Assessment of organic substrates as sites for zebra mussel (Dreissena polymorpha) attachment in four West-Central Minnesota Lakes

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\textbf{ABSTRACT}

Zebra mussels (Dreissena polymorpha) are an aquatic invasive species generalist with known ecological and economic impacts due to their settlement and attachment characteristics as well as their filtration abilities. Although zebra mussel attachment to abiotic substrates has been extensively studied, the importance of organic substrates for established zebra mussel populations in North American waters has not been evaluated. We assessed organic substrates in four west-central Minnesota lakes. Using qualitative analysis, we found most substrates were used proportionally to their availability. A quantitative assessment revealed significantly more zebra mussels attached to detritus than pondweeds (P < 0.05). Algae (filamentous and Chara spp.) were a significant suitable substrate for zebra mussel attachment (P < 0.05). Furthermore, more juvenile zebra mussels were found on organic substrates than were adults (P < 0.001). Although not always a consistent substrate, biological material as a vector for zebra mussel spread and settlement should be considered in further research to mitigate subsequent invasions and manage already naturalized populations.

\textbf{INTRODUCTION}

Every continent has been affected by non-native species (Cassey et al. 2005) and zebra mussels (Dreissena polymorpha) are one of the most damaging to aquatic systems (Vrtilek and Reichard 2012). Originally from the Ponto-Caspian region, zebra mussels were introduced into the Great Lakes between 1986 (Johnson and Padilla 1996; McMahon 1996) and 1988 (Timar and Phaneuf 2009). By 2005, dreissenid mussels (zebra mussels and quagga mussels [Dreissena bugensis]) were observed in the Lake Superior harbor (Duluth, MN), with the first observation of zebra mussels as early as 1989 (United States Geological Society [USGS] 2021). Vander Zanden and Olden (2008) found that to slow...
the spread of aquatic invasive species (AIS), the prevention of secondary range expansion to adjacent water bodies was paramount. Minnesota range expansion of quagga mussels slowed after 1989 (USGS 2021). Zebra mussels, however, utilized available vectors and rapidly invaded inland Minnesota waters from Lake Superior.

Zebra mussel colonization of hard substrates that are subsequently relocated (e.g., watercraft and boat lifts) and the transfer of ballast water containing veligers are well-documented introduction mechanisms (Oldham 1930; Kobak 2001; Porter and Marsden 2008; Depew et al. 2021). Zebra mussels have also been known to redistribute on floating plant fragments and via macrophytes entangled on watercrafts (Minchin et al. 2002). In 2020 and 2021, the MnDNR reported 6% of inspected watercrafts entering Minnesota waters had zebra mussels attached to aquatic plants entangled on the boat or trailer (Minnesota Department of Natural Resources [MnDNR] 2021). By December 2021, approximately 550 Minnesota surface waters were deemed infested because of known zebra mussel populations or downstream connectivity (Minnesota Department of Natural Resources [MnDNR] 2017a).

As a relatively new invader to Minnesota, zebra mussel establishment and range expansion is ongoing, and the ability to predict and manage colonization is limited. Because one adult zebra mussel can filter 1 liter of water per day, water clarity often increases where zebra mussels become established, facilitating deeper photic zones and increasing favorable habitats for aquatic macrophyte growth (Scheffer et al. 1994; Strayer 1999; Zhu et al. 2006; Higgins and Vander Zanden 2010; e.g., Figure 1). Increased macrophyte abundance and frequency of occurrence amplifies zebra mussel settlement, recruitment opportunities, and overall densities (Kobak 2001; Muskó and Bakó 2005; Porter and Marsden 2008). Although submerged macrophytes are not a homogenous or sturdy substrate (Lewandowski and Ozimek 1997), plants provide zebra mussels with detrital organic carbon and periphytic algae as a food source (Ozimek 1997).

The relations between zebra mussel ecology and aquatic plants, including flora as attachment substrata, have been evaluated in the European zebra mussel range (e.g., Muskó and Bakó 2005). Stańczykowska and Lewandowski (1993) demonstrated that zebra mussel populations occur in higher densities on submerged macrophytes than other fine substrates, such as sand and silt. However, less research has been directed at aquatic flora as a colonization habitat factor. Therefore, the objectives of this research were to 1) assess

![Figure 1](http://cf.pca.state.mn.us/water/watershedweb/wdip/search_more.cfm).

**Figure 1.** Mean water clarity indexed with a Secchi (m) from 1980 to 2016 in four study lakes of west-central Minnesota. The vertical line denotes when zebra mussels were first detected in the four lakes. Data source: Minnesota Pollution Control Agency, EDA: Surface water data and watershed data project (http://cf.pca.state.mn.us/water/watershedweb/wdip/search_more.cfm).
the potential associations zebra mussels may have with various types and biomasses of organic substrates in mid-continental lakes, 2) determine zebra mussel attachment electivity for different types of organic substrates, and 3) determine whether there are any adult-juvenile settlement differences.

Materials and methods

Organic substrates and zebra mussels from populations naturalized since at least 2009 were collected from four west-central Minnesota lakes located within 6.8 km of lat: 45.939488˚ N, lon: 95.356769˚ W. Self-contained underwater breathing apparatus (SCUBA) was utilized to collect samples along transect lines in the summer of 2014. A geographical center point was located for each lake and a transect line from that point was drawn due north until it intersected with the shoreline. From that transect line, five additional transects were identified at 60˚ angles and drawn in from the center point to the shoreline (6 transects per lake). At the shoreline end of each transect, a 50-m tape was secured at the land-water interface and extended toward the center point of the lake. Divers then placed 0.25-m² quadrats at 10-m intervals along the transect line, with the first interval placed 10 m from the shoreline. Therefore, 5 quadrats were assessed per transect (Figure 2).

At each quadrat, a diver collected all organic substrates and any associated zebra mussels by digging into the underlying sediment with a gloved hand to a depth of 8 cm. Quadrat materials were placed into a collection bag by the diver with the lake name, transect number, quadrat number, and collection date transcribed on the outside of the bag. Samples (4 lakes, 6 transects per lake, 5 quadrats per transect, N = 30 quadrats per lake, or 120 total samples) were frozen for laboratory processing (Tóth et al. 1996; Ravera et al. 2003; Baker and Hornbach 2008). Samples were thawed and sorted into the groupings of detrital deposits (i.e., organic-based sediments), filamentous algae, Chara spp., and macrophyte species. Detrital deposits included organic-based allochthonous and autochthonous materials less than 7.6 cm in length (e.g., decomposing wood, leaves, and other plant material). The filamentous algae were not identified beyond growth form because of post-
freezing cell degradation. Macrophytes were identified to species (Borman et al. 1997; Skawinski 2014).

Zebra mussels were then separated, enumerated, and systematically measured from each organic substrate. Zebra mussel attachment to, compared with loose association with, filamentous algae was analyzed carefully due to the sheer chance that unattached zebra mussels may have become tangled in the algae during sample collection and processing (See Figure 3). Only zebra mussels with byssal threads fused with, or otherwise intertwined with filamentous algae were categorized as attached. For all other organic substrata, resistance felt when pulling on the zebra mussel corresponded to byssal attachment.

After separation from the organic substrates, zebra mussels were measured using a systematic random sampling method. All zebra mussels removed from each group of organic substrates were placed in a clear 22.86 cm x 33.02 cm (9 in x 13 in) rectangular pan placed on white paper inscribed with a 12-cell (7.62 cm x 8.26 cm; 3 in x 3.25 in) grid. Umbo-central margin distances were measured on mussels (< 50 mussels for each substrate in each lake quadrat) in a random series of the 12 cells. Individuals with an umbo-central-margin distance < 8 mm were distinguished as juveniles ([adults were ≥ 8 mm] Skyler and Edds 2014).

Figure 3. Zebra mussel attachment to filamentous algae and the incorporation of algae into the zebra mussel's shell. (a) Filamentous algae at 40x magnification wrapped around Vallisneria americana. Filamentous algae attached to the zebra mussels’ shell. (b) Microscopic view at 100x magnification of the filamentous algae attachment to the zebra mussel and therefore was not enumerated into the zebra mussel “attached to algae” total.
After zebra mussel removal, each organic substrate sample was blotted dry, placed in a glass 100 mm x 15 mm petri dish, and dried at 105˚C (Newman and Biesboer 2000; Gross et al. 2001) to determine organic biomass density (g dry weight•0.25-m-2). Organic substrate samples were monitored at 48-hr intervals until weight loss diminished to a constant within ± 0.03 g (Newman and Biesboer 2000; Gross et al. 2001). For simplification, only those substrate types (n = 12 substrates) comprising ≥ 1% of the total biomass were included in the analyses. If zebra mussel densities did not differ (P > 0.05) among similar organic substrates they were combined. The following organic substrate groupings were established for further analyses: algae (filamentous algae and Chara spp.), coontail (Ceratophyllum demersum), detritus, naiad (Najas spp.), northern milfoil (Myriophyllum spicatum), wild celery (Vallisneria americana), and pondweeds (Potamogeton spp.). Substrate use was measured as the number of mussels per dry mass of each substrate. Substrate availability was the total dry mass of substrate per quadrat. Substrate electivity was measured as the dry mass of mussels attached to a substrate type within each quadrat divided by the dry mass of the substrate within each quadrat. Mussel electivity was tested for normality and homogeneity of variances and tested with either an ANOVA or Kruskal-Wallis test to detect potential differences in mussel density among organic substrates. When significant differences were present, multiple comparison tests were used to determine which pairs of means were significantly different. Sigma Plot software was used for all statistical analyses.

Historically, indices of electivity have been used to quantify feeding ecology of organisms based on prey availability compared with prey selection (Kohler and Ney 1982; Lechowicz 1982). The same premise can be applied to using a linear electivity index (LEI) to assess zebra mussel selection or avoidance of available organic substrate types (Strauss 1979; Fisher et al. 1996). Positive electivity was defined as substrate use disproportionately greater than substrate availability. The LEI allows for the determination of the degree of electivity:

\[ \text{LEI} = \frac{r_i}{p_i}, \]

where \( r_i \) is the relative abundance of organic substrate category “i” with attached zebra mussels and \( p_i \) is the relative abundance of organic substrate category “i” in the total sample. Output values for the LEI range from 1 (strong electivity) to -1 (complete avoidance). Therefore, a LEI value of 0 suggests zebra mussels are using the category at a rate proportional to its presence in the environment. LEI values were calculated for all organic substrate groupings, although Chara spp. and filamentous algae were separated for potential electivity differences based on life stage.

All data used in these analyses for the current study are available at the Dryad repository, https://datadryad.org/stash/share/1_dIcdIJT6DBxvNwO5bPyZ45cAW6Sjr5DGV-FTC_4DE

**Results**

Twenty-two types of organic substrates, including 19 macrophyte species, one macroalgae genus (Chara spp.), detrital deposits, and filamentous algae were collectively found in the four sample lakes with a mean dry weight organic mass of 2.9 g•0.25-m-2 (SE = 0.3). More than half of the quadrats sampled had filamentous algae present. Chara spp. was the greatest single-category proportion of the biomass (40.7%) while white water lily (Nymphaea odorata) had the lowest proportion of the biomass (< 0.1%) and was the only macrophyte devoid of zebra mussels. A total of 16,334 zebra mussels were found attached to organic substrata for all samples combined (N = 120), resulting in an overall mean
density of 46.9 zebra mussels g dry weight of organic substrates (SE = 4.4). Based on mean organic biomass dry weight (g m\(^{-2}\)), the area-based zebra mussel density that is attached to organic substrates is 552 zebra mussels m\(^{-2}\). Of the 22 organic substrate types, detritus had the most attached zebra mussels with a total of 896 (29.6% of total).

Data substantially differed from normal distribution, nullifying attempts to utilize parametric tests to analyze for main effects and interactions among main effects. Therefore, effects were assessed using non-parametric tools. The mean number of attached zebra mussels (adults and juveniles combined) among the organic substrate groupings was significantly different (P = 0.001). A multiple comparison test revealed that detritus had significantly (P < 0.05) more attached zebra mussels than coontail, northern milfoil, the pondweeds, and wild celery, and statistically similar densities with the algae and naiads. Wild celery had significantly fewer attached zebra mussels than all other groupings (P = 0.01). In terms of LEI selection, results indicated minimal selection or avoidance (i.e., neutral selection) by zebra mussels for the organic groupings, with LEI scores only ranging from −0.02 for detritus and pondweeds to 0.06 for algae (Table 1).

Within-grouping comparisons of adult and juvenile attachment revealed no significant differences (P > 0.05) for detritus, naiad, and wild celery (Figure 4). Significantly more juveniles per dry biomass (P < 0.03) were observed on coontail, northern milfoil, algae, and the pondweeds (Figure 4). Juvenile use of the organic groupings was found to be significantly lowest for wild celery and highest for detritus (P = 0.005). Adult attachment was most significant for detritus and naiads, followed by the pondweeds (P = 0.001; Figure 4). No difference in adult attachment was detected among coontail, northern milfoil, wild celery, and algae (P = 0.05).

**Discussion**

**Attachment to detritus**

In the current study, it should be noted allochthonous and autochthonous material may offer a suitable substrate for settling and developing zebra mussels much like other invertebrates. In addition, many benthic invertebrates and aquatic biofilms use material with no definite dimension (e.g., large and medium-sized woody debris < 1.5 cm) as an important substrate (Spänhoff and Cleven 2010; Andersen et al. 2016). Detritus also provide invertebrates with a valuable food source and offers shade and a reprieve from predation (Minshall 1966; Gonçalves et al. 2004). Zebra mussels are negatively phototaxic and prefer shaded conditions on the underside of larger detrital substrates - a behavior that also offers some protection from known predators (e.g., freshwater drum

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**Table 1.** Linear electivity index (LEI) for each organic substrate type making up more than 1% of the total biomass of all samples from four Minnesota lakes, 2012–2015. Negative values denote avoidance and positive values indicate preference.

| Substrate          | LEI (All) | LEI (Juveniles) | LEI (Adults) |
|--------------------|----------|-----------------|--------------|
| Filamentous Algae  | 0.09     | 0.12            | 0.02         |
| Chara spp.         | −0.04    | −0.07           | 0.00         |
| Coontail           | 0.01     | 0.02            | −0.02        |
| Detritus           | 0.01     | −0.01           | 0.06         |
| Naiad spp.         | 0.00     | 0.00            | 0.01         |
| Northern Milfoil   | −0.02    | −0.01           | −0.03        |
| Potamogeton spp.   | −0.02    | −0.01           | −0.03        |
| Water Celery       | −0.02    | −0.03           | −0.01        |
Shrubs, riparian trees, and leaf litter are major contributors to lotic system energy cycles (Gessner and Chauvet 1997) and decomposition of these organic materials offers a link between primary and secondary producers (Fenchel 1970), offering zebra mussels a slower-changing attachment site. Detrital decomposition, specifically wood break-down, is a regional-temporal process that depends on local temperature, moisture, nutrient availability (Andersen et al. 2016), metabolic activity (Reddy and DeBusk 1991) and microbial community (Reshi and Tyub 2007). In areas where there are seasonal temperature changes, cooler fall and winter temperatures slow decomposition (Godshalk and Wetzel 1978) and offer zebra mussels a relatively stable attachment substrate until their reproductive months the following May or June. Although detritus has been well documented for zebra mussel settlement their effects on overland spread is likely very limited.

**Attachment to macrophytes**

In the present study, zebra mussels were shown to be generalists when attaching to macrophytes. Although the LEI suggested that zebra mussels were attaching to organic substrates largely based on the substrate’s abundance in the environment, other assessments suggest that zebra mussel attachment behaviors, based on life stage, may be different among the substrates (Table 1). Nevertheless, aquatic plants offer many benefits to aquatic systems, such as providing habitat and food for aquatic and terrestrial biota, stabilizing sediment, and improving water clarity (Smart et al. 1996; 2005; Knopik and Newman 2014).
The majority of annual aquatic plants are viable during the spring and summer months and start to senesce by early to late fall in Minnesota, while some perennial plants remain present year-round. Although not always homogenous, vertically available organic substrates are important for young zebra mussel settlement (Lewandowski and Ozimek 1997). Juvenile zebra mussels have the ability to form temporary byssal threads and can move more readily to a more optimal substrate (Toomey et al. 2002). In addition, juvenile zebra mussels possess the ability to settle out of the water column onto macrophytes and remain attached until decomposition (Lewandowski and Ozimek 1997). Despite zebra mussel juveniles’ ability to settle on macrophytes post-larval stage, not all macrophytes are elected equally.

Wild celery was used significantly less than all other available biologic substrates. Given wild celery’s thin leaves and vertical growth often reaching the surface, the plant’s morphology does not possess the characteristics often associated with zebra mussel settlement (seemingly preferring branching or horizontal movement within the water). Conversely, Skrip (2005) found that zebra mussels used water celery for attachment and development over the invasive water chestnut (Trapa natans). In these areas of dense Trapa beds, there was overall less dissolved oxygen present, resulting in fewer attached mussels. Water quality data were not collected on a regular basis nor did we have the ability or resources to collect these data in the current study. Settlement and attachment to organic substrates in different water quality conditions should be considered for future research.

Ozimek (1997) found the most suitable macrophyte substrates to be perennial, had long-term stability, and were branching. Najas spp. often form dense beds and offer heavily branched areas with a higher horizontal surface area that could assist in attachment, much like macroalgae. Ozimek (1997) and Lewandowski and Ozimek (1997) found the majority of the aquatic flora with attached zebra mussels included coontail, macroalgae, starry stonewort, and water-soldier (Stratiotes aloides), two of which are found in our study lakes. In addition, Eurasian watermilfoil (Myriophyllum spicatum), another invasive perennial plant species in Minnesota, has been noted as a reliable substrate for zebra mussel attachment most likely due to its branching morphology much like other native milfoils (Muskó and Bakó 2005; McComas et al. 2010). Mutualistic relationships among invasive species have been noted by others. For example, Crane et al. 2020 noted a relationship between European invaders, particularly between Nuttall’s waterweed (Elodea nuttallii) and zebra mussels. The authors also observed the presence of zebra mussels decreased the competition between native and invasive plants (Crane et al. 2020). There are several ways invasive plants can spread, including fragmentation, natural reproduction, and lastly through the movement of water-related equipment. If invasive plants such as Eurasian watermilfoil (and European invasive Nuttall’s waterweed) are a suitable substrate for zebra mussels, the accidental movement of these plants could also increase the likelihood of facilitating the introduction of zebra mussels.

**Attachment to algae**

The change in algal communities after an invasive species (e.g., zebra mussel) invasion has been widely studied. In Brazil, López and Coutinho (2010) found there to be a positive temporal correlation between the presence of macroalgae (Sargassum spp.) and the abundance of non-native bivalve Imbricaria bicolor. Much like macroalgae, filamentous algae abundance can also be altered with the introduction of zebra mussels. Multiple studies (e.g., Francoeur et al. 2015; Lowe and Pillsbury 1995; Stankovich 2004) noted an
increase in filamentous algae growth has been common in areas of the Great Lakes where zebra mussels may have altered the benthic environment. Vaughn et al. (2007) found dreissenid mussel filtration capabilities increased light penetration and relocated nutrients to the sediment in fecal deposits, thus creating a positive feedback loop that can enhance algal growth. In addition, both Chara spp. and zebra mussels require moderately hard water to maintain their growth. In areas where zebra mussels have completed their life cycles, decomposing shells could offer a rich calcium environment for Chara spp. to proliferate. Ultimately this cycle allows for the increase in opportunities for settling juvenile zebra mussels. Although this symbiotic relationship is widely understood and other marine relatives (e.g., Mytilus edulis) have been known to use algae for metamorphosis and development (Eyster and Pechenik 1988), no literature has cited or investigated the likelihood of zebra mussels to use algae as an attachment site.

Our research indicated a relationship between filamentous algae and zebra mussels that may be explained by their life cycle. Most zebra mussel juveniles appear in their planktonic form in May or June, grow up to 220 μm, until becoming heavy enough to settle out of the water column (Martel 1995; Kobak 2001). Similarly, depending on species, filamentous algal blooms occur in spring and summer (May through August) when chlorophyll-a is abundant (Kiirikki and Lehvo 1997; Berry and Lembi 2000; Nozaki et al. 2003). Shortly after, filamentous algae rapidly photosynthesizes, creating oxygen underneath algal aggregates, allowing algae to range from benthic to floating (Berry and Lembi 2000). If filamentous algae mats are present, juvenile zebra mussels may often settle on top of the mats or become passively entangled in filaments. The LEI indicated slight selection for filamentous algae and slight avoidance of Chara spp. by juveniles, an observation that could simply be explained by the position of the organic substrates in the water column (Table 1). Nevertheless, macroalgae grows in dense patches (e.g., >300 g·m⁻²) in many Minnesota lakes, creating ample opportunities for adult zebra mussel attachment and possible refuge from predatory fishes (Engel 1988; Ozimek 1997). Ozimek (1997) found that coontail and Chara spp. are the dominant organic substrates harboring zebra mussels in Europe. Other invertebrates such as ostracods (Cypridopsis vidua) were found to use Chara spp. as refuge from predators with an 80.2% survival rate in high density locations, while only 30.75% survived without plant cover (Roca et al. 1993).

In Minnesota waters, there are several macroalgae and filamentous algae often including filamentous taxa such as spirogyra and cladophora (Minnesota Department of Natural Resources [MnDNR]) 2017b) that could be used as an attachment site in infested waters. Starry stonewort (Nitellopsis obtusa), an invasive macroalgae, was discovered in 2015 and may theoretically serve as yet another suitable attachment substrate for zebra mussels. Starry stonewort has been suggested to be favorable for zebra mussel attachment, but the relationship has not been fully investigated (Crawford 2011). However, in 2020, Harrow-Lyle and Kirkwood (2020) found zebra mussel biomass being facilitated by the presence of N. obtusa, most likely due to the macroalgae’s branching calcified structure. In contrast to Chara spp, starry stonewort can attain denser growth and extend higher (7 feet and to a water depth of 29 feet [Pullman and Crawford 2010]) in the water column, creating a much higher physical habitat than native macroalgae. In areas where starry stonewort has been introduced, its colonization has increased the biomass available for zebra mussel settlement and recruitment. Minnesota DNR watercraft inspectors have observed this invader wrapped around boat propellers, ultimately increasing the likelihood of zebra mussel movement.
Conclusion

Organic substrates for zebra mussels’ attachment have not been given enough attention in the North American invaded range. While organic substrates such as detritus, macrophytes, and algae may make up a smaller habitat component than inorganic substrates, they are nonetheless important to zebra mussel populations, especially in new juvenile zebra mussel recruitment. Detritus and algae, such as Chara spp., offer ample attachment sites and reprieve from predators. LEI indicated notable juvenile selection for filamentous algae but all other substrates were being used randomly based on their abundance in the environment. Although filamentous algae may not serve as a long-term sustainable substrate for zebra mussel attachment, this observation has the potential to be something of interest in areas with hypereutrophic and eutrophic lakes and is worthy of additional study.

Benthic changes in nutrients and plant growth patterns caused by zebra mussel introduction can facilitate novel relationships and create opportunities for other invasive species to establish and become transported by boaters. Pathways of invasive plant spread include fragmentation, natural reproduction, and the movement of water-related equipment between waterbodies. Given humans’ highly transient use of water resources, coupled with the zebra mussel’s perceived attachment to submersed aquatic macrophytes and algae, the involuntary movement could increase the likelihood of zebra mussel spread and invasion. Therefore, organic substrates should be considered when searching for new populations, monitoring existing populations, and preventing spread via watercraft. An additional consideration for lake managers may be to consider aquatic vegetation management at heavily used public water access sites in invaded lakes to reduce the risk of zebra mussel spread. Understanding these complex relationships could inform aquatic invasive species policies and management decisions moving forward.

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