SPREAD, POPULATION DYNAMICS AND ECOSYSTEM IMPACTS OF ZEBRA *VERSUS* QUAGGA MUSSELS: WHAT DO WE KNOW AND WHAT WE DO NOT?

Alexander Karatayev
Great Lakes Center, SUNY Buffalo State
The most aggressive invaders in freshwaters of the Northern Hemisphere have similar life habits and similar life history characteristics. They co-occur in their native habitat but are very different in the timing of spread:

- Zebra mussel has been an important invader in Europe since early 1800s, while quagga mussels - since late 1940s.
- Both species colonized North America at the same time (1980s).
By the time of invasion of North America, zebra mussel was much better studied than quagga mussel

- Many aspects of the spread, biology, and ecosystem impacts of *Dreissena* on the North American freshwaters could be predicted based on European experience for zebra, but NOT for quagga mussels.
- North American studies became critically important in improving our knowledge on quagga mussel.

<table>
<thead>
<tr>
<th>Period</th>
<th># <em>Dreissena</em> spp. papers</th>
<th>Papers per year</th>
<th>% Quagga mussels</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1771-1963</td>
<td>1180</td>
<td>6</td>
<td>2 (15)</td>
<td>Limanova 1964</td>
</tr>
<tr>
<td>1964-1978</td>
<td>740</td>
<td>39</td>
<td>8 (60)</td>
<td>Limanova 1978</td>
</tr>
<tr>
<td>1964-1993</td>
<td>885</td>
<td>30</td>
<td>6 (53)</td>
<td>Schloesser et al. 1994</td>
</tr>
<tr>
<td>1993-2010</td>
<td>1147</td>
<td>64</td>
<td>17 (192)</td>
<td>Schloesser &amp; Nalepal 2012</td>
</tr>
<tr>
<td>TOTAL</td>
<td>3950</td>
<td></td>
<td>320</td>
<td></td>
</tr>
</tbody>
</table>
Outline:

- Review what is known about:
  - life history parameters
  - population dynamics
  - environmental factors
  - spread
  - impacts

- Identify similarities and contrast important differences between these species

- Identify important gaps in our knowledge that should be research priorities for these two important invaders
Life History Characteristics

Reproduction:

- Because of fewer studies on quagga mussels, often biology and potential impacts of quagga are assumed to be the same as zebra mussels (Keller et al. 2007; Ward, Ricciardi, 2007; Higgins & Vander Zanden 2010; Kelly et al. 2010)

- Fecundity of zebra mussels are well-known, but comparable information for quagga mussels is lacking

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Zebra mussel</th>
<th>Quagga mussel</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fecundity</td>
<td>300,000 – 1,700,000 (Lvova 1977; Sprung 1991; Neumann et al. 1993)</td>
<td>???</td>
</tr>
</tbody>
</table>
Life History Characteristics

Reproduction:

**Zebra mussel**

- **In warm water** gonads are fully developed by spring and spawning occurs in summer. Unspawned eggs resorb in winter *(Lvova & Makarova 1994)*

- **In cold deep water** mussels have ripe gonads for extended periods of time and may spawn fewer eggs at once over many months *(Bacchetta et al. 2010)*

**Quagga mussel**

- There are few data following gonad production throughout the year in either shallow or deep waters, and few studies have examined gonad development in quagga mussels *(Nalepa et al. 2010)*
Reproduction:

- Zebra mussels usually initiate spawning in May-June, at 12 - 15°C and continue to spawn until August-September (Sprung 1987; Borcherding 1991; Lvova et al. 1994a; Karatayev et al. 1998, 2010; Pollux et al. 2010).

- Quagga mussels may spawn at colder temperatures in the profundal zones of deep lakes (Roe & MacIsaac 1997; Claxton & Mackie 1998; Nalepa et al. 2010).

- In Lake Michigan at 25 m depth, all females had mature oocytes in early April but did not spawn until September (when temperature reached maximum 19.7°C) and lasted through November (Nalepa et al. 2010).

- At 45 m depth, all females were mature by late April and spawning started in early June (temperature increased from 2°C to 6.0°C) and was complete by early August (Nalepa et al. 2010).

**More work is needed to determine spawning cues for quagga mussels, especially those found at different water depths**
# Life History Characteristics

## Growth:

<table>
<thead>
<tr>
<th>Factor</th>
<th>Zebra mussel</th>
<th>Quagga mussel</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td><strong>Faster in the water column than on the bottom</strong> <em>(Kachanova 1963, Spiridonov 1971, Kornobis 1977, bij de Vaate 1991, Yu &amp; Culver 1999)</em></td>
<td><strong>No data</strong></td>
</tr>
<tr>
<td>Depth</td>
<td><strong>Growth decreases with depth</strong> <em>(Mikheev 1964, Garton &amp; Johnson 2000)</em></td>
<td><strong>No data</strong>*</td>
</tr>
</tbody>
</table>

*We do not know the effects of depth on the quagga mussel growth, however their average length in deep parts of Lake Erie was larger than in the littoral zone, suggesting either the faster growth or greater longevity.*

However, studies based on field observations during the winter, when low temperatures are coincident with low phytoplankton abundance

During summer, in Lake Erie water, both zebra and quagga mussels grow at <7°C, supporting the hypothesis that it is the lack of food rather than low temperatures per se that limits the growth during winter (Karatayev et al. 2010)

Quagga grow faster and had lower mortality than zebra mussels both at the low and high temperature (Karatayev et al. 2010)
**Life History Characteristics**

*Growth:*

- Quagga have a positive growth rate at low food concentration compared to zebra mussels, which lose weight when subjected to low food levels *(Baldwin et al. 2002; Stoeckmann 2003)*

- In the benthic environment of Lake Erie zebra mussel size much smaller than that of quagga mussels, and their growth rate is also likely to be slower *(Karatayev et al. in review)*

- In contrast, in the water column young-of-the-year zebra mussels are significantly larger than quagga mussels, suggesting either higher growth rate (due to better food and other conditions) or size selective survivorship *(Karatayev et al. in review)*
Population Dynamics

- Few studies have followed zebra mussel populations from initial invasion through time and even fewer studies have been done on quagga mussels.

- Initially, populations attain very high densities, but because of density-dependent processes, total sustainable biomass declines, and densities well below the maximum achieved persist \( (Karatayev \text{ et al.} \ 1997, \ 2002) \).
The time lag between when a species was first detected and when it reached its maximum population density is 5 times shorter for zebra than for quagga mussels ($P < 0.001$) (Karatayev et al. 2011).

- **zebra mussel:** $2.4 \pm 0.2$ years ($n = 12$)
- **quagga mussel:** $12.2 \pm 1.5$ years ($n = 9$)

The shorter lag time for zebra mussels may be the key to their invasion success and the more rapid spread of zebra mussels relative to quagga mussels. The longer lag time for quagga may indicate that their fecundity is lower than zebra mussels, especially in profundal zone, or they do not reproduce every year.
As *D. polymorpha* was first found in Lake Erie in 1986 \cite{Carlton2008}, zebra mussels likely reached their maximum around 1989.

However, the first lake-wide study of *Dreissena* spp. distribution was conducted in Lake Erie only in 1992, when *D. polymorpha* may have already passed its maximum and had already been in decline.

Although it is likely that quagga plays an important role in the decline of zebra mussels, we do not know what the population dynamics of the zebra mussels would be in the absence of quagga mussels.

We need more studies that follow *Dreissena* spp. populations from initial invasion through time.
### Environmental factors

<table>
<thead>
<tr>
<th>Factors</th>
<th><em>D. polymorpha</em></th>
<th><em>D. r. bugensis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper temperature limit (°C)</td>
<td>33</td>
<td>31</td>
</tr>
<tr>
<td>Minimal temperature for reproduction (°C)</td>
<td>12 - 15</td>
<td>6</td>
</tr>
<tr>
<td>Lower oxygen limit at 20°C (mg L⁻¹)</td>
<td>1.8 - 2.4</td>
<td>1.5</td>
</tr>
<tr>
<td>Upper salinity limit</td>
<td>6</td>
<td>3.5</td>
</tr>
<tr>
<td>Lower calcium limit (mg L⁻¹)</td>
<td>23 - 25</td>
<td>No data</td>
</tr>
<tr>
<td>Lower pH limit</td>
<td>7.3 - 7.5</td>
<td>No data</td>
</tr>
<tr>
<td>Tolerance to wave activity and currents</td>
<td>Higher</td>
<td>Lower</td>
</tr>
</tbody>
</table>

- **Zebra mussels** are better adapted to the unstable littoral zone with high fluctuations in water current, temperature, and waves *(Peyer 2009)*
- **Quagga mussels** may prefer the stable environment of the cold deep profundal zone
- **During Miocene-Pliocene, in the Pannon basin, Europe, over 130 dreissenid species occupied all substrates from shallow littoral to silty profundal zone** *(Geary et al. 2000)*
Reports from Europe (Zhuravel 1952, 1965; Orlova et al. 2004, 2005; Zhulidov et al. 2010) and North America (Mills et al. 1996; Watkins et al. 2007; Dermott & Dow, 2008; Nalepa et al. 2009, 2010) show that in waterbodies where both species co-occur, quagga mussels replace zebra mussels after 9 or more years of coexistence (Karatayev et al. 2011).
Lake Erie

(Karatayev et al. in review)
• In invaded lakes with a small or no profundal zone and rivers, zebra mussels often dominate, or the two species co-dominate, even after 20 years of coexistence.

• Within their native range in the Dnieper-Bug Liman, zebra mussels and quagga mussels are co-dominants; each species may be more abundant in different years.

**Don River, Russia (Zhulidov et al. 2006)**

**Western Basin**

**Relative abundance of quagga mussels in Don River (from Zhulidov et al. 2010)**

**Dreissena spp. dynamics in Western Erie (Karatayev et al., in review)**
Mechanisms for Displacement

- Quagga mussels may have higher filtering rates, allowing them to outcompete zebra mussels if food is limited (Diggins 2001)

- Quagga mussels may spawn at lower temperatures earlier in the season, allowing them to outcompete zebra mussels for open space for attachment (Roe & MacIsaac 1997; Claxton & Mackie 1998)

- Genetic adaptation may allow quagga mussels to expand from deep, cold-water habitats into shallow waters (Mills et al. 1996)

- Quagga mussels may have a higher energetic efficiency, allowing them to achieve higher growth rates at low food concentrations (Mills et al. 1996, 1999; Baldwin et al. 2002; Stoeckmann 2003)
• By creating extremely high densities in profundal zone, quagga produce more larvae than the zebra mussels, and simply outnumber *D. polymorpha*.

• With time, *D. r. bugensis* becomes dominant in all habitats, including the littoral zone.

• In contrast, in rivers and shallow lakes quagga may not outcompete zebra mussels.

• Therefore, in contrast to the deep eastern basin, in the shallow western basin of Lake Erie zebra mussels may sustain a significant presence for decades without being displaced by quagga mussels.
Because dreissenids are important invaders, we have very good data on the geographic extent of their spread as well as the timing of invasion by each species in different waterbodies and different countries.
Cumulative spread of zebra mussel on a global scale

- **Initial exponential spread**: After the construction of interbasin canals in late 1700 – early 1800s, zebra mussels spread across Europe for 70 years.

- At the time of the industrial revolution and increased pollution, the spread of zebra mussels in Europe stopped.

- **Second exponential spread**: Zebra mussels invasion into North America, and expansion in Europe (Alpine lakes, Ireland, Italy and Spain).

- During the **initial spread**, zebra mussels colonized ~3.9 regions per decade.

- During the **second spread**, zebra mussels colonized ~6.6 regions per decade.

Zebra mussel spread at a global scale *(Karatayev et al. 2011)*
Although there was extensive ship traffic, the quagga mussel remained restricted to their native range until the middle of the 20th century.

Why did the mechanisms and vectors of spread used successfully by zebra mussels not work for quagga mussels?
In the 19th century *Dreissena* spread through canals and rivers in Europe attached to vessels and rafts, therefore, attachment strength was critically important for successful invasion.

Zebra mussel has a greater rate of byssal thread production and higher attachment strength than quagga mussel (Peyer et al. 2009), which may facilitate its attachment to boats.

Habitats initially colonized by zebra mussels were mostly shallow areas of rivers and canals. These habitats are excellent environments for zebra mussels, but quagga mussels prefer quiet areas of deep waterbodies.
What facilitated Quagga Mussel Spread??

1. Newly constructed reservoirs became the “stepping stones” for the invasion

2. New vectors of spread became available:
   - ballast water
   - canals became larger than in the 19th century
   - increased rate of commercial and recreational ship traffic
   - overland movement of pleasure boats
The rate of quagga mussel spread on a global scale

- is significantly faster than that of zebra in the 19th century
- not different from the recent rate of zebra mussels spread
Although both species were introduced into North America at the same time, by 2010 *D. polymorpha* had colonized:

- **twice** as many states as *D. r. bugensis*
- **7 times** more counties
- **15 times** more waterbodies than *D. r. bugensis*

...why?
Zebra and quagga spread in US at different spatial scales

- The lag time between initial introduction and when the population reaches maximum abundance is **5 time shorter for zebra** than for quagga mussels.
- This shorter lag time may be the key to zebra mussel invasion success.
- The ability of zebra mussels to rapidly capitalize on secondary spread is likely responsible for the escalating rates of spread.
- However, as more lakes are invaded by quagga mussels it is likely that secondary spread will become more important, allowing quagga mussels to have an increased rate of spread at all spatial scales.

![Graphs showing spread of zebra and quagga mussels](image-url)
Could Lower Great Lakes still be a source of zebra mussels invasion?
Initially zebra mussels dominated the Great Lakes, the major source for the secondary spread in the US.

Recently, quagga mussels almost completely replaced zebra mussels in Lake Ontario and eastern basin of Lake Erie.

As a consequence, we may suggest that recreational boats from the Great Lakes are now more likely to be transporting quagga than zebra mussels.

![Relative abundance of quagga mussels in the Lower Great Lakes](chart.png)
Lower Great Lakes are still a source of zebra mussels invasion

- Surveyed 200 boats from eastern Erie and Ontario (*Vadim Karatayev in review*)
- Although quagga mussels compose ~ 99% of dreissenids in lakes, on boats, zebra mussels were often more abundant and were larger than the quagga mussels
- Lower Great Lakes are still a source for the spread of zebra mussels, and for some vectors, the propagule pressure from zebra mussels is likely greater than for quagga mussels
Both zebra and quagga mussels have all of the properties of ecosystem engineers (Karatayev et al. 2002, 2007; Vanderploeg et al. 2002; Higgins and Vander Zanden 2010).

They change the characteristics of both abiotic and biotic environments in aquatic systems by creating 3-D structure and providing food and shelter for benthic invertebrates (Local effects).

System-wide changes are caused by their feeding and filtering activities.

Although both species have similar life history characteristics, they have different population dynamics and distributions within waterbodies and therefore may have different local or system-wide effects.
• Zebra have higher attachment strengths *(Peyer et al. 2009)*, which allows them to create larger druses than quagga mussels and therefore **have greater local impacts**

• Zebra mussels are limited to the littoral zone while quagga mussels can also colonize profundal zone and therefore the **extend of their local impacts may be larger**
Local impacts of zebra mussels in littoral zone:

- Increased habitat complexity in zebra mussel aggregations, coupled with organic enrichment, induced profound changes in community diversity, trophic structure, and interspecies links, creating different community in druses compared to nearby sediments (Lvova-Kachanova & Izvekova, 1978; Sokolova et al., 1980a; Karatayev & Burlakova, 1992; Burlakova et al., 2005; 2011; Ward & Ricciardi, 2007; Higgins & Vander Zanden, 2010).

- However, due to the patchy distribution of druses, part of the littoral is not colonized and supports community typical of bare sediments.

- We do not have parallel data for the quagga mussel.
Littoral vs. profundal zone:

- In the littoral zone, zebra mussels multilayered druses attract isopods, amphipods, gastropods, mayflies, trichopterans, oligochaetes, chironomids, etc. by providing shelters and food (Sokolova et al. 1980a; Karatayev & Lyakhnovich 1990; Karatayev & Burlakova 1992; Botts & Patterson, 1996; Ricciardi et al. 1997; Stewart et al. 1998a; Karatayev et al. 2002; Ward & Ricciardi 2007; Burlakova et al. 2011).

- In the profundal zone, quagga mussels are often more evenly distributed across silty bottom without forming multilayered isolated druses. Therefore, habitat provided by the zebra and quagga mussels could be different.

- In contrast to the littoral zone, there are no similar invertebrates in the profundal that may take advantage of the presence of *Dreissena*.

High unionid mortality is typical during initial invasion, when zebra mussels density is high. The effects on unionids may decrease with time as the population of zebra mussel stabilizes or decreases.

Studies from waterbodies colonized with zebra mussels for long periods of time show that unionids have not been extirpated from any of them (Lewandowski 1976; Karatayev et al. 1997; Miroshnichenko 1987; Ponyi 1992; Burlakova et al. 2000).
Although there are no comparable information on the impacts of quagga, their impacts may be smaller than those of zebra mussels

Lower Great Lakes, 2011-2012 data:

- > 90% of all *Dreissena* in these lakes were quagga mussels
- > 60% of all mussels attached to unionids were zebra mussels
  - From 3,614 live unionids collected only 30% had attached *Dreissena*
  - Additional 42% had byssus threads remains on their shells
  - Median number of attached *Dreissena* per live unionid was 3
System wide impacts:

- The system-wide effects of dreissenids are associated with their role as biofilters and is determine by their total population size in a waterbody.
- By clearing large volumes of water, dreissenids transfer materials from the water column to the benthos, providing a strong direct link between planktonic and benthic components of the ecosystem, and induce major changes including:

  **increase in:**
  - water transparency
  - macrophyte growth

  **decrease in:**
  - phytoplankton
  - zooplankton, suspended mater

![Diagram showing system-wide impacts](image)
**Zebra vs. quagga mussels:**

- Depending on water mixing rates, lake morphology, and turnover rates, zebra mussels will have very different effects *(Reed-Andersen et al. 2000)* and may be very local in deep water lakes *(Ackerman et al. 2001)*.

- Because quagga are found throughout the whole waterbody, rather than concentrated in the littoral zone, they are likely to have larger total population sizes than zebra mussels.

- Therefore, quagga may have a greater system wide effect than zebra mussels in deep lakes and reservoirs with large profundal zones.

- However, zebra mussels in the well mixed littoral zone may have a greater impact on the whole water column above them, while quagga mussels below thermocline may not have strong impacts on the epilimnion.
Dianna Padilla
Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY USA

Lyuba Burlakova
Great Lakes Center, Buffalo State College, Buffalo, NY, USA
Questions?