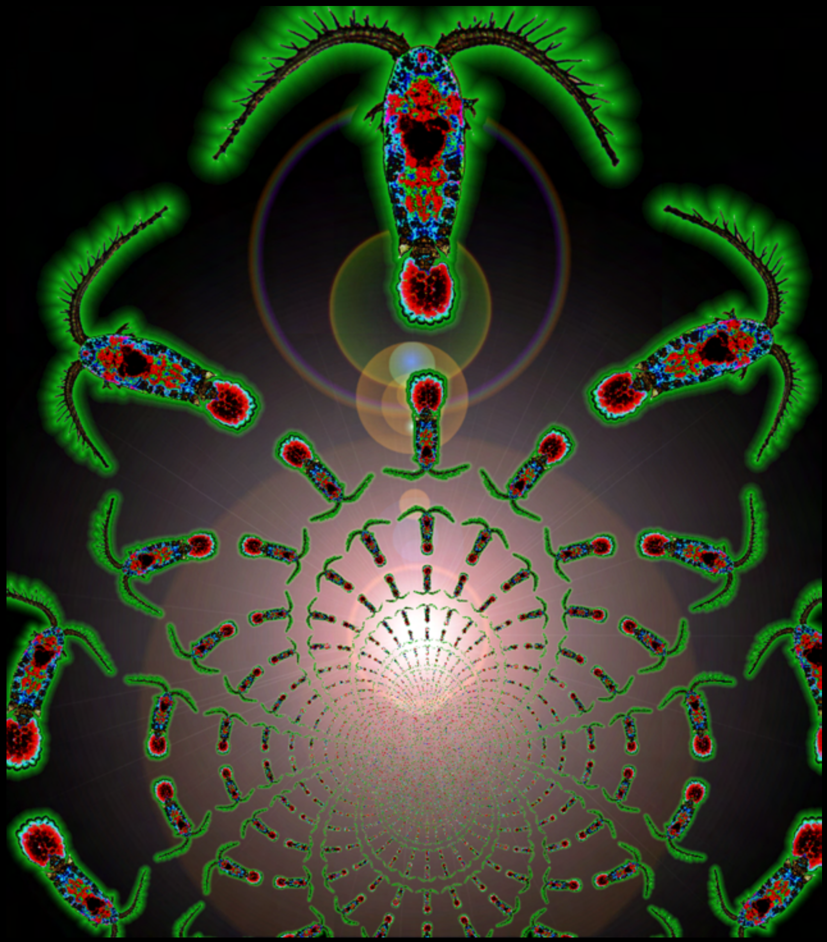
Rapid Evolution during Habitat Change



Carol Eunmi Lee

Center of Rapid Evolution *(CORE)*

University of Wisconsin, Madison

Outline

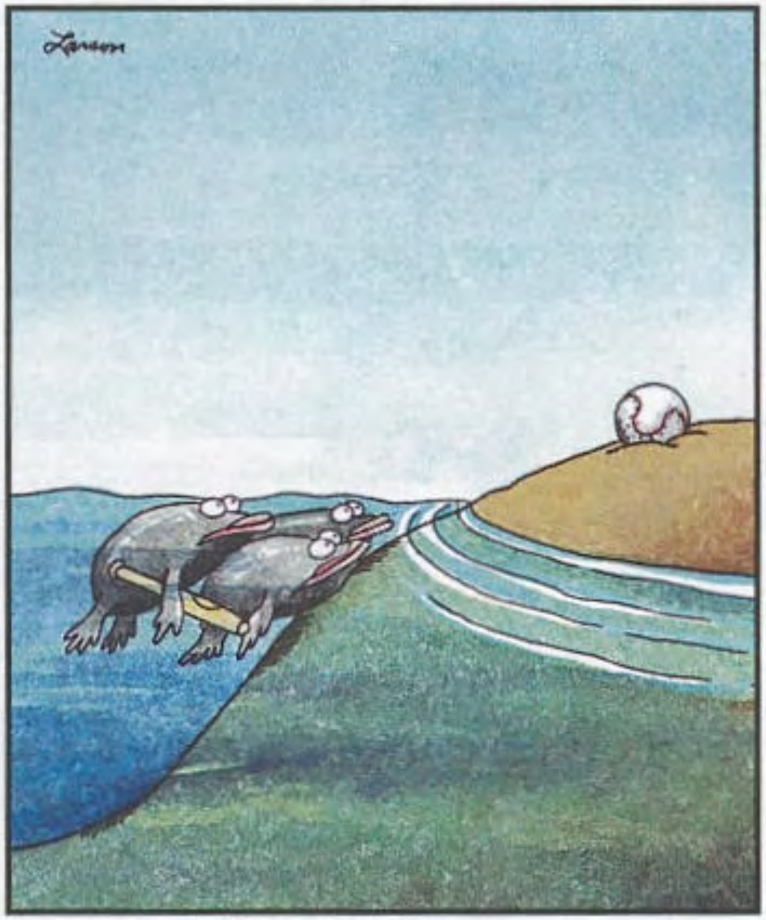
- **What conditions enable Rapid Evolution?**
- **How do we detect Rapid Evolution?**

  Comparative Common-Garden Experiments
  Selection Experiments

- **Examples of Rapid Evolution in Copepods**:

  Salinity Adaptation
  Response to Deep Horizon Gulf Oil Spill
  Temperature Adaptation

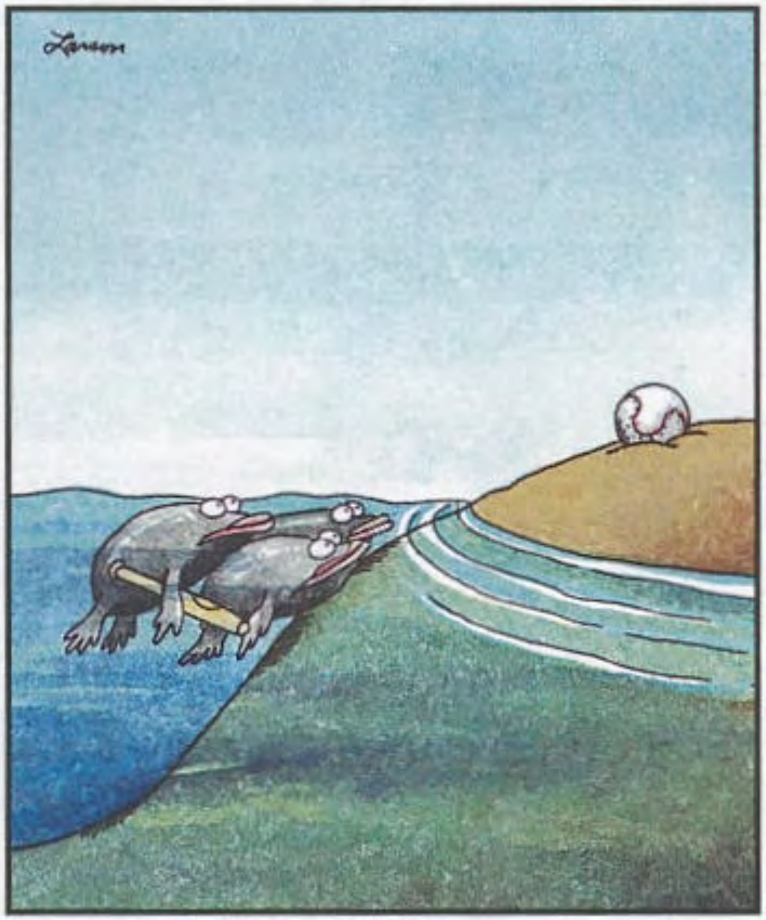
A fundamental problem in ecology and evolution regards limits to species distributions



Great moments in evolution

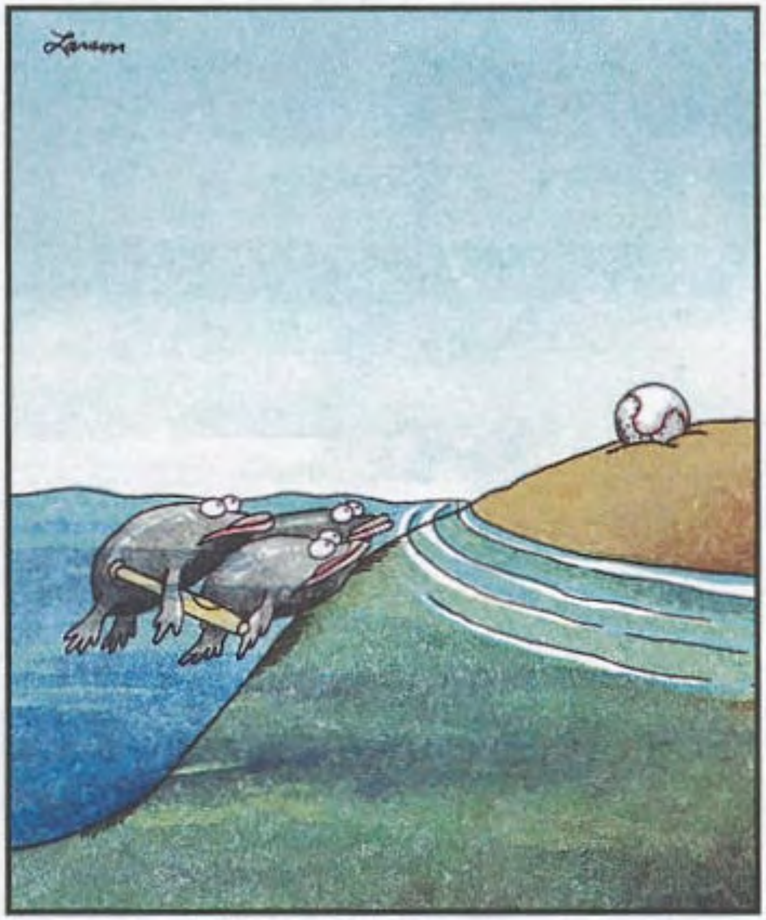
What constrains species distributions?

What mechanisms allow those distributions to shift?



Great moments in evolution

Adaptation during Extraordinary Environmental Change

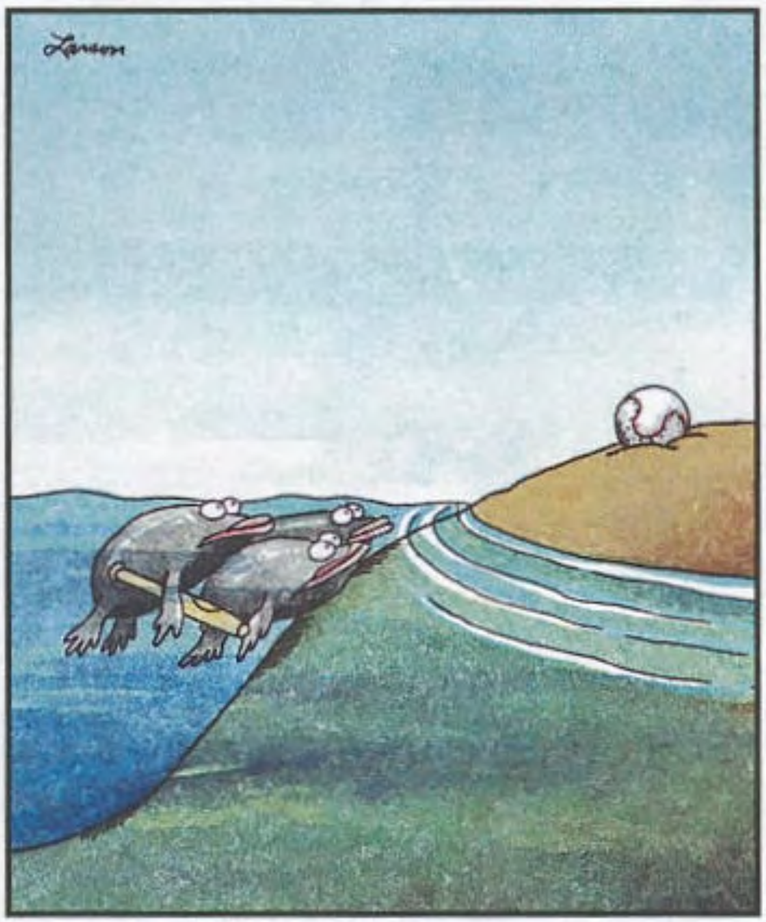


Great moments in evolution

Over longer time scales, colonizations across habitat boundaries represent major events in the history of life, leading to the **evolution of key innovations.**

In general, transitions into more stressful environments have been accompanied by the **evolution of increased physiological regulation**.

Examples of extraordinary environmental change:



Great moments in evolution

Transitions between

Saltwater → Freshwater

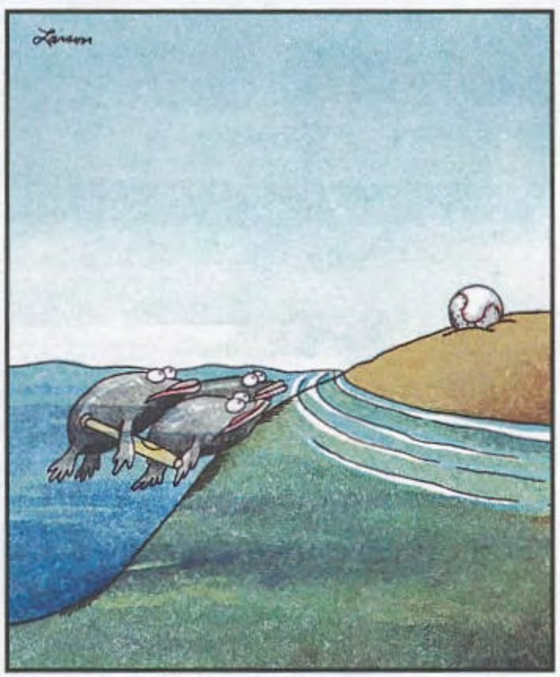
and

Freshwater → Land

Constitute Major Evolutionary Transitions in the History of Life

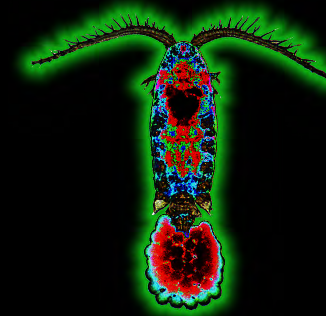
Life evolved in the sea, and freshwater and terrestrial habitats impose profound physiological challenges for most taxa (Hutchinson 1957; Lee & Bell 1999)

Of ~35 Animal Phyla, only 16 invaded fresh water, and only 7 invaded land



Great moments in evolution

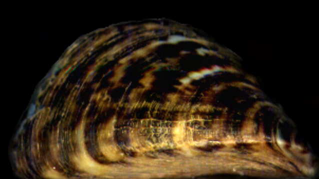
Partial List of Taxa	Sea	Fresh	Land
Protista	X	X	
Porifera	X	X	
Placazoa	X		
Cnideria	X	X	
Ctenophora	X		
Entoprocta	X		
Platyhelminthes	X	X	X
Nemertea	X	X	X
Rotifera	X	X	
Gastrotricha	X	X	
Gnathostomulida	X		
Kinorhyncha	X		
Chaetognatha	X		
Loricifera	X		
Nematoda	X	X	
Nematomorpha	X	X	
Entoprocta	X	X	
Annelida	X	X	X
Mollusca	X	X	X
Xenoturbellida	X		
Phoronida	X		
Bryozoa	X	X	
Brachiopoda	X		
Sipunculida	X		
Echiuroida	X		
Priapulida	X		
Tardigrada	X	X	
Onychophora			X
Arthropoda	X	X	X
Echinodermata	X		
Pogonophora	X		
Hemichordata	X		
Chordata	X	X	X



Over geological time scales, such major habitat transitions have been relatively rare…

However, some **invasive species are extraordinary** in their ability to breach such habitat boundaries (Lee and Bell 1999; Lee and Gelembiuk 2008; Lee 2010).

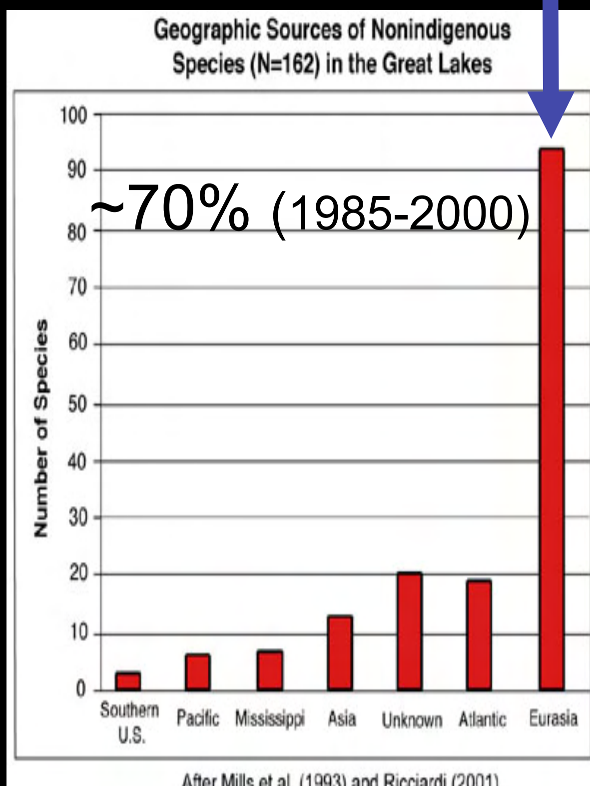
Hence, such **invasive species provide valuable models** for understanding **how organisms could adapt to radical environmental change**.



Many invasive species are undergoing fundamental niche expansions:

For example, many freshwater habitats are overrun with <u>brackishwater</u> invaders

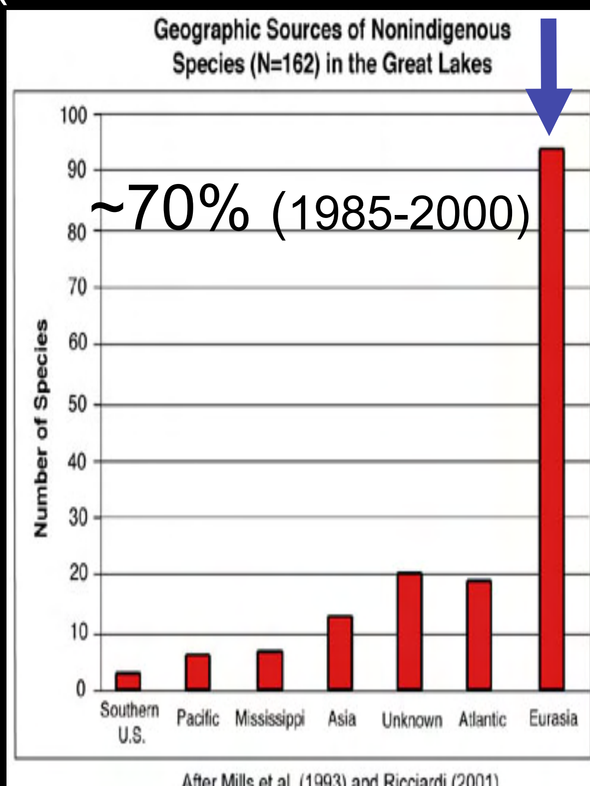
(Lee & Bell 1999; Ricciardi & MacIsaac 2000)



Many invasive species are undergoing fundamental niche expansions:

But, 5 PSU is a major biogeographic barrier for most aquatic invertebrates

(Khlebovich and Abramova 2000)



Question

What accounts for the ability of some populations to invade novel habitats, when most cannot?

386 Review TRENDS in Ecology & Evolution Vol.17 No.8 August 2002

Evolutionary genetics of invasive species

Carol Eunmi Lee

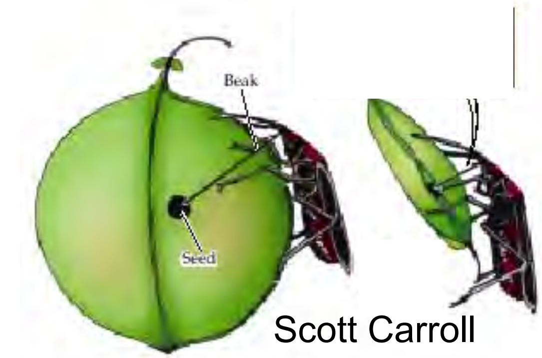
The evolutionary genetics of invasive species has been relatively unexplored, but could offer insights into mechanisms of invasions. Recent studies suggest that the invasion success of many species might depend more heavily on their ability to respond to natural selection than on broad physiological tolerance or plasticity. Thus, these studies stress the importance of genetic architecture, selection upon which could result in evolutionary adaptations and possibly speciation. For instance, epistatic interactions and the action of a few genes could facilitate invasion success. These findings emphasize the utility of genomic approaches for determining invasion mechanisms, through analysis of gene expression, gene interactions, and genomic rearrangements that are associated with invasion events.

INVASIVE SPECIES (see Glossary) and populations pose major threats to biodiversity, ecosystem integrity, agriculture, fisheries, and public health. Economic costs associated with the more publicized exotic invaders, such as weeds, agricultural pests, zebra mussels and plant pathogens, total ~US$137 billion y^{-1} in the USA [1]. The rapid spread of exotics has received considerable attention within the international community, and has mobilized substantial ecological research. By contrast, LOCI (QTL) MAPPING) and BIOINFORMATICS offer many opportunities for exploring GENETIC ARCHITECTURE and gene expression patterns of invading populations. Effective application of these tools requires an assessment of the current literature. Thus, here I review recent studies on genetic characteristics and adaptative responses of successful invaders, and recommend topics for future research.

Genetic architecture of invasive species

The importance of natural selection

Biological invasions present interesting evolutionary problems because they are stochastic events often involving small populations that can survive rapid habitat transitions. The classic symposium volume *The Genetics of Colonizing Species* [8] was influential for focusing on evolutionary mechanisms of invasions. In this text, C.H. Waddington asked how genetic architecture might impact the propensity to invade. Mounting evidence supports the importance of genetic attributes for invasion success, such as ADDITIVE GENETIC VARIANCE (AGV) [7,9–11], EPISTASIS [7,12–14],



Increasingly, we are learning that a rapid evolutionary response is important

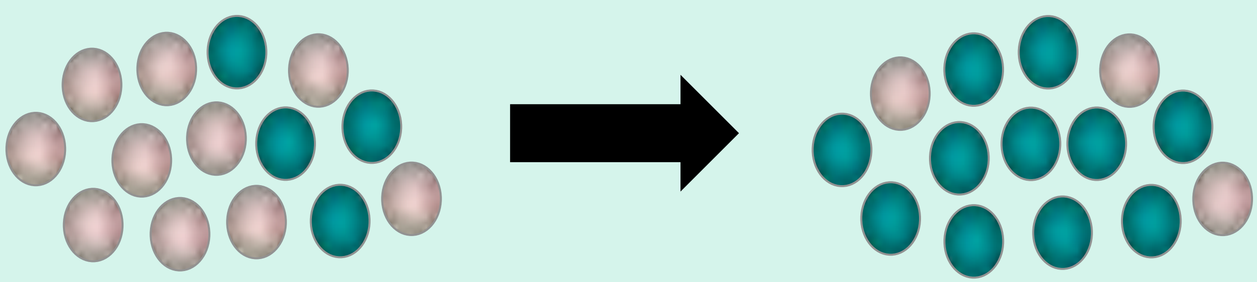
What do we need for an Evolutionary Response (in this case Adaptation) to occur?

Adaptation occurs through Natural Selection

- **Natural Selection occurs by culling genetic variation in a population**

Frequency shift in a population, so that the average characteristics of a population is changed

***Need genetic variation upon which selection could act, <u>at the relevant traits</u>

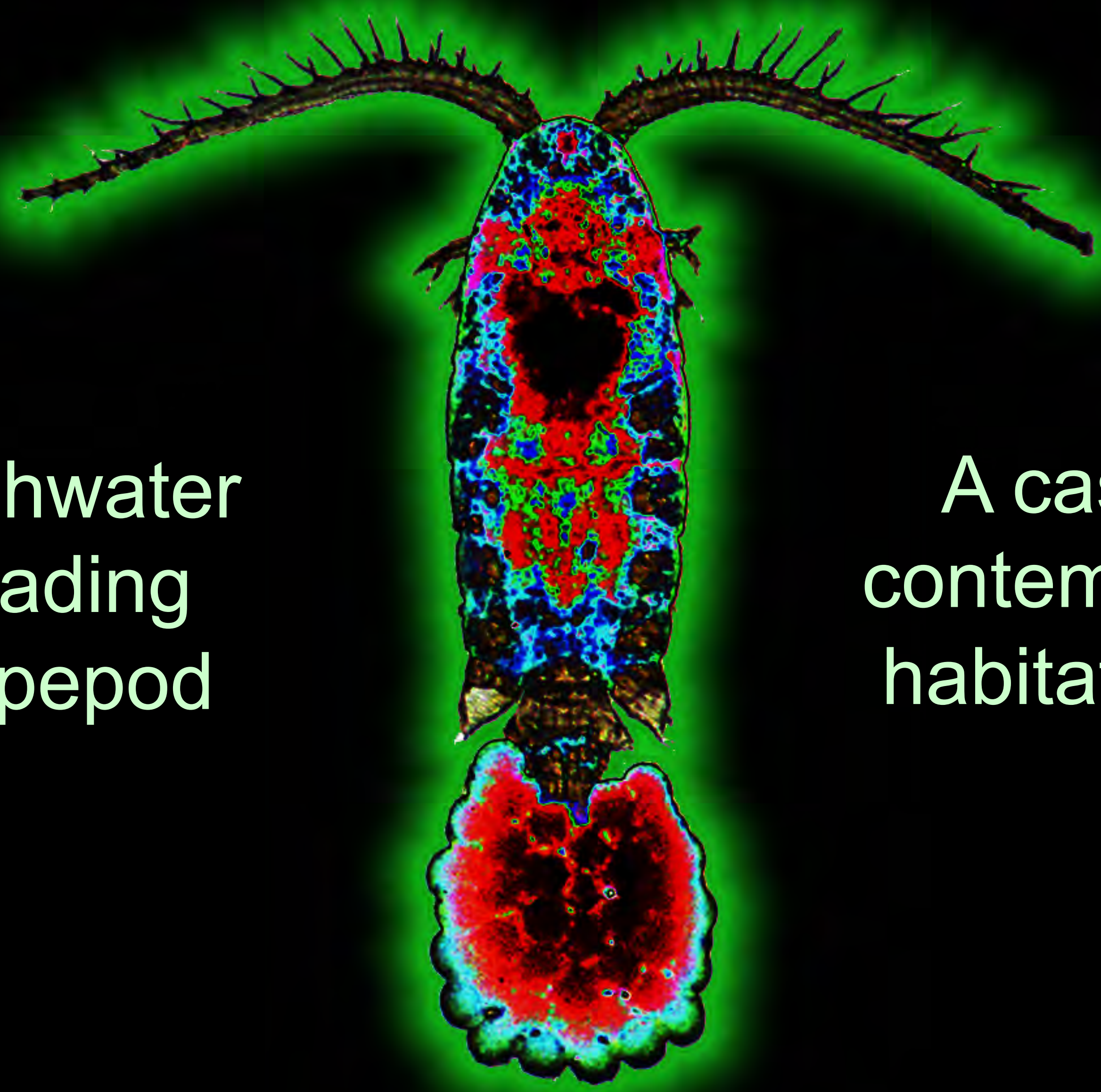


Adaptation occurs through Natural Selection

***Need genetic variation upon which selection could act

- **Sources of Genetic Variation:**
  - Smaller organisms (bacteria, viruses, phytoplankton): New Mutations can arise quickly after habitat change
  - Larger organisms: Generation times are too long and mutation rate is too slow → often must rely solely on **standing genetic variation** in a population
    - **Need mechanisms for the maintenance of genetic variation ***at the relevant traits***** (not at neutral loci, not at microsatellites)

Freshwater
Invading
Copepod

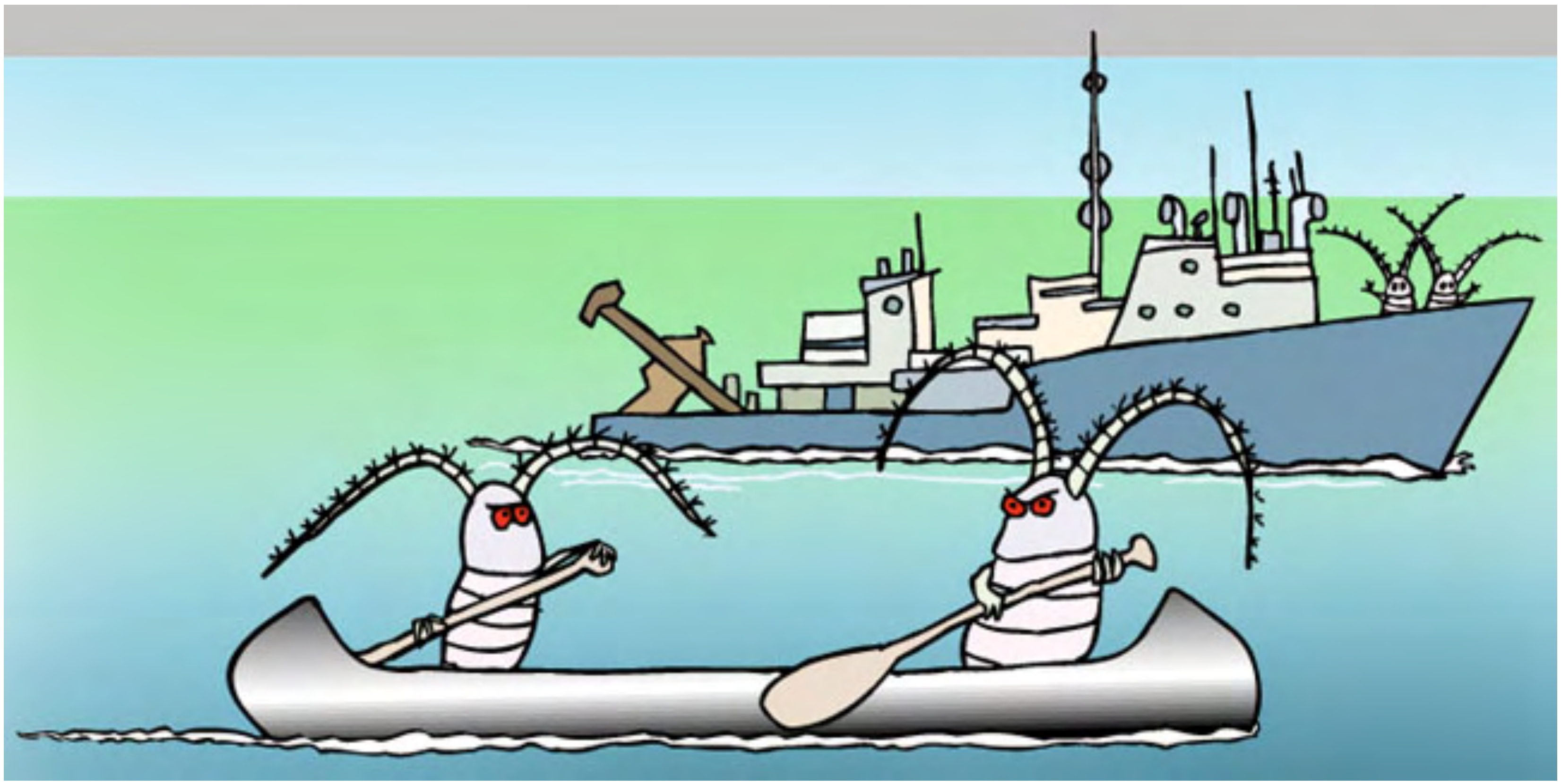


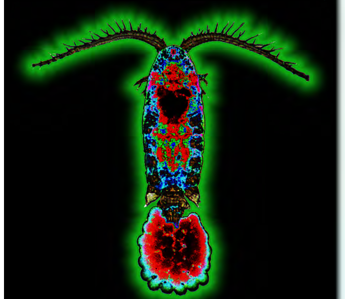
A case of
contemporary
habitat shifts

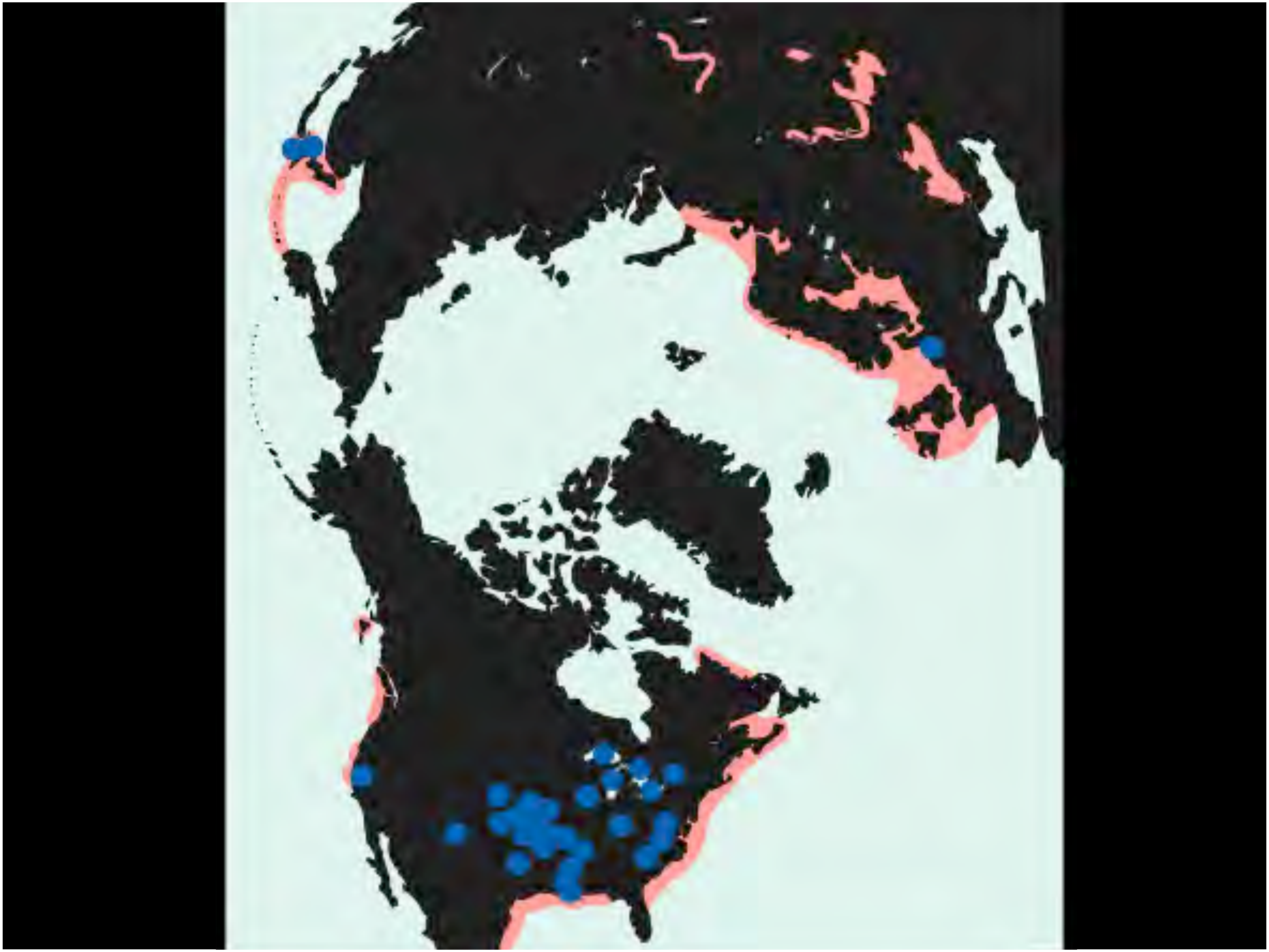
Eurytemora affinis

Copepods are common as invaders

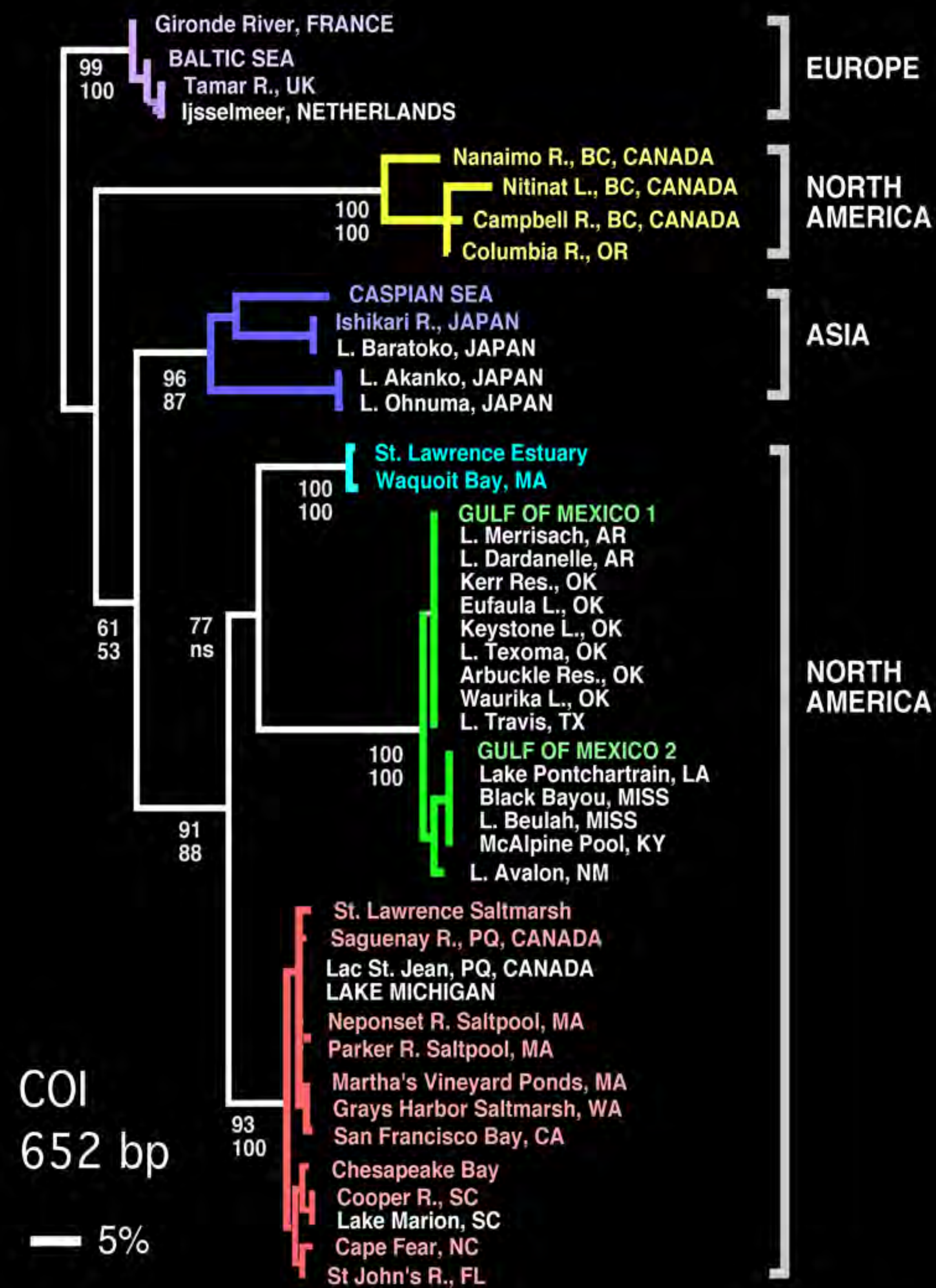
- Copepods form the largest biomass of metazoans in the world's oceans (Hardy 1970; Verity & Smetacek 1996)
- Copepods also form the largest biomass in ship ballast water
- ~12 billion tonnes of ballast water transported annually

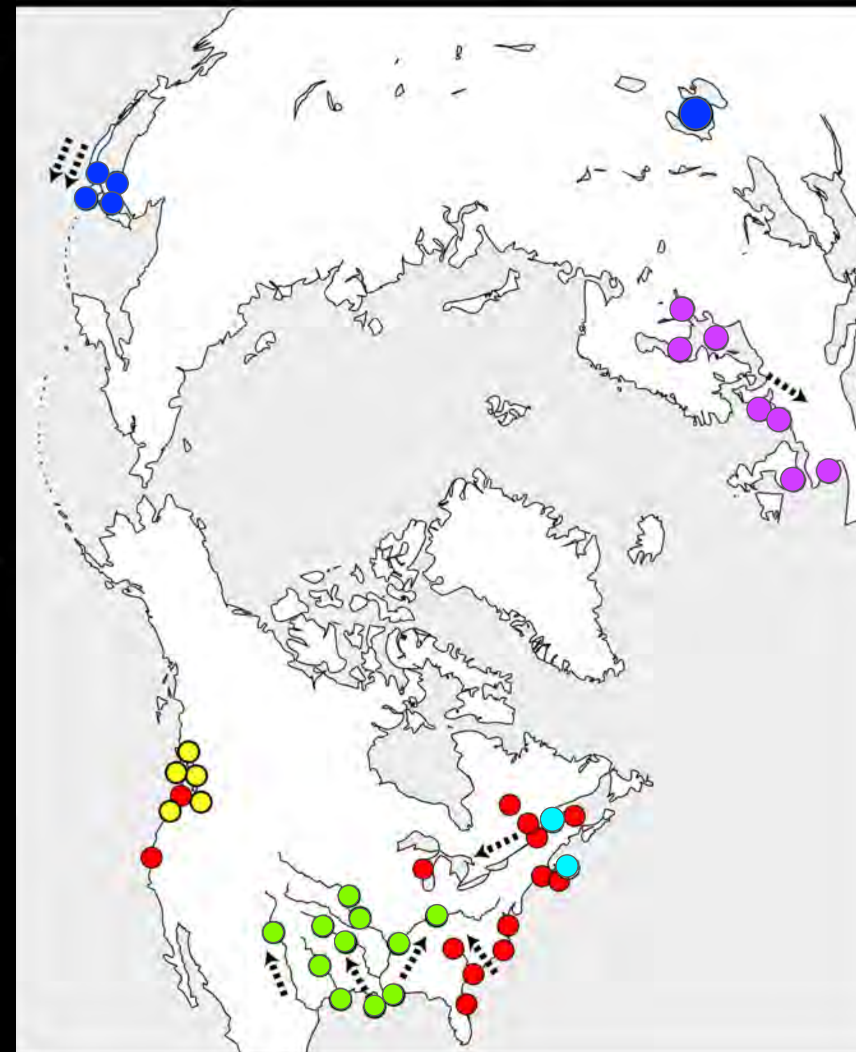






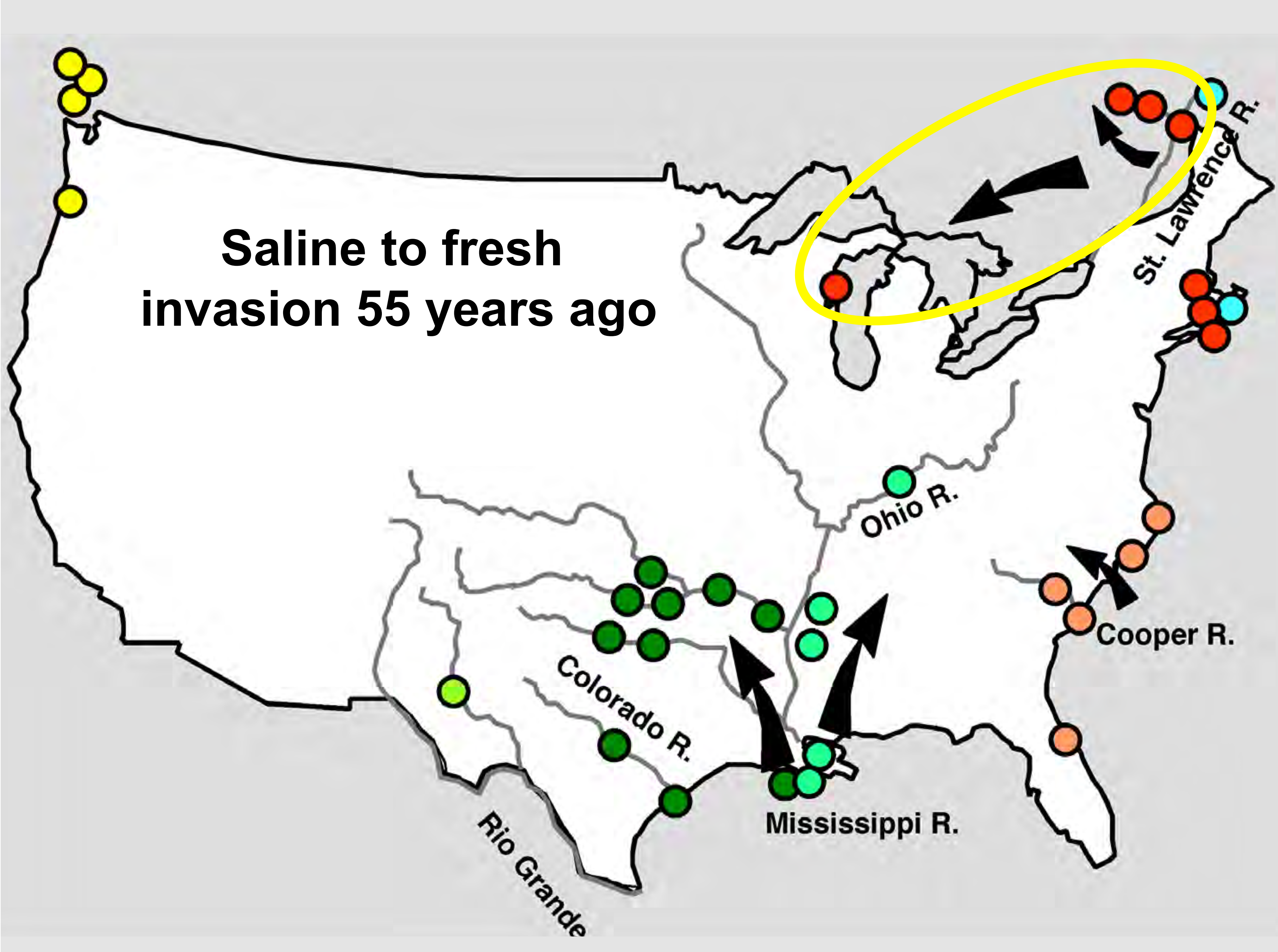
Eurytemora affinis species complex



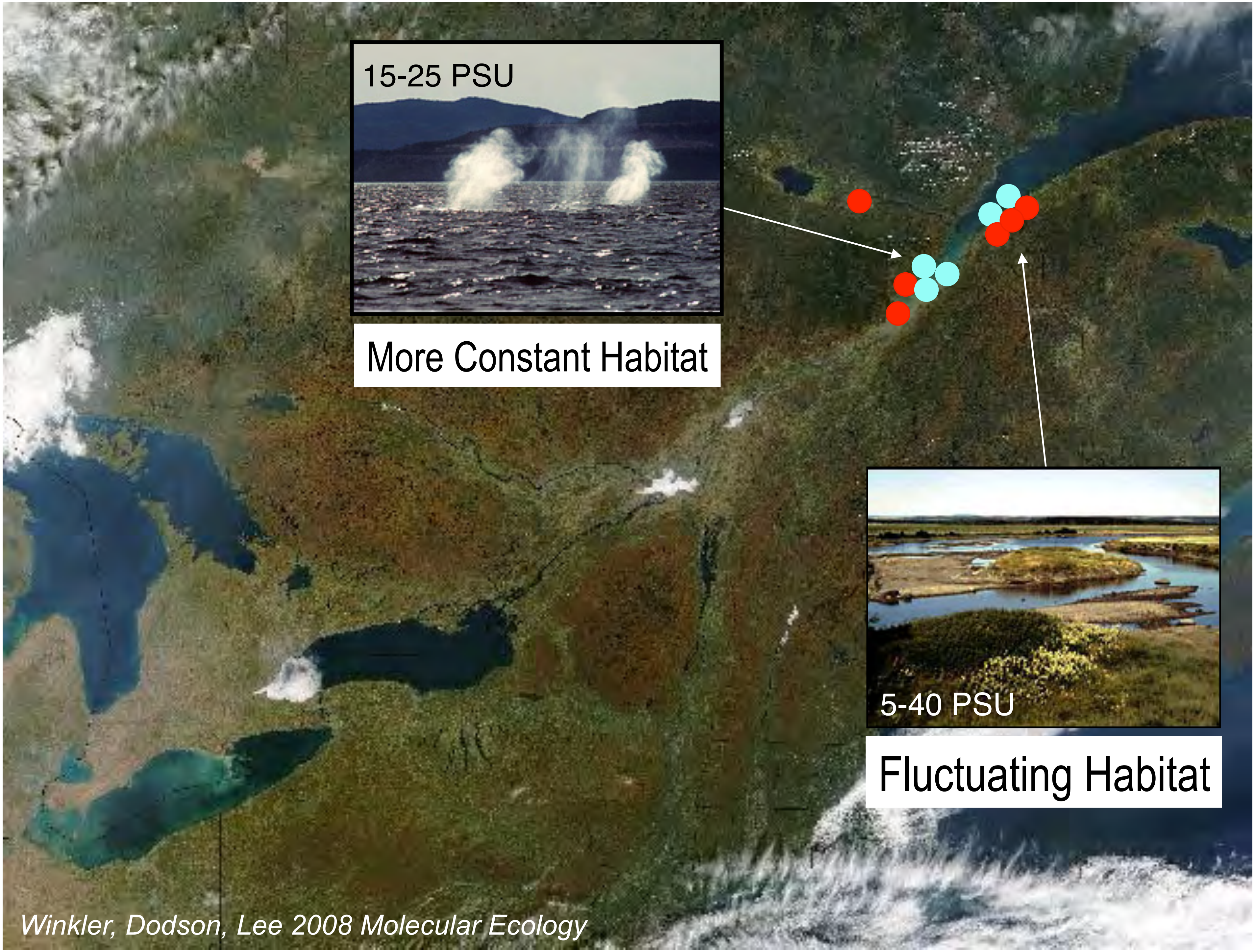


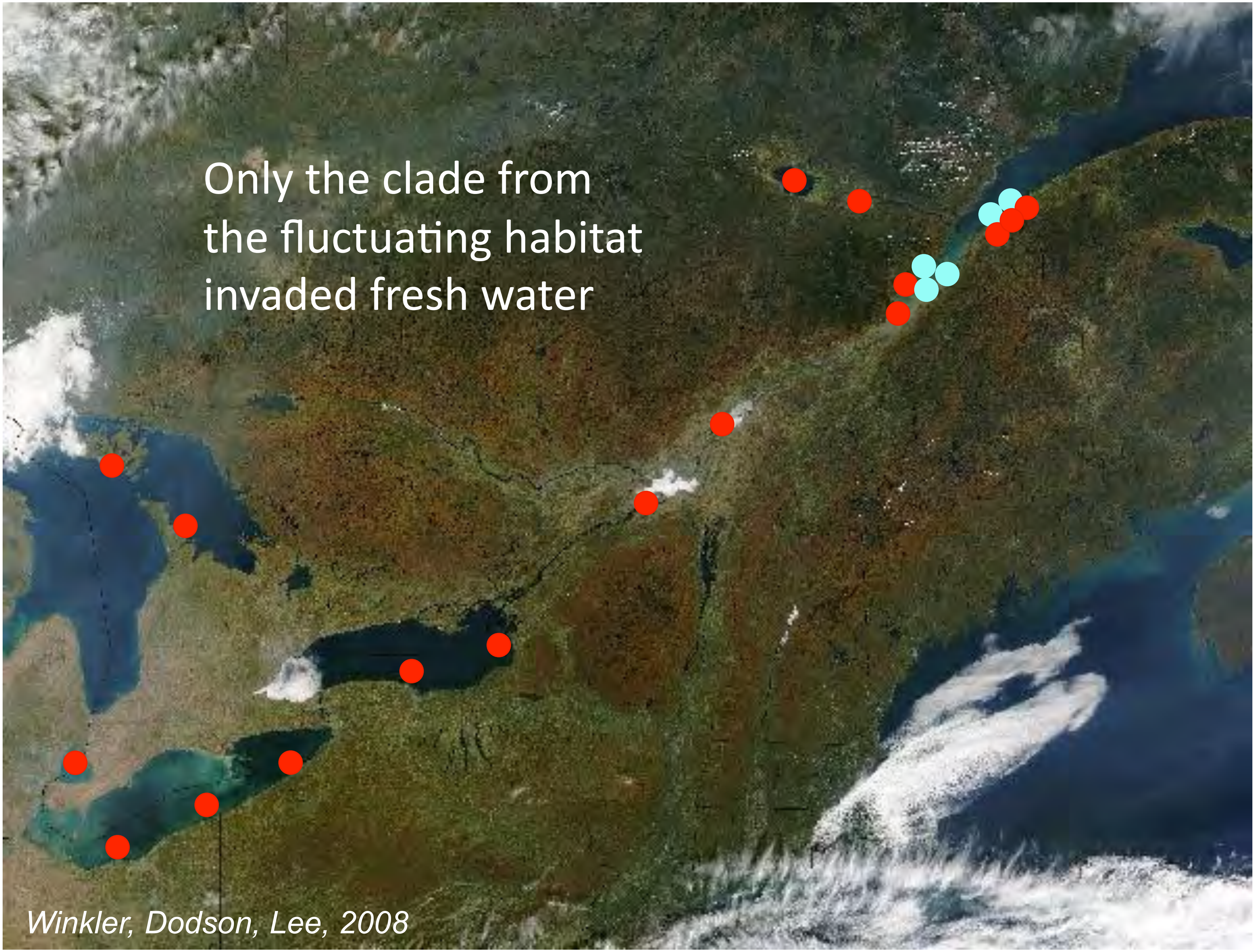
Lee 1999, 2000, Evolution

Saline to fresh invasion 55 years ago

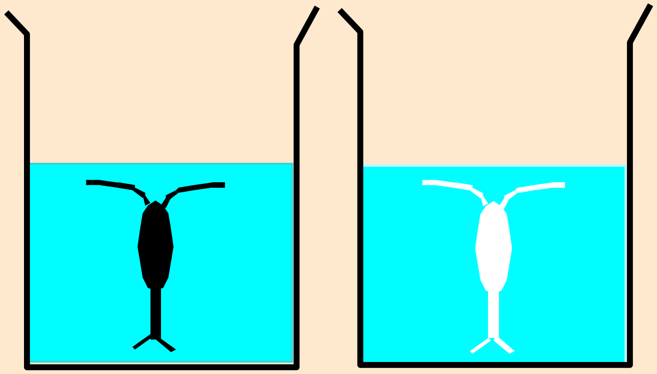


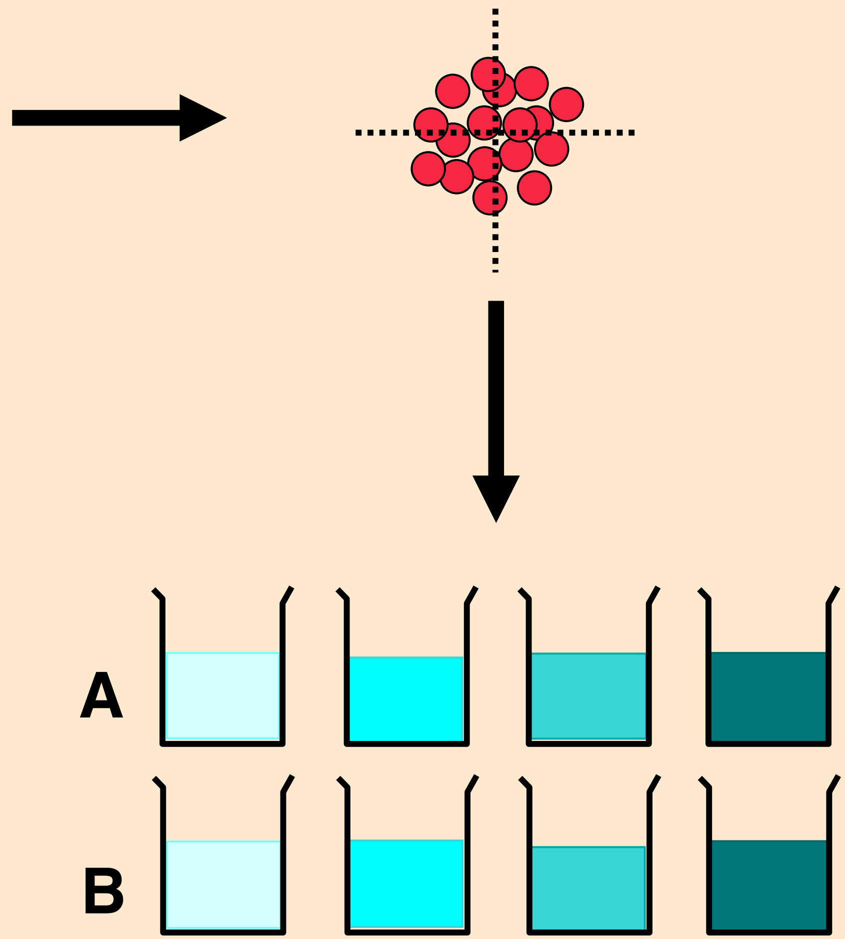

Winkler, Dodson, Lee, 2008


15-25 PSU
More Constant Habitat
5-40 PSU
Fluctuating Habitat
Winkler, Dodson, Lee 2008 Molecular Ecology


Only the clade from
the fluctuating habitat
invaded fresh water
Winkler, Dodson, Lee, 2008

What is the pattern of physiological evolution?

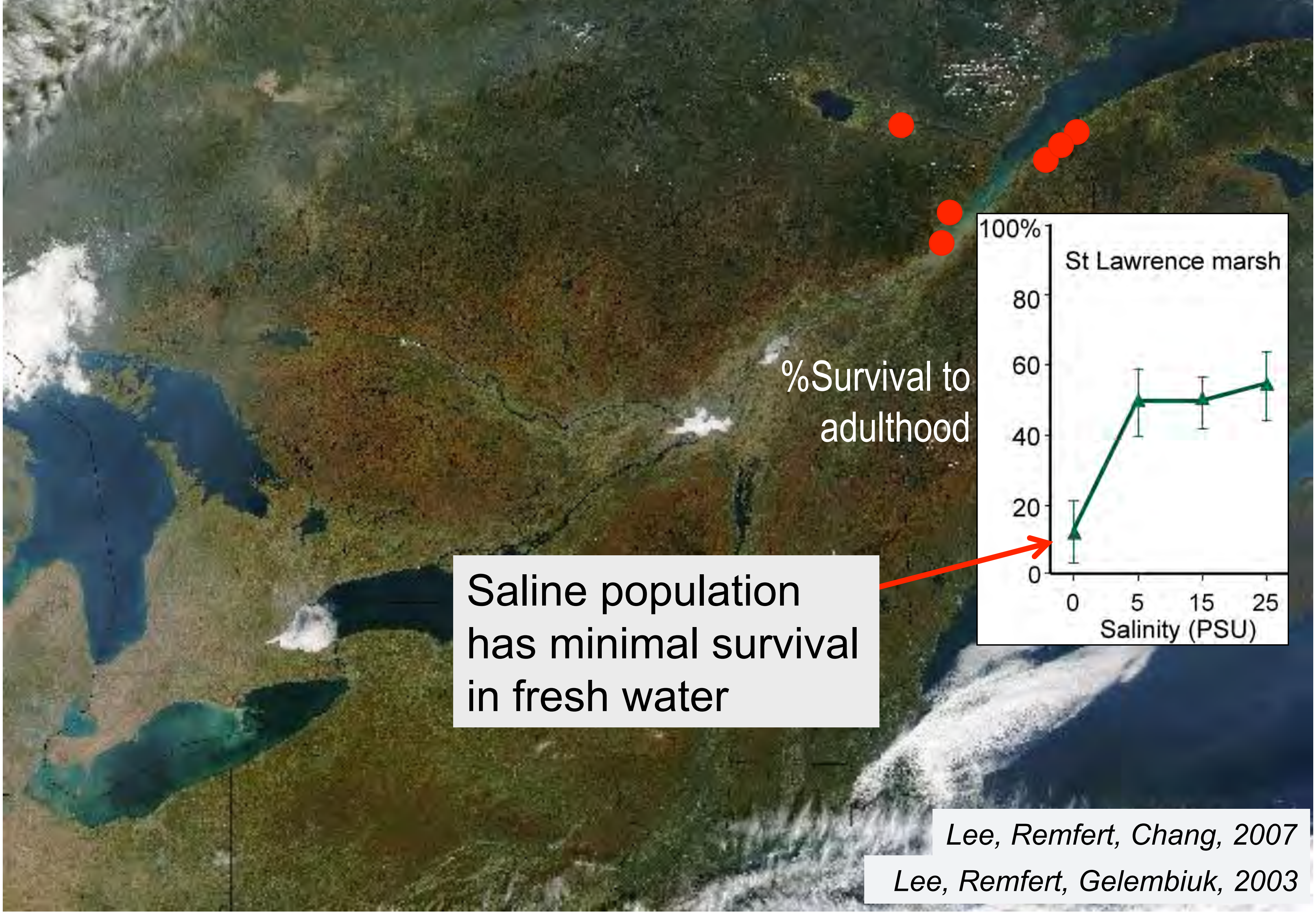




Common-garden reaction norm experiment

Jane Remfert

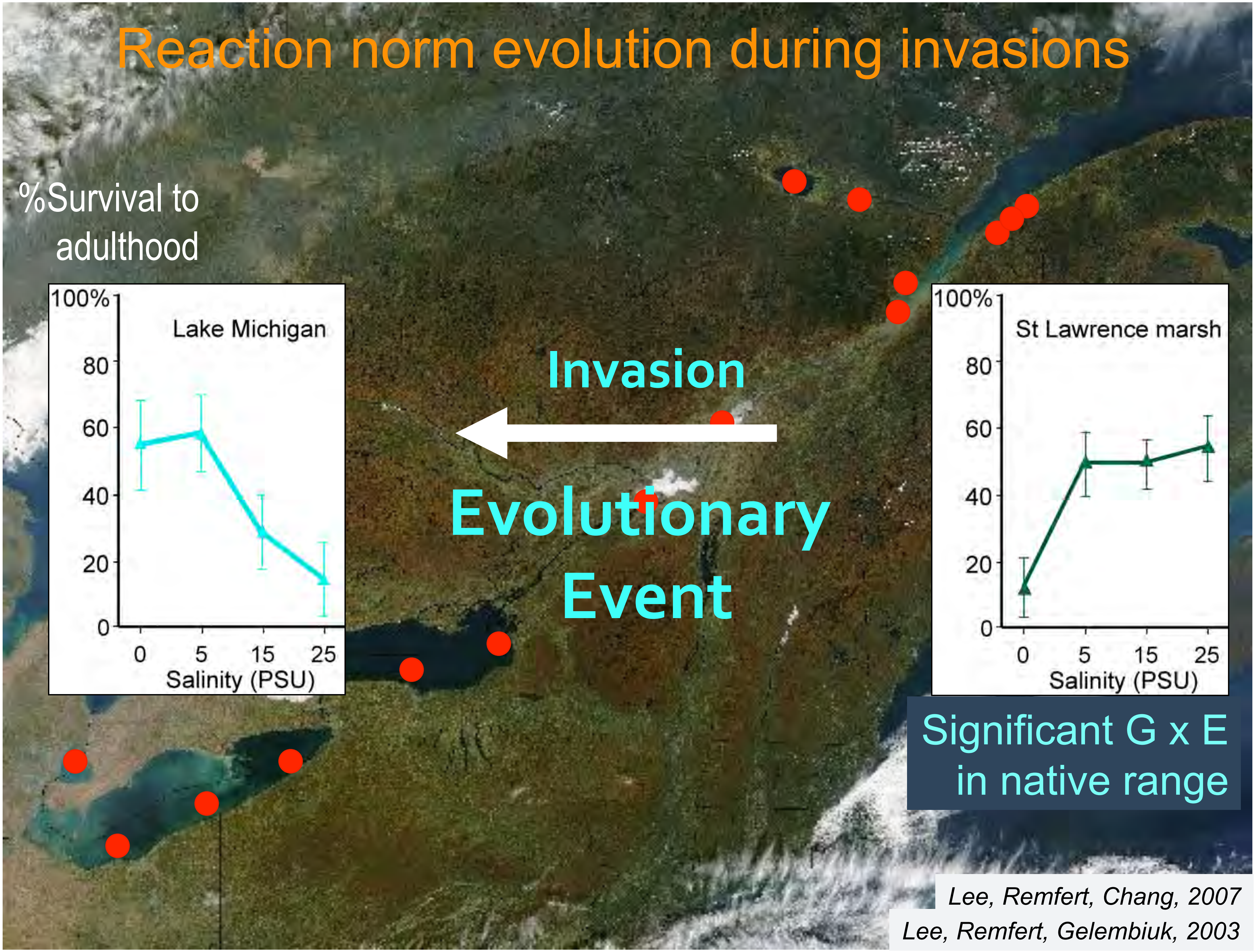
Reaction norm evolution during invasions

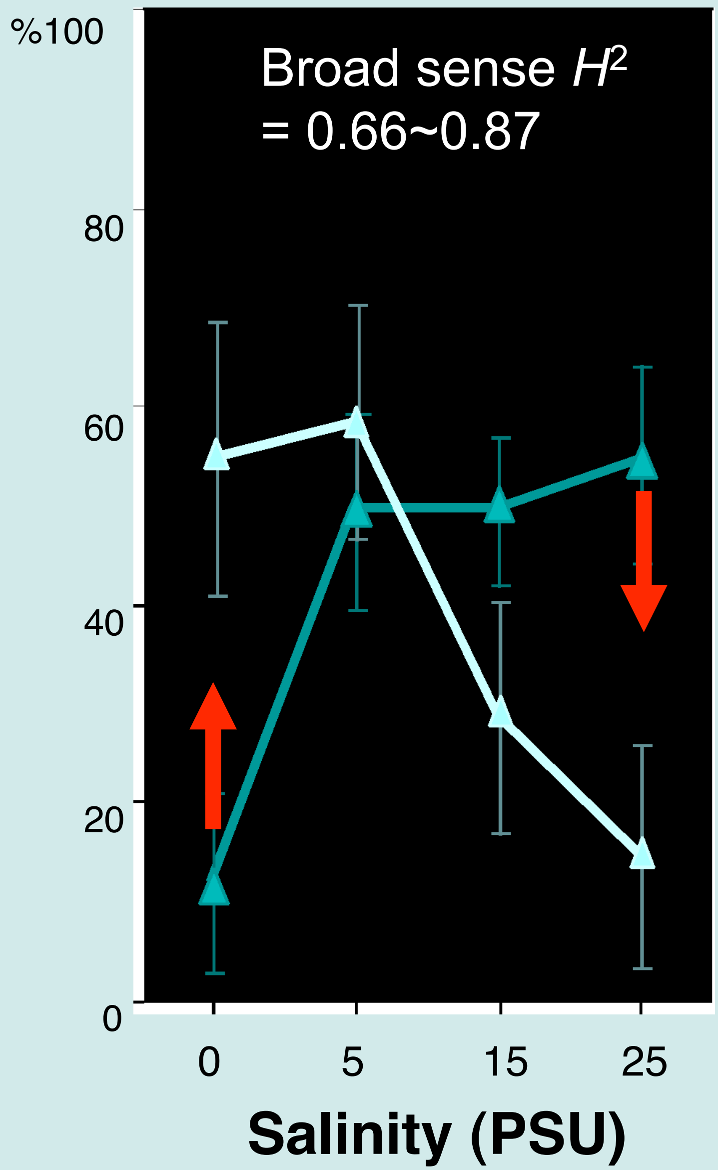


Saline population has minimal survival in fresh water

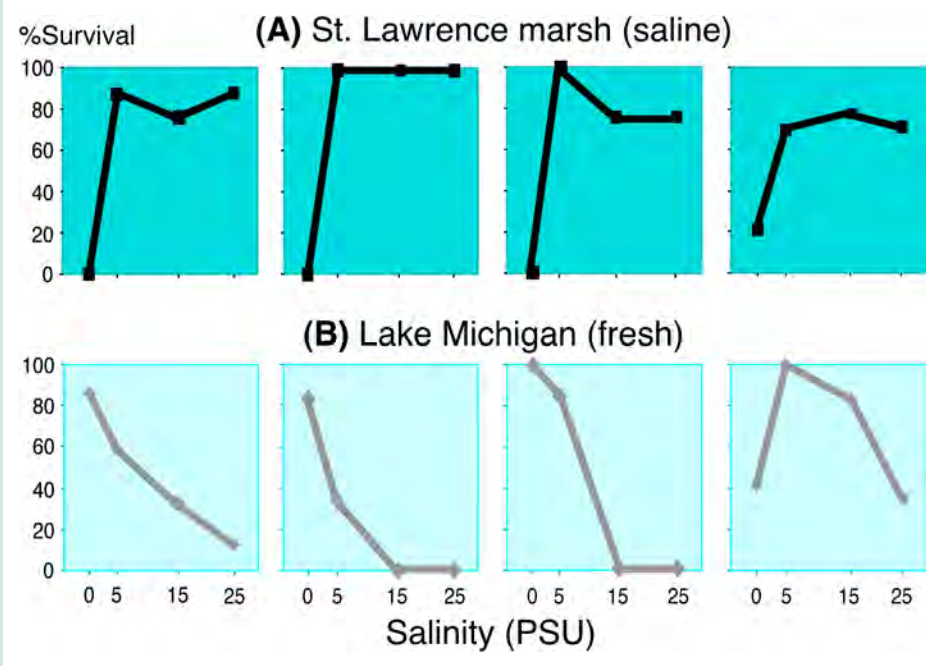
Lee, Remfert, Chang, 2007

Lee, Remfert, Gelembiuk, 2003


Reaction norm evolution during invasions
%Survival to adulthood
100%
80
60
40
20
0
Lake Michigan
0 5 15 25
Salinity (PSU)
Invasion
Evolutionary Event
100%
80
60
40
20
0
St Lawrence marsh
0 5 15 25
Salinity (PSU)
Significant G x E in native range
Lee, Remfert, Chang, 2007
Lee, Remfert, Gelembiuk, 2003

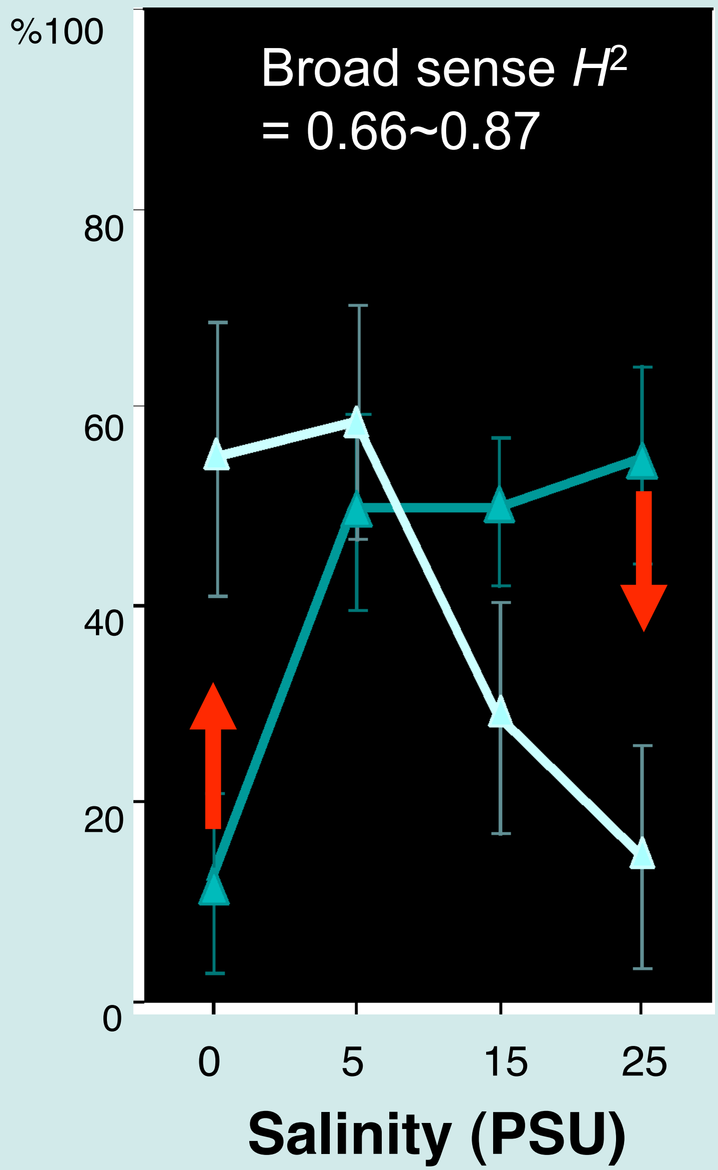


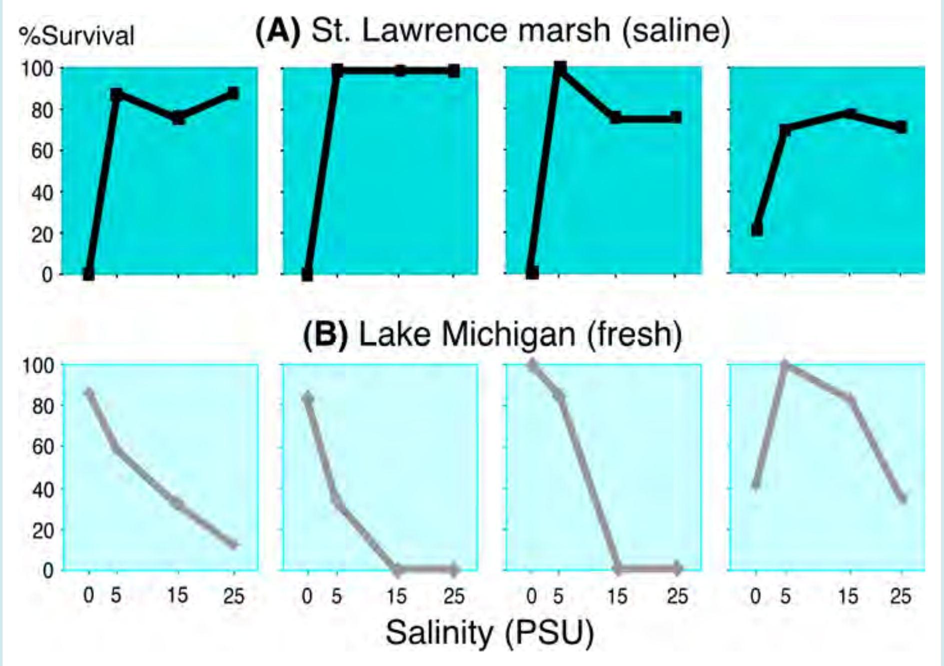
Lee, Remfert, Gelembiuk, 2003, 2007



BUT, what's interesting from an evolutionary point of view is the **variance**, more so than the mean response

Because Natural Selection acts on the variance

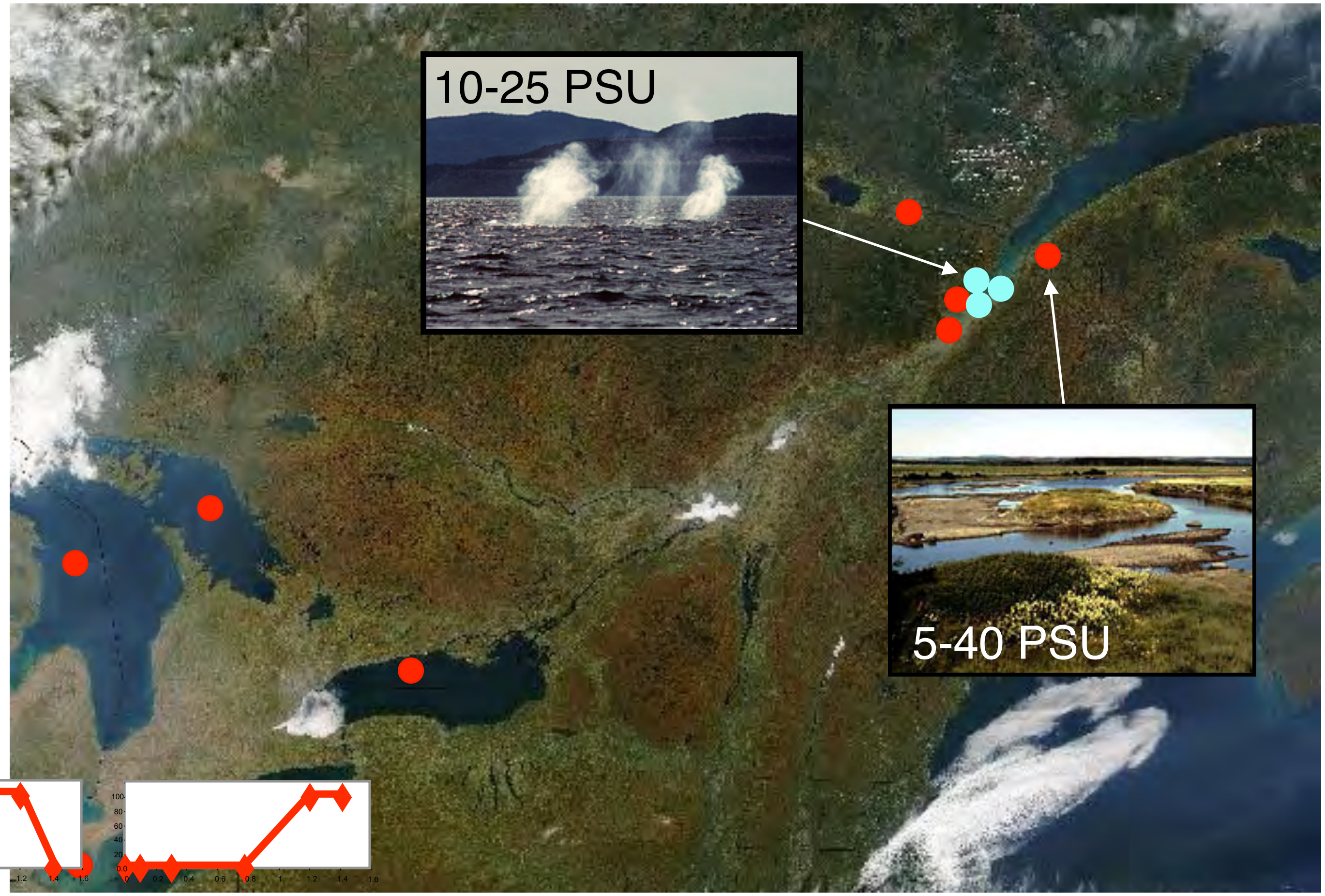


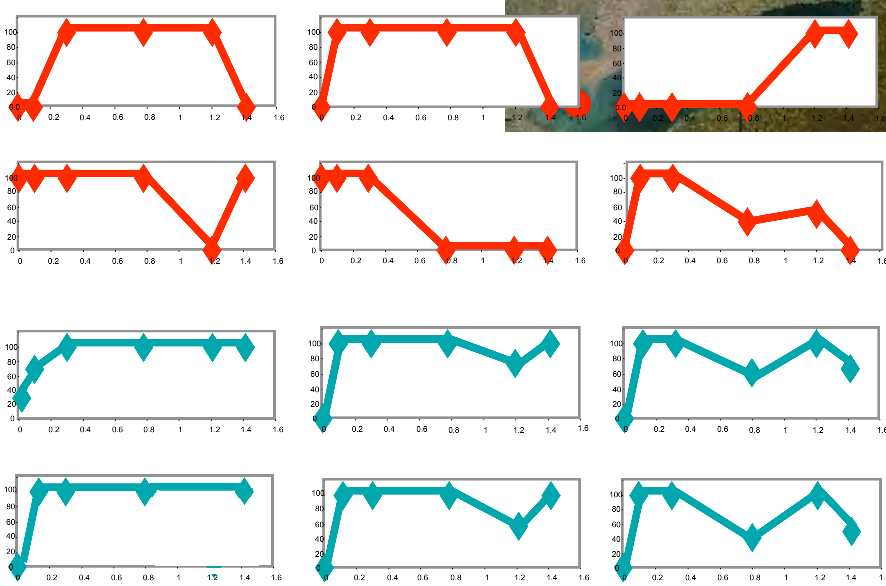


Much genetic variation in physiological tolerance in the native range

This genetic variation from the native range would allow Natural Selection to act during invasions

Lee, Remfert, Gelembiuk, 2003, 2007





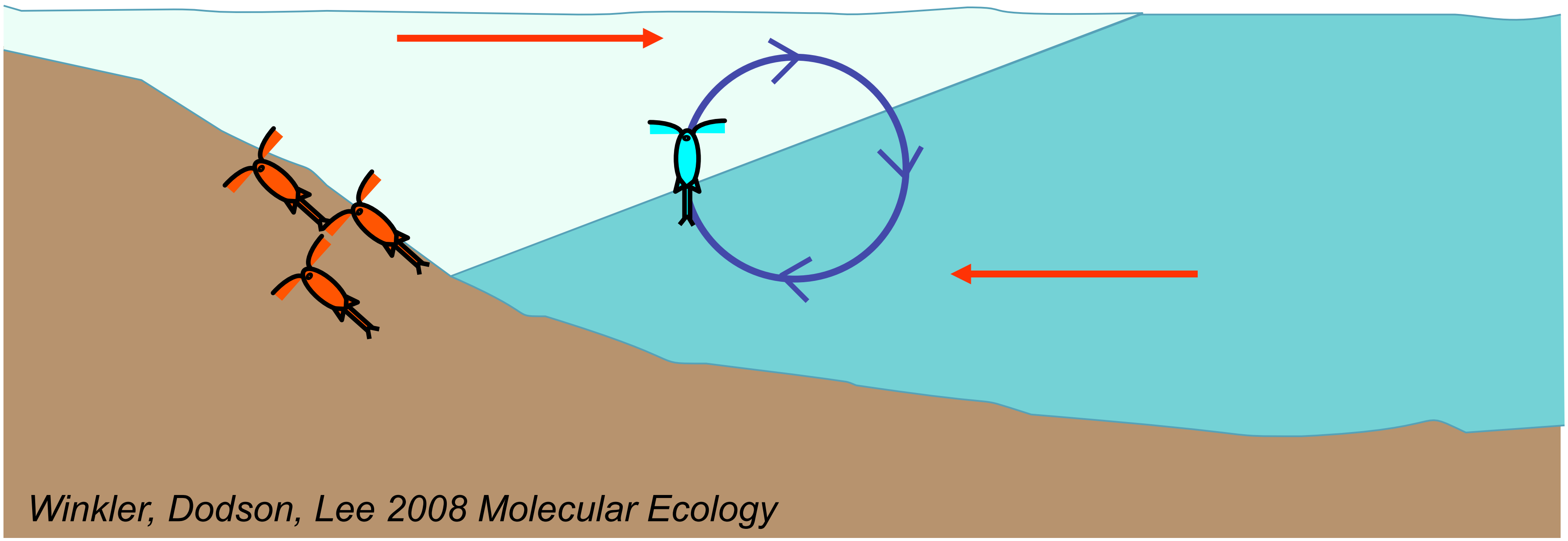
Significantly higher genetic variation in reaction norms in the invasive clade

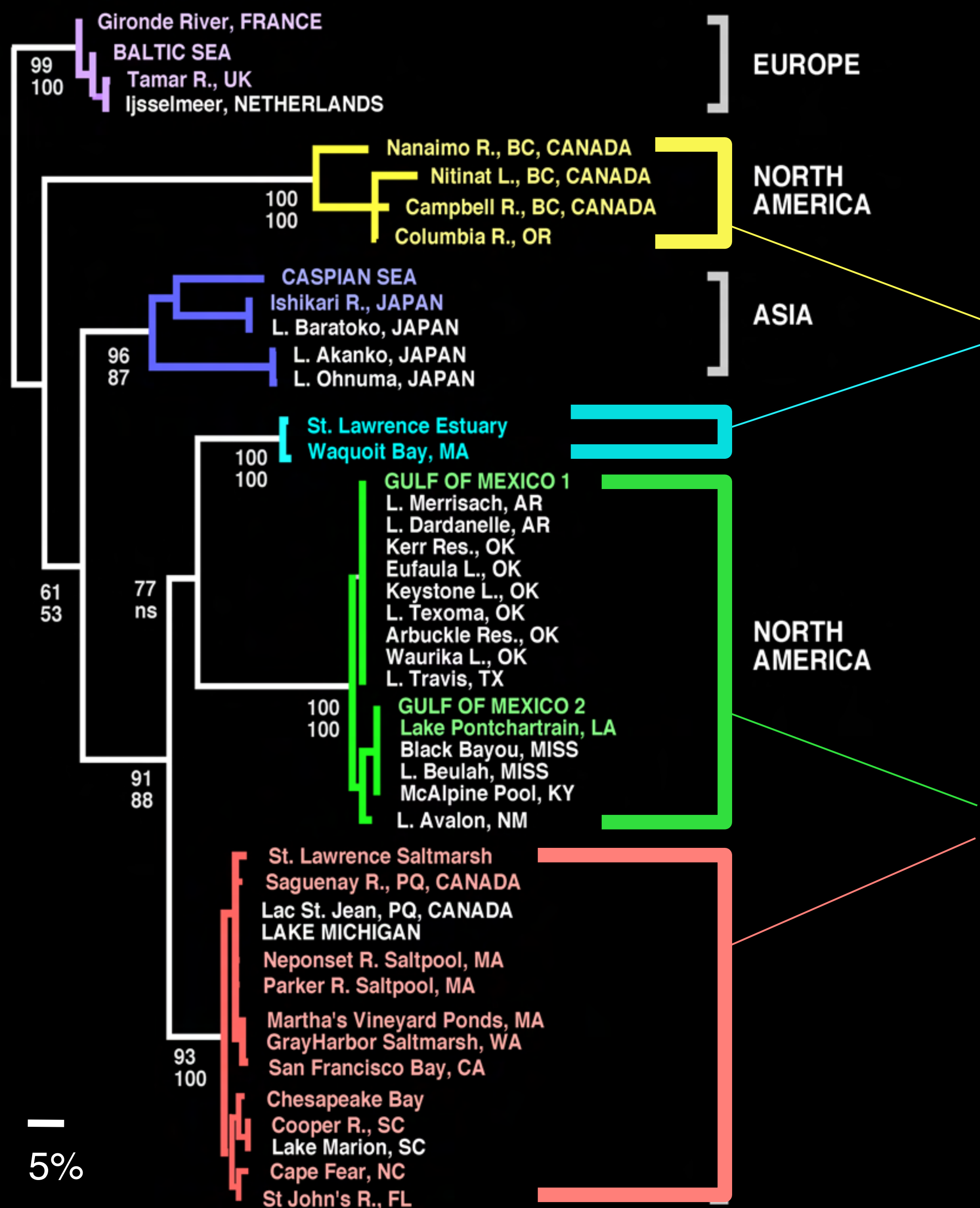
(Shannon's entropy, N = 15 clutches, $P = 0.03$)

Skelly, Chang, Winkler Lee, In Prep.

- **Invasive clade:** Nearshore and salt marsh
  Seasonal salinity fluctuations
  Select for different genotypes across seasons

- **Noninvasive clade:** Central portion of estuary
  Maintain more constant salinity
  No seasonal fluctuations





Noninvasive clades:

More Constant Habitats

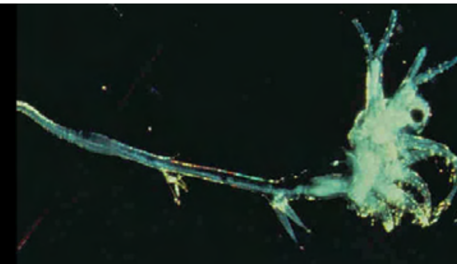
(Restricted to central portions of estuaries and bays)

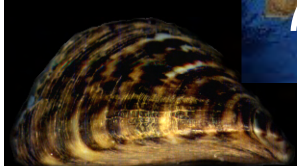
Invasive clades:

Fluctuating Habitats

(Nearshore, salt marsh ponds, marginal portions of estuaries)

Ponto-Caspian Basin:
Hot-spot for invasive populations?



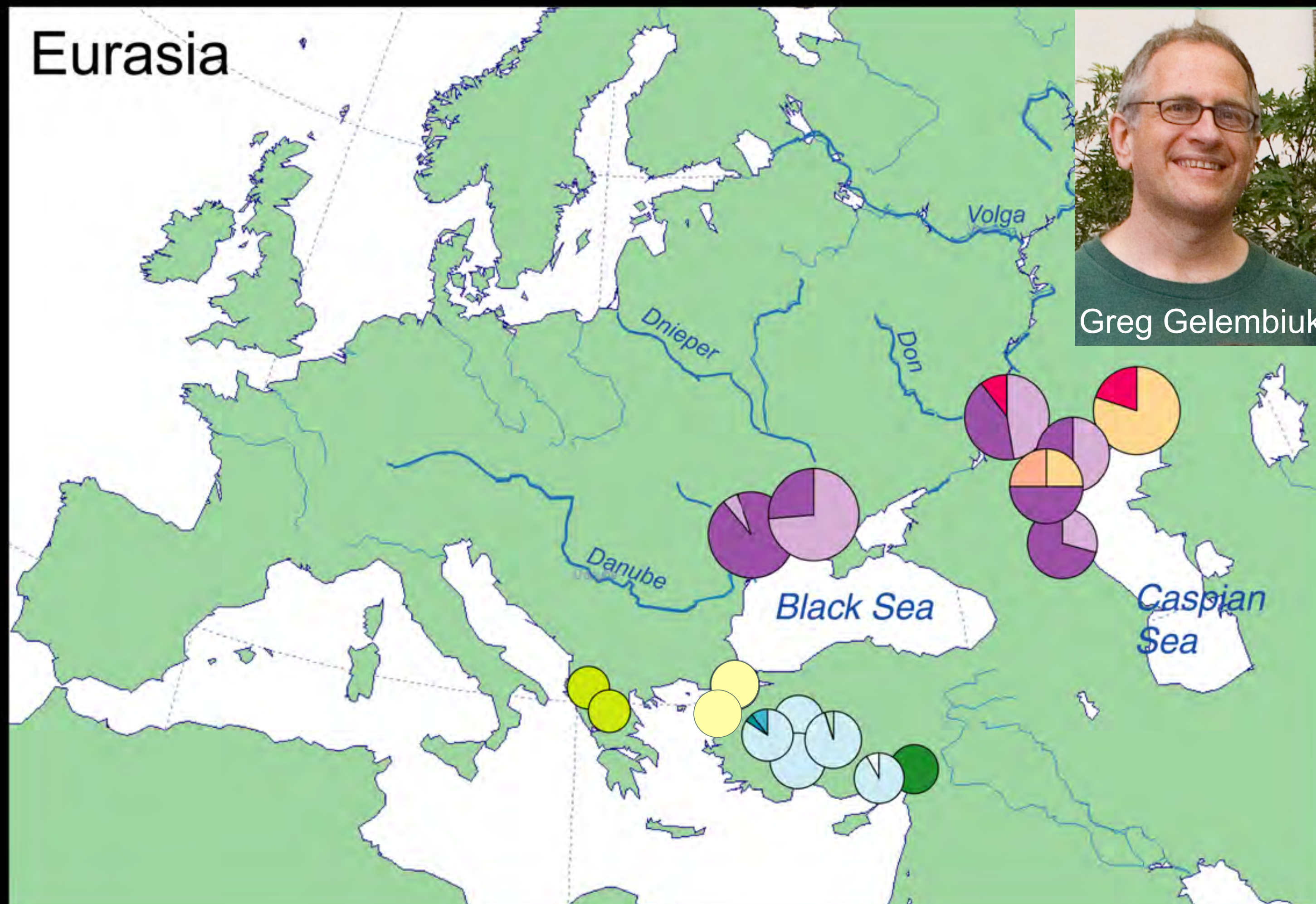


Lee and Bell 1999
Ricciardi and MacIsaac 2000

Zebra Mussel *Dreissena polymorpha*
COI Haplotypes in the Endemic Range

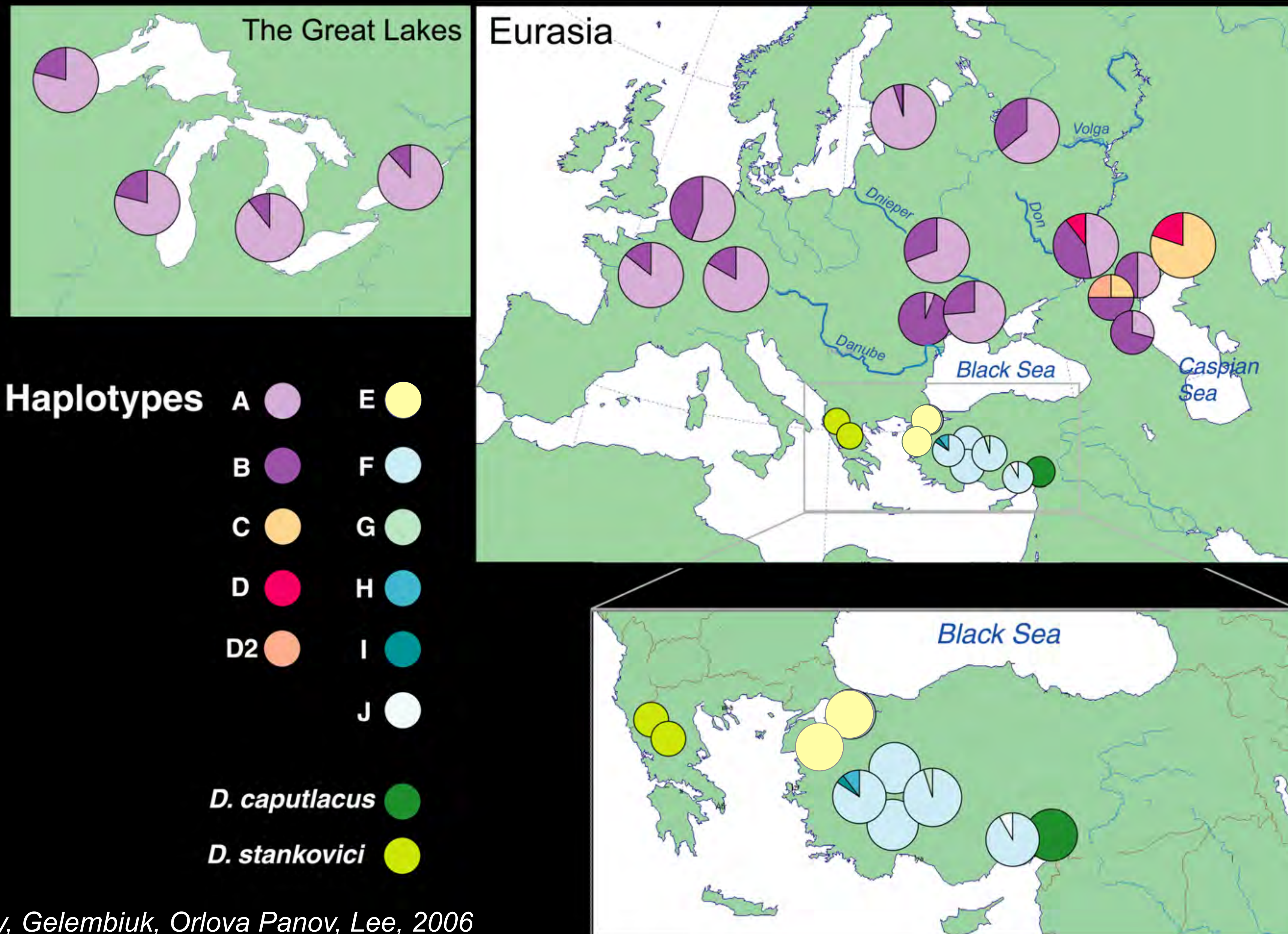
Haplotypes

- **A** · **E**
- **B** · **F**
- **C** · **G**
- **D** · **H**
- **D2** · **I**
- **J**
- ***D. caputlacus***
- ***D. stankovici***



May, Gelembiuk, Orlova Panov, Lee, 2006
Gelembiuk, May, Lee, 2006

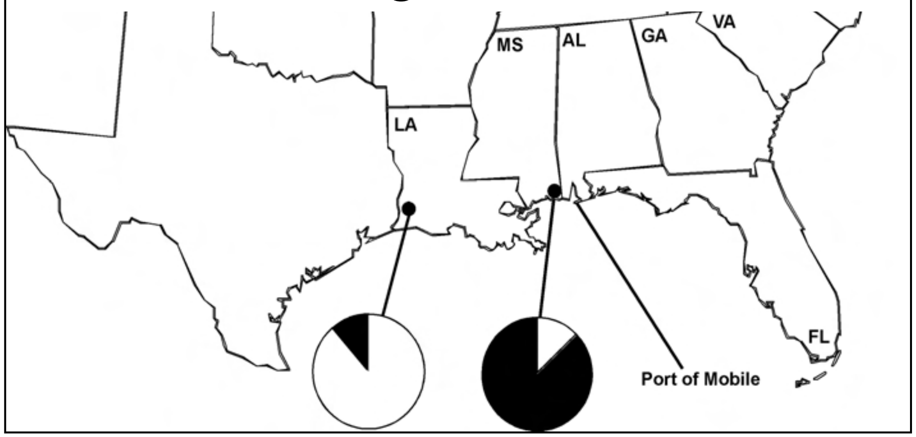
Invasive populations likely arose from the Black-Caspian Sea



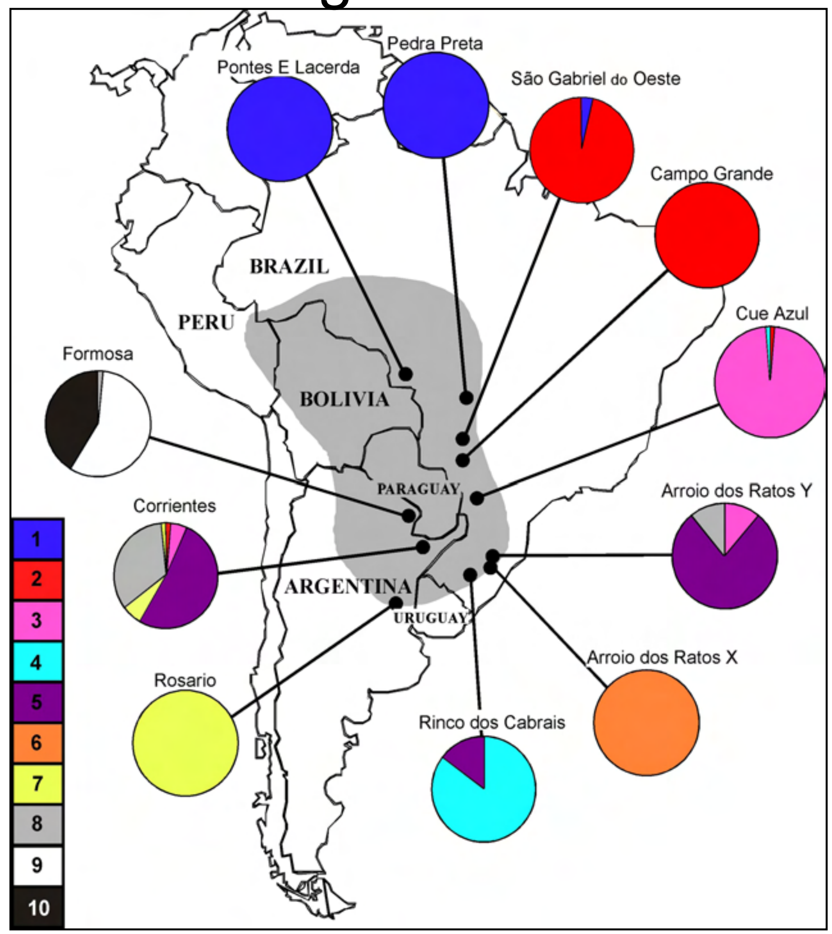
May, Gelembiuk, Orlova Panov, Lee, 2006
Gelembiuk, May, Lee, 2006

Fire Ant *Solenopsis invicta*

Invaded Range: North America



Native Range: South America

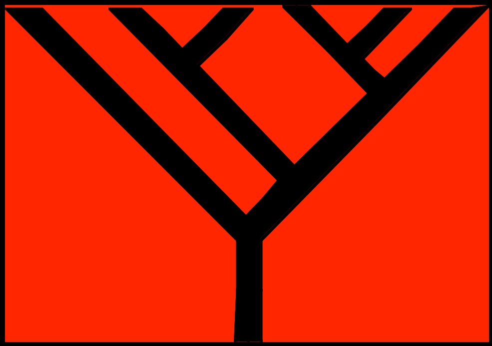


At least 6 invasive ant species in North America likely originated from the unstable floodplains of Argentina

- Fire Ant *Solenopsis invicta* (Caldera *et al.* 2008)
- Argentine Ant *Linepithema humile* (Tsutsui *et al.* 2001)

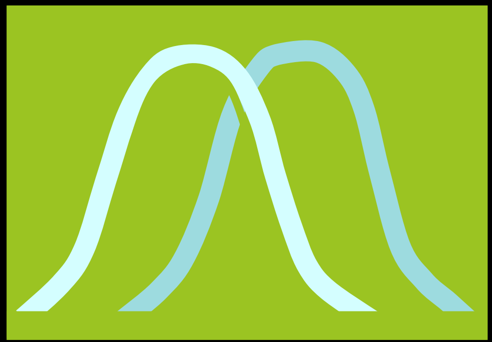
Review in Lee & Gelembiuk 2008, *Evolutionary Applications*

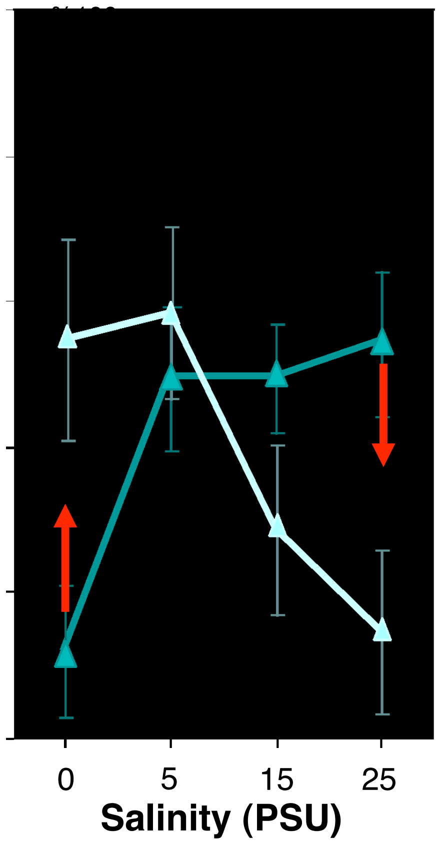
- Invasive species often contain **populations** that are **genetically and physiologically diverse → not all populations within a species are invasive** (Lee, 1999; May et al, 2006; Gelembiuk et al. 2006; Caldera et al. 2008)



- Invasive populations often originate from **fluctuating habitats**, with an evolutionary history of **fluctuating selection** (Lee & Gelembiuk 2008)

- **Fluctuating selection across generations** would result in the creation and maintenance of **standing (existing) genetic variation upon which Natural Selection could act during habitat change**

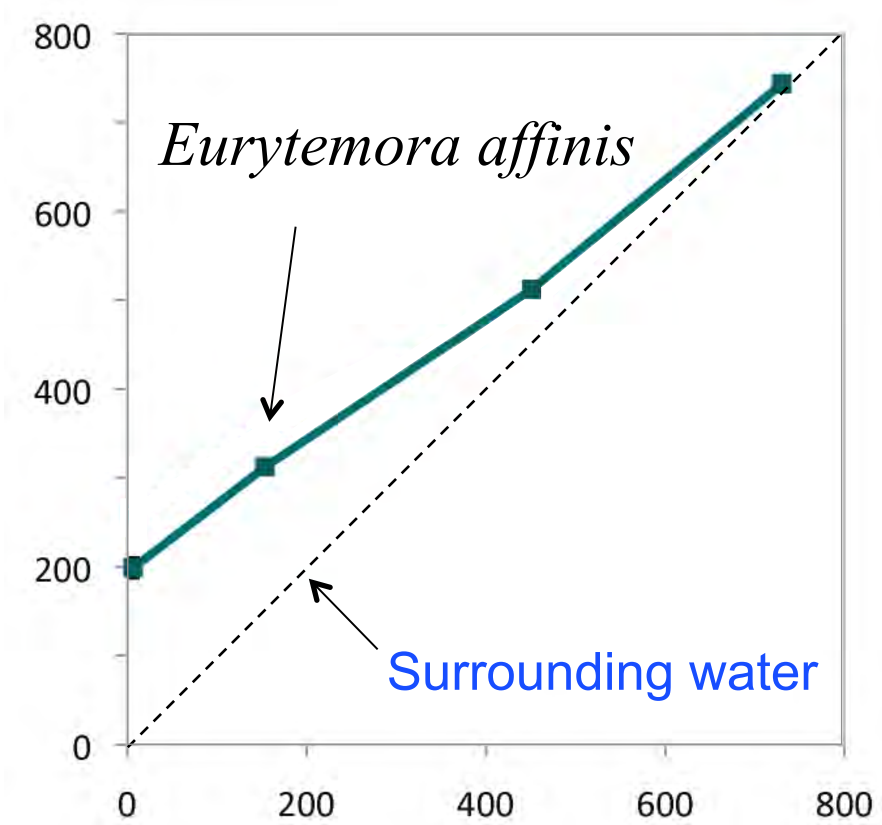




Which particular traits are undergoing natural selection, allowing freshwater invasions to occur?

Problem: "Blood" must be Thicker than Water

Hemolymph Osmolality (mOsm/kg)



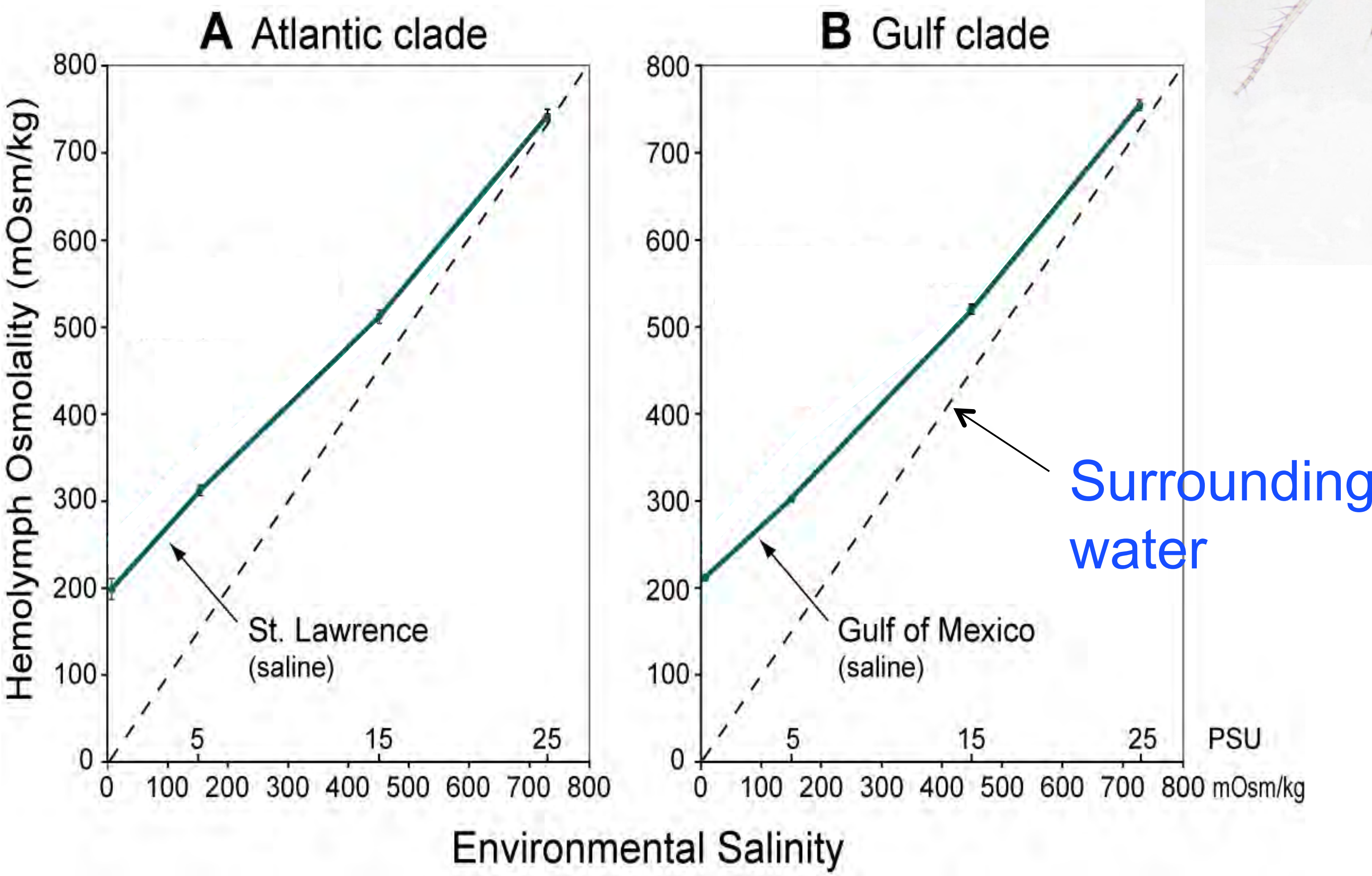
Environmental Concentration (mOsm/kg)

Must maintain steep concentration gradient between hemolymph and dilute water

Lee, Posavi, Charmantier, 2012

Problem: "Blood" must be Thicker than Water

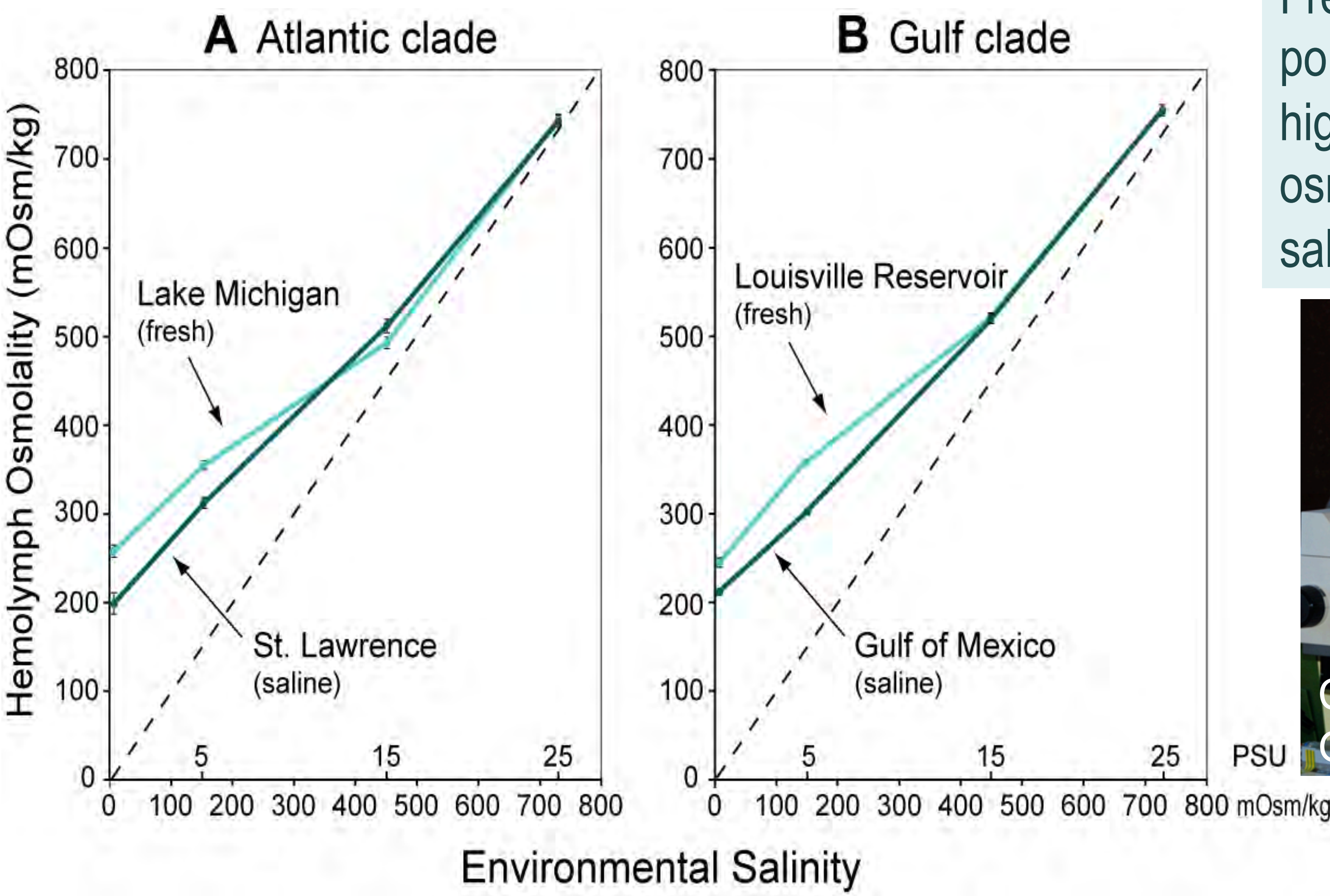
Saline Ancestral Populations



Lee, Posavi, Charmantier, 2012

For Freshwater Populations, "Blood" is even thicker

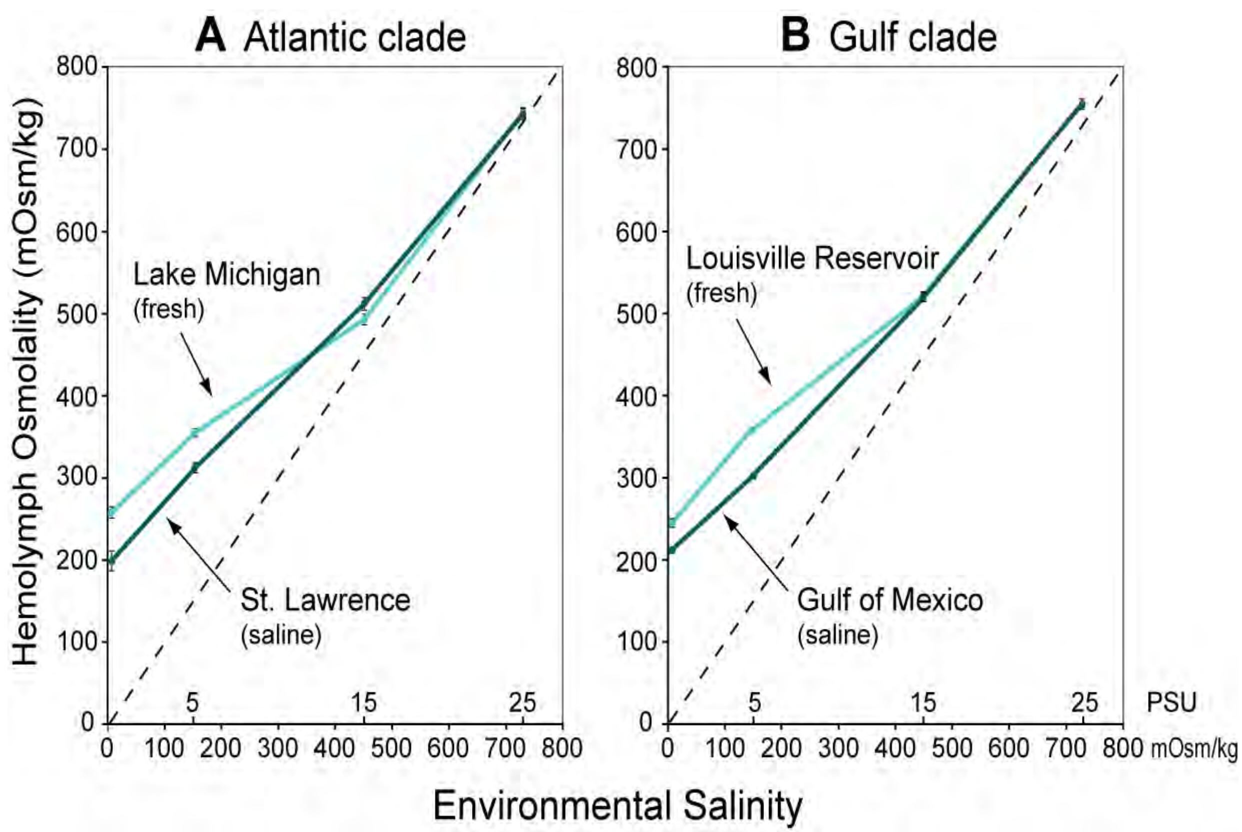
Evolution of increased body fluid regulation



Freshwater populations show higher hemolymph osmolalities at low salinities ($P < 0.001$)

Lee, Posavi, Charmantier, 2012

For Freshwater Populations, “Blood” is even thicker



Evolution of increased body fluid regulation

Maintaining this higher hemolymph concentration in fresh water would require i**ncreases in ion uptake** from the environment (and/or reduced ionic loss)

Gene Expression Analysis

↑ **Up in freshwater populations:**

Ion transport enzyme V-type H^+ ATPase**

some cuticle proteins

Mitochondrial proteins (ADP/ATP carrier protein)

Prohibitin

Malate dehydrogenase

S-adenosyl methionine synthase

↓ **Down in freshwater populations:**

Ion transport enzyme Na^+,K^+-ATPase*

some cuticle proteins

Eukaryotic translation elongation factor 1 alpha

Nicotinic acetylcholine receptor

Parallel shifts in expression of ion transport enzymes from saline to freshwater habitats

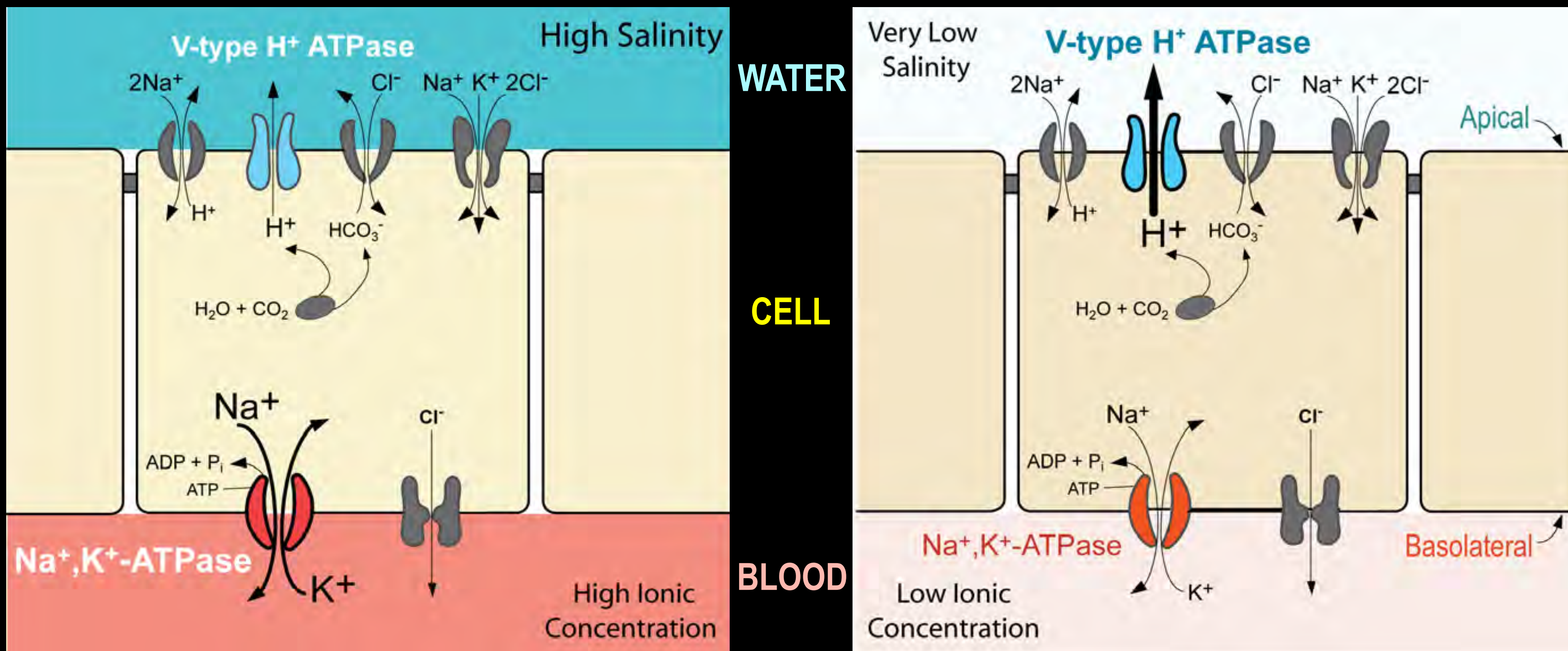
Lee et al. 2011 Evolution; Gelembiuk et al. In Prep.

MODELS OF ION TRANSPORT

Lee et al. Evolution 2011

Saline Habitats

Freshwater Habitats

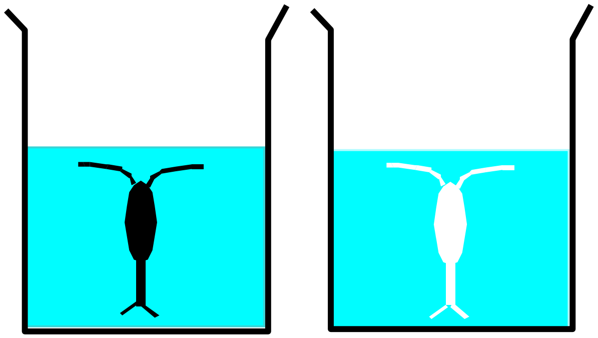


- In salt water, Na^+ transport into the cell is not a problem
- But, Na^+ transport from the cell to the hemolymph is more difficult; so, ***Na^+, K^+-ATPase*** is the rate limiting step

- In fresh water, ***V-type H^+ ATPase*** creates a H^+ gradient on apical side, enabling Na^+ to enter cell against steep concentration gradient
- But then, transport from the cell to the hemolymph is not a problem

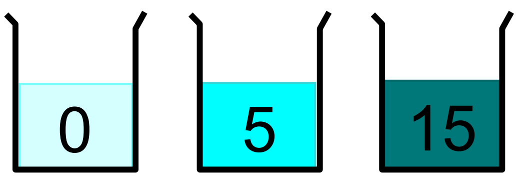
Does ion-transport ATPase function evolve during invasions?

Classic "**common-garden**" experiment, to remove effects of environmental acclimation



5 PSU

Larval Development

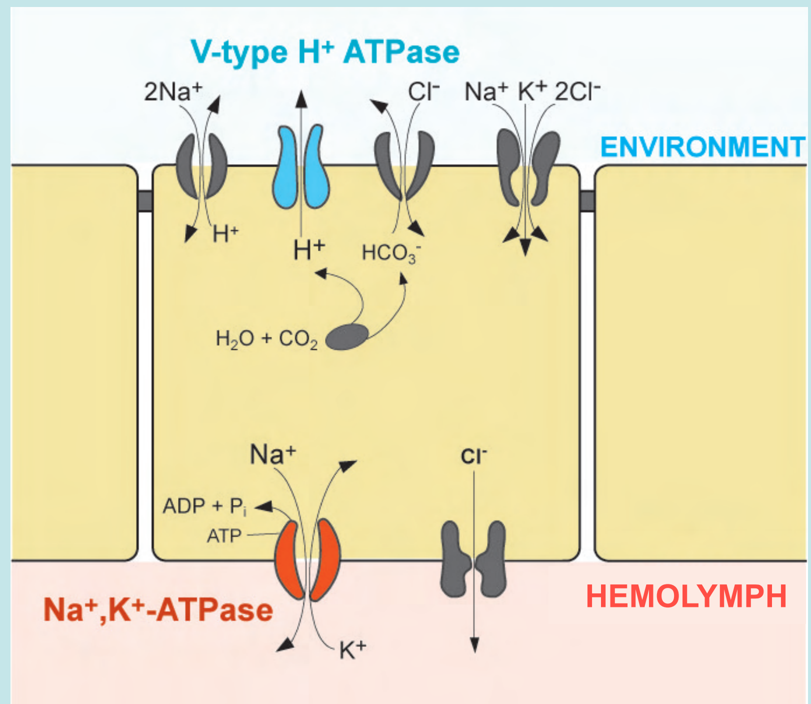


PSU

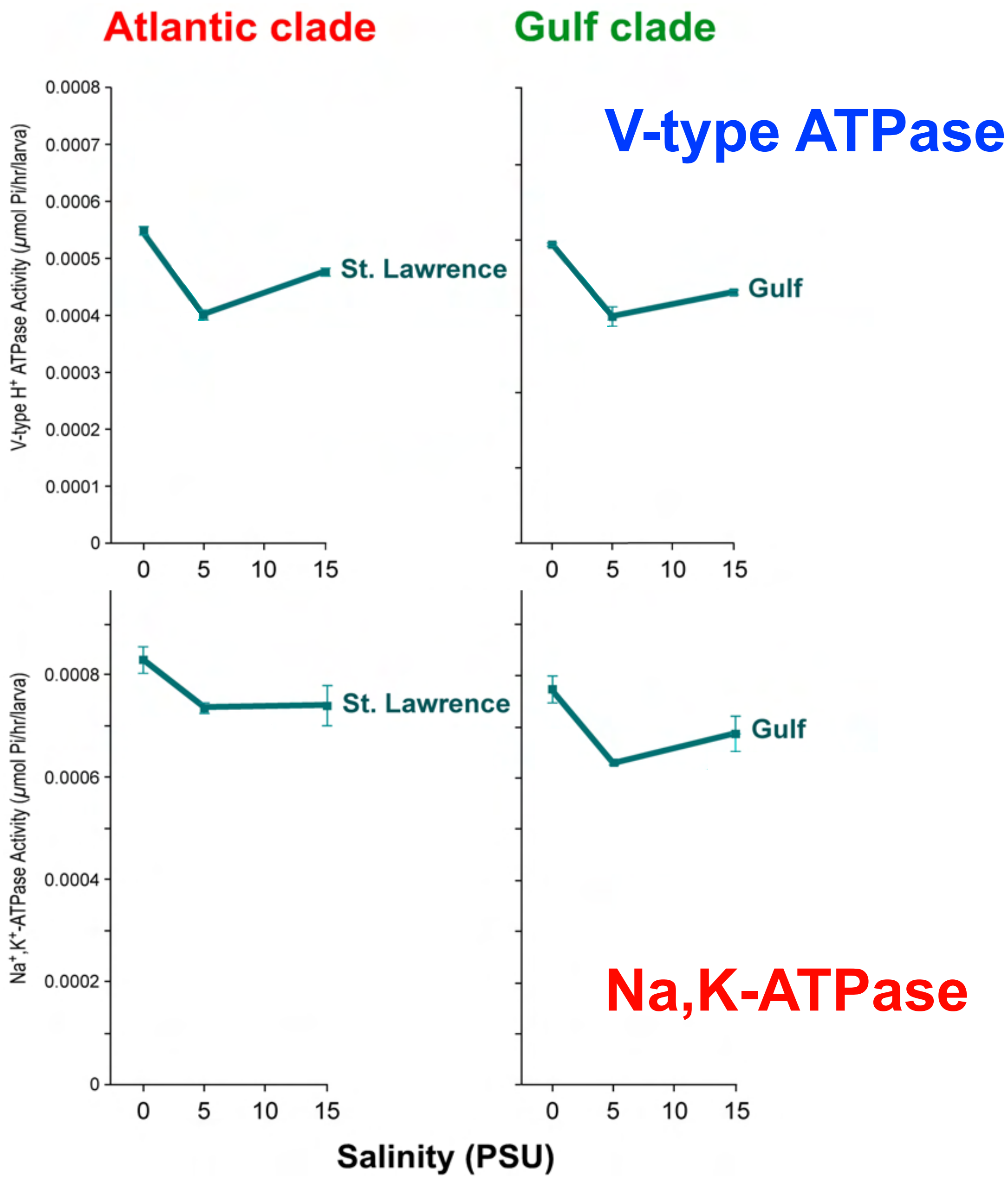
7 150 450 mOsm/kg

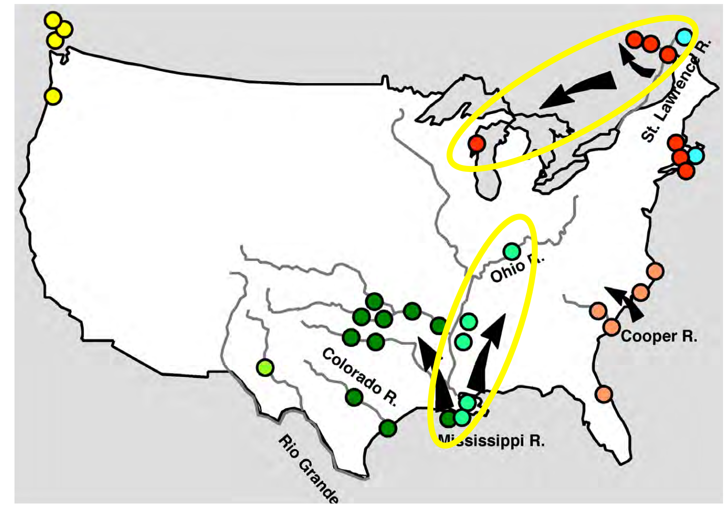
Enzyme Kinetics:
V-type ATPase, Na,K-ATPase activity

Mike Kiergaard



Evolution of Ion Transport Activity in Larvae



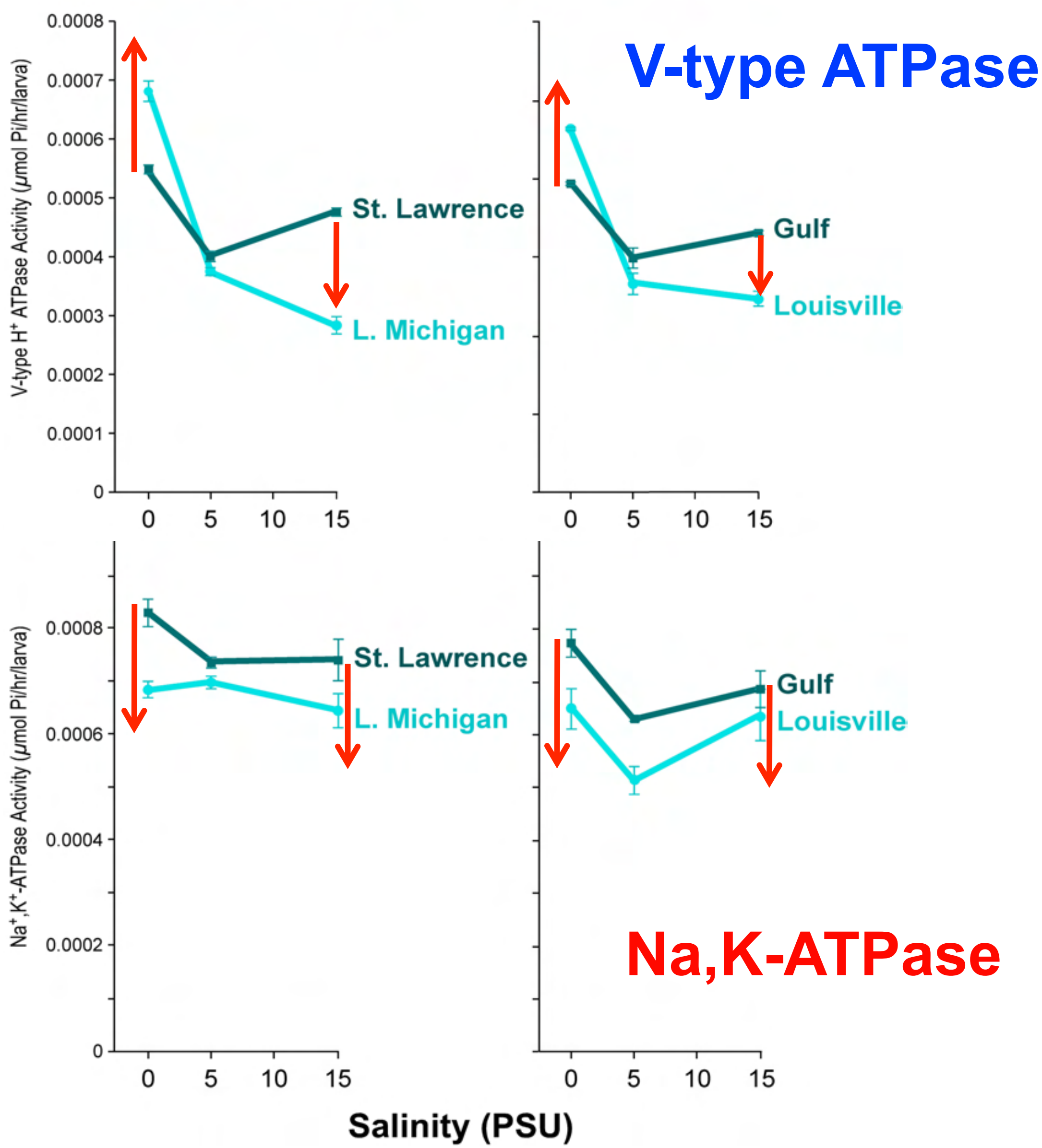


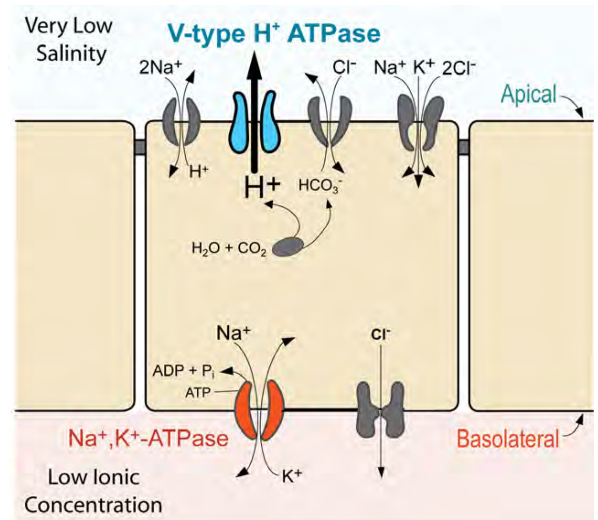
- Enzyme activity in the ancestral saline populations

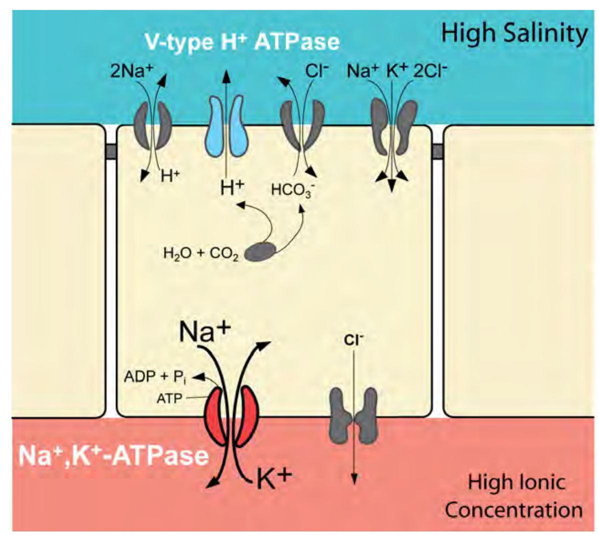
Lee et al., 2011 Evolution

Evolution of Ion Transport Activity in Larvae

Atlantic clade **Gulf clade**

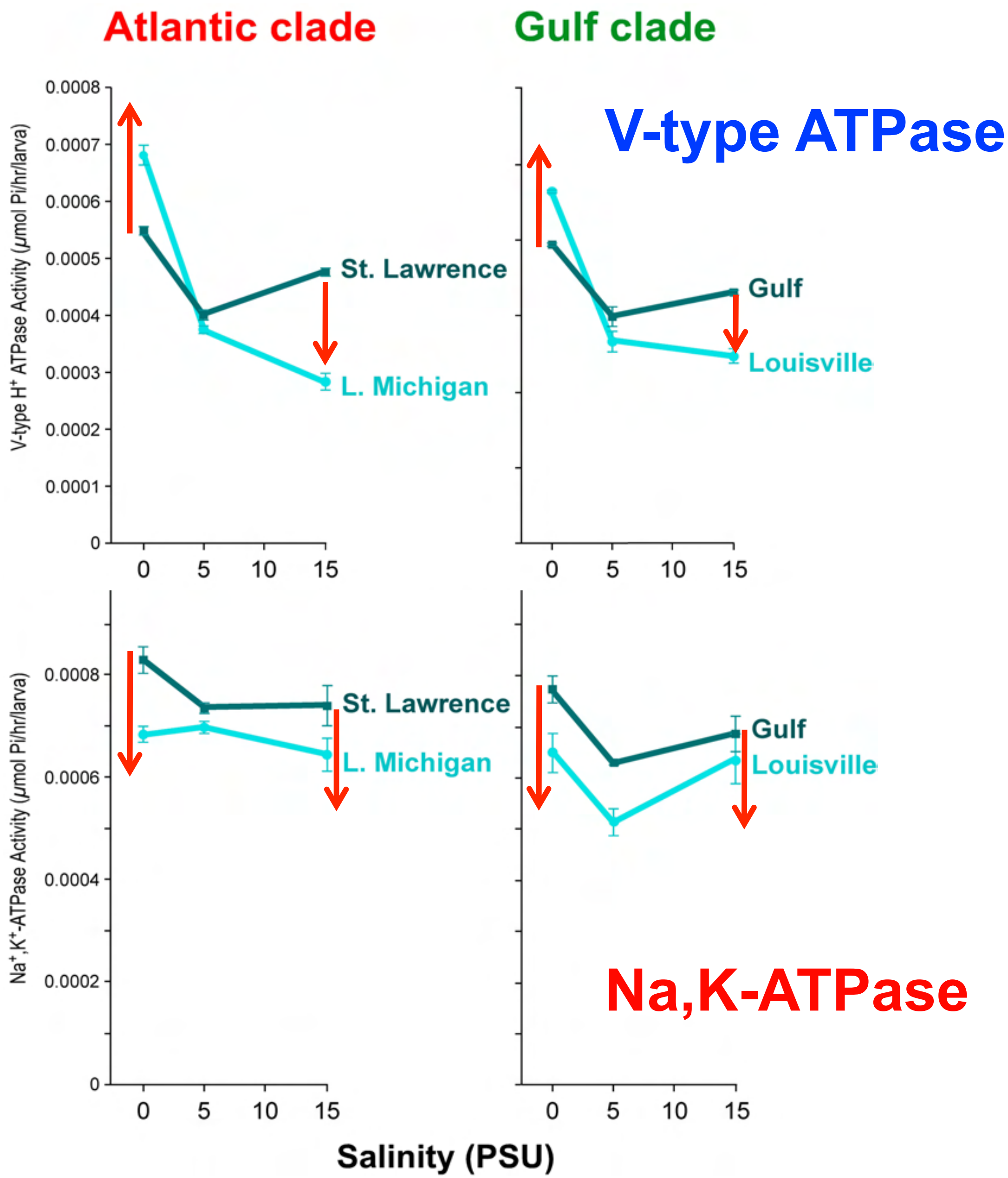


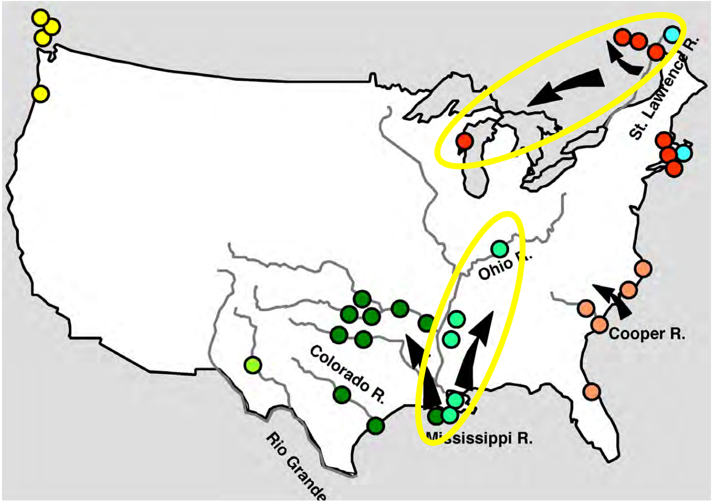




Lee et al., 2011 Evolution

Evolution of Ion Transport Activity in Larvae





- **Parallel evolution** in ion transport activity during independent invasions
- Suggests common mechanisms during independent invasions

Lee et al., 2011 Evolution

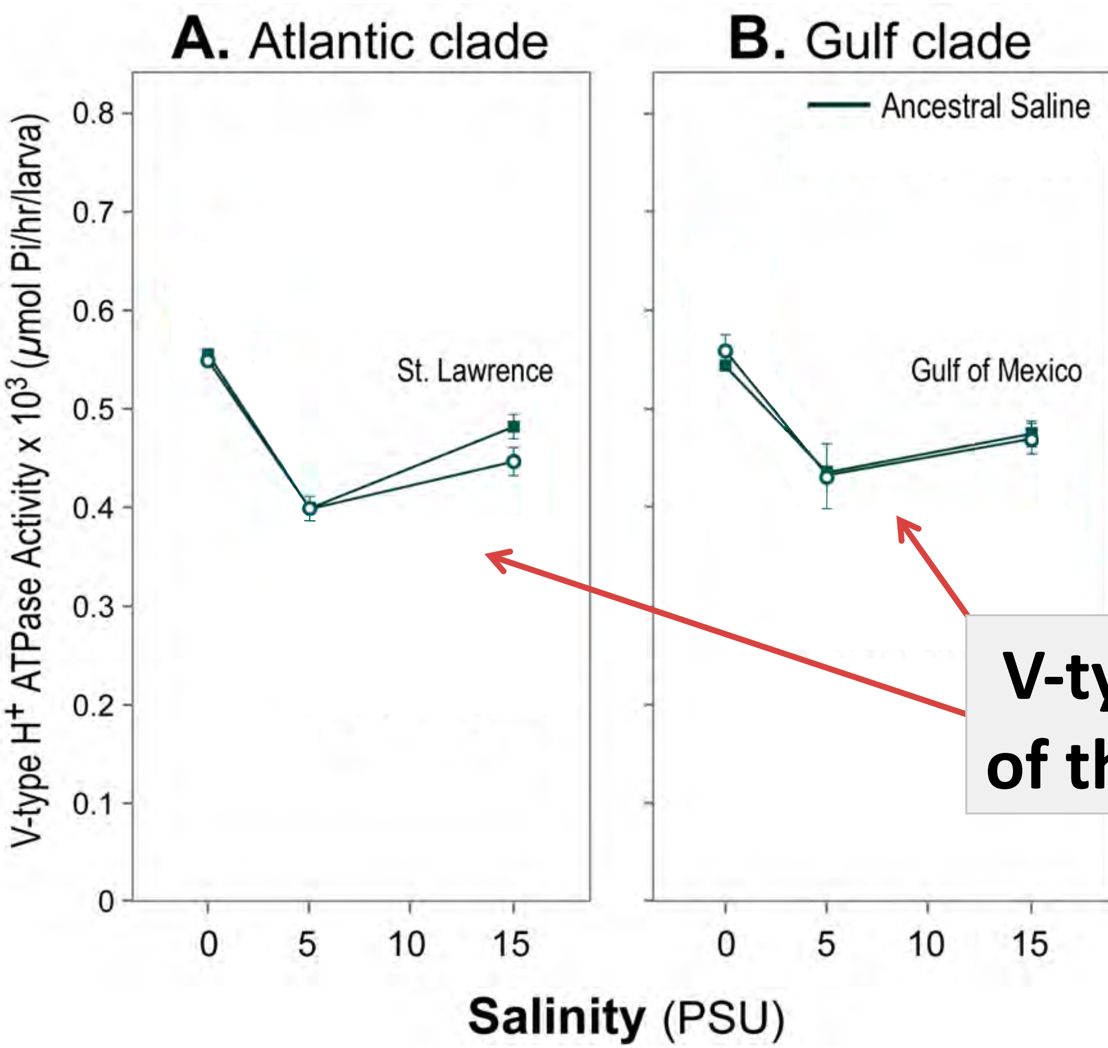
Laboratory Selection Experiments

- **But is salinity really the factor causing the evolutionary change?**

- Performed **selection experiments** to test whether the evolutionary change happens in response to salinity alone (and to establish a causal link between salinity and V-ATPase activity)

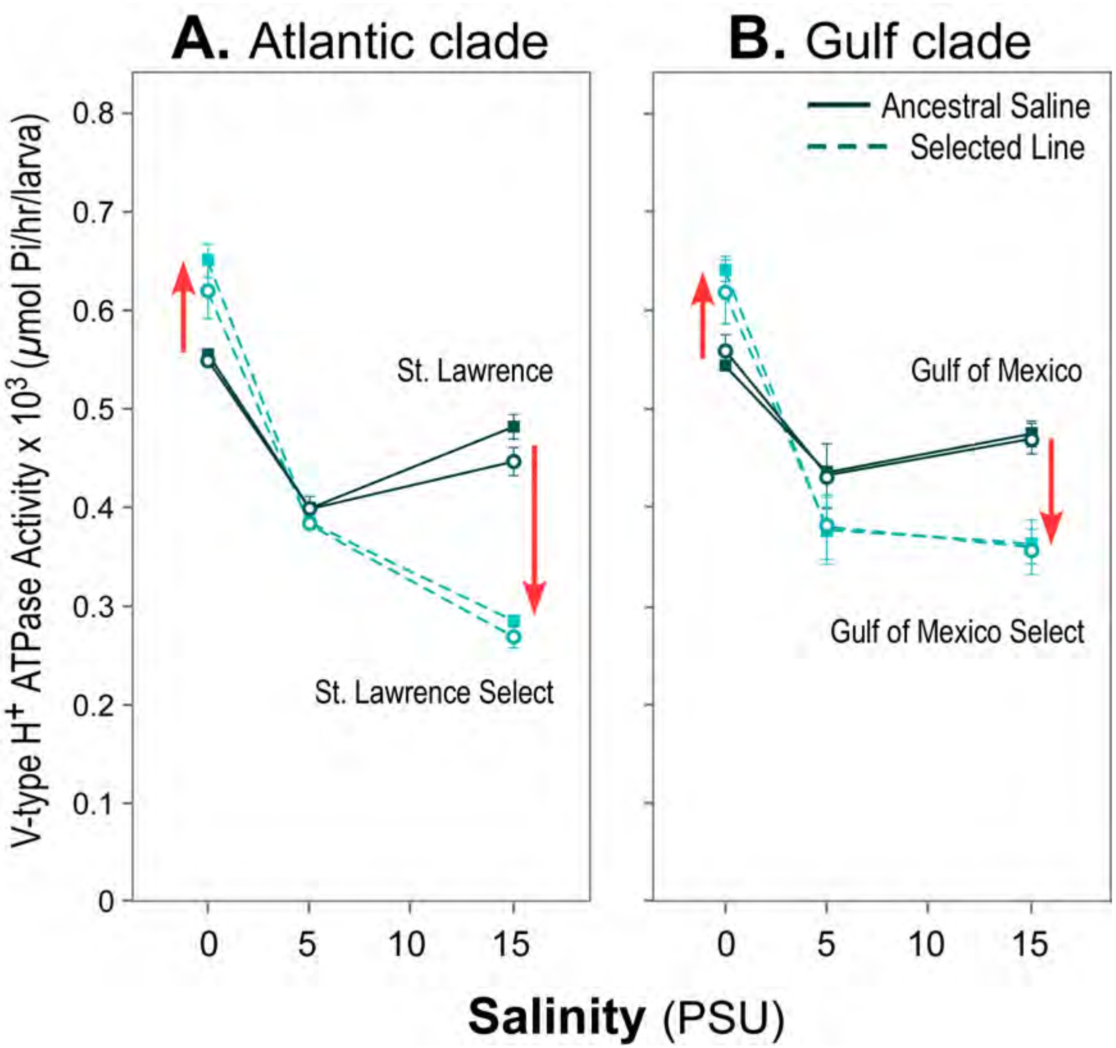
- Imposed laboratory selection on saline populations for freshwater tolerance over 12 generations

Selection in the Laboratory



V-type ATPase activity of the saline populations

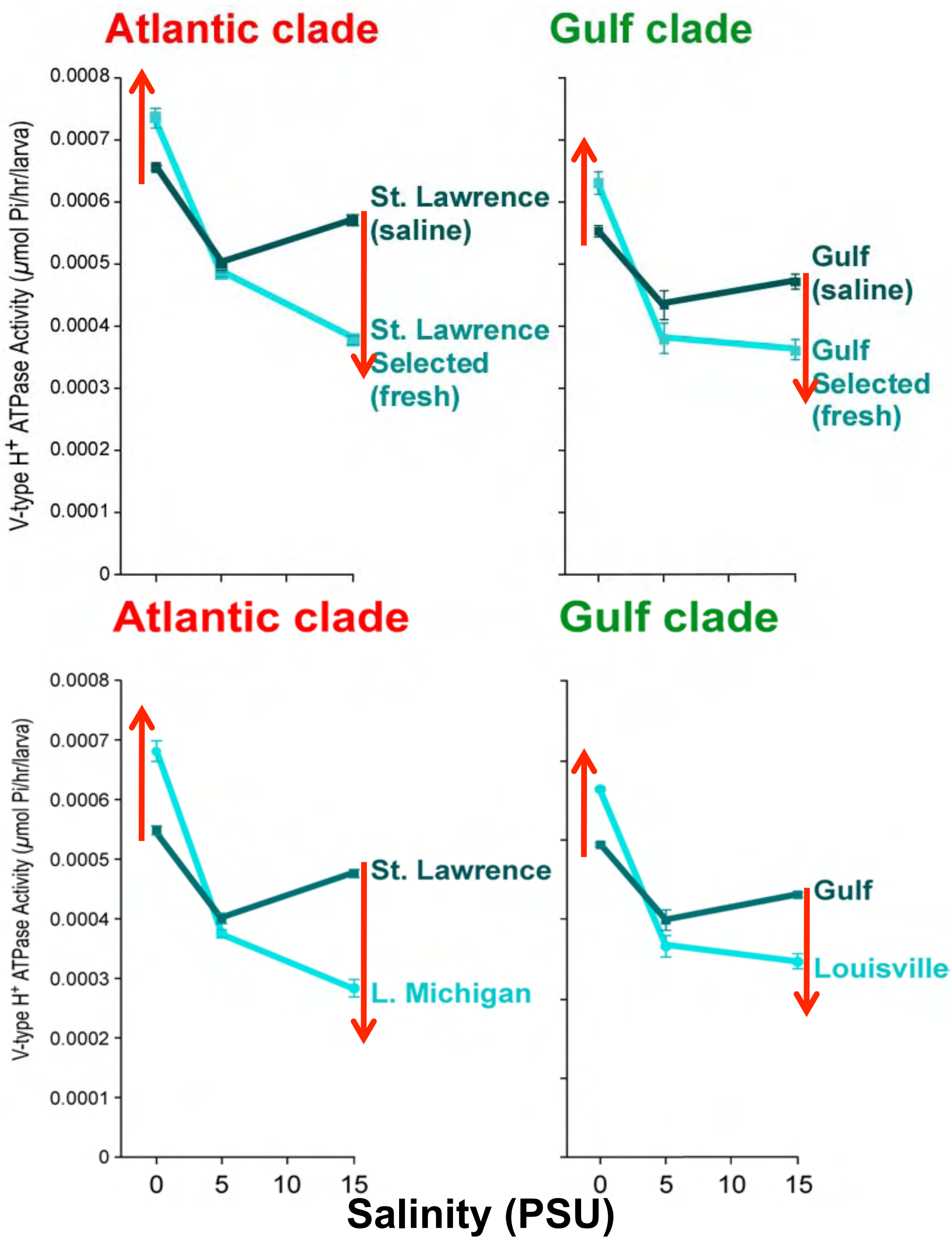
Selection in the Laboratory



Lee et al., 2011 Evolution

- Selected lines show same pattern of evolution as wild fresh populations
- Parallel Evolution across independent selection lines
- Varying salinity alone reproduced the same evolutionary shifts as in the wild, suggesting that **salinity** is indeed the factor imposing selection

Laboratory Selection Mimics Natural Invasions

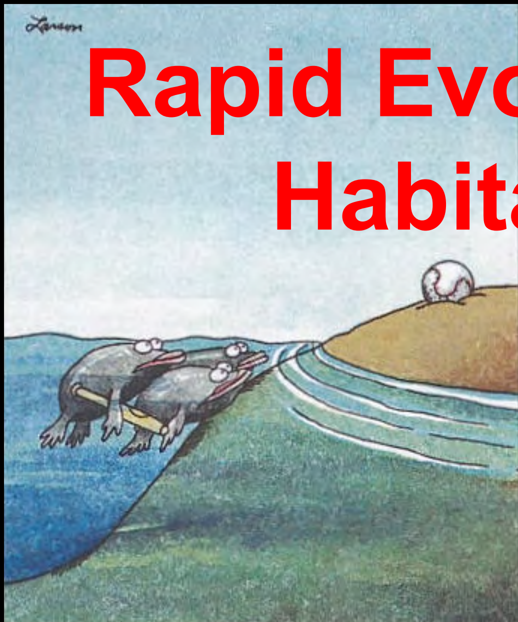


Selected Lines

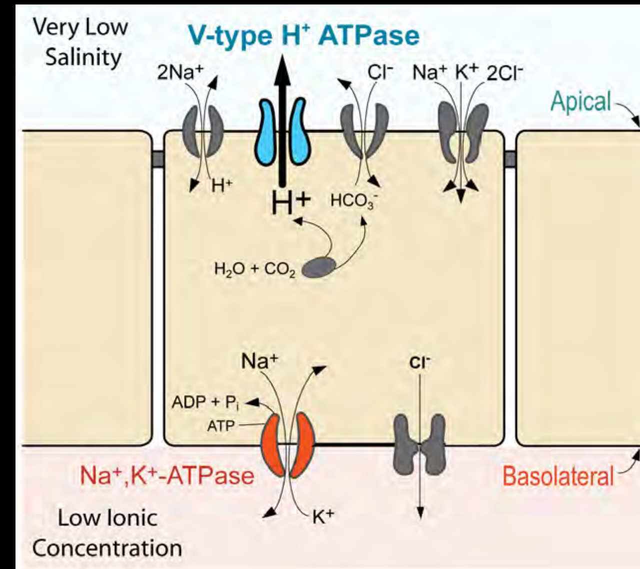
Reproducibility of evolutionary pathways suggests that this is an evolutionary labile trait

Natural Populations

Lee et al., 2011 Evolution



Rapid Evolution during Habitat Change

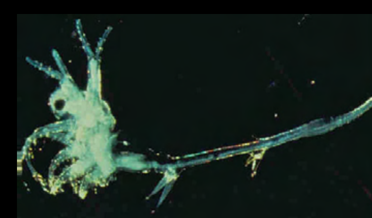


- **Parallel repeated mechanism of evolution**
  - **Parallel physiological mechanisms**

- **The capacity to evolve revealed by comparative reaction norm and selection experiments**

- **What is remarkable here is the high speed to which these evolutionary shifts could occur (~50 years in the wild, only 12 generations in the laboratory)**

Mechanisms observed here might have relevance for different taxa crossing similar habitat clines



…and might yield powers of prediction on populations that are likely to invade

Deep Horizon Oil Spill

Can zooplankton evolve in response to crude oil toxicity?

Compare pre-Oil Spill and post-Oil Spill populations to determine if adaptation has occurred

Evolutionary Response to the Deep Horizon Oil Spill

The Post-Oil Spill population shows a significant increase in survival and reduction in development time in water soluble fraction of crude oil

Unpublished Data

Funded by NSF RAPID

Lee et al. In Prep.

Evolutionary shift in response to crude oil

- Considerable genetic variation in oil tolerance exists in the pre-oil spill population

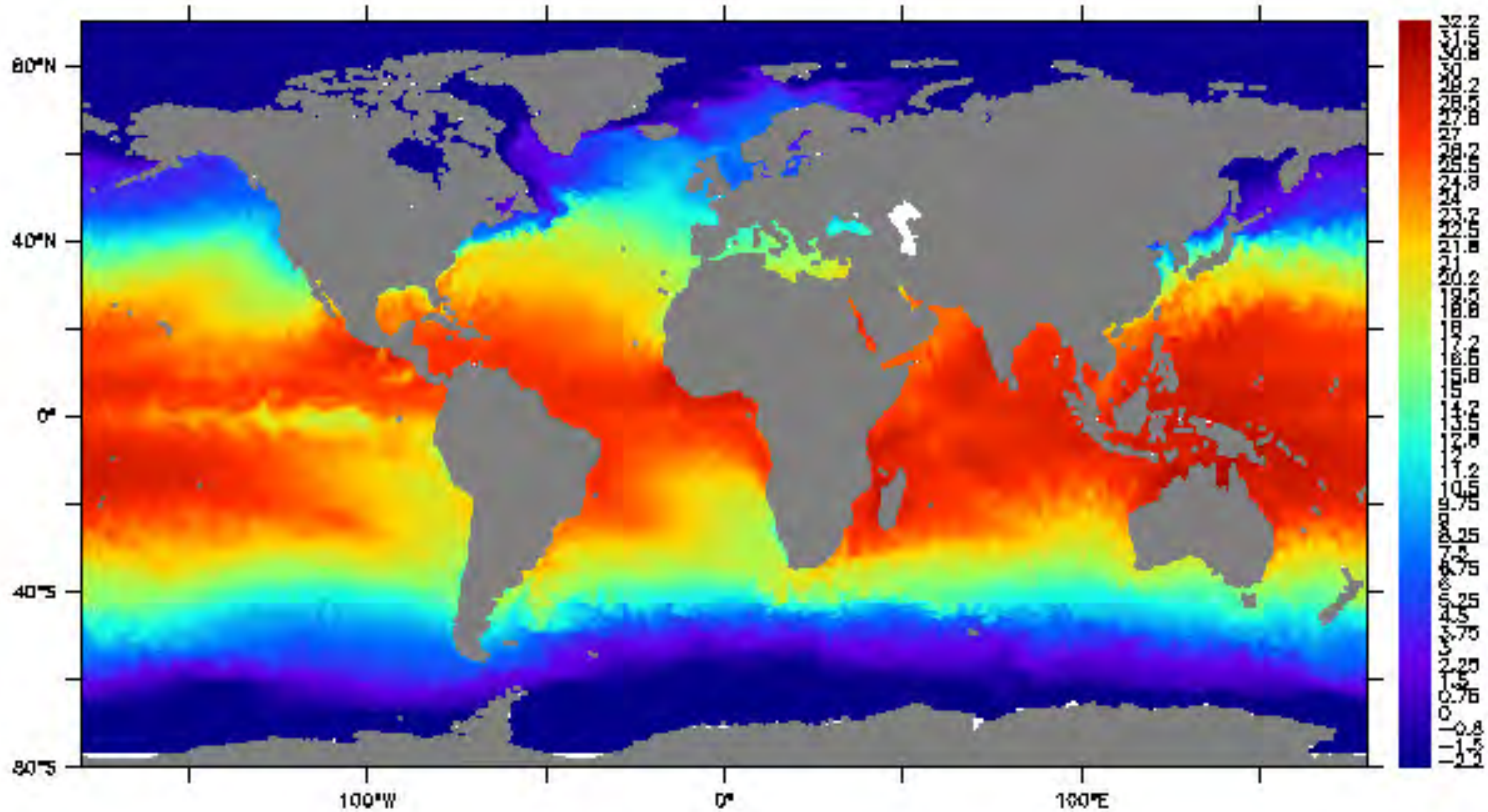
- Natural selection on standing genetic variation in the pre-Oil Spill population

Unpublished Data

Red = after oil spill
Blue = before oil spill

Lee et al. In Prep.

Temperature Adaptation?



Can Zooplankton populations evolve in response to temperature?

Example: Copepods in Chesapeake Bay

- Fluctuating temperature across seasons, and across generations
- That is, individuals do not experience the full temperature range of the environment
- Generation time shorter than seasonal fluctuations: ~20 day generation time at 15°C
- Seasonal change in temperature from 0 to 30°C

Prediction:

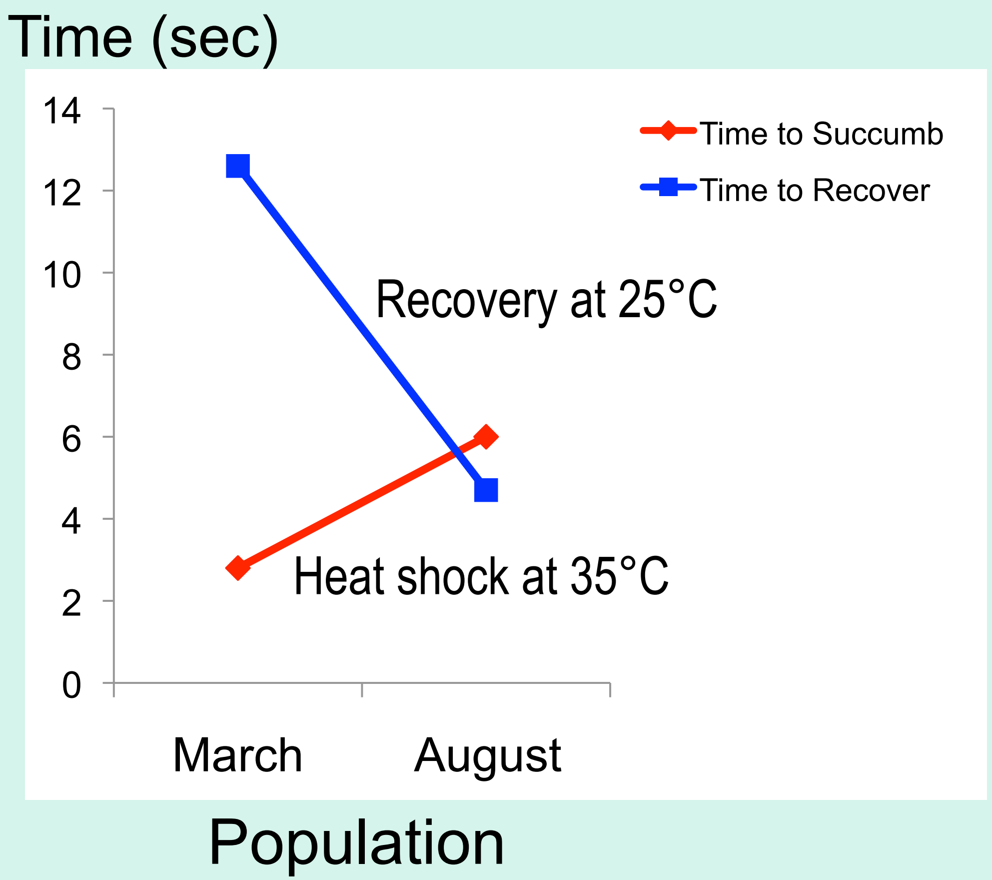
- Selection would favor different temperature tolerances at different generations (seasons), leading to the increase and maintenance of genetic variance in the population

- Fluctuating selection + the presence of an egg bank would help preserve genetic variation in the population

Difference in temperature tolerance across seasons

- Two populations from different seasons in the Chesapeake showed different temperature tolerance ($P < 0.01$)
  (Bradley 1975)

- March (colder) population experienced heat shock faster and took longer to recover

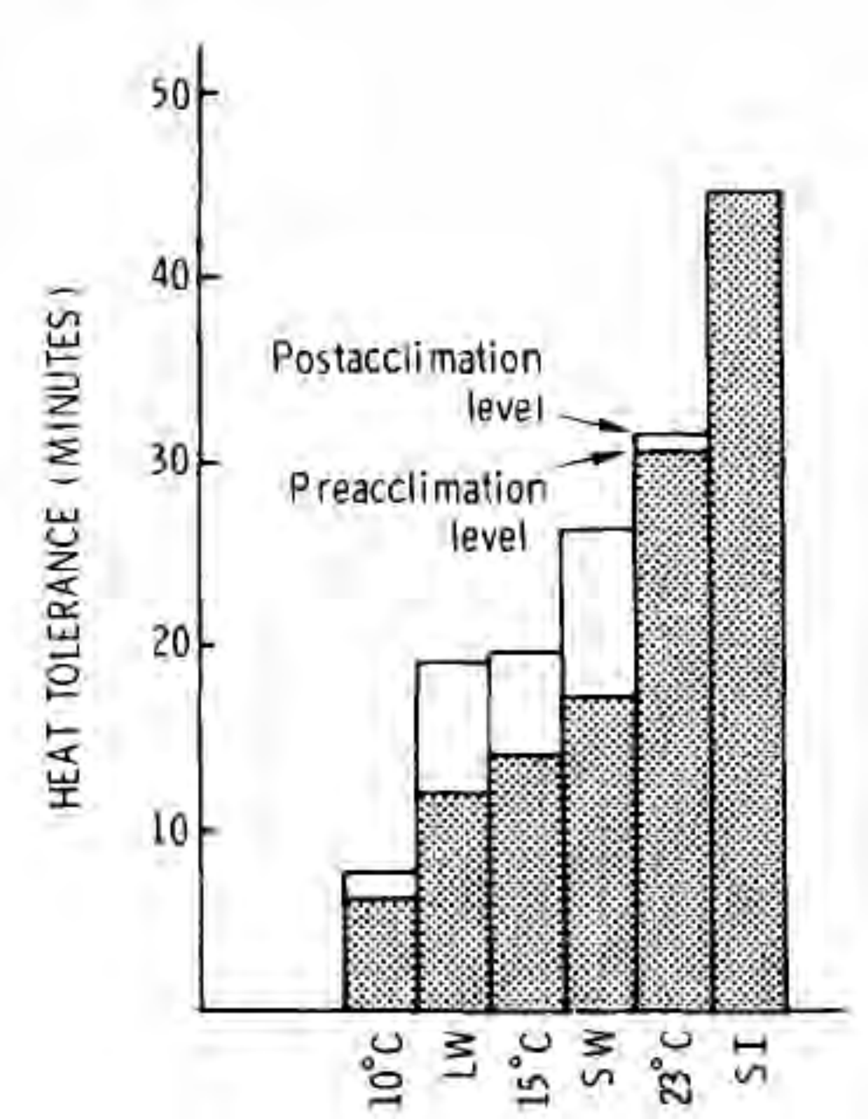


- Difference persisted for multiple generations in the lab (common-garden) revealing that the difference is heritable (genetically-based) and not due to phenotypic plasticity (acclimation)

Significant Selection Response to Temperature

Significant difference in temperature tolerance among selected lines ($P < 0.01$)

Selected lines reared at higher temperature for ~25 generations (~2 years) had greater tolerance to heat shock (32°C) (Ketzner & Bradley 1982)



Reared at higher Temp →

Evolutionary Potential

- Genetic variance in temperature tolerance is present in the Chesapeake Bay *E. affinis* population **due to seasonal fluctuations** (<u>not necessarily true of all *E. affinis* populations</u>)

- **<u>Common-garden Experiment → Evolution Happened</u>**: revealed significant heritable differences in temperature tolerance between two populations originating in different seasons

- **<u>Selection Experiment → Evolution can Happen</u>**: revealed that populations of *E. affinis* can undergo natural selection in response to temperature

What about the Open Ocean?

- **Do the populations contain genetic variance for the relevant traits?**
  - Is there a mechanism to maintain genetic variation in temperature tolerance?
    - → For instance, is there fluctuating temperature across different generations?
    - → The storage effect of an egg bank? Overlapping generations?

What about the Open Ocean?

Data Needed:

Amount of genetic variation for temperature tolerance ≠ genetic variation at neutral markers (e.g. microsatellites)

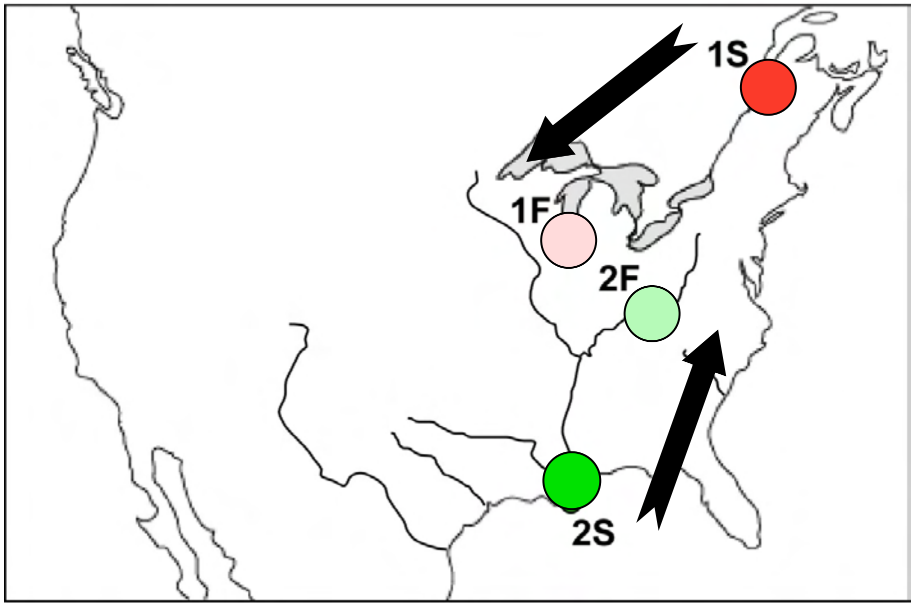
Mechanism to maintain genetic variance? Period of temperature fluctuations relative to generation time of organisms? Overlapping generations (egg bank)?

Rate of Evolution? Generation time (unit of evolution); mutation rate of smaller organisms (Bacteria, Archaea, Viruses)

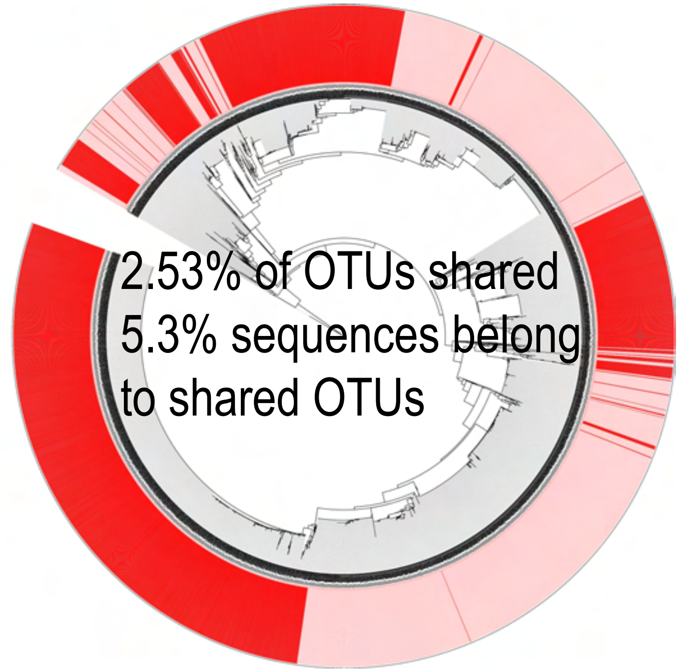
Another issue to consider:
The Host's Microbiome

- Shift in the microbiome during habitat change
- The microbiome is a biogeochemical reactor
- Will affect host physiology
- Will affect the ecosystem

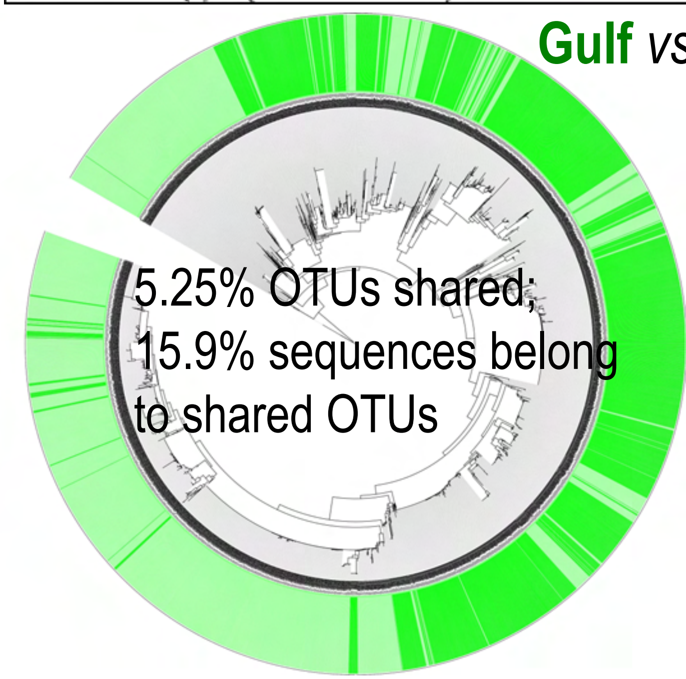
Dramatic Shift in Microbial Composition during Invasions



St. Lawrence *vs.* L. Michigan



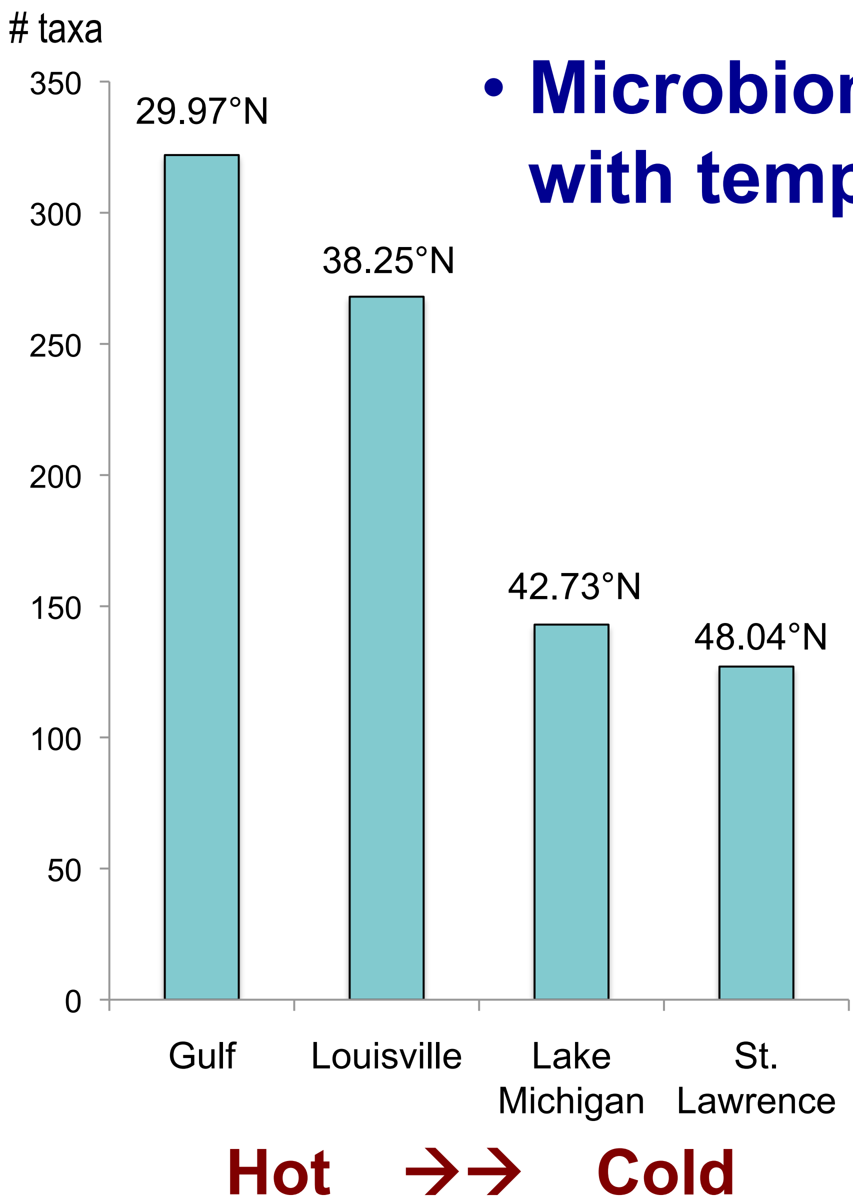
Gulf *vs.* Louisville



- **Microbiome composition shifts radically with salinity change**
- Significant Unifrac distances between saline *vs.* fresh microbial communities ($P < 0.01$)

Gelembiuk, Silva, Metzger, Lee, In Prep.

Microbial community diversity across latitudes

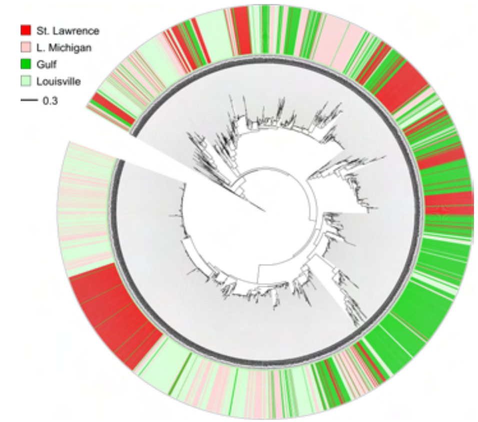


- **Microbiome composition shifts with temperature**

- Microbial community diversity increases at lower latitudes (r = -0.95, $P < 0.05$)
- This pattern has been found in free-living bacteria, and here it is found for host-associated microbiomes

Gelembiuk, Silva, Metzger, Lee, In Prep.

Potential roles in Biogeochemical Cycles



Enormous Copepod Biomass, Anaerobic Compartment in Guts

Affecting the fate of Nitrogen:

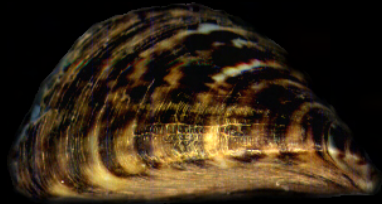
→ **Zooplankton gut flora have been speculated to partly account for deficits in N_2 Fixation Budgets in some ocean basins:** nitrogen loss exceeding the gain from dinitrogen fixation by approximately 200 Tg N yr^{-1} (Mahaffey et al. 2005)

- **Denitrification ($NO_3^- \rightarrow N_2$):** Many species of denitrifying bacteria (e.g. Comamonadaceae, Pseudomonadaceae, Vibrionaceae, Rhodobacteraceae, Shewanellaceae)
- **Nitrogen fixation ($N_2 \rightarrow NH_3$):** All copepod microbiomes contained *Klebsiella* spp.

Summary

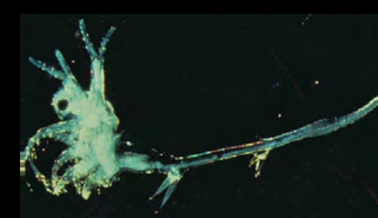
- **Rapid Physiological Evolution can occur during Habitat Change**
- **Ample Genetic Variation <u>for the relevant phenotype traits</u> is essential for Natural Selection to occur**
- **Evolutionary history in the native range likely affects the levels of standing genetic variation and the potential to respond to habitat change (fluctuating habitats)**
- **Common-garden and selection experiments could provide insights into whether populations have evolved or could evolve**
- **When habitat changes, microbiome will also change; the Copepod Microbiome might play critical functional roles for the host, and might have profound ecosystem impacts given its huge size as a biogeochemical reactor**

Mechanisms observed here might have relevance for different taxa crossing similar habitat clines



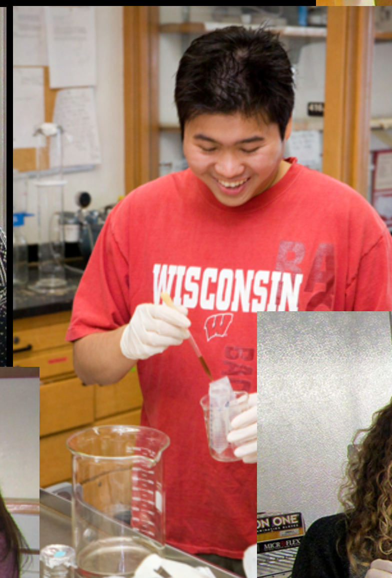


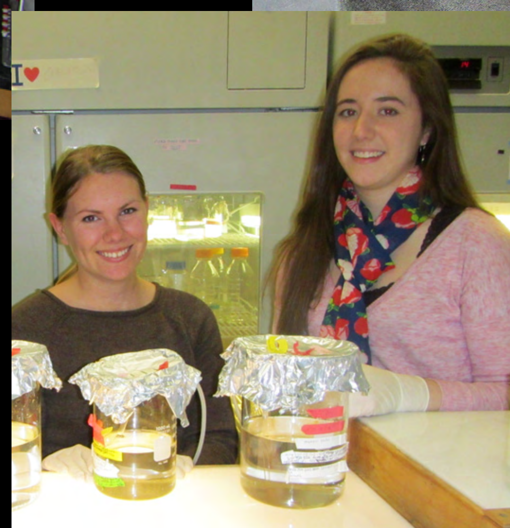


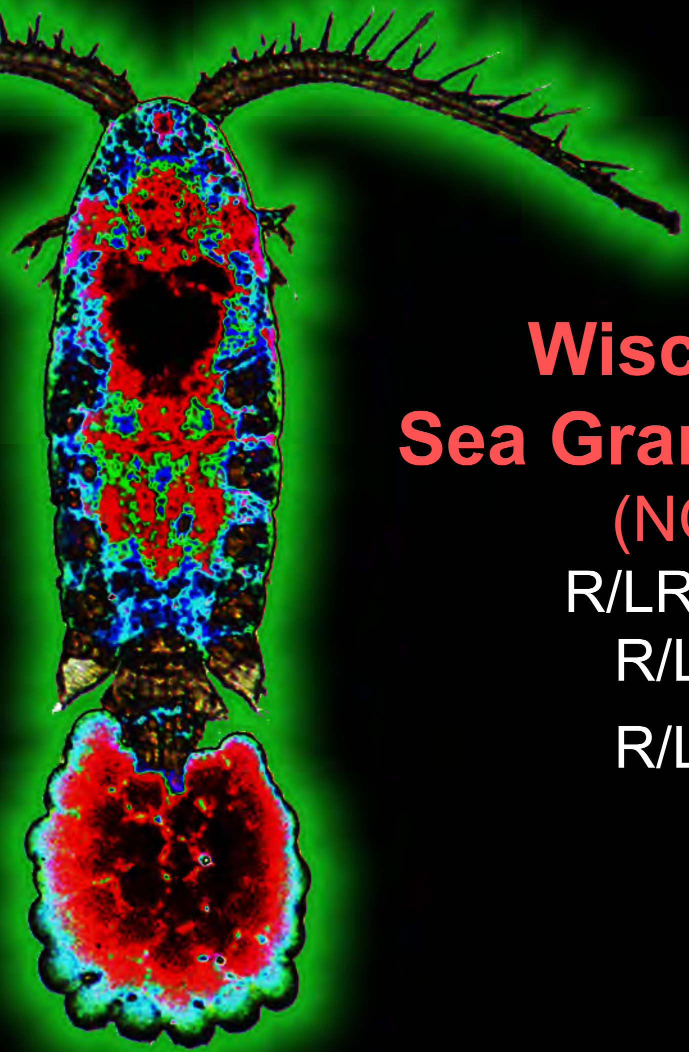
…and might yield powers of prediction on how populations will respond to habitat change

Lee Lab Members





Federal Funding



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