# The benthification of freshwater lakes: Exotic mussels turning ecosystems upside down Collaborators

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### **Dreissenid Mussels & Benthification**

- High population density
- High filtration rate

**Increased water clarity** 

**▶** Form clusters

**Increased benthic structure** 





### Dreissena are Ecosystem Engineers

Organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials.

Jones et al. 1994

#### Ecology, Ricklefs & Miller, 2000

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### **Population Interactions**

**Resources and Consumers** 

**Competition Theory** 

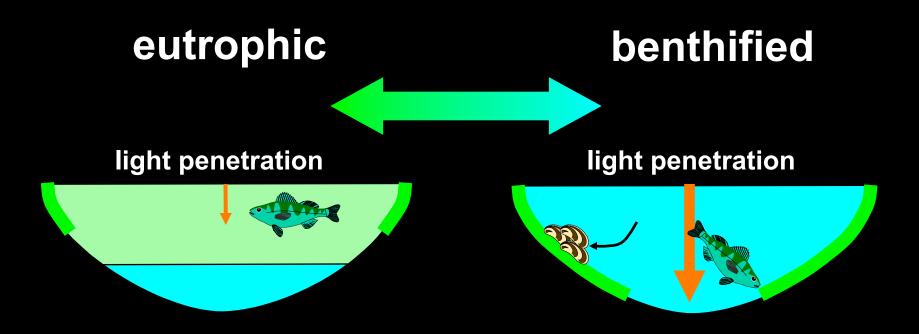
**Competition in Nature** 

**Predation** 

**Herbivory and Parasitism** 

**Coevolution and Mutualism** 

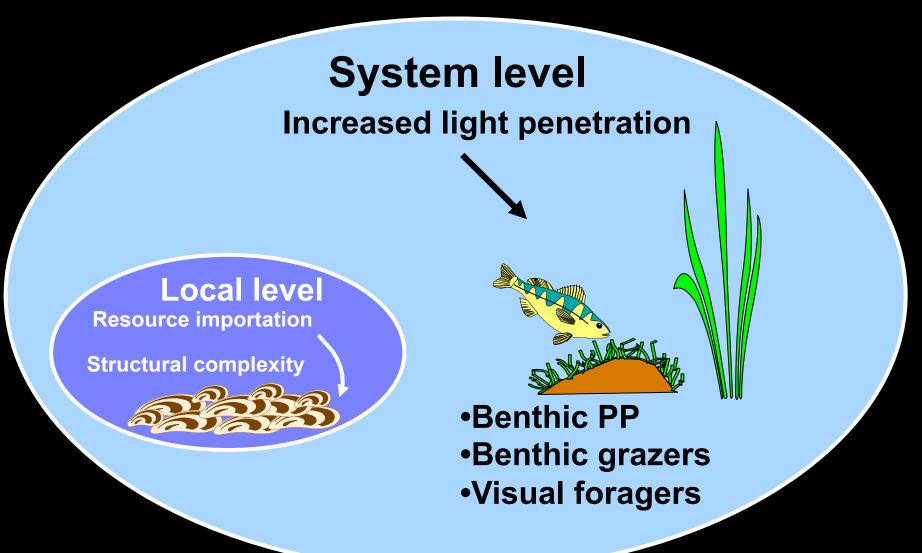
### Suite of expected changes with benthification



- → Limited benthic production
- **→** Low benthic complexity
- → Low foraging efficiency by benthic fish (low benthic to pelagic flux)

- **→**Extensive benthic production
- → High benthic complexity
- → High foraging efficiency by benthic fish (high benthic to pelagic flux)

# Dreissena affect lakes at multiple spatial scales and across trophic levels



**→** Primary production

**Macrophytes:** System-wide

Algae: System-wide & Local

Benthic populations

**Microbes: Local** 

Macroinvertbrates: System-wide & Local

**→** Primary production

**Macrophytes: System-wide** 

Algae: System-wide & Local

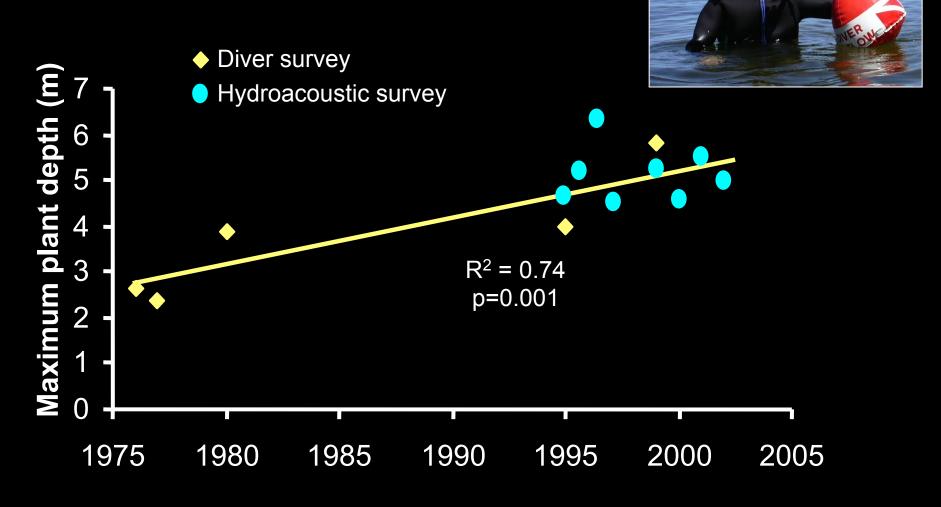
**→** Benthic populations

**Microbes: Local** 

Macroinvertbrates: System-wide & Local



- → SAV maximum depth increased after *Dreissena*
- → Species evenness increased
- → Myriophylum only spp to decrease



Zhu et al. 2006 Ecosystems 9:1-12

**→** Primary production

**Macrophytes: System-wide** 

Algae: System-wide & Local

**Oneida Lake** 

**Experiments** 

Local mechanisms

**→** Benthic populations

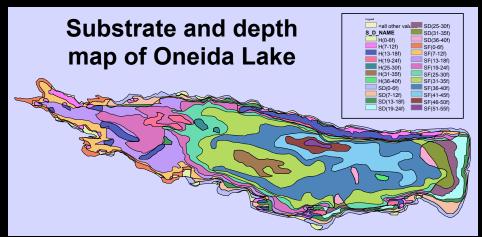
Microbes: Local

Macroinvertbrates: System-wide & Local

# Response of benthic algal primary production to increased clarity in Oneida Lake



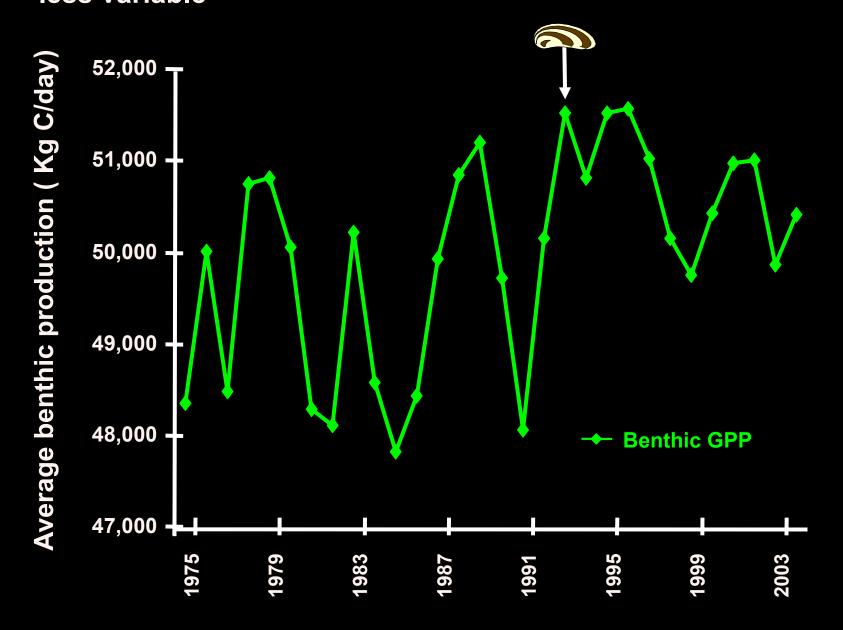
- o Whole lake GPP 2003 & 2004
- oLight response curves (N ~ 200) & modified Fee model to estimate production
- Back casting using long-term clarity data



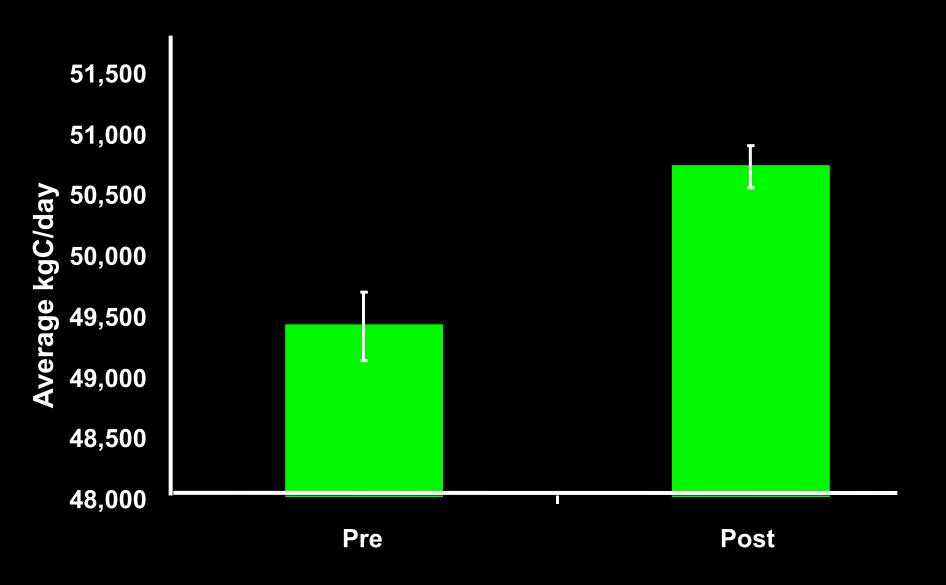
# Diver collecting surface core to measure primary production on soft sediment



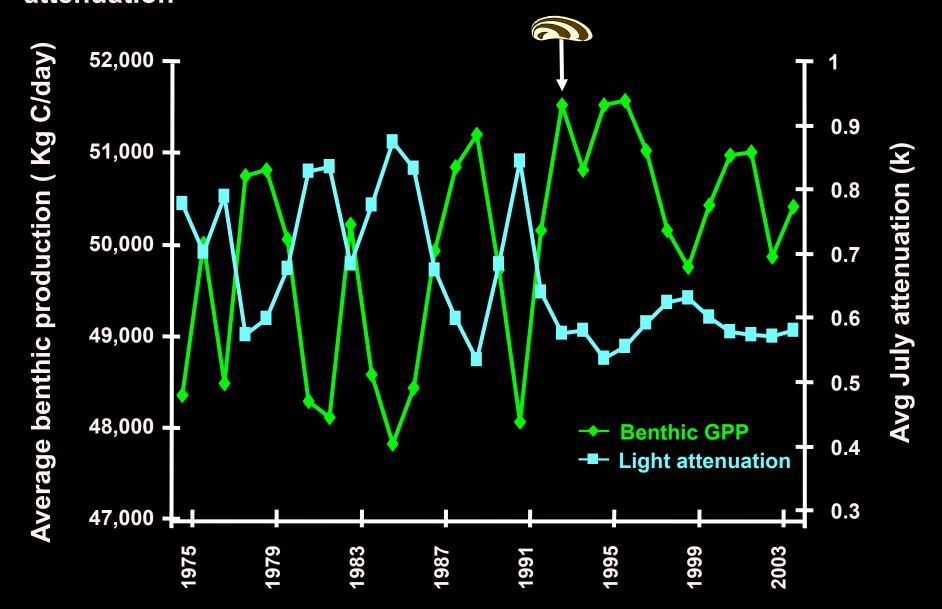
Whole-lake summer benthic GPP has increased and become less variable



## ~4% increase, was net change & included areas of reduced production due to photoinhibiton



Benthic GPP has become less variable following changes in attenuation



**→** Primary production

**Macrophytes: System-wide** 

Algae: System-wide & Local

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**→** Benthic populations

Microbes: Local

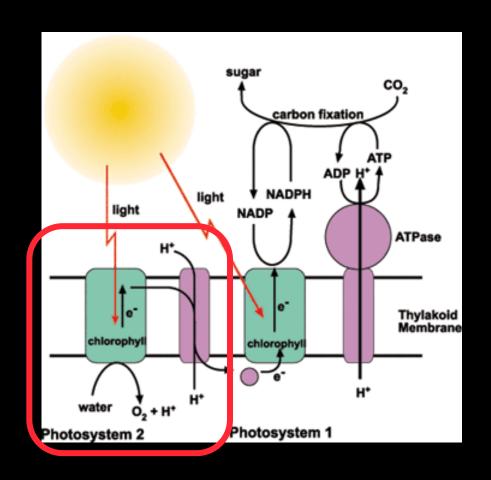
Macroinvertbrates: System-wide & Local

# Experimental Approach: light x *Dreissena* x P x other grazers w/ Kim Schulz, Peibing Qin, Xinli Xi



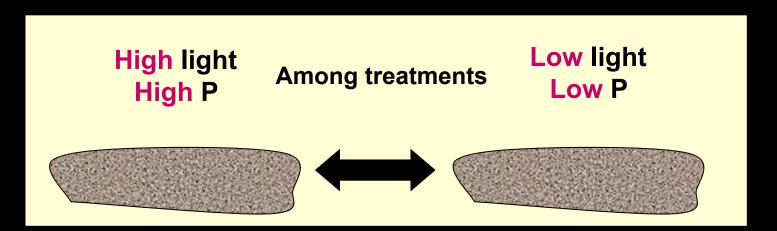
# Fluorometric measure of photosynthesis



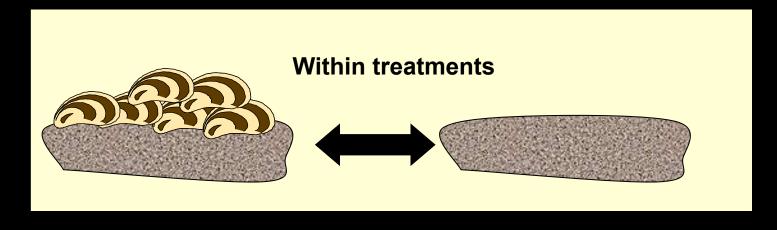


Electron Transport
Rate (ETR) =
proportional to
photosynthesis

# ⇒ System wide and localized effects of *Dreissena* on *Cladophora*-dominated algal community



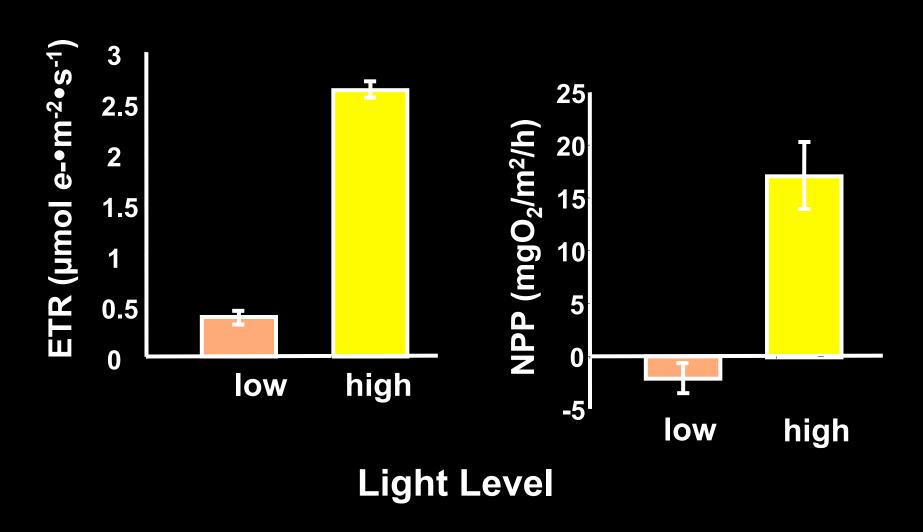
Systemwide effects



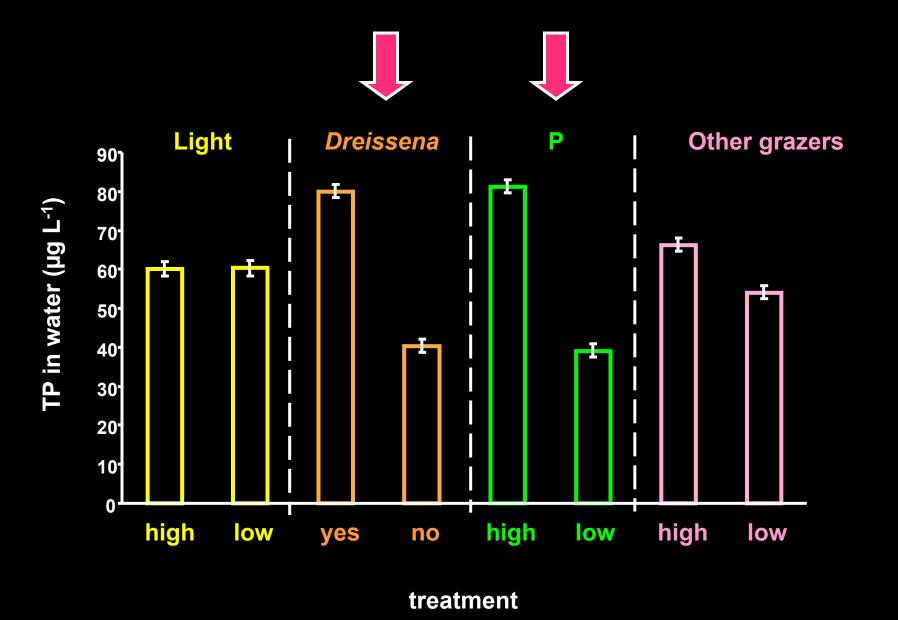
Localized effects

#### ⇒ Light (but not P) strongly affected both NPP and ETR

Non-colonized rocks (system wide effect)

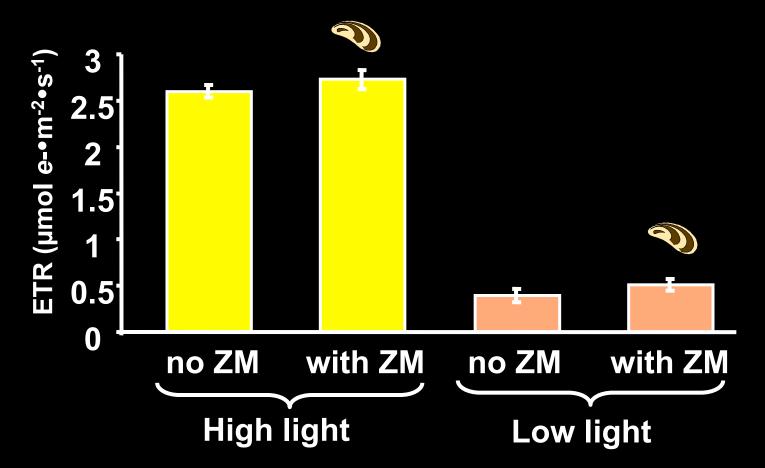


### ⇒ *Dreissena* sequestered P in experimental mesocosms, mimicking near shore shunt



### **Localized Effects**

- ⇒ETR higher with *Dreissena* at both high & low light
- ⇒Statistical model accounts for other- treatment variance
- **⇒ Difference small compared to light effect**



→ Primary production macrophytes: System-wide algae: System-wide & Local Oneida Lake Experiments Local mechanisms

→ Benthic populations microbes: Local macroinvertbrates: System-wide & Local

# Do *Dreissena* contribute nutrients to promote algal blooms? Manipulative experiment with *Lyngbya wollei*



Patricia Armenio; MS student U. Toledo



Live *Dreissena* (N=10)



Dreissena shells (N=10)

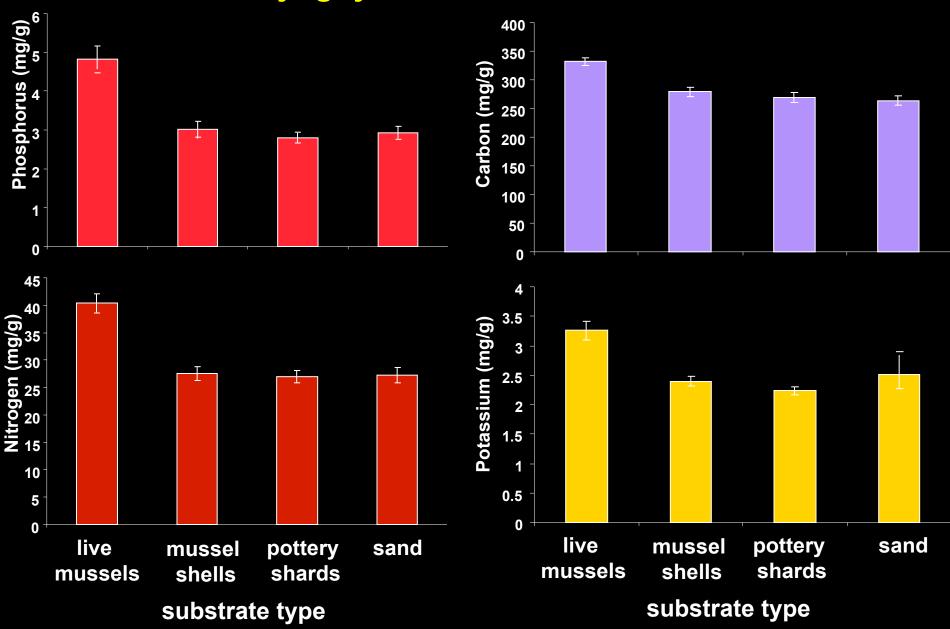


Pottery shards (N=10)

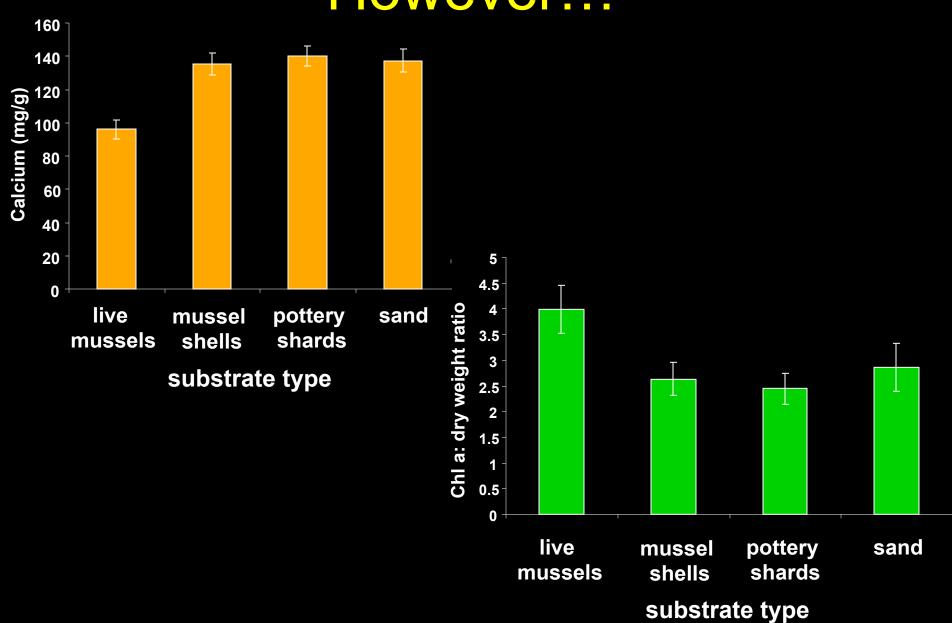


Sand (N=10)

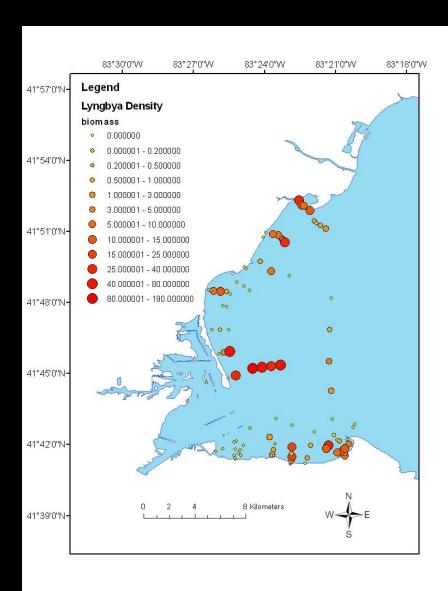
# No mass change, but *Dreissena* contributed some nutrients to *Lyngbya*

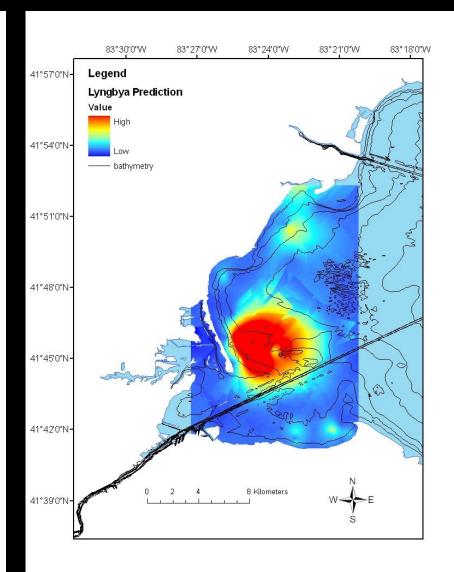


### However...



### Lyngbya density in western Lake Erie





### **Conclusions**

- 1. Increased water clarity, hence bottom light promotes increased benthic PP, both plants and algae
- 2. Dreissena also increase benthic algal photosynthesis at local scale
- 3. Transfer of nutrients is a possible mechanism for local-scale effects— work in progress
- 4. When ZM aggregations are large, they may elevate water column P and other nutrients and thereby increase benthic algal photosynthesis, Near Shore Shunt

**→** Primary production

**Macrophytes: System-wide** 

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Local mechanisms

Benthic populations

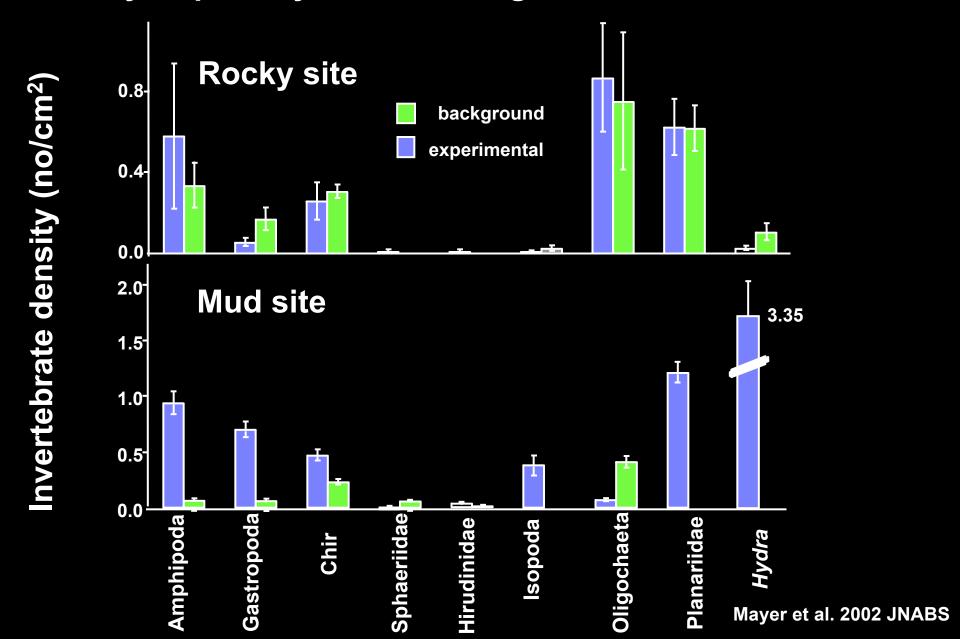
**Microbes: Local** 

Macroinvertbrates: System-wide & Local

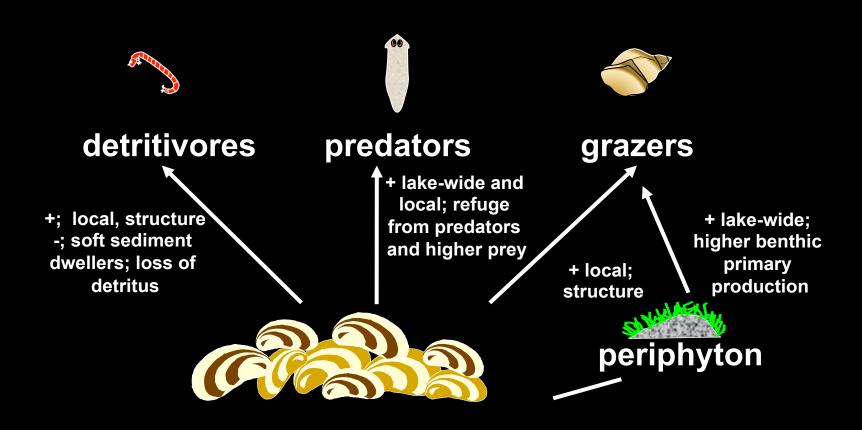
**Hard substrate-Oneida Lake** 

Soft substrate-western Lake Erie

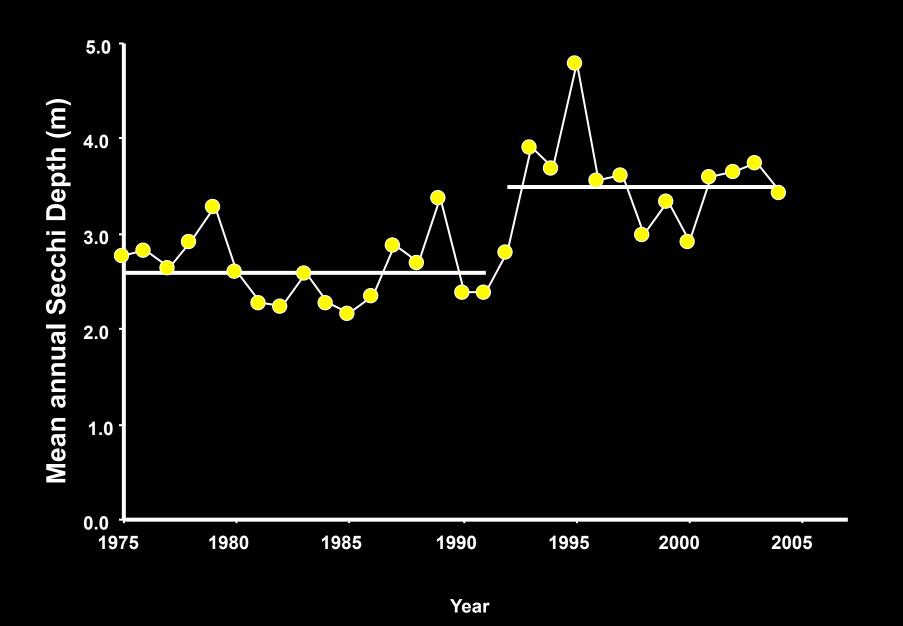
Dreissena attached to hard substrate increase invertebrate density, especially on soft background



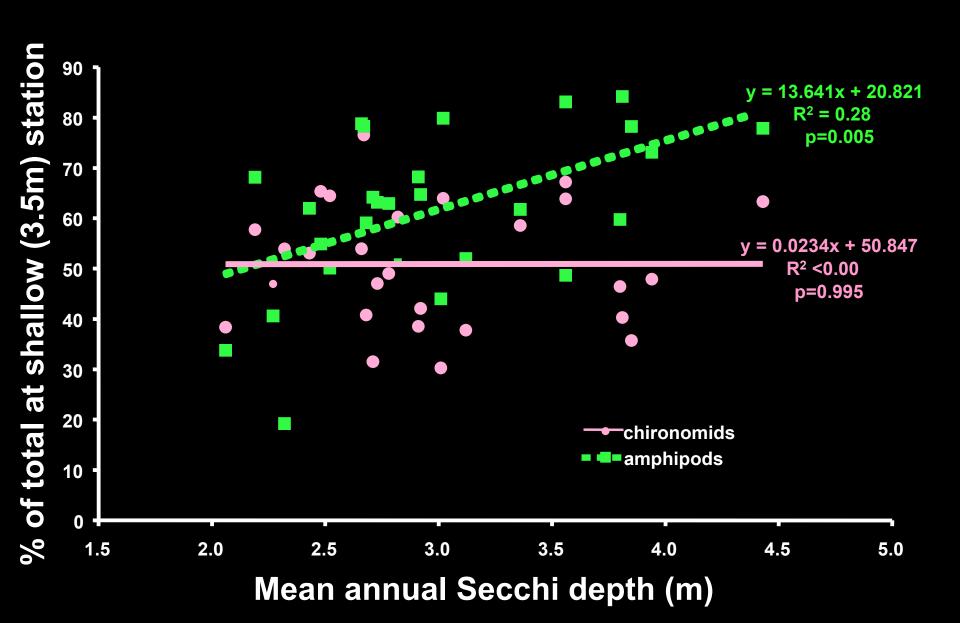
## Combined lake-wide and local effects of *Dreissena* may favor grazers and predators



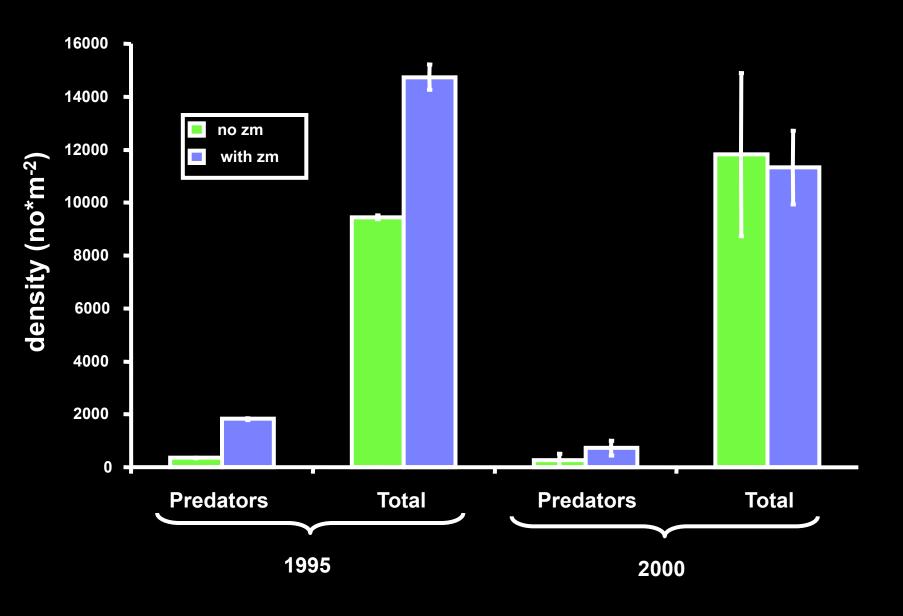
#### Water clarity and benthic GPP have increased in Oneida Lake



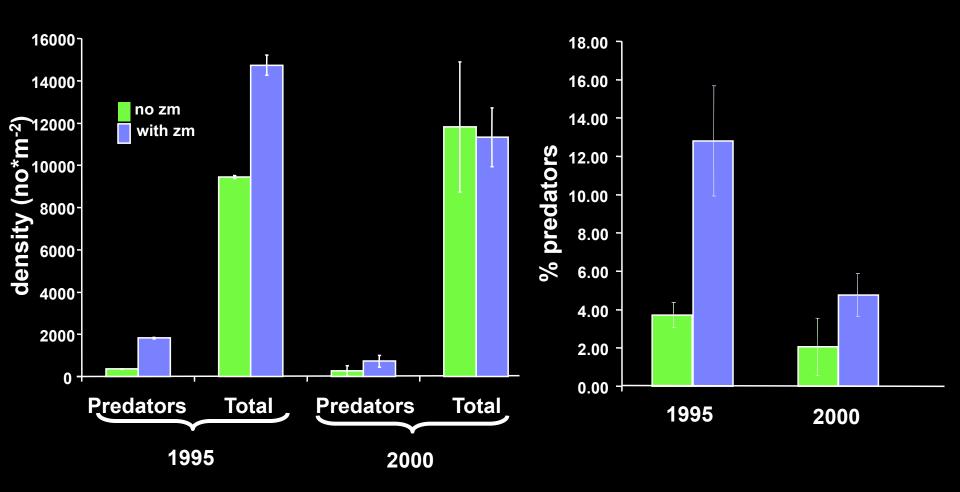
### As water clears, relatively more amphipods, but not chironomids found at shallow station



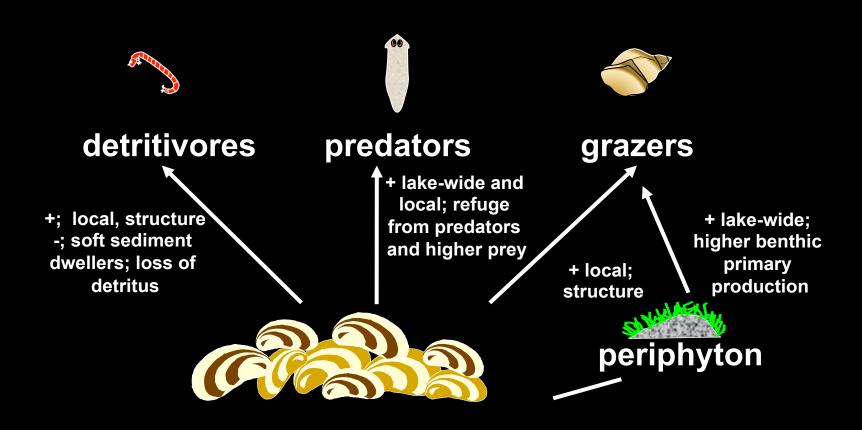
### Periodic intensive survey of embayment shows predatory taxa higher in *Dreissena*-colonized habitats



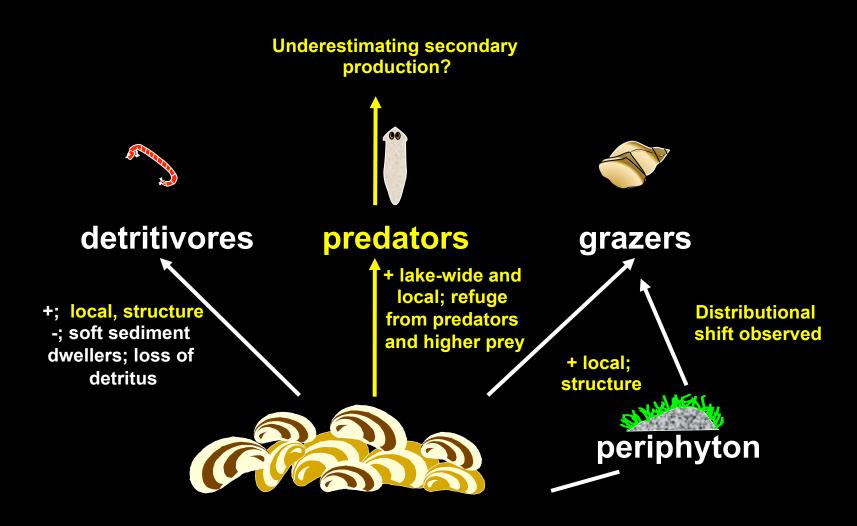
#### Percent predatory taxa consistently higher with Dreissena



### Combined lake-wide and local effects of *Dreissena* may favor grazers and predators



### Combined lake-wide and local effects of *Dreissena* may favor grazers and predators



#### Benthic Processes Affected by Dreissena

**→** Primary production

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Algae: System-wide & Local

**Oneida Lake** 

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Local mechanisms

**→** Benthic populations

**Microbes: Local** 

Macroinvertbrates: System-wide & Local

**Hard substrate-Oneida Lake** 

Soft substrate-western Lake Erie

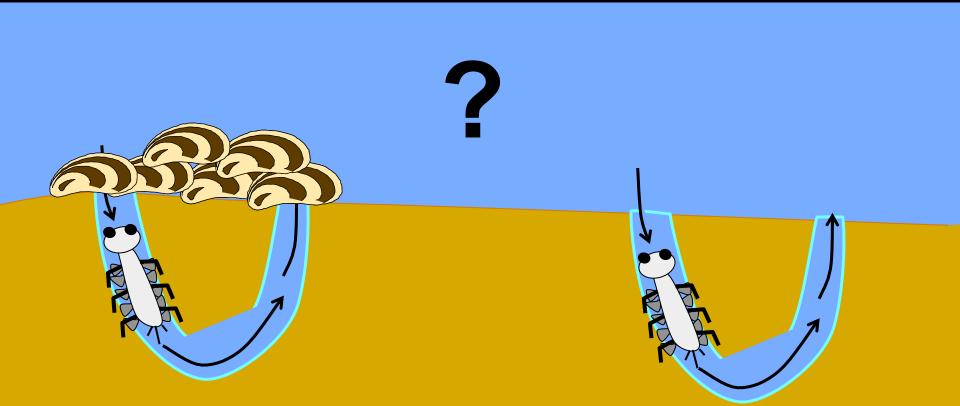
→ Visual foragers: System-wide & Local



Kristen DeVanna; PhD student U. Toledo

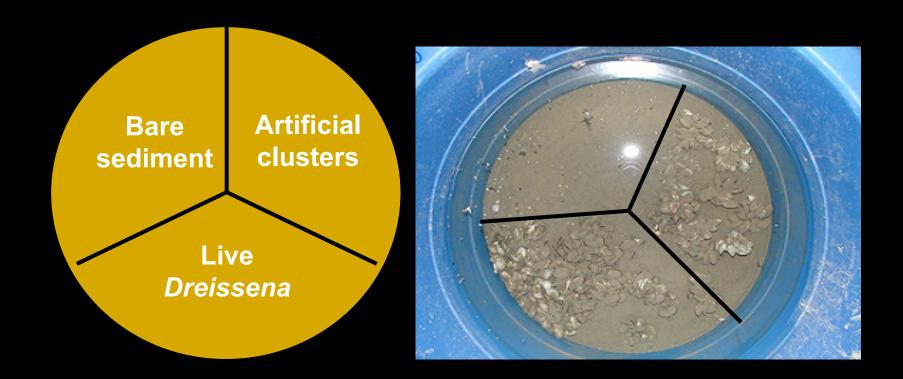
Dreissena clusters on hard substrate repeatedly shown to elevate localized invertebrate density

How do *Dreissena* affect soft sediment invertebrates such as *Hexagenia*?

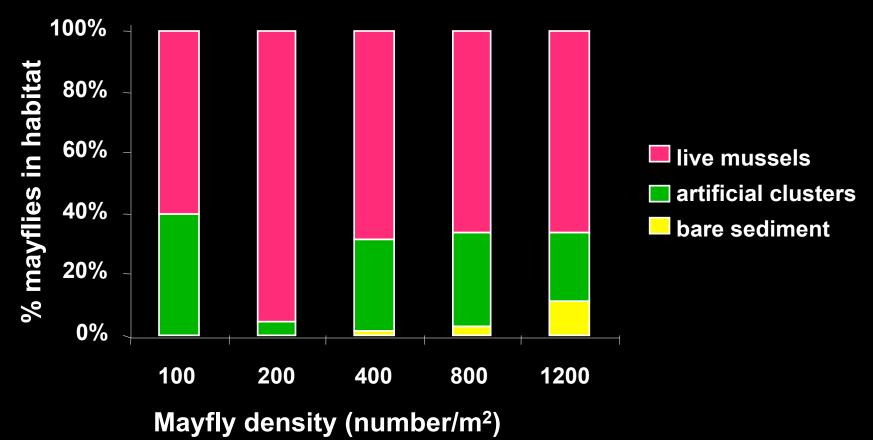


#### Hexagenia habitat selection experiments

5 mayfly densities; 100 -1200/m<sup>2</sup> Mayflies allowed to chose habitat Removed after 48 hr

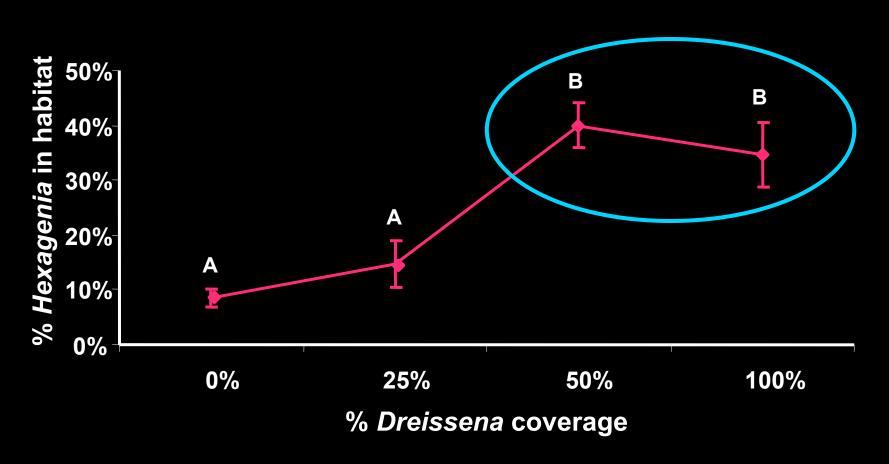


- ⇒Hexagenia prefer live *Dreissena* clusters
- **⇒**Suggests resource importation
- ⇒Only go to bare sediment at high density



DeVanna et al. in review

#### 75% of *Hexagenia* inhabited highdensity *Dreissena* habitats

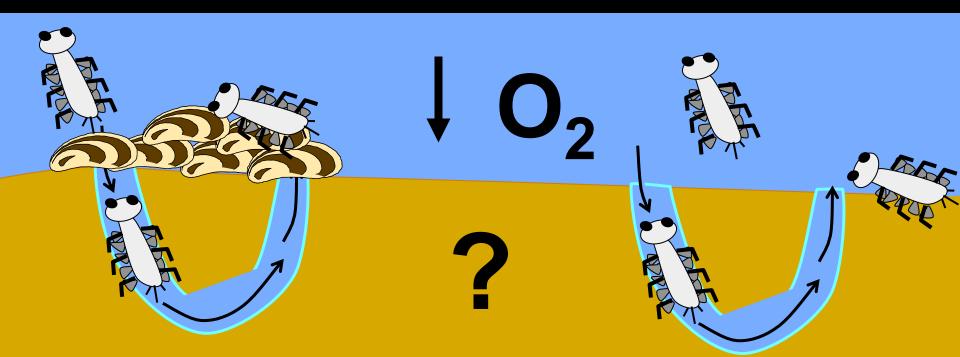


DeVanna et al. in review

## Do Hexagenia always prefer Dreissena habitat: hypoxia?

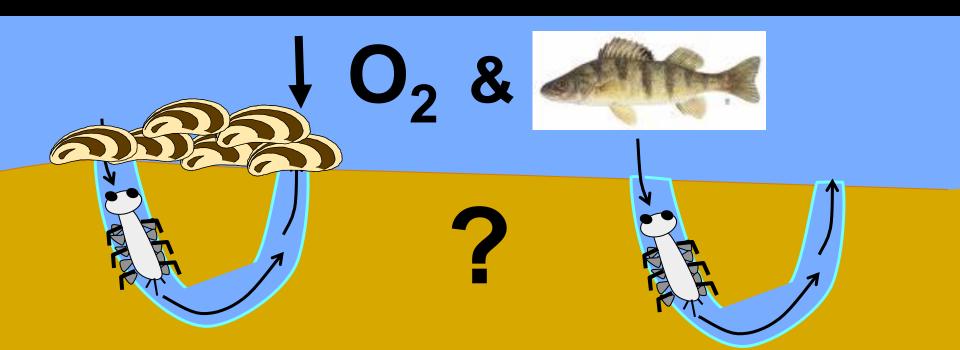
H<sub>1</sub> → Hexagenia avoid *Dreissena* clusters during hypoxic conditions

H<sub>2</sub> → Hexagenia leave burrows more often in hypoxic conditions compared to normoxic conditions



### Does predation threat change Hexagenia behavior under different O<sub>2</sub> conditions?

- H<sub>1</sub> Hexagenia select for *Dreissena* clusters and leave burrows less when fish predation threat is present
- H<sub>2</sub> Hexagenia leave burrows under low O<sub>2</sub> even when predation threat is present



#### **Methods**

- Hexagenia Behavioral Arenas
  - 2 habitat types:
     Dreissena and sediment



#### Treatments

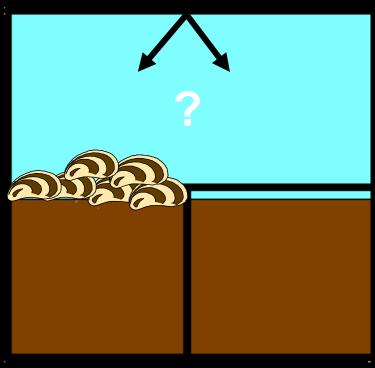
- Fish presence (N=5) vs. no fish (N=5)
- High oxygen vs. hypoxia (imposed at 24 hr to both treatments)

#### **Methods**

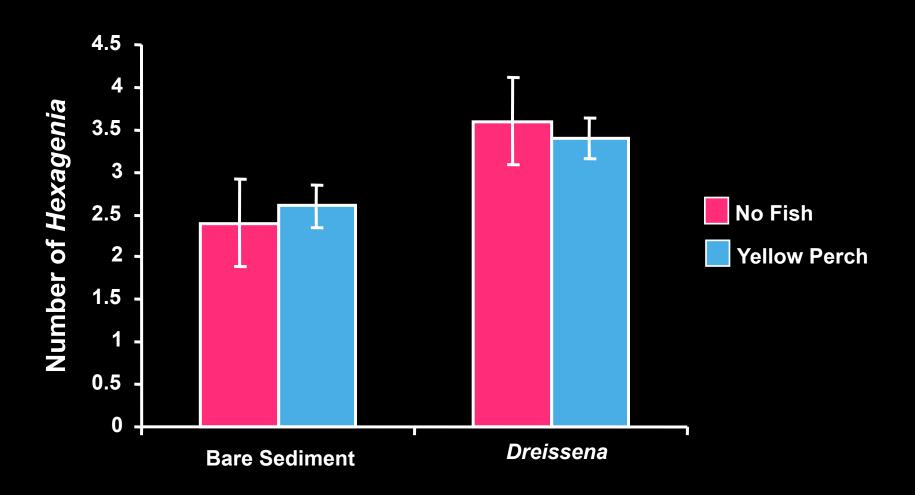
- Day 1
  - Introduced 6 mayflies
  - Observed for 15 minutes (Initial)
- Day 2
  - Initial Observations (Pre-hypoxia)
  - Lowered oxygen (<30% saturation)</li>
  - Observed for 15 minutes (post-hypoxia)
  - Observed after 3 hours of hypoxia



**X** 6

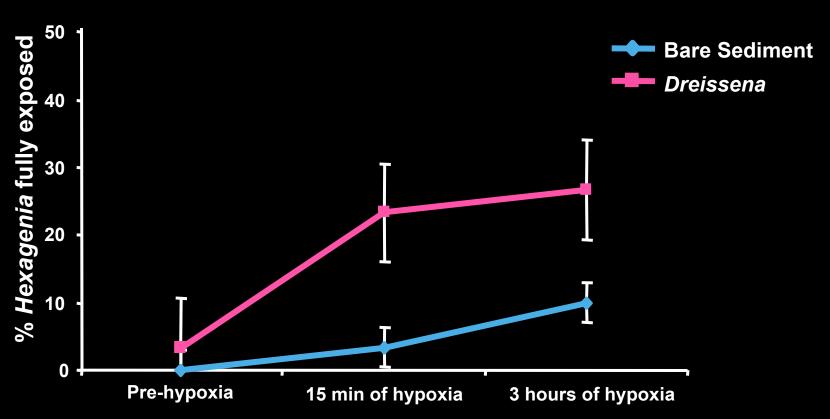


# Initial Selection for *Dreissena*-covered sediment

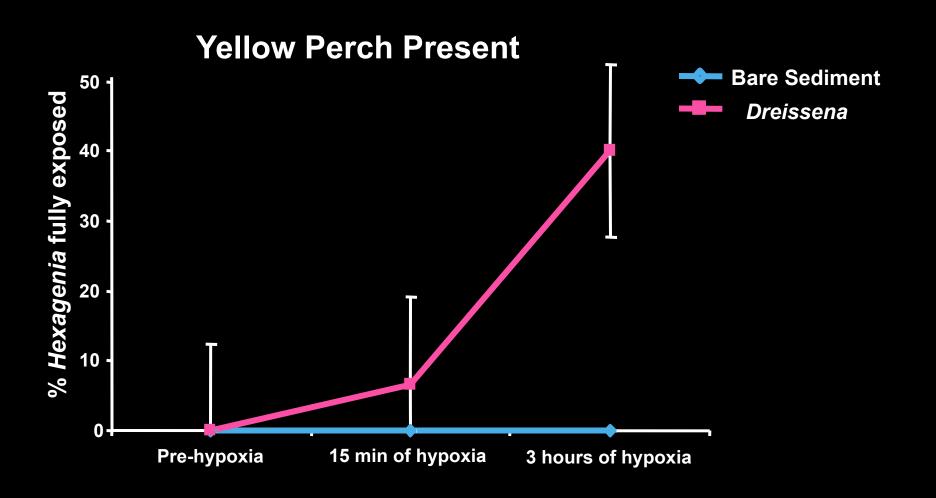


# More *Hexagenia* were exposed in the structured habitat during hypoxia





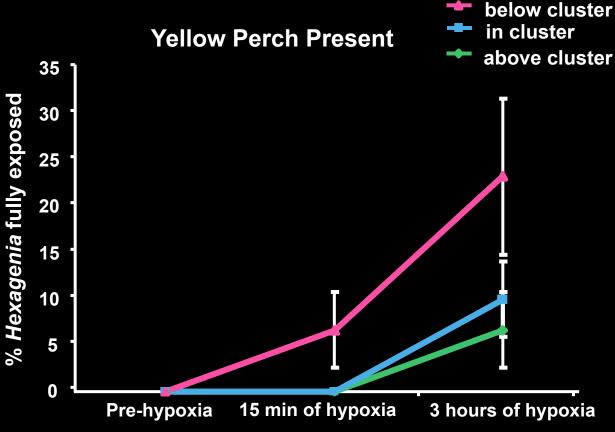
# Hexagenia waited longer to expose themselves when fish were present



# Hexagenia left their burrows during hypoxia, but many were still sheltered beneath cluster







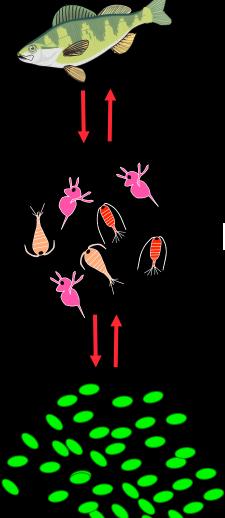
#### **Conclusions:**

- Hexagenia select for habitat with Dreissena
- → May be exploiting microbial, algal or other resources in clusters
- → Ongoing experiments to determine factors controlling habitat choice, e.g. fish predation, hypoxia

Preliminary results show that hypoxia results in neutral habitat selection and *Hexagenia* exit burrows and expose heads and bodies



#### **Trophic Cascade**



Effects
transmitted
among trophic
levels; up, down,
or middle out

#### **Ecosystem Engineering Cascade**

