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

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I. Introduction

This paper represents an extensive review of the literature on the zebra mussel and its predators, parasites and ecological competitors that interact to restrict its spread and control its population density. It is especially valuable in containing extensive international research, particularly that published in Cyrillic. Since most of the literature discussed here relates to research done on *Dreissena polymorpha,* the term zebra mussel or *Dreissena* refers to that species unless otherwise stated.

Zebra mussels originated in Eurasia and a great deal of the research on predation and naturally occurring parasites has been done there. Since the immigration to the Great Lakes region of both the zebra mussel *(0. polymorpha)* and the related quagga mussel *(Dreissena bugensis)* in the ballast water of transoceanic vessels, an explosive expansion of these animals within littoral hardwater habitats throughout North America has been observed. Besides significant economic impact as a macrofouling nuisance, they have become key players in the ecology of lakes and rivers in North America. Competition with native bivalves, declines in phytoplankton productivity, and restructuring of benthic communities have all been attributed to zebra mussel colonization.

Once introduced into a suitable habitat, their high fecundity and growth rate, coupled with a tolerance of a wide variety of environmental conditions, generally result in a rapid increase in numbers. A lack of a natural enemy complex in North America doubtless contributed to their rapid establishment and range expansion, but to what extent is subject to debate. This paper attempts to address the issue of natural controls through a review of the international literature on natural enemies of *Dreissena* and the impact these enemies have on mussel populations.

II. Predators

A variety of predators exist for attached *Dreissena,* but relatively little research exists for the planktonic stages. Field observations of 10 European and 5 North American fish species (Cyprinidae (7 species), Clupeidae (3 species), Osmeridae (2 species), Percidae (2 species), Percichthyidae (1 species)) have shown planktonic dreissenid larvae in the alimentary tracts of the fry. Predatory copepods such as *Mesocyclops* and calanoid copepods are reported to take veligers, with the stages before the first "D" (90 - 100 pm) stage being particularly vulnerable. Coelenterate predation on veligers has also been reported in Europe and North America. Cannibalism of pelagic larvae by adult zebra mussels has also been documented in Europe and North America, and this may be a density dependent population control.

Attached mussel predation is more extensively documented. Records from Europe and North America indicate that at least 38 species of fish consume attached mussels. For many of these species, however, zebra mussels may comprise a relatively small portion of their diet. In North America, some 13 additional species are considered potential predators based on their natural consumption of other bivalves. In North America, freshwater drum *(Aplodinotus grunniens)* is the best documented fish predator. This is in contrast to Europe where cyprinids comprise the largest class of consumers. Predatory species capable of taking adult mussels typically have either molariform pharyngeal teeth or strong crushing jaws and even then, predation is limited by the size class of both the mussel and the fish.

Zebra mussels can quickly become a significant food resource for molluscivorous fish when introduced into new habitat. Additionally, they can be a high quality food supplement for a plant-dominated diet. Biomass of black carp *(Mylopharyngodon piceus)* in the Tsimlyanskoe Reservoir and roach in the Rubyinsk Reservoir increased following the invasion of *D. polymorpha* with concomitant increase on the yields of the fisheries. Predation on zebra mussels can also result in increased exposure of fish to parasites as well as toxins such as heavy metals which bioaccumulate in mussel tissue.

At least 36 species of birds are recorded as consumers of attached *Dreissena,* although they are not a major dietary component for all these species. The best documented of the avian predators are all diving birds, including the tufted duck *(Aythya fuligula),* greater scaup *(Aythya marila),* lesser scaup *(Aythya afinis),* goldeneye *(Bucephala clangula)* and a diving rail, the coot *(Fulica atra).* The greater scaup *(A. marila),* goldeneye *(B. clangula),* oldsquaw *(Clangula hyemalis),* herring gull *(Larus argentatus),* and white-winged scoter *(Melanitta fusca)* are all known to consume mussels in both Europe and North America.

Factors influencing selection of *D. polymorpha* as prey include seasonal availability and migratory patterns, depth and density of mussel populations, and prey size. Fall, winter, and spring are times of peak mussel predation by birds. Flocking for seasonal migration results in high bird densities and plants are often not available during the winter. Migratory or overwintering populations can consume large quantities of zebra mussels. Shallow water areas with a high mussel density are generally preferred for foraging. Medium length mussels (ca. S-20 mm) are preferred.

Waterfowl predation can substantially decrease zebra mussel densities in a limited area over the short term. It can also result in the removal of a size class, but the change is often short-lived as space available is generally recolonized within a year. Lasting reductions in zebra mussel numbers are seen only when recruitment is low and predation is intense.

Dreissena! is published six times per year by the Zebra Mussel Information Clearinghouse, a project of New York Sea Grant. ***Dreissena!*** presents summaries of research, meetings, legislation, and sightings of *Dreissena polymorpha* (the zebra mussel) and *Dreissena bugensis* (the "quagga" mussel), to encourage and facilitate communication among stakeholders.

Submissions for inclusion in ***Dreissena!*** are encouraged. Please direct correspondence to:

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Zebra mussels can be a significant food source for waterfowl. Increases in flock size as *Dreissena* colonized a water body have been observed in Lake Erie, and lakes in Germany and Switzerland. In Europe, both distribution and timing of migration routes are influenced by availability of zebra mussels. Large standing populations of mussels have caused thousands of waterfowl to overwinter on Swiss lakes rather than continue their migration south.

Detrimental effects can be seen with narrow reliance on zebra mussels as a food source. In Europe, a decline in mussel populations in the bitterly cold winter of 1986 was a contributing factor in the population crash due to starvation of pochard and tufted duck. Zebra mussels tissues also harbor contaminants and intermediate stages of parasites, both of which can have adverse affects on their avian predators.

Crustaceans and reptiles may also be predators in North America. Both laboratory and field data suggest that blue crabs *(Callinectes sapidus)* can be aggressive consumers of large mussels. Crayfish *(Orconectes)* are documented predators in European waterbodies and are suspected to be consuming dreissenids in North America also. *Astacus leptodactylus* and *Cambarus affinis* are also predatory species in European waters. Predation was generally higher among female crayfish. Intensity of predation was related to temperature and prey size. Predation increased with increasing water temperature and smaller (<8 mm) mussels were preferred. Laboratory studies suggest turtles may also feed on *Dreissena,* although not as preferred prey.

III. Parasites

The relationship between many of the microscopic organisms found in and on *D. polymorpha* is unclear. Therefore, some symbionts are discussed that have an obligate association with zebra mussels but whose precise relationship may actually prove to be mutualistic or commensal.

Over 30 species of parasites are described that have been reported within attached zebra mussels. There is no reported research on parasites of planktonic mussels, although such parasites may exist. Parasites are commonly thought to enter the adult mussel via the inhalant siphon. They then migrate to the specific tissue within the mussel. In some cases, the mussel may be the sole host, while others such as digenetic trematodes spend only a portion of their life cycles within the mussel before being passed ultimately to the definitive host, often a fish or waterfowl.

To date, 5 species of host specific ciliates *(Conchophthirus acuminatus, Conchophthirus klimentinus, Sphenophrya dreissenae, Sphenophrya naumiana,* and *Hypocomagalma dreissenae)* (Figure l A-E) have been reported within the mantle of *D. polymorpha.* In addition, ophryoglenine species have been reported in the digestive gland (Figure lF-G). In a low stress environment, a healthy mollusc is generally in equilibrium with the ciliates that inhabit it; only when conditions alter to permit uncontrolled growth will significant damage to the mollusc occur.

Throughout the world *Conchophthirus* spp. are found on gills, viscera, and within the mantle cavities of both freshwater and marine bivalve species. Based on vacuole contents analysis, they are generally thought to be a commensal since only one species, *Conchophthirus magna,* has been reported consuming epithelial cells as a parasite. No detrimental effects have been reported even with extremely heavy infestation. To date, only two species have been reported in *Dreissena, C. acuminatus* (Figure lA, 2A) and *C. klimentinus* (Figure 1B). In the absence of vacuole analysis for *Conchophthirus* spp. in *Dreissena,* it is assumed that the more general commensal pattern is followed.

Hypocomagalma dreissenae (Figure 1C) is the only ancistrocomid ciliate reported in *Dreissena.* It is widely distributed throughout Europe. The entire family exhibits morphological characteristics typical of the parasitic form. Ciliation is reduced and the mouth has been replaced with a suctorial tentacle which is inserted into the epithelial cell of the host. In *Dreissena,* as well as other bivalves, this group is clearly parasitic; however, the infections seem to be of low intensity and produce few pathological effects.

Sphenophrya spp. are also considered parasitic. The adults of this genus have lost their mouth, apparently feed osmotically, and lack cilia - all traits consistent with parasitism. Two species are reported in *D. polymorpha* (Figure lD-E). Infection records are few in number and limited geographically, with *S. naumiana* reported only in Macedonia and *S. dreissenae* in Macedonia and Poland.

Ciliates of the order Hymenostomatida, separated into small (Figure 1G) and large forms (Figure 1F) and tentatively placed in the suborder Ophryoglenina, have been reported in the digestive gland of *D. polymorpha* in Russia. Degeneration of the digestive gland has been noted. In Lake Erie, *Ophryoglena* was observed in the mantle cavity of living and dead mussels, but it is highly probable that they were not the same ophryoglenine species as in European *D. polymorpha* and may simply have been free-living histophagous species - not parasites at all.

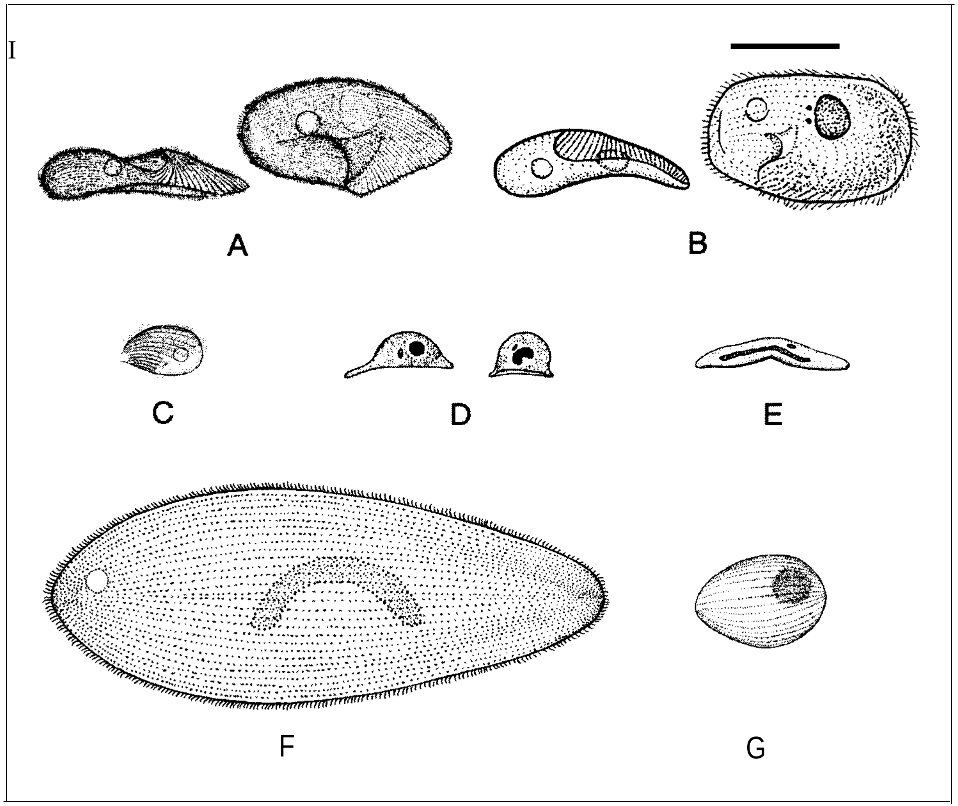

FIGURE 1. Ciliates from *Dreissena* (bar = *50* pm). A - *Conchophthirus acuminatus;* B *Conchophthirus klimentinus; C Hypocomagalma dreissenae; D Sphenophrya dreissenae;* E *Sphenophrya naumiana;* F - Large ophryoglenine associated with digestive gland; G - Small ophryoglenine associated with digestive gland. (Reprinted with permission of *Rev. Fish. Sci..* CRC Press.)

Dreissena spp. have seven genera of trematodes capable of infecting them as either intermediate hosts in a complex life cycle or as the sole host. Most trematodes are digenetic species and require more than one host to complete their life cycle. *Bucephalus polymorphus* is a digenetic trematode that inhabits three hosts during its life cycle. *Dreissena* is the first intermediate host parasitized by the miracidium after hatching. Within the visceral mass of the mussel, the sporocyst develops into a knotted white mass of tubules (Figure 2B). This mass is found primarily in the gonads and typically renders the mussel sterile; however, these tubules can also extend into surrounding tissues such as the gills, digestive gland, and mantle epithelium. Cercariae released from infected mussels attach to fish, encyst, and metamorphose into metacercariae. Cyprinids are most commonly infected, but not the only fish hosts for *B. polymorphus* metacercariae. In France, pathologies have been observed in cyprinids, although not on a consistent basis. The definitive hosts for *B. polymorphus* are predatory fish that consume infected forage fish. Northern pike *(Esox lucius),* Eurasian perch *(Perca fluviatilis),* zander *(Stizostedion lucioperca),* and brown bullhead *(Ictalurus nebulosus)* have all been documented as harboring adult worms in their intestines. No pathologies associated with the infection have been reported in these host species. A growing body of evidence suggests *B. polymorphus* is host specific for *Dreissena.* Although found throughout Europe, infected populations are not common. Prevalence varies widely. Rates of infection peak during the warmest months resulting in subsequent shedding of cercariae 1 - 2 months later. *B. polymorphus* has not been reported in North America.

Phyllodistomum spp. require only one other host, a fish, to complete their life cycle. After hatching, a miracidium enters the mantle cavity of a dreissenid through the siphon and encysts in a gill demibranch where it forms a mother sporocyst. Daughter sporocysts are produced, with 200 - 300 infecting various locations within the gills (Figure 2C). Mature sporocysts containing metacercariae are then shed to be eaten by a variety of fish genera where the adult worms are ultimately develop in the urinary tract. Zebra mussels infected by *Phyllodistomum* demonstrated reduced dry weight and higher concentrations of toxic substances. No adverse effects were observed in the fish host. Although widely distributed throughout Europe, prevalence of infection is generally low. Increasing water temperatures generally increases prevalence of infection. Both prevalence and intensity of infection increase with mussel size.

Dreissena acts as one of several possible intermediate hosts for *Echinoparyphium recurvatum.* Freshwater snails and sometimes tadpoles act as first intermediate hosts for the miracidium. Sporocysts develop within these hosts with subsequent release of free swimming cercariae. The cercariae enter the second intermediate host which can be a tadpole, snail or *Dreissena* and encyst as metacercariae. Such infected hosts are ingested by waterfowl and sometimes mammals. The adult parasite infests the small intestine sometimes producing a fatal infection in waterfowl. The infection is thought to be insignificant to the zebra mussel, but the increased availability of intermediate host species may prove detrimental to waterfowl populations.

Aspidogaster limacoides has been reported in Russian zebra mussels. *Aspidogaster conchicola* is native to both Europe and North America and is a documented parasite of *Dreissena* as well as unionids and snails. These trematodes require only one host to complete their life cycle. No known pathological effects are evident with infection, but histological studies are lacking. Additional species of trematode reported in *Dreissena* are *Leucochloridiomorpha* spp. in the Ukraine and plagiorchiid metacercariae at Port Colbome (Lake Erie).

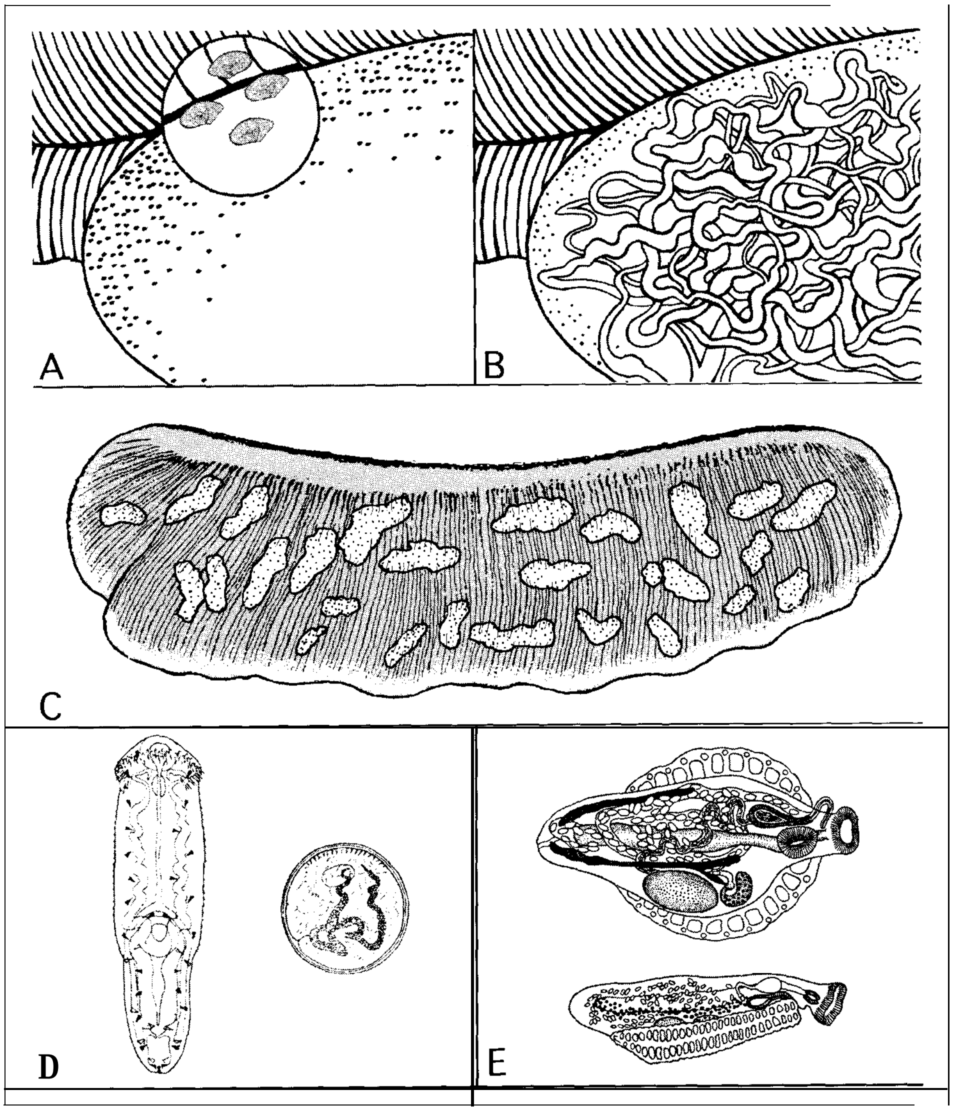

FIGURE 2. Ciliates and trematodes from Dreissma. A - *Conchophthir-us* ac~uminatus (each black dot represents one ciliate) on the surface of the visceral *mass* and gills, with magnified view of four specimens: B - *Bucephalus* pol~morphus sporocyst within the gonads; C Dozens of *Phyllodisronzunz* sporocysts within a gill demibranch; D *Echinoparyphium* recurw~um metacercaria, encysted (right) and released from the cyst (left): E - Adult of *Asr~ido~asrrr* limucoidrs (top) and *Aspidogasrrr conchic&* (bottom). (Reprinted with permission of Rel,. Fish.'%?., CRC Press.)

Lethal infections putatively attributed to an ascetosporan protozoan have been reported in the Netherlands. The oligochaete *Chaetogaster limnaei* has been reported in *Dreissena* in both the Dnestr River/Liman in the Ukraine and the St. Lawrence River in North America. Erosion of gill and mantle epithelium has been observed in histological sections. In England, infection by rod shaped bacteria produced tumor-like lesions on the gills of *D. pofymorpha.* Other groups reported within the mantle cavity include nematodes, leeches, chironomids, and mites.

IV. Ecological competitors

Zebra mussels are a very aggressive colonizer of the benthic environment in the presence of the proper environmental conditions and substrate. They can rapidly come to dominate the benthic environment, but there are reports of species capable of excluding *D. polymorpha* from substrates thus inhibiting colonization.

Sponges are successful competitors for substrates. Rapid growth also permits some species to overgrow mussel colonies blocking siphons and impairing feeding and respiration resulting in tissue weight loss and slow death. Once established, sponges seem successful in preventing settling and attachment of veligers.

Competition from sponges is limited. They are generally restricted to vertical surfaces, and numbers tend to be low in open waters.

Another native of the Black Sea-Caspian basin, the amphipod Corophium *cuwispinum* is another filter-feeder present in Europe which out-competes dreissenids for space on hard substrates. Its colonization is facilitated by the presence of crevices produced in dense mussel colonies. Mud tubes constructed by the amphipod smother adults and hinder attachment by veligers.

The marine species *Mytilaster lineatus* .was inadvertently introduced into the Caspian Sea and was able to displace *Dreissena andrusovi* in shallow waters with salinity levels 1.5 ppt.

Intraspecific competition within a *Dreissena* sp. can act as a regulator of the population. Mussels in bottom layers can die as colonies reach several centimeters of thickness. It has been suggested that adult mussels in high densities compete with their planktonic larvae for food resources. Interspecific competition between *D. polymorpha* and *D. bugensis* apparently results in the displacement of the former by the latter in both European and North American waters.

V. Discussion

A diverse and abundant community of natural enemies is beneficial not only because of its inhibiting effect on zebra mussel population growth, but also because of its impact on energy flow. The introduction of these filter-feeding bivalves has modified this flow in many North American aquatic ecosystems by redirecting large amounts of energy from the planktonic to the benthic community. Predators, in particular fish and waterfowl, are serving to redistribute this energy flow back into open waters.

Approximately 220 species (176 predators, 34 parasites, and 10 competitors) are discussed as natural enemies of *Dreissena* spp. This paper questions the relatively low number of parasitic compared to predatory organisms reported and suggests that the reason lies essentially in the relative size of these natural enemies. Compared to predators, parasites are simply too small to be commonly noticed. A wide variety of virulent parasites are known for commercially valuable marine molluscs. Comparatively, zebra mussels seem to have few diseases, but even in the European literature, scant attention has been paid to parasites compared to predators.

Although the vast majority of organisms that are natural enemies in Europe are not present in North America, ecologically similar species do exist, and zebra mussels represent a novel and abundant organism for these native predators, parasites, and ecological competitors -the new natural enemies of *Dreissena.* The idea that these organisms might eliminate zebra mussel populations, even in limited areas of North America, however, is far more hopeful than realistic. As in Europe, there will likely be isolated reports of major impacts by natural enemies, and on the whole we will likely see a cumulative effect of a suite of enemies having a constant. but limited, role in suppressing zebra mussel populations.

(Daniel P. Molloy, New York State Museum and Diane J. Oleson, Clearinghouse Editorial Assistant)