Zebra mussels belong to the phylum Mollusca, the group bivalves (unique among them--the only species that attaches to a hard substrate), which are native to the Black, Caspian, and Azov seas (USGS NAS). They were first observed in areas nearby Indiana, Michigan, and Ohio in 1986 (USGS NAS). Zebra mussels likely originated in Europe, establishing a population in Lakes St. Clair and Erie when ships dispersed ballast water (Hebert et al. 1989). The influence of bivalves on ecosystems includes the following: removal of particles from the water column, reducing populations of consumers depending on these particles as food source, increasing populations that use bivalves or their waste products, and making available particles previously used by phytoplankton (Strayer et al. 1999). As a result, their introduction into the United States as a result of commercial trade has had cascading effects on ecosystems, affecting multiple trophic levels and altering the abiotic conditions of the water bodies in which they reside.

The outcome of invasions depends in part on the tolerance of environmental conditions in the area of introduction. Introduced environments with conditions similar to those found in the native range may be more conducive to invasive establishment (reference). Additionally, reproductive and physiological characteristics of the invading organism play a role in whether populations become established in the new range. In the case of zebra mussels, free swimming larvae and high fecundity (eggs per female) have been implicated in its proliferation success (Hebert et al. 1989). That zebra mussels are amenable to a wide range of habitats with a flexible reproductive system has aided their spread and establishment in North America where they were introduced via the release of ballast water from ships (Nichols 1996).

Physiological constraints of organisms determine the optimal range in which reproduction can occur, an important factor in the spread and establishment of an invasive species (or any species, for that matter). One such constraint is thermal tolerance, and temperature was shown to affect the timing of gametogenesis (Wacker & Elert 2003). The two experimental groups were raised at different depths to generate the temperature difference, and variation in environmental quality in the surrounding region may explain the differences in egg mass released at the two different depths (Wacker & Elert 2003). In addition, metabolic rates increase with temperature, so that differences in food availability at the two depths could further influence reproductive investment. Without respective to temperature differences, availability of polyunsaturated fatty acids and food quality in general resulted in changes to reproductive investment (Wacker & Elert 2003). An additional study confirms a threshold of 12 C for the onset of spawning and further identifies two spawning cohorts as the season proceeds from May to August (Borcherding 1991). Gametes are released into the water column over a period of 6 to 8 weeks, where they are fertilized and develop—30,000 to 40,000 eggs may be released by one female, though the actual number may be closer to 1.5 million. Egg release corresponds with temperature, beginning at 12C and peaking at 22C. As a result, juvenile proliferation should track these temperature changes (Hebert et al. 1988). High temperatures alongside low food availability results in reduction in the size of the gonads (Borcherding 1991).

*Dreissena* tends to colonize structures below 1.2 m. Zebra mussels may spread to larger structures through water intake pipes. Zebra mussels tend to increase water clarity through digestion of suspended sediments—for this reason zebra mussels have been intentionally stocked in lakes outside North America. Food deprived mussels fed indiscriminately on particles of all sizes, but satiated individuals felt only on those in a much smaller size range (MacIsaac 1996).

Ambient temperature, seston concentration, and mussel size frequency are three factors that influence *Dreissena* filtering impact. Maximal filtering rate has been hypothesized to be 5 and 20 C, declining outside of this range. Ingestion rate may also be temperature dependent; however, the results of experiments investigating the effect of temperature are variable. It may still be an important performance factor, and impose a range limitation in southern states. Depending on size, zooplankton may succumb to or evade ingestion by zebra mussels—smaller individuals cannot escape the inflow current and are not rejected, whereas larger individuals may dodge the current or be expelled as a result of irritating the feeding apparatus (MacIsaac 1996).

In addition to the direct effects caused by the introduction and proliferation of an alien species, management strategies may themselves cause additional disruption, such as the use of molluscicides (reference).

To observe the spread of zebra mussels in the United States, occurrence data was plotted on a map and combined with temperature records to observe patterns in the invasion process.

1. slide on life cycle (Mackie 1991)
   1. graphic
   2. image of adult
2. graphs showing relationship to temperature

Ecological and Genetic Studies on Dreissena polymorpha (Pallas): A New Mollusc in the Great Lakes

The larval stage of the zebra mussel life cycle is planktonic and free-living, with a sessile adult phase. Though mostly dioecious, some hermaphrodism is observed. Sexual maturity is a function of size, sometimes taking two years to reach the necessary 5 mm or greater.

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Swimming blastula, trocophore, straight-hinge larvae, umbonal larvae, pediveliger, plantigrade, and juvenile are the phases of the life cycle; settlement occurs in the plantigrade phase, and marks the transition between the free-living larval stages and benthic adult form.

Zebra mussels may be moved passively via vegetation dislocation in the fall to deeper waters.

Temperature regulates the temporal development of fertilized egg to juvenile—development proceeds faster in warmer waters and slower in cooler waters. Developmental times have been reported in a range between 8 days to 240 days, but are considered to develop fairly quickly, though certain phases of the life cycle display different growth rates.

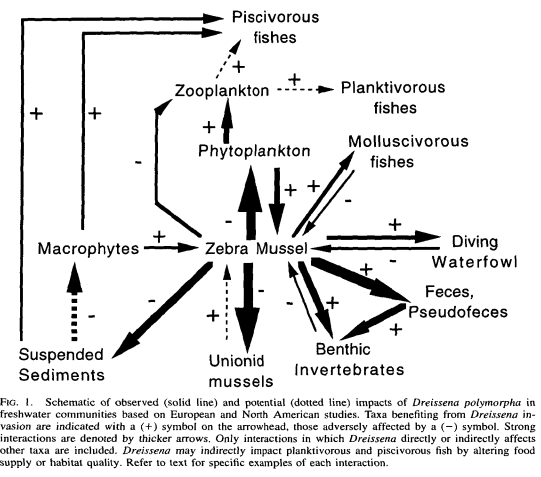
Settlement of larvae upon reaching juvenile stage may take place some distance from the parent mussels: vertical distribution in the water column varies diurnally while horizontal distribution is affected by water currents and wind.

In Lake Erie, initial attachment requires a hard substrate of minimal size, such as a pebble, where the surrounding stratum may be soft and muddy. Colonization by subsequent populations may take place on top of previously established zebra mussel shells.

Failure to colonize northern and central portions of the lake is likely attributable to flow patterns, but the explanation for nonrandom colonization patterns in southeastern portions of lake is uncertain. Long distance dispersal is restricted only to large colonies, suggesting that veliger dispersal is curtailed.

Potential Abiotic and Biotic Impacts of Zebra Mussels on the Inland Waters of North America

*Dreissena* tends to colonize structures below 1.2 m. Zebra mussels may spread to larger structures through water intake pipes. Zebra mussels tend to increase water clarity through digestion of suspended sediments—for this reason zebra mussels have been intentional stocked in lakes outside North America. Food deprived mussels fed indiscriminately on particles of all sizes, but satiated individuals felt only on those in a much smaller size range (MacIsaac 1996).

Ambient temperature, seston concentration, and mussel size frequency are three factors that influence *Dreissena* filtering impact. Maximal filtering rate has been hypothesized to be 5 and 20 C, declining outside of this range. Ingestion rate may also be temperature dependent; however, the results of experiment investigating the effect of temperature are variable. It may still be an important performance factor, and impose a range limitation in southern states. Depending on size, zooplankton may succumb to or evade ingestion by zebra mussels—smaller individuals cannot escape the inflow current and are not rejected, whereas larger individuals may dodge the current or be expelled as a result of irritating the feeding apparatus (MacIsaac 1996).

The accumulation of zebra mussels results in biofouling whereby the function of structures is compromised, the extent of which depends on the type of substrate.

Include figure that plots water turbidity as a function of zebra mussel density. A heat map with concentrations of particulate matter with zebra mussel sightings superimposed.

Examine the relationship between lake bathymetry and water clarity related changes from zebra mussels.

Total zebra mussel sightings by lake.

# Food quality controls reproduction of the zebra mussel (*Dreissena polymorpha*)

One of the reasons for prolific spread is likely high fecundity of its reproduction. Spawning in spring begins at a temperature threshold of about 12C, so it is often delayed in the hypolimnion of lakes. Food quality is another factor determining the number and quality of gamete production. Summer cyanobacterial blooms comprise low food quality and may thus interfere with gametogenesis of zebra mussels. This study examined the effects on reproduction of two different temperatures (as achieved by differing depths) and feeding regimes. Mussels raised at 15 m depth released eggs later than those raised at 4 m depth. In addition to the differences in temperature between these two groups, food availability also differed in that fewer fatty acids were available at 15 m.

# Zebra Mussel Effects on Benthic Invertebrates: Physical or Biotic?

Zebra mussels create living mats of many individuals attached to one another known as druses. These assemblages were observed to increase the abundance of multiple groups of invertebrates.

References

# Zebra Mussel Effects on Benthic Invertebrates: Physical or Biotic?

Biology of the exotic zebra mussel, Dreissena polymorpha, in relation to native bivalves and its potential impact in Lake St. Clair

Food quality controls reproduction of the zebra mussel (Dreissena polymorpha)

Ecological and Genetic Studies on Dreissena polymorpha (Pallas): A New Mollusc in the Great Lakes

Potential Abiotic and Biotic Impacts of Zebra Mussels on the Inland Waters of North America

Variations in the Reproductive Cycle of Dreissena Polymorpha in Europe, Russia, and North America

Transformation of Freshwater Ecosystems by Bivalves A case study of zebra mussels in the Hudson River

<https://www.glerl.noaa.gov/res/HABs_and_Hypoxia/rtMonSQL.php#WLEMap>

Evaluation of Hemlock (Tsuga) Species and Hybrids for Resistance to Adelges tsugae (Hemiptera: Adelgidae) Using Artificial Infestation MICHAEL E. MONTGOMERY,1 S. E. BENTZ,2 AND RICHARD T. OLSEN2

The progrediens generation matures about 8 to 9 weeks after the crawler phase. Analyze sexually reproducing individuals genetically as well? Pinpoint the population from which the eastern NA introduction was a part?

The spring generation beginning in April is the progrediens, the eggs of which mature and produce eggs of their own by late July, which then become the sistens generation. The sisten first instar nymphs settle at a feeding site and subsequently enter diapause that extends through the summer and into fall, at which time growth resumes, to complete in early spring.

The first instar nymph is the only mobile stage and is known as the crawler, which can be carried via wind or animals to other host trees. Once a feeding site at the base of a hemlock needle is established, they remain settled and stationary for the remainder of the life cycle. Progredien crawlers emerge from the characteristic woolly white ovisacs beginning before the vegetative buds have broken and ending after.

Hypersensitive responses result from infestation by certain herbivores with the function of starving and isolating the invader through increase in levels of reactive oxygen species such as hydrogen peroxide.

Used image analysis by counting the number of stained pixels in the image and generating a percentage of needle containing hydrogen peroxide. Insect herbivores with similar feeding modes can elicit very different defense responses from plant host.

The presence of elevated levels of hydrogen peroxide even in new growth absent settled HWA could be the result of diffusion from that produced in high quantities in needles with HWA.

HWA settles at the base of the petiole, feeding on xylem ray parenchyma cells, which are involved in nutrient storage. High levels of HWA saliva may be toxic and result in the sustained systemic response

forest structure and composition (Orwig and Foster [1998](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR102); Heard and Valente [2009](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR59); Spaulding and Rieske [2010](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR127)), hydrological processes (Ford and Vose [2007](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR47)), decomposition rates (Cobb et al. [2006](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR23); Cobb [2010](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR22)), and carbon and nitrogen cycling (Jenkins et al. [1999](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR71); Nuckolls et al. [2009](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR97); Albani et al. [2010](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR1); Templer and McCann [2010](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR130)). Shifts in the community structure and diversity of birds (Tingley et al. [2002](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR131); Allen et al. [2009](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR2)), fish (Ross et al. [2003](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR118); Siderhurst et al. [2010](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR123)), amphibians (Brooks [2001](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR16)), and terrestrial and aquatic arthropods (Snyder et al. [2002](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR126); Jetton et al. [2009](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR74); Rohr et al. [2009](https://link.springer.com/article/10.1007/s10592-011-0301-2#CR117)

**Widespread inbreeding and unexpected geographic patterns of genetic variation in eastern hemlock (Tsuga canadensis), an imperiled North American conifer at high densities of HWA.**

Maturity is reached after 20 or 30 years, and is pollinated by the wind with short distance seed dispersal.

Sample HWA from same sample set as was collected for genetic variability of hemlock?

CHAPTER 1: HEMLOCK WOOLLY ADELGID AND ITS HEMLOCK HOSTS: A GLOBAL PERSPECTIVE

Hemlock woolly adelgid was introduced to eastern North America in Virginia around 1950 from Japan; since then, it has ravaged hemlock forests throughout their natural range. The loss of hemlock, a long-lived, shade-tolerant coniferous species, has implications for wildlife habitat, nutrient cycling, and forest composition. For this reason, understanding the ecology and genomics of the insect, alongside the character of its interaction with hemlock, is important to inform management strategies and hopefully avoid decimation of Eastern and Carolina hemlock.

There are currently identified nine species of hemlock, five in Asia and four in North America, all of which grow in cool, humid conditions in a moist soil environment. These conditions can be found from sea-level to the subalpine zone.

\*Include a map of hemlock distribution (Alabama in south, Minnesota in west, New Brunswick in north), explaining the biophysical gradients present throughout\*

The two eastern North American populations are not closely related--Carolina hemlock diverged later and is more closely related to the Asian species while Eastern hemlock represent a more individual divergence. As a result, hybridization between Carolina and Asian hemlock species has been successful, while crossing with eastern hemlock has not.

Eastern hemlock has low genetic variability compared to other conifers and other hemlock species. Perhaps this is the result of the early divergence and subsequent isolation of genetic material into the newly established species at the time of divergence--an inbreeding of sorts. Two periods of decline in Eastern hemlock occurred likely as a result of increased climatic variability, in particular drought, due to hemlock’s increased susceptibility in comparison to other trees. Range contracted to the southern area, which served as a source of refuge until reexpansion occurred.

Evolutionary diversity of HWA corresponds to evolutionary diversity of hemlock--both were diversifying at the same time.

There are two distinct lineages of HWA that feed on T. seiboldii and T. diversifolia. Though the two hemlock species may exist in close proximity, they are rarely found in the same stand and the HWA populations have not experienced gene flow. Those HWA found in eastern North America originated from the population inhabiting T. seiboldii from Japan. Adelgids from China and Taiwan are markedly different from all others--perhaps species differentiation. HWA in eastern North America is less genetically variable than those in western North America, which do not resemble any Asian populations. This is typical of the population bottleneck following introduction into a new range.

NA

canadensis, heterophylla, caroliniana, mertenensis

Asian

chinensis, sieboldii

The HWA population inhabiting T. seiboldii in Japan alternates its hemlock host with the tiger spruce, on which sexual reproduction occurs.

The sistens generation of HWA in eastern North America (originating in Japan on T. seiboldii and tiger spruce) hatches in late spring to early summer, subsequently entering diapause throughout the summer and into the fall. Nymphs overwinter, becoming adults in early spring at which time they lay eggs, which form the winged sexuparae (which do not survive) and wingless progrediens. The progrediens develop quickly into adults, laying eggs in late spring to early summer.

HWA impacts on hemlock include:

-increased foliar nitrogen

-abnormal xylem tissue and associated water transport

-changes in amino acid composition and concentration

-high levels of starch at the feeding site

T. caroliniana and T. canadensis are not closely related, but they are similar in composition of two substances, isobornyl acetate and alpha-humulene (higher and lower than that found in all other hemlock species, respectively).

Eastern hemlock has evolved with more chewing insects than piercing sucking insects, which may explain the poorly adapted hypersensitive response that leads to tree death.

Souto, D., Luther, T. & Chianese, B. (1996) Past and current status of HWA in eastern and Carolina hemlock stands. *Proceedings of the First Hemlock Woolly Adelgid Review* (ed. S.M. Salom, T.C. Tignor and R.C. Reardon), pp. 9–15. USDA Forest Service, Morgantown, WV.

is migrating at a rate of approximately 30 km year–1 ([McClure, 1989, 1990, 1991](https://onlinelibrary.wiley.com/doi/full/10.1046/j.1365-2699.2002.00765.x?casa_token=NEZjY970If4AAAAA%3AuNd8M4SY4A69GG4a-ZCNvMzPafbu-D2of3--s-eRXxPBPtLy7tOXc6dNPbohhEgK_Bm2bAx71WXtmF4m#b28%20#b22%20#b25)

Landscape and local edaphic and biotic factors have been shown to play important roles in pest and pathogen spread and impact by influencing pathogen dispersal and population growth ([Eager, 1984](https://onlinelibrary.wiley.com/doi/full/10.1046/j.1365-2699.2002.00765.x?casa_token=NEZjY970If4AAAAA%3AuNd8M4SY4A69GG4a-ZCNvMzPafbu-D2of3--s-eRXxPBPtLy7tOXc6dNPbohhEgK_Bm2bAx71WXtmF4m#b37); [Mitchell & Preisler, 1991](https://onlinelibrary.wiley.com/doi/full/10.1046/j.1365-2699.2002.00765.x?casa_token=NEZjY970If4AAAAA%3AuNd8M4SY4A69GG4a-ZCNvMzPafbu-D2of3--s-eRXxPBPtLy7tOXc6dNPbohhEgK_Bm2bAx71WXtmF4m#b38)), host distribution ([Smith & Nicholas, 1998](https://onlinelibrary.wiley.com/doi/full/10.1046/j.1365-2699.2002.00765.x?casa_token=NEZjY970If4AAAAA%3AuNd8M4SY4A69GG4a-ZCNvMzPafbu-D2of3--s-eRXxPBPtLy7tOXc6dNPbohhEgK_Bm2bAx71WXtmF4m#b39)) and susceptibility ([Liebhold *et al*., 1994](https://onlinelibrary.wiley.com/doi/full/10.1046/j.1365-2699.2002.00765.x?casa_token=NEZjY970If4AAAAA%3AuNd8M4SY4A69GG4a-ZCNvMzPafbu-D2of3--s-eRXxPBPtLy7tOXc6dNPbohhEgK_Bm2bAx71WXtmF4m#b40); [Trial & Devine, 1994](https://onlinelibrary.wiley.com/doi/full/10.1046/j.1365-2699.2002.00765.x?casa_token=NEZjY970If4AAAAA%3AuNd8M4SY4A69GG4a-ZCNvMzPafbu-D2of3--s-eRXxPBPtLy7tOXc6dNPbohhEgK_Bm2bAx71WXtmF4m#b41); [MacLean & MacKinnon, 1997](https://onlinelibrary.wiley.com/doi/full/10.1046/j.1365-2699.2002.00765.x?casa_token=NEZjY970If4AAAAA%3AuNd8M4SY4A69GG4a-ZCNvMzPafbu-D2of3--s-eRXxPBPtLy7tOXc6dNPbohhEgK_Bm2bAx71WXtmF4m#b42); [Powers *et al*., 1999](https://onlinelibrary.wiley.com/doi/full/10.1046/j.1365-2699.2002.00765.x?casa_token=NEZjY970If4AAAAA%3AuNd8M4SY4A69GG4a-ZCNvMzPafbu-D2of3--s-eRXxPBPtLy7tOXc6dNPbohhEgK_Bm2bAx71WXtmF4m#b43))

Is the only relevant factor determining “duration of infestation” the time since HWA colonized a stand to present?

Gray, D.R. & Salom, S.M. (1996) Biology of the hemlock woolly adelgid in the southern Appalachians. *Proceedings of the First Hemlock Woolly Adelgid Review* (ed. S.M. Salom, T.C. Tignor and R.C. Reardon), pp. 26–35. USDA Forest Service, Morgantown, WV.

**Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid**

Does infestation intensity correlate with genetic variability? Is genetic composition of a population predictive of infestation intensity?

HWA infestation level shows weak correlations with aspect, slope, and location, but is most strongly related to latitude, with greater mortality in southern than northern stands.