalence of infection with large metacercariae in *D. polymorpha* varied from 25 to 70% and in *D. r. bugensis* from 6.7 to 100%. Prevalence of infection with small metacercariae ranged from 4.5 to 80%, and from 60 to 90% in *D. polymorpha* and *D. r. bugensis*, respectively.

3.3. Other parasites

3.3.1. Haplosporidium raabei (Haplosporidia: Haplosporidiidae)

3.3.1.1. Life cycle. Haplosporidians are spore-forming, endoparasitic protists that are well documented as pathogens of marine invertebrates, especially of commercially important bivalves (Burreson and Ford 2004; Ford et al. 2018; Lauckner 1983; Sparks 1985). For example, *Haplosporidium nelsoni*, responsible for the MSX disease, has devastated oyster populations of the Delaware and Chesapeake Bays and other regions of the eastern United States coast (Burreson and Ford 2004; Ford and Tripp 1996; Ford et al. 2018; Haskin and Andrews 1988). Reports of haplosporidian infections in freshwater invertebrates, however, are rare (Burreson and Ford 2004), and the first case of a haplosporidian in *D. polymorpha* was reported from the Netherlands (Bowmer and van der Meer 1991; de Kock and Bowmer 1993). In 1988 Bowmer and van der Meer (1991) observed a putatively lethal infection in the blood system and all key organs of *D. polymorpha*. Based on genetic sequencing, morphology, and host, this protist was described as a new species—*Haplosporidium raabei*, representing the first haplosporidian species from a freshwater bivalve (Molloy et al. 2012, Figure 8).

In *D. polymorpha,* infections with multinucleate plasmodia and sporocysts were observed systemically in connective tissues and organs, such as gills, gonads, and digestive gland often exhibited the most severe infections, but there was no evidence of haplosporidian cells in epithelial or muscle tissue (Molloy et al. 2012). Plasmodia, sporocysts, and mature spores were observed in spring through fall with no evidence of seasonality. Plasmodial development and sporogenesis within individual mussels are relatively synchronous. Multinucleate plasmodia are irregular in shape with a maximum dimension of 73 µm. Sporocysts are generally spherical and typically ≤40 µm in diameter. Mussels containing spores liberated from sporocysts or nearing completion of sporogenesis were observed in the Baggersee Reeserward, Meuse, and Moselle rivers, with mean spore dimensions ($L \times W$) of 8.9 × 6.5, 7.5 × 5.2, and 8.0 × 5.4 µm, respectively (Molloy et al. 2012).

3.3.1.2. Effect of infection. Hemocyte infiltration is associated with infection, and plasmodia were observed being phagocytosed by hemocytes (Molloy et al. 2012). Sporogenesis is accompanied by degeneration of host tissues, but no major signs of disease are evident during dissection. Histological examinations revealed that gills can be very swollen in advanced infections. Extensive connective tissue lysis is a common consequence of advanced infection by *H. raabei* as sporogenesis is accompanied by systemic tissue degeneration. When sporogenesis is completed, mature spores typically appear densely packed throughout much of the host's connective tissues, with their subsequent liberation into the environment dependent on host death. Bowmer and van der Meer (1991) observed that advanced infection of *D. polymorpha* can be severe, completely destroying the gonads, and appears to be lethal since there is little to no functional tissue left in the digestive gland. According to Molloy et al. (2012), gross signs of disease were not observed in infected mussels and their dissected tissues appear normal. Only two epizootics have been documented in *D. polymorpha*: in 1990 Bowmer and van der Meer (1991) reported infection in 26% of the mussels in Lake Volkerak, and in 1992 Molloy et al. (2012) described an infection prevalence of 20% in the Hollands Diep. Both waterbodies, located in the Netherlands, are part of the freshwater confluence of the Meuse and Rhine basins.

3.3.1.3. Geographical distribution and prevalence. Although *D. polymorpha* populations from 11 countries across Europe were examined by histological analyses, *H. raabei* infections were detected only in the Rhine and Meuse river basins in France, Germany, and The Netherlands. It is likely that the spread of *H. raabei* between these two river basins was facilitated by the freshwater estuary they share in the Netherlands. Moreover, infection outbursts were only intermittently observed in this region during the 17-year sampling period, and when *H. raabei* was detected, the prevalence of infection was typically <4%, with a maximum of 20% (Molloy et al. 2012).

3.3.2. Bacteria

3.3.2.1. General description and biology. Molloy et al. (2001) characterized intracytoplasmic infections by prokaryote microorganisms in a *Dreissena* sp. from Lake Volvi (northeastern Greece). Light microscope observations of stained tissues revealed basophilic, cytoplasmic inclusions in 87.5% of the mussels sectioned. Inclusions in epithelial cells and connective tissues were noted in 34.4 and 71.9% of the specimens, respectively, with five mussels (15.6%) having both tissue types infected. Epithelial cell infections were observed in histological sections only in digestive gland tubules and ducts; within the tubules, inclusions were present more often in secretory than in digestive cells. Connective tissue infections, however, were systemic; among the 32 mussels sectioned, inclusions were found in the gills (65.6%), foot (12.5%), mantle (9.4%), labial palps (6.3%), digestive gland (6.3%), stomach (6.3%), and gonads (3.1%). In the gills, cytoplasmic inclusions were prominent enough to be visible in 17.0% of the 247 mussels dissected. Ultrastructurally, prokaryote cells in gill connective tissues were characteristic of Chlamydiales-like organisms, with each intracytoplasmic inclusion containing a loosely packed mixture of elementary, reticulate, intermediate bodies, and blebs. Prokaryotes in the epithelial cells of the digestive gland contained only one of the four morphological cell types and were considered Rickettsiales-like organisms (RLO) (Minguez and Giambérini 2012; Minguez et al. 2012, 2013). Hexagonal, virus-like particles were present in the cytoplasm of the largest of these prokaryotes.

3.3.2.2. Effect of infection. Although host stress was evident from localized cell necrosis and dense hemocyte infiltration, overall infection with RLO was fairly benign, with no major adverse impacts on the body condition of the mussels analyzed. A possible negative effect was the partial constriction of gill water tubes, but at the infection intensity observed (typical range 1–7 inclusion bodies per section), significant interference with respiration and other metabolic functions of the gills was considered highly unlikely. Host response was observed in *D. carinata* tissues only in intense infections. In such cases, connective tissues of the digestive gland, the mantle, and the gills exhibited cell necrosis. These connective tissues were infiltrated with numerous hemocytes, but only in regions containing relatively numerous inclusions (Molloy et al. 2001).

3.3.2.3. Geographical distribution and prevalence. Intracytoplasmic infections by prokaryote microorganisms in *Dreissena* have been reported in Greece (Molloy et al. 2001), France (Minguez and Giambérini 2012; Minguez et al. 2012, 2013), and United States (Minguez et al. 2013) (Table 10). The prevalence of infection varied from low to moderate: 9–22% (Minguez and Giambérini 2012; Molloy et al. 2001, 2010).

3.3.3. Nematodes

3.3.3.1. General description and biology. Among *Dreissena* endosymbionts, nematodes are likely the most common (Tables 10 and 11). They have been reported from all dreissenid species examined: *D. polymorpha* (Karatayev et al. 2000a, 2003a; Kuperman et al. 1994; Mastitsky and Gagarin 2004; Mastitsky et al. 2008), *D. r. bugensis* (Pryanichnikova et al. 2011; Reid et al. 2012), and *D. carinata* (Molloy et al. 2010). Evidence to date suggests that they are likely free-living species, without any obligate association with dreissenids (Karatayev et al. 2003a; Mastitsky and Gagarin 2004; Mastitsky et al. 2008; Molloy et al. 1997; Reid et al. 2012). Free-living nematodes probably enter the mantle cavity unintentionally by crawling along the byssal threads (Karatayev et al. 2003a; Molloy et al. 1997) or carried with water currents through the inhalant siphon (Mastitsky and Gagarin 2004). Nematodes have been frequently reported in the mantle cavity of *Dreissena* populations both in Europe (Karatayev et al. 2000a, 2003a; Kuperman et al. 1994; Mastitsky and Gagarin 2004; Mastitsky et al. 2008; Pryanichnikova et al. 2011) and in North America (Conn et al. 1994; Reid et al. 2012; Toews et al. 1993).

As specific identification of this group is challenging, their identifications vary greatly, from species (Karatayev et al. 2003a; Mastitsky and Gagarin 2004; Mastitsky et al. 2008; Reid et al. 2012) to phylum (Karatayev et al. 2000a; Pryanichnikova et al. 2011). Currently, 25 species and genera of nematodes have been reported from *D. polymorpha* from Europe and 10 taxa from *D. r. bugensis* species in North America. In Europe, the highest diversity (22 species) was reported by Mastitsky and Gagarin (2004) in *D. polymorpha* from Narochanskie Lakes (Belarus). In North America, 10 species and higher taxa of nematodes were reported in *D. r. bugensis* from the Colorado River Aqueduct (Copper Basin Reservoir and Lake Skinner, USA) (Reid et al. 2012). All these nematodes are free-living organisms common in benthic and/or periphytic freshwater communities. It is interesting to notice that in all studies that reported nematodes in *Dreissena*, the most common species was *Chromadorina bioculata*. The relative abundance of this species among the nematodes found in the mantle cavity of *D. polymorpha* is 24–90% in Narochanskie Lakes (Belarus) (Mastitsky and Gagarin 2004), 82% in Drozdy Reservoir (Belarus) (Karatayev et al. 2003a), and 96.9% in Lake Erken (Sweden) (Mastitsky et al. 2008). Surprisingly, *C. bioculata* is also the most common species in the mantle cavity of *D. r. bugensis* from the Colorado River Aqueduct (Reid et al. 2012). These data suggest that, in contrast to other nematode species reported from dreissenids, *C. bioculata* may have a rather high affinity with the mussels (Mastitsky et al. 2008). Further investigations are required to understand the nature of *C. bioculata/Dreissena* relationships.

3.3.3.2. Geographical distribution. In European populations of *D. polymorpha* nematodes were reported from 15 countries (Table 10). In addition to *D. polymorpha*, nematodes were reported from *D. r. bugensis* in Russia (Pryanichnikova et al. 2011; Tyutin et al. 2013a) and Ukraine (Yuryshynets 2019), and from *D. carinata* in the Republic of North Macedonia (Molloy et al. 2010). In North America, nematodes were reported from both *D. polymorpha* (Conn et al. 1994; Toews et al. 1993) and *D. r. bugensis* (Reid et al. 2012).

3.3.3.3. Prevalence and infection intensity. Nematodes are among the most common organisms found within the mantle cavity of dreissenids. Reported prevalence usually ranges from moderate to high: 10–15% (Chuševė et al. 2012), 10–50% (Burlakova et al. 2006a), 40% (Conn et al. 1994), 52% (Karatayev et al. 2000a), 50–72% (Mastitsky and Gagarin 2004), and 17–82% (Mastitsky et al. 2008). In contrast to prevalence, the number of worms per host is almost always low, from 1 to 4.2 worms/mussel (Burlakova et al. 2006a; Chuševė et al. 2012; Conn et al. 1994; Karatayev et al. 2000a; Mastitsky and Gagarin 2004; Mastitsky et al. 2008). Similar values of prevalence (31%) and infection intensity (1–3 worms/mussel) were reported for *D. carinata* from the Republic of North Macedonia (Molloy et al. 2010), although higher prevalence (85%), but low intensities (5.3 worms/mussels) were reported in *D. r. bugensis* from North America (Reid et al. 2012).

There is only one report of seasonal dynamics of the prevalence and intensity of nematode infection in *D. polymorpha* (Karatayev et al. 2003a). In this two-year study in Svisloch River (Belarus) the mean prevalence ranged from 6.7 to 76.7%, and mean intensity from 1 to 3.7 worms/mussel. This survey found a significant negative correlation between temperature and both infection prevalence and intensity, with the highest numbers of nematodes in mussels in January–February. This suggests that during the winter either more nematodes may actively use zebra mussels for shelter or that free-living nematode population densities are simply higher in the benthos during winter (Karatayev et al. 2003a).

3.3.4. Oligochaetes

Oligochaetes (Annelida: Oligochaeta) have been frequently reported from the mantle cavities of freshwater bivalves in North America, but the nature of this relationship remains unclear (Conn et al. 1994, 1996; Curry 1979; Karatayev et al. 2000a; Klemm 1976; Sickel and Lyles 1981). In many instances, these oligochaetes are likely free-living species that have unintentionally entered the mantle cavity and could be considered as commensals (reviewed in Molloy et al. 1997). Among oligochaetes *Chaetogaster limnaei*, however, is one of the very few species that has likely evolved in association with gastropods and bivalves. According to Conn et al. (1994, 1996), in dreissenids the vast majority of *C. limnaei* inhabit the mantle cavity of their hosts, frequently occurring between the gill lamellae with only slight evidence of pathologic effects. Only once a *C. limnaei* was found inside the ovary of a mussel, where it had caused appreciable damage by feeding on the host's oocytes and gonadal tissues (Conn et al. 1994, 1996). The relationship could actually be in part mutualistic, since *C. limnaei* was reported to eat miracidia in snails in Europe, thus, possibly reducing trematode infections (Conn et al. 1996).

In Europe, Chernogorenko and Boshko (1992) reported *C. limnaei* in 8% of *D. polymorpha* from the Dniester River/Liman (Ukraine). Karatayev et al. (2000a) found *C. limnaei* in 11 of 17 *D. polymorpha* populations in Belarus with a prevalence and intensity ranging from 1.4 to 11.9%, and 1 to 1.5 worms/mussel, respectively. In addition, *C. limnaei* was also recorded in *D. polymorpha* from Germany (Molloy et al. unpublished data). Kuperman et al. (1994) observed the free-living species *Psammoryctides barbatus* and *P. moldavensis* in *D. polymorpha* in the Volga Basin (Russia). Unidentified oligochaetes were reported from European populations of *D. polymorpha* from Belarus (Karatayev et al. 2000a), Ireland (Burlakova et al. 2006a), Denmark, and Ukraine (Molloy et al. unpublished data, Table 10). In addition, there are two reports of unidentified oligochaetes from European populations of *D. r. bugensis* in Russia (Pryanichnikova et al. 2011; Tyutin et al. 2013a) and Ukraine (Yuryshynets 2019). According to Pryanichnikova et al. (2011), the prevalence of infection in *D. r. bugensis* with oligochaetes is 0.53%.

In North America *C. limnaei* was reported in both *Dreissena* species from the St. Lawrence River (USA) (Conn et al. 1996). The prevalence of infection ranged from 0 to 80%, depending on the collection site and date. The mean prevalence and intensity of infection in *D. r. bugensis* were 27.4% and 2.7 worms/mussel, and in *D. polymorpha*—25.5% and 2.9 worms/mussel. The mean and maximum intensity of infection were ca. 3 and 18 worms, respectively, and peaks of prevalence and intensity occurred during July and August (Conn et al. 1996).

3.3.5. Leeches

At least a dozen leech species have evolved in close association with Unionidae since the Miocene (Bolotov et al. 2019). In contrast, there are no reports of any obligate associations between *Dreissena* and leeches. In fact, only two studies, both from Europe, reported leeches from dreissenids (Karatayev et al. 2000a; Kuperman et al. 1994). Two species *Caspiobdella fadejewi* and *Helobdella stagnalis* (Annelida: Hirudinea) were found associated with "internal organs" of *D. polymorpha* in the Volga Basin, Russia (Kuperman et al. 1994). Leeches *Erpobdella octoculata* and *H. stagnalis* were observed in the mantle cavity of molluscs from one and three, respectively, of a total of 17 *D. polymorpha* populations sampled in Belarus (Karatayev et al. 2000a). The prevalence was <1%, and typically only one leech per infested mussel was present. Young specimens of *Erpobdella* sp. and *Helobdella* sp. were reported from *D. r. bugensis* in Russia (Tyutin et al. 2013a). Since both these leech species are free-living predators, they were considered to have inadvertently entered the mantle cavity.

3.3.6. Chironomids

Chironomid larvae (Insecta: Chironomidae) have been observed in the mantle cavities of *Dreissena* both in Europe and in North America (Conn et al. 1994; Kuperman et al. 1994; Mastitsky and Samoilenko 2005; Ricciardi 1994, 1994). In Europe, *Chironomus bathophilus* was observed in *D. polymorpha* in the Volga Basin (Kuperman et al. 1994), and 14 species and higher taxa were reported from the mantle cavity of *D. polymorpha* from seven Belarussian lakes with *Limnochironomus* gr. *nervosus* being the most common (Table 10) (Mastitsky and Samoilenko 2005). All chironomids reported from dreissenids are free-living species commonly found in the benthos (Mastitsky and Samoilenko 2005). In addition, unidentified chironomids were recorded from *D. polymorpha* populations in Belarus (Karatayev et al. 2000a), Ireland (Burlakova et al. 2006a), Sweden (Mastitsky et al. 2008), Russia (Pryanichnikova et al. 2011), Czech Republic, Denmark, Germany, Greece, and Ukraine (Molloy et al. unpublished data, Table 10). Chironomid larvae were also reported from *D. r. bugensis* in Ukraine (Yuryshynets 2019).

In North America, *Paratanytarsus* sp. was reported from both *Dreissena* species in the St. Lawrence River (New York State and Quebec Province) (Conn et al. 1994; Ricciardi 1994). Up to 38% of *D. polymorpha* and 10% of *D. r. bugensis* hosted larvae of *Paratanytarsus* sp. Dreissenids are typically colonized by either the third or the fourth instar larvae and are more common in larger mussels. Chironomid larvae *Paratanytarsus* sp. inhabits the mantle cavity of dreissenid mussels around the gills, gonads, and siphonal tissue, and are most frequently found near the inhalant siphon. They were never observed feeding on dreissenid tissues, and no tissue damage was ever detected (Ricciardi 1994), which indicates that these associations are commensal (Mastitsky and Samoilenko 2005; Ricciardi 1994). The chironomid larvae probably benefit from the association since the mussels might provide refuge from predation, as well as a source of oxygenated water and suspended food particles (Mastitsky and Samoilenko 2005; Ricciardi 1994).

3.3.7. Mites

In Ukraine, *Unionicola* sp. (Arachnida: Hydrobatidae) was observed in 3.2% of the specimens of *D. polymorpha* examined (Chernogorenko and Boshko 1992). At several locations in the Volga Basin (Russia), *Unionicola* eggs were present on the gills of both *D. polymorpha* (Kuperman et al. 1994) and *D. r. bugensis* (Tyutin et al. 2013a). In Belarus, unidentified hydracarinid mites were recorded from 6 of 17 *D. polymorpha* populations; the prevalence ranged from 0.4 to 1.8%, with typically one mite per host (Karatayev et al. 2000a). A single unidentified aquatic mite was found in the mantle cavity of a *D. polymorpha* from Sweden (Mastitsky et al. 2008). In the St. Lawrence River, one *D. polymorpha* had one mite in its mantle cavity, but many mussels had hydracarinid egg masses glued to their shells (Conn et al. 1994). Adult *Unionicola* spp. are known to be common parasites of freshwater mussels, living on the gills, mantle, and foot of their hosts and using these tissues as sites of oviposition (Edwards and Vidrine 2006). Therefore, in *Dreissena*, *Unionicola* are likely parasitic (rather than commensal) as well, but their impact on host populations is probably negligible.

4. Ecological competitors

Dreissenids are sessile bivalves feeding on seston from the water column, and therefore potentially vulnerable to competitors for substrate and/or for food suspended in the water-column. Although both *D. polymorpha* and *D. r. bugensis* belong to the same genus and have similar life history characteristics, they are not identical and have different invasion dynamics and distribution patterns within waterbodies (Karatayev and Burlakova 2022a, 2022b; Karatayev et al. 2015, 2021a; Nalepa et al. 2010). In shallow lakes, both species can colonize the entire bottom, if appropriate substrate for attachment is available, but in deep lakes, *D. polymorpha* is largely limited to the shallow well-mixed warm littoral zone, while *D. r. bugensis*, in addition to the littoral fringe, can also colonize the entire profundal zone. In nearshore environments, attachment to a suitable substrate is essential for both dreissenids to withstand wave activity, but here they can be outcompeted by other organisms, including sponges, amphipods, algae, bryozoans, hydrozoan coelenterates, and other bivalves (reviewed in Balogh et al. 2008, 2018; Jantz and Schöll 1998; Lauer and Spacie 2000, 2004; Molloy et al. 1997) (Table 12). In contrast to the nearshore, in deep, cold, and calm offshore environments, where wave action does not reach the bottom, *D. r. bugensis* do not require hard substrates for attachment and can form large aggregations on soft sediments (Karatayev and Burlakova 2022a, 2022b; Karatayev et al. 2021a). Here, the role of the aforementioned competitors for space is negligible, but competition for food resources can be important. In this regard, in dreissenids both intraspecific and interspecific competition can play an extremely important role in affecting their population size and dynamics (reviewed in bij de Vaate et al. 2014; Hetherington et al. 2019; Karatayev and Burlakova 2022a, 2022b; Karatayev et al. 2011a, 2015, 2021a; Strayer et al. 2019).

4.1. Sponges

The ability of sponges (Porifera) to overgrow and kill dreissenids was first reported in Europe by Arndt (1937) for *Ochridaspongia rotunda* in Lake Ohrid, inhabited by *D. carinata*. In Lake Balaton (Hungary) Sebestyén (1937) reported *Spongilla carteri* and *Eunapius* (=*Spongilla*) *fragilis* to overgrow and embed *D. polymorpha's* colonies. Local negative impacts of the sponge *Ephydatia fluviatilis* on *D. polymorpha* were also reported in Poland (Piesik 1983) and in Italy (Lancioni and Gaino 2009) (Table 12).

In the first comprehensive North American (Great Lakes-St. Lawrence River system) investigation, Ricciardi et al. (1995) found that sponges (*E. fragilis*, *Ephydatia muelleri*, and *Spongilla lacustris*) are always successful in overgrowing dreissenids. Overgrowth occurred either by lateral growth from an existing

Table 12. Competitors of *Dreissena* spp. reported from Europe (E) and North America (NA).

Competitor	Conti-nent	*Dreissena* species, location, references
Sponges		
Ochridaspongia rotunda	E	*D. carinata*, Macedonia (Arndt 1937)
Spongilla carteri	E	*D. polymorpha*, Hungary (Sebestyén 1937)
S. lacustris	NA	*D. polymorpha*, Quebec, Ohio (Ricciardi et al. 1995)
	NA	*D. r. bugensis*, Quebec, Ohio (Ricciardi et al. 1995)
Eunapius (=Spongilla) fragilis	E	*D. polymorpha*, Hungary (Sebestyén 1937)
	NA	*D. polymorpha*, Quebec, Ohio (Ricciardi et al. 1995)
	NA	*D. polymorpha*, Indiana (Early and Glonek 1999; Lauer 1997; Lauer and Spacie 2000, 2004)
	NA	*D. r. bugensis*, Quebec, Ohio (Ricciardi et al. 1995)
Ephydatia fluviatilis	E	*D. polymorpha*, Poland (Piesik 1983)
	E	*D. polymorpha*, Italy (Lancioni and Gaino 2009)
Ephydatia muelleri	NA	*D. polymorpha*, Quebec, Ohio (Ricciardi et al. 1995)
	NA	*D. polymorpha*, Indiana (Lauer 1997; Lauer and Spacie 2000)
	NA	*D. r. bugensis*, Quebec, Ohio (Ricciardi et al. 1995)
Bryozoans		
Plumatella repens	E	*D. polymorpha*, Poland (Piesik 1983)
Pectinatella magnifica	NA	*D. polymorpha*, New York (Conn and Conn 1993)
Lophopodella carteri	NA	*D. polymorpha*, Indiana (Lauer et al. 1999)
Other competitors		
Chlorophytes		
Cladophora sp.	E	*D. polymorpha*, Hungary (Sebestyén 1937)
	E	*D. polymorpha*, The Netherlands (Smit et al. 1993)
Crustaceans		
Chelicorophium curvispinum	E	*D. polymorpha*, Hungary (Sebestyén 1937)
	E	*D. polymorpha*, The Netherlands (Paffen et al. 1994; Smit et al. 1993; van den Brink et al. 1993; van der Velde et al. 1994)
		D. polymorpha, Germany (Jantz and Schöll 1998)
Hydrozoans		
Cordylophora caspia	E	*D. polymorpha*, The Netherlands (Smit et al. 1993)
	E	*D. polymorpha*, Poland (Piesik 1983)
Bivalves		
Mytilaster lineatus	E	*D. elata*, Caspian Sea (Karpinsky 2010; Karpinsky et al. 2005; Logvinenko and Starobogatov 1968)
	E	*D. caspia*, Caspian Sea (Karpinsky 2010; Karpinsky et al. 2005; Logvinenko and Starobogatov 1968)
D. r. bugensis	E, NA	*D. polymorpha*, multiple waterbodies in Europe and North America (Balogh et al. 2018; bij de Vaate et al. 2014; Heiler et al. 2013; Hetherington et al. 2019; Karatayev and Burlakova 2022a, 2022b; Karatayev et al. 2011a, 2015, 2021a, 2021b; Noordhuis et al. 2016; Orlova et al. 2004, 2005; Strayer et al. 2019)

nearby sponge colony or by settlement of sponge larvae on the shells. Overgrowth starts as early as in May (at water temperatures ca. 10 °C) and typically declines in late autumn. Lauer (1997) also observed that in the Great Lakes, sponge overgrowth was generally limited to the May to October period, with the most severe fouling from June through August. Ricciardi et al. (1995) observed that adhesion of gemmule (overwintering structures) patches occur in autumn, giving rise to new colonies the following year. Surviving mussels are, thus, subject to annual overgrowth from successive sponge generations, resulting in a slow death, with 50–79% of the sponge-covered mussels dying, respectively, after 1–3 to 4–6 months. No significant differences in mortality rates were observed between small and large mussels, or between *Dreissena* species (*D. polymorpha* and *D.* r. *bugensis*). Because of the adverse effects of siltation on sponge colonies, high growth rates are generally restricted to vertical surfaces. Thus, sponges may control mussel abundance only locally, particularly on vertical surfaces, such as in canals. Ricciardi et al. (1995) concluded that the overall impact of sponges on *Dreissena* populations in the Great Lakes-St. Lawrence River system is negligible due to the high rate of mussel recruitment and the environmental constraints on sponge growth.

The actual causes of mussel death due to sponge overgrowth are likely a combination of factors. Ricciardi et al. (1995) hypothesized that sponge overgrowth blocks the mussel's siphons, seriously impairing mussel feeding and respiration. In overgrowth studies with *Eunapius fragilis*, Early and Glonek (1999) reported that dreissenid adenosine triphosphate (ATP) was depleted suggesting anoxic stress. Lauer and Spacie (2000, 2004) observed that fouled mussels in Lake Michigan suffer significant reductions in both their soft tissue weight and glycogen content, suggesting that in addition to starvation and reduction in energy stores, other processes likely contribute to mortality, including the increased metabolic demand and inhibition of gas exchange or waste excretion.

4.2. Amphipods

Amphipod *Chelicorophium curvispinum* is a small (adult length 2.5–7.0 mm), filter-feeding species that build mud tubes on hard substrates, and therefore can potentially compete for space with dreissenids. Native to the Ponto-Caspian basin, *C. curvispinum* began to expand its range into Europe at the beginning of the twentieth century *via* various river systems and interconnecting canals (Paffen et al. 1994). According to Sebestyén (1937), the establishment of *C. curvispinum* in Lake Balaton (Hungary) was facilitated by the suitable substratum offered by the numerous crevices in dreissenid colonies, and in addition, he observed that dreissenids were sparse where this amphipod's population was dense. Recently, Balogh et al. (2008, 2018) reported that *D. polymorpha* and *C. curvispinum* populations in Lake Balaton, both with a long history of coexistence characterized by competition and intermittent population fluctuations, currently suffer population reductions due to the introduction of another competitor, *D. r. bugensis*.

After having been discovered in 1987 in the River Rhine, in the 1990s *C. curvispinum* underwent a population explosion causing the displacement of *D. polymorpha* from hard substrates in the Lower Rhine (Jantz and Schöll 1998; Smit et al. 1993; van den Brink et al. 1993; van der Velde et al. 1994). Since both *C. curvispinum* and *D. polymorpha* are filter-feeders, competition may have existed for suspended particles, but it was in the battle for attachment sites where *D. polymorpha* appears to have been no match for *C. curvispinum* (reviewed in Molloy et al. 1997). This amphipod typically covers available stones in the Lower Rhine (both breakwaters and riverbanks) with a 1–4 cm thick layer of their mud tubes, thereby smothering dreissenids. Moreover, mussel larvae are unable to settle successfully on these tubes. In some sections of the Dutch Rhine, *C. curvispinum* became the dominant macroinvertebrate species, and densities of dreissenids were dramatically reduced (Paffen et al. 1994). In 2001, however, *C. curvispinum* decreased in numbers, most likely due to top–down regulation caused by the increased predatory pressure of the recent invasion by the Ponto-Caspian amphipod *Dikerogammarus villosus* (van Riel et al. 2006).

4.3. Other competitors for surface

Other competitors with a documented negative impact on *D. polymorpha* include the green alga *Cladophora*, the hydroid *Cordylophora caspia*, and the bryozoans *Plumatella repens*, *Pectinatella magnifica*, and *Lophopodella carteri* (reviewed in Lauer et al. 1999; Molloy et al. 1997). In Lake Balaton, dense colonies of *D. polymorpha* are occasionally entirely smothered by *Cladophora* (Sebestyén 1937). Zebra mussel is also absent from stones covered with *Cladophora* in the Rhine and Meuse rivers (Smit et al. 1993). In the Netherlands, the colonial hydroid *Cordylophora caspia* was observed to compete for substrate with *D. polymorpha* on stones in the Rhine River and in Lake Markermeer (Smit et al. 1993). This species was reported as a substrate competitor along with the bryozoan *Plumatella repens* in an Oder River canal in Poland (Piesik 1983). In the St. Lawrence River (USA), adult dreissenids can be overgrown and killed by the bryozoan *Pectinatella magnifica* (Conn and Conn 1993). In Lake Michigan (USA), colonies of the bryozoan *Lophopodella carteri* on pier posts inhibit the successful settling of mussel larvae, but mussels >10 mm long are not affected by this overgrowth (Lauer et al. 1999).

4.4. Bivalves

4.4.1. Mytilaster lineatus

The marine, byssus-producing bivalve *Mytilaster* (=*Brachyodontes*) *lineatus*, which is widespread in the Mediterranean and Black Sea, was inadvertently introduced into the Caspian Sea in 1919, where it colonized the entire sea, except its less saline northern reaches (reviewed in Karpinsky et al. 2005). By 1934–1938, its biomass rose from 11 to 42% of the overall benthos (up to 7 kg/m^2 in wet weight). New bivalve invaders started competing with the endemic Caspian dreissenids *D. elata* and *D. caspia*, which were still present in 1938, but disappeared by 1955–1957 (Kostianoy and Kosarev 2005) and are now considered extinct (Leroy et al. 2020). According to Karpinsky et al. (2005), the mechanism of *Dreissena* replacement is in the ability of *M. lineatus* to create high biomass and deplete dissolved oxygen to levels intolerable for dreissenids. It should be noticed, however, that *M. lineatus* coexists with *D. rostriformis*. Surveys conducted in 1986–1987 showed that near the Middle Caspian eastern coast, the biomass of *M. lineatus* peaks at depths of 10–25 m, where it exceeds the biomass of the second most abundant species, *D. rostriformis* by a factor of 5–8 (Karpinsky 2010). The fact that the dreissenid is still very abundant indicates that it can coexist with *M. lineatus*, although the competition involved is likely very strong.

4.4.2. *Intraspecific dreissenid competition*

Could *Dreissena* be its own worst enemy? Intraspecific competition in dreissenids can be a significant mortality factor and a major density-dependent, population-regulating mechanism. Population abundance of invasive species often exhibits an invasion cycle characterized by very strong initial growth in abundance and a subsequent marked decline (Karatayev et al. 2015; Simberloff and Gibbons 2004; Strayer et al. 2017). This cyclicity might be due to various factors, including density-dependent changes in the abundance of the invader. For example, when mussels attach to each other and colonies become several centimeters thick, the ones at the bottom may die (Lewandowski 1982). In Uchinskoe Reservoir (Russia), substrate limitation for *D. polymorpha* attachment due to the accumulation of feces and pseudofeces was concluded to be the major reason for the decline in mussel biomass in 1960s (Lvova 1977). Likewise, adults in high-density populations may compete with their planktonic larvae for limited food resources, thus, reducing settling rates and/or survival of postveligers. Strayer et al. (1996) provided evidence that adult dreissenids may outcompete their pelagic larvae for phytoplankton in the Hudson River (USA) and suggested that such food-limited dreissenid populations may be especially frequent in rivers and estuaries, where the ratio of food supply to available substratum is small. Dreissenids are known to reduce their food resources (e.g., seston and chlorophyll) through their feeding and filtering activities (reviewed in Higgins and Vander Zanden 2010; Karatayev et al. 1997, 2002a; Pothoven and Fahnenstiel 2013; Rowe et al. 2015), especially below the thermocline (Karatayev et al. 2018b, 2021a). In the eastern basin of Lake Erie, early in *D. r. bugensis* invasion (before 2006), seston concentrations were similar at the surface and in the near bottom layers, and mean mussel length and recruitment rates were also similar in both zones (Karatayev et al. 2018b). After 2006 however, in the deepest zone, there was a 3-fold decline in near bottom summer seston concentrations, suggesting a strong depletion of food resources in the hypolimnion during stratification due to grazing by *D. r. bugensis*, which coincided with a strong increase in average mussel length as recruitment and growth of young-of-the-year mussels became unsuccessful in this zone in 2007–2021 (Karatayev and Burlakova 2022b).

4.4.3. *Interspecific dreissenid competition*

There are a multitude of reports, both from North America and from Europe, indicating that there is interspecific competition between *D. polymorpha* and *D. r. bugensis*, with the latter generally displacing the former (Balogh et al. 2018; bij de Vaate et al. 2014; Heiler et al. 2013; Hetherington et al. 2019; Karatayev and Burlakova 2022a, 2022b; Karatayev et al. 2011a, 2015, 2021a, 2021b; Noordhuis et al. 2016; Orlova et al. 2004, 2005; Strayer et al. 2019). The outcome of this competition, however, may vary from an almost complete extirpation of *D. polymorpha* to the co-existence of both species and sometimes even reversals to a predominance of *D. polymorpha* (Karatayev et al. 2011a, 2021c; Rudstam and Gandino 2020; Strayer and Malcom 2006; Strayer et al. 2019; Zhulidov et al. 2006, 2010). Among the most important factors determining the outcome of the competition are lake morphometry, prevalent substrate types, food availability, predation, and others (Balogh et al. 2022; bij de Vaate et al. 2014; Burlakova et al. 2006b; Hecky et al. 2004; Hunter and Simons 2004; Jackson et al. 2020; Karatayev and Burlakova 2022a, 2022b; Karatayev et al. 1997, 2002a, 2011a, 2021a; Rudstam and Gandino 2020). In general, in shallow polymictic lakes, *D. r. bugensis* becomes dominant 4–12 years after coexisting with previously established *D. polymorpha*, but it does not appear to fully replace the zebra mussels (Balogh et al. 2018; Hetherington et al. 2019; Karatayev et al. 2014, 2021a, 2021c; Noordhuis et al. 2016; Orlova et al. 2004). There are several examples suggesting that the dominance of *D. r. bugensis* could be reversed due to species-selective predation (Rudstam and Gandino 2020; Zhulidov et al. 2006, 2010), periodic mass mortality due to hypoxic events, or other factors (Karatayev et al. 2021c). Due to its thinner shells, weaker aggregation behavior, and lower attachment strength, *D. r. bugensis* is more vulnerable to predation than *D. polymorpha* (Balogh et al. 2019, 2022; Czarnoleski and Muller 2013; Kobak and Kakareko 2009; Naddafi and Rudstam 2013; Peyer et al. 2009, 2010). After mass die-offs induced by hypoxia or other factors, *D. polymorpha* can recolonize faster areas in waterbodies with mixed dreissenid populations (Karatayev et al. 2021c). Interestingly, within their native range in the Dnieper-Bug Liman, Ukraine, a shallow productive polymictic waterbody, the two species have been intermittently dominant in different areas and/or periods for thousands of years since the last glaciation (reviewed in Karatayev et al. 2011a).

In a recent study, Karatayev et al. (2021a, 2022b) compared the outcome of the competition between these two dreissenid species in the Laurentian Great Lakes. All these lakes and embayments were initially colonized by *D. polymorpha* and later by *D. r. bugensis*. In shallow polymictic lakes and lake basins (Lake

St. Clair, western basin of Lake Erie, and Saginaw Bay), although *D. r. bugensis* is currently dominant, both species still coexist after 30 years since the initial invasion and in the western basin in 2019 the reverse trend was recorded with zebra mussels again becoming the dominant species (Karatayev et al. 2021a, 2021c). In contrast, in deep, well-stratified lakes (lakes Michigan, Huron, Ontario, and eastern basin of Lake Erie), *D. r. bugensis* became dominant, spread to greater depths, reached much higher densities, and drove *D. polymorpha* to virtual extirpation (Karatayev et al. 2021a; Madenjian et al. 2015; Nalepa et al. 2010).

Several hypotheses have been suggested to explain the displacement of *D. polymorpha* by *D. r. bugensis* (reviewed in Karatayev et al. 2013, 2015, 2021a; Zhulidov et al. 2006). Although the mechanisms and conditions under which *D. r. bugensis* displace *D. polymorpha* still remain incompletely known (Strayer et al. 2019), it is most likely that they are associated with the higher physiological activity of *D. r. bugensis*, including higher filtration rates at low food concentrations, greater assimilation efficiency (Baldwin et al. 2002; Diggins 2001; Stoeckmann 2003), and greater plasticity in shell production allowing more energy allocation to growth and reproduction (Karatayev et al. 2011b; Mills et al. 1999; Nalepa et al. 2010; Pryanichnikova 2012). Other studies reported higher growth rates (Baldwin et al. 2002; Casper et al. 2014; Karatayev et al. 2011b; Marescaux et al. 2015; Metz et al. 2018; Stoeckmann 2003), a larger size of larvae at settlement (Martel et al. 2001), and longer reproduction period, especially for mussels below the thermocline (Nalepa et al. 2010; Wong et al. 2012). These advantages allow *D. r. bugensis* to outcompete *D. polymorpha* in many lakes and reservoirs and make them especially successful in deep stratified waterbodies (Karatayev and Burlakova 2022a, 2022b; Karatayev et al. 2021a).

5. Conclusions and future research needs

For a freshwater bivalve, dreissenids can create unusually high biomasses, often exceeding the combined biomass of all pelagic and benthic invertebrates in a waterbody by an order of magnitude. Therefore, it is not surprising that in their native range, 156 species of predators, parasites, and commensals use these bivalves as a food resource or shelter. A diverse and abundant array of natural enemies is beneficial not only because of its controlling effect on dreissenid population growth but also because of its enhancement of energy flow. The introduction of these filter-feeding bivalves into new waterbodies has modified this flow by redirecting large amounts of energy from planktonic to benthic communities. Predators, in particular molluscivorous fish and waterfowl, redirect this energy flow back to the pelagic environment.

In agreement with the enemy release hypothesis, more natural enemies of *Dreissena* spp. were initially present in their native range in Europe compared to North America. During the early years after the invasion, North American native species were likely "naïve" to the new potential prey, which may at least in part explain why fewer natural enemies were reported from the New World (19 species of fish) than from Europe (30 species). Interestingly, even in the 1990s, virtually no difference was found between the number of birds recorded preying on *Dreissena* in Europe (21 species) compared to North America (20). With time, however, more indigenous North American fishes were observed feeding on dreissenids, and currently, their respective numbers are very similar (Europe: 42 predators; North America: 39) (Table 13). Likewise, some indigenous North American parasites with a broad host range have also been reported to be capable of infecting *Dreissena* (Karatayev et al. 2012; Toews et al. 1993), and the inventory is expected to increase as more studies are conducted.

5.1. Fish

Twenty-two species of fish were documented to feed on planktonic larvae of *Dreissena*, 11 in the Old World, and 11 in North America. During the summer, *Dreissena* veligers often comprise a large part of the zooplankton biomass and production, and are likely utilized by many species of fish, especially when other food items are rare. Relatively little research, however, had been conducted to quantify the importance of this resource for their consumers and the potential impact on dreissenid populations.

A total of 64 fish species have been documented to feed on attached dreissenids, including 37 species in Europe, 31 in North America, and 4 in both continents (Table 13). Generally, smaller (<15 mm) mussels are most vulnerable to fish predation. Only a few fish species have been reported to consume large zebra mussels (e.g., ide, up to 30 mm, and large carp, up to 42.5 mm). Although fish predators, including round gobies, may cause declines in dreissenid densities, these declines are usually limited to shallow lakes or the shallow areas of deep lakes, are likely temporary, and have little lake-wide effects at the scale of large, deep lakes like the Laurentian Great Lakes.

Table 13. Total number of *Dreissena* spp. natural enemies recorded in Europe and North America according to Molloy et al. (1997) and current study (2022).

	Europe		North America		Both continents		Total	
Natural enemy	1997	2022	1997	2022	1997	2022	1997	2022
Fish	30	42	19	39	3	4	46	77
Birds	21	22	20	22	5	5	36	39
Crayfish	3	10	3	4	0	0	6	14
Others	5	7	3	7	1	1	7	13
All Predators	59	81	45	72	9	10	95	143
Parasites	17	20	3	6	3	5	17	21
Commensals	15	55	2	15	0	5	17	65
All endosymbionts	32	75	5	21	3	10	34	86
Competitors	8	10	5	6	2	2	11	14
All natural enemies	99	166	55	99	14	22	140	243

This list includes *C. klimentinus* and *S. naumiana* found exclusively in *D. carinata* in Lake Ohrid. The total number of predators and competitors in Molloy et al. (1997) were reported erroneously as 176 and 10.

More studies are needed not only on fish diets but especially on quantitative assessment of the impact of predation on dreissenids populations.

In general, the effect on fish varies depending on the feeding mode of the consumer, the morphology of the waterbody invaded, time since mussel invasion, co-evolutionary history, and *Dreissena* species, and is different in Europe and in North America.

5.2. Birds

An identical number of birds (22 species) are known to consume attached dreissenids in Europe and in North America (Table 13). Birds prey on dreissenids because they are often very abundant, requiring low search and handling times. Since diving effort increases with depth (and depth increases with the distance from shore) and the energy content of mussels decreases with depth, predation rates tend to be higher in shallow, coastal areas. Therefore, shallow waterbodies with dense mussel populations are the most attractive foraging areas for waterfowl, where they can exert high predation pressure on dreissenid populations. High rates of bird predation have been most commonly reported between autumn and spring when flocks are either temporarily present on waterbodies during their migration or overwintering and can be enhanced by the seasonal absence of other food items.

The intensity of avian predation on dreissenid populations depends on several factors, including predator densities, depth, substrate, mussel accessibility, and *Dreissena* species. Multiple studies documented significant declines in mussel populations due to bird predation, but these reductions tend to be temporary. Significant long-term reductions in mussel densities are most likely to occur only in localized areas where waterfowl overwinter (not just stage during the fall migration), and mussel recruitment is limited. Birds benefit from direct consumption of dreissenids as a reliable and abundant food source, and from feeding on the invertebrates, macrophytes, and bottom algae facilitated by and associated with the mussels. As a result, waterfowl flock sizes increase, and overwintering, timing, and routes of bird migration change.

In summary, while predation has been cited as one of the factors responsible for declines in dreissenid population densities and/or biomass, its effectiveness in steadily reducing *Dreissena* densities over the long term has yet to be demonstrated. The high fecundity and recruitment rates are precisely the traits that preclude its enemies from causing steady, long-term declines in dreissenid populations. The notion that predators or other enemies can succeed in extirpating the mussels, even in limited areas, seems unrealistic. As in Europe, there will likely be isolated reports of major impacts, but in general, the cumulative effects of a suite of enemies will likely have a constant, but limited, role in suppressing dreissenid populations.

5.3. Endosymbionts

Seventy-five species and higher taxa of endosymbionts have been found within the mantle cavity and/or associated with *D. polymorpha* in Europe, and 21 in North America (Table 13). The number of *Dreissena*-specific endosymbionts in a given population depends on many factors, in particular the *Dreissena* species (*D. polymorpha* hosts more symbionts than *D. r. bugensis*), the life stage of the mussel (attached or planktonic), as well as the number of mussels initially introduced, and/or the number of introduction events involved. The fact that *C. acuminatus* is present in virtually all European freshwater populations of *D. polymorpha,* but has not been found in North America, supports the hypothesis that planktonic larvae (rather than attached *Dreissena)* invaded North America. Therefore, analysis of *Dreissena* endosymbionts may help us to reconstruct the mechanisms of *Dreissena* invasion. Several records of *O. hemophaga* from North America, however, conflict with the hypothesis of the introduction of *D. polymorpha* at the planktonic stage, and additional investigation is required.

Among the most significant ecological and economic impacts of exotic species are those associated with their role as vectors for the introduction of parasites and commensals into the areas invaded, as well as new hosts for native parasites that promote preexisting diseases. Both processes were documented for *D. polymorpha*. For example, in Belarus—a country colonized by *D. polymorpha* in the early 1800s—at least six species-specific endosymbionts were introduced with the mussel, while in Ireland, colonized only in 1997, only two species-specific endosymbionts have been recorded so far. In addition to ciliates that spend their entire life within their host, *D. polymorpha* may host trematodes that can increase parasite loads on fish. Thus, increases in infection by metacercariae of *B. polymorphus* were documented in several water systems in Europe for many fish species. These infections were due to the expansion of both the first intermediate *B. polymorphus* host, *D. polymorpha*, and the second intermediate host, gobiid fishes, which in turn are heavily preyed upon by piscivorous fish. Dreissenids can also become a new reservoir for indigenous parasites, promoting native diseases in fish and waterfowl populations that otherwise would not have happened in the waterbodies invaded. To determine the level of endosymbiont specificity requires additional studies since it is not entirely clear if endosymbionts reported from *D. polymorpha* are species-specific or genus-specific.

In strong contrast to the evidence presented in the "Predators" section of this article, suggesting that predators can be responsible for some declines in dreissenid populations, even if these declines are limited in space and time, there is no published evidence to date that parasites can control dreissenid populations to any extent. Usually, infectious diseases are mentioned as a possible cause only when the decline studied has no explanation, and the putative infection is speculation unsupported by actual data. This does not imply that parasites capable of killing dreissenids have not been observed—they exist and occasionally their lethal effects have been thoroughly documented. Compared to the wide diversity of virulent parasites known from other bivalves, particularly commercially valuable marine species, dreissenids appear to have relatively few serious diseases. As a result, clear evidence of lethal parasites killing a sizable portion (e.g., >20%) of a dreissenid population has never been reported. Such infections leading to mass mortalities (e.g., >20%) potentially may occur in dreissenid populations, but they go unreported. This is most likely because these rare events require a very swift research response and the availability of uncommon experience and skills, as well as considerable financial resources. The identification of parasitic, infectious organisms among the myriad of creatures swarming in the body cavities and inside the tissues of dying or recently dead mussels, and distinguishing the parasites from the hordes of saprophytic microscopic organisms that invade and proliferate in the animal is a very difficult task that few scholars are able and willing to undertake. In short, so far the understanding of the role that infectious diseases play in dreissenid population declines is extremely limited. Intensive research efforts employing histological techniques to detect diseases are currently underway both in Europe and in North America (Molloy, unpublished data). These investigations will likely reveal a much broader range of parasites, particularly microbial parasites, and shed more light on their pathogenicity.

5.4. Ecological competitors

Fourteen competitors were reported to have some impact on dreissenids. Although some of them have been shown to be able to occasionally outcompete *D. polymorpha*, but the effect was always very limited in space and time, and no significant impacts on entire populations were found. In contrast, impacts on *D. polymorpha* by its congener *D. r. bugensis* were shown to be able to cause dramatic declines of the former in many European and North American water bodies, especially in deep stratified lakes.

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