# Evolutionary Transitions between Marine and Freshwater Environments in Fish


*Andrew Whitehead*

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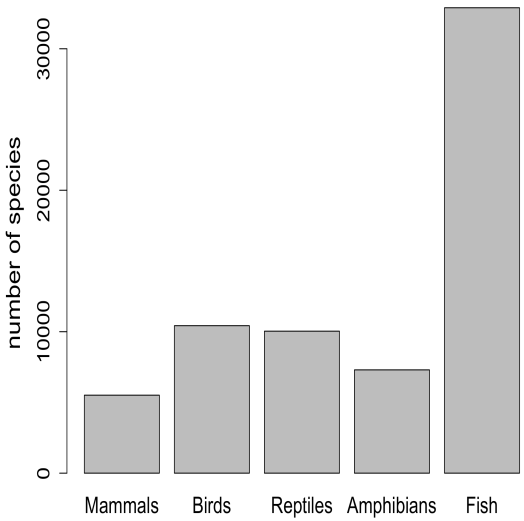
UC DAVIS UNIVERSITY OF CALIFORNIA

# Marine to FW → steepest biodiversity gradient on the planet?




World Conservation Union. 2014

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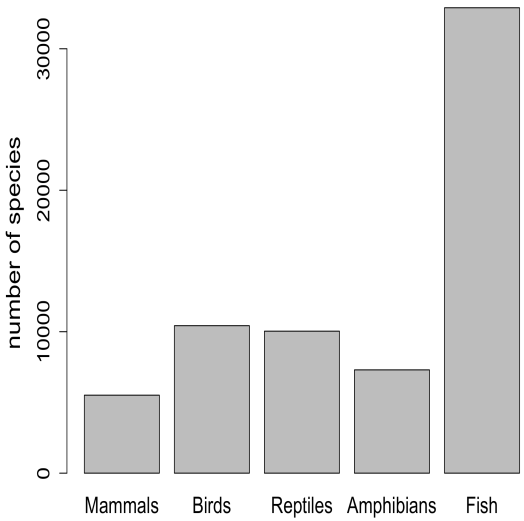


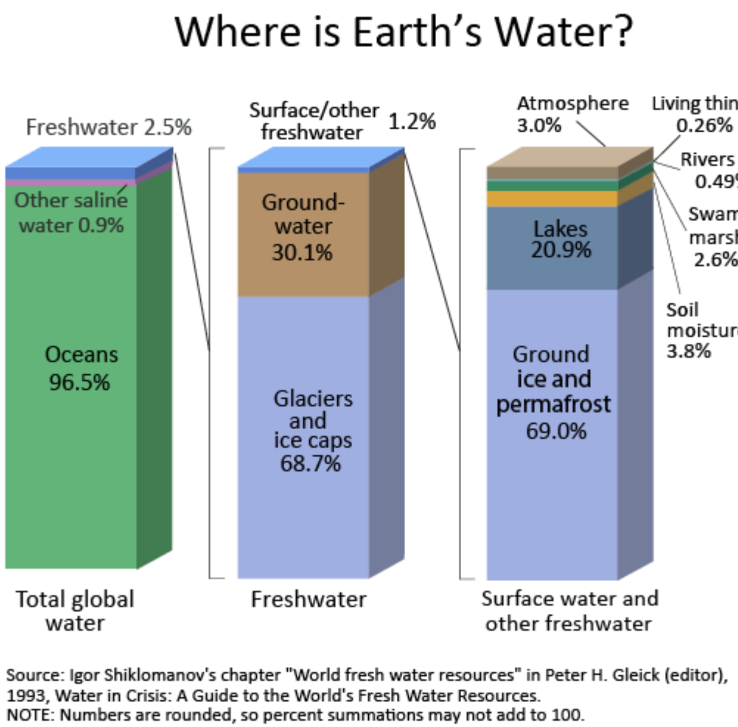


World Conservation Union. 2014

https://water.usgs.gov/edu/earthwherewater.html

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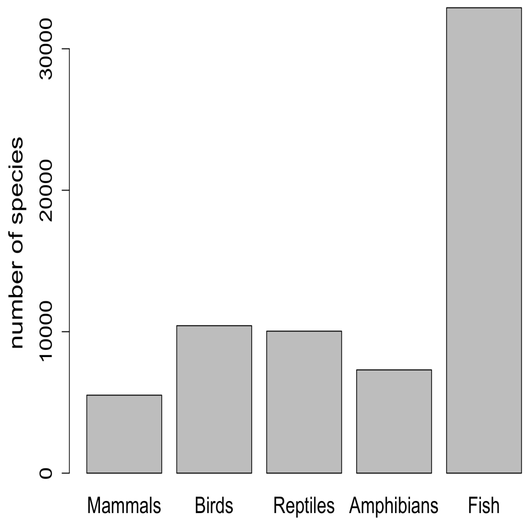
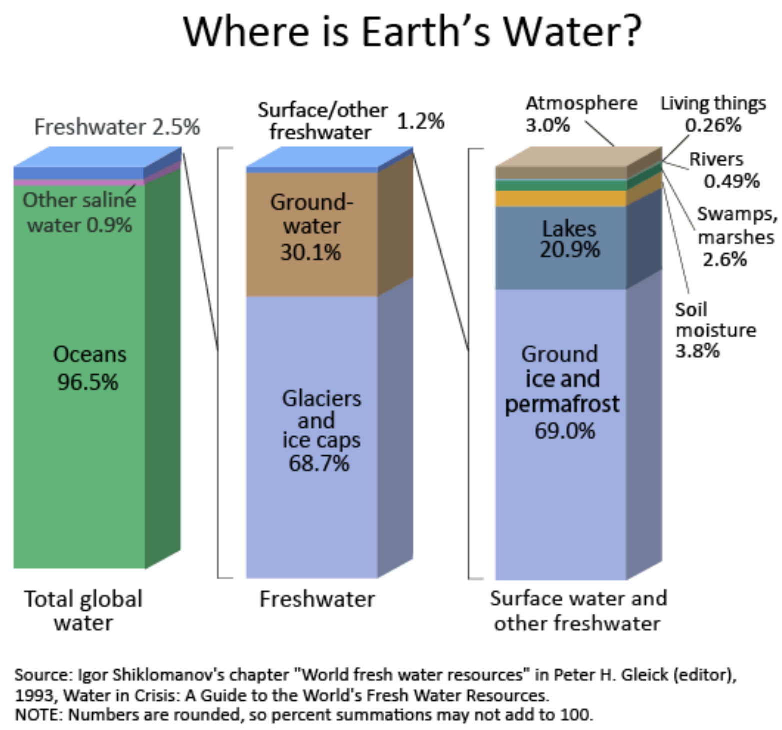
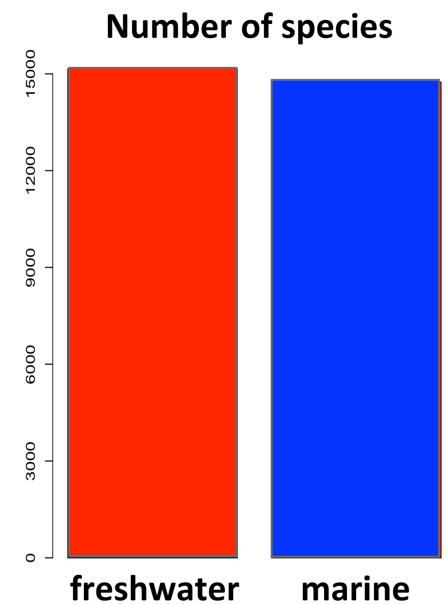


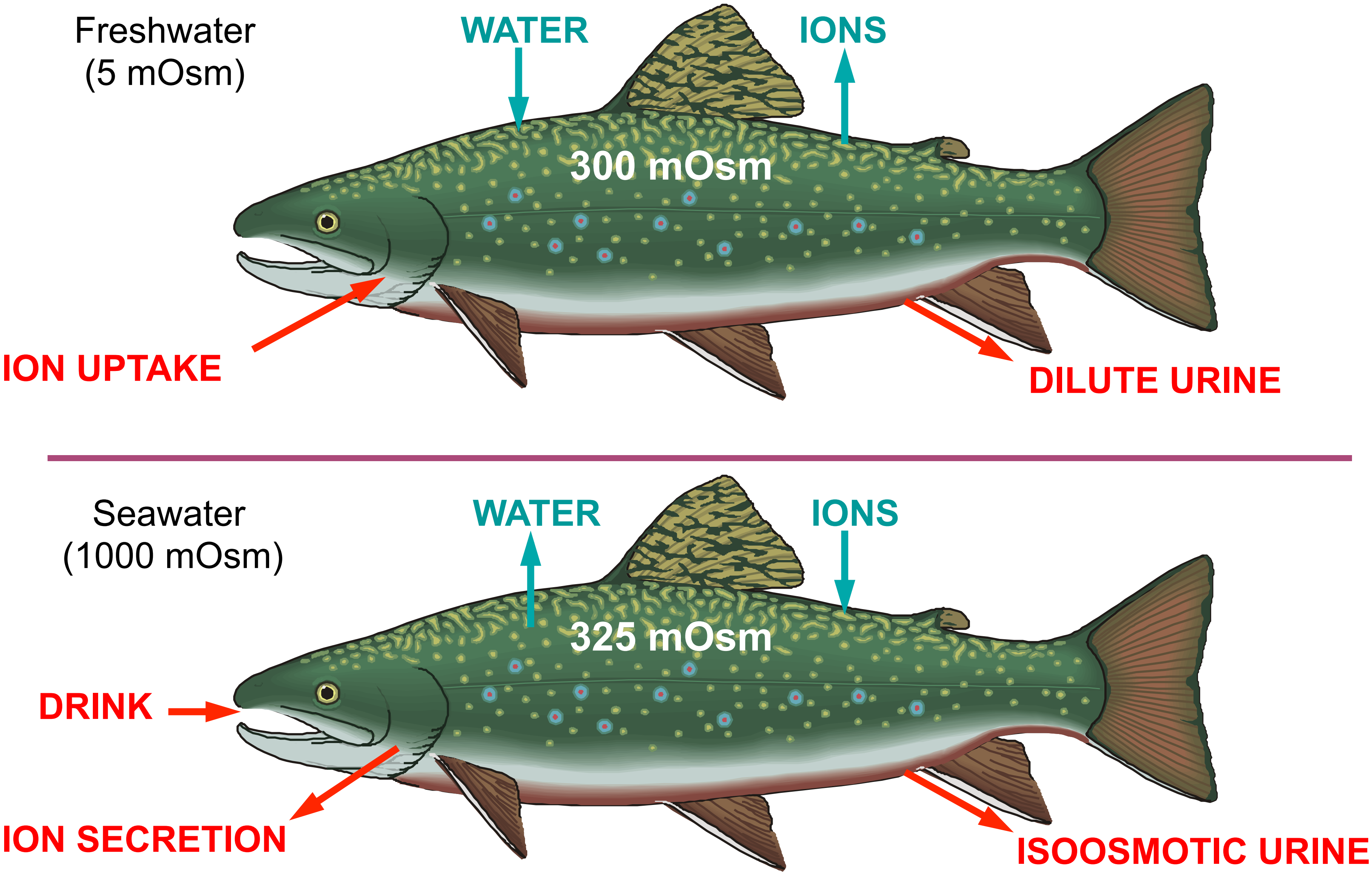




World Conservation Union. 2014

https://water.usgs.gov/edu/earthwherewater.html

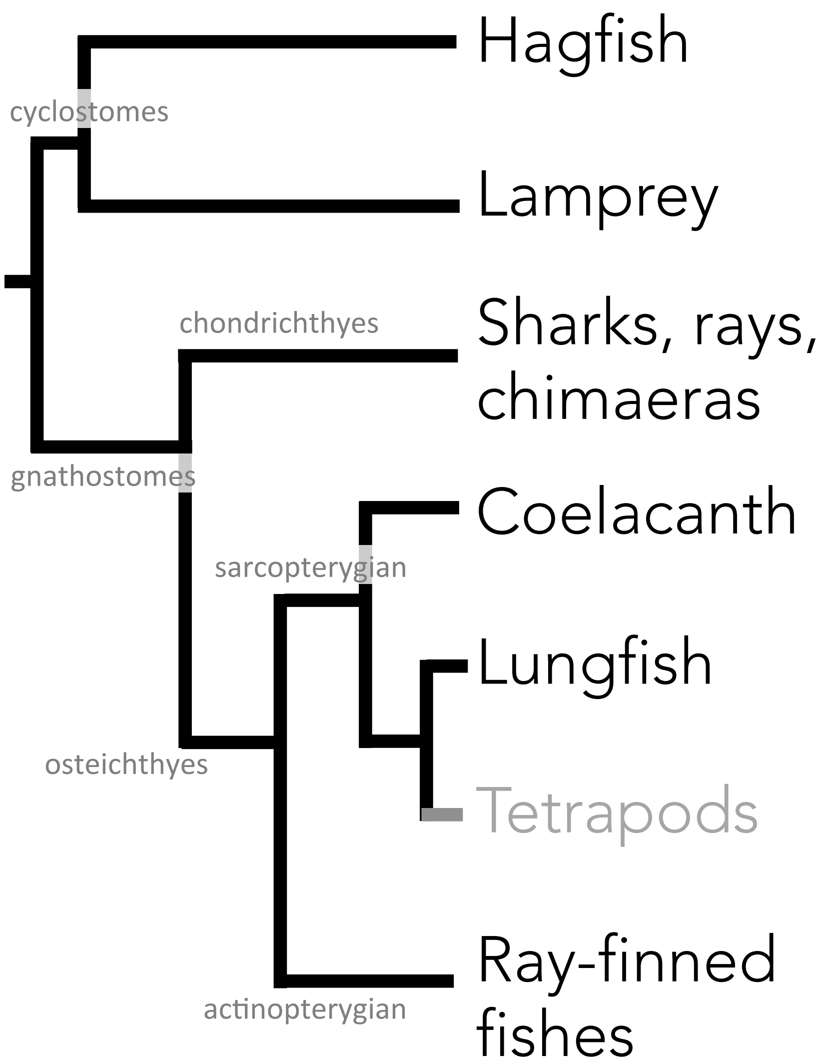
May, 1994

# Osmoregulatory physiology of teleost fish

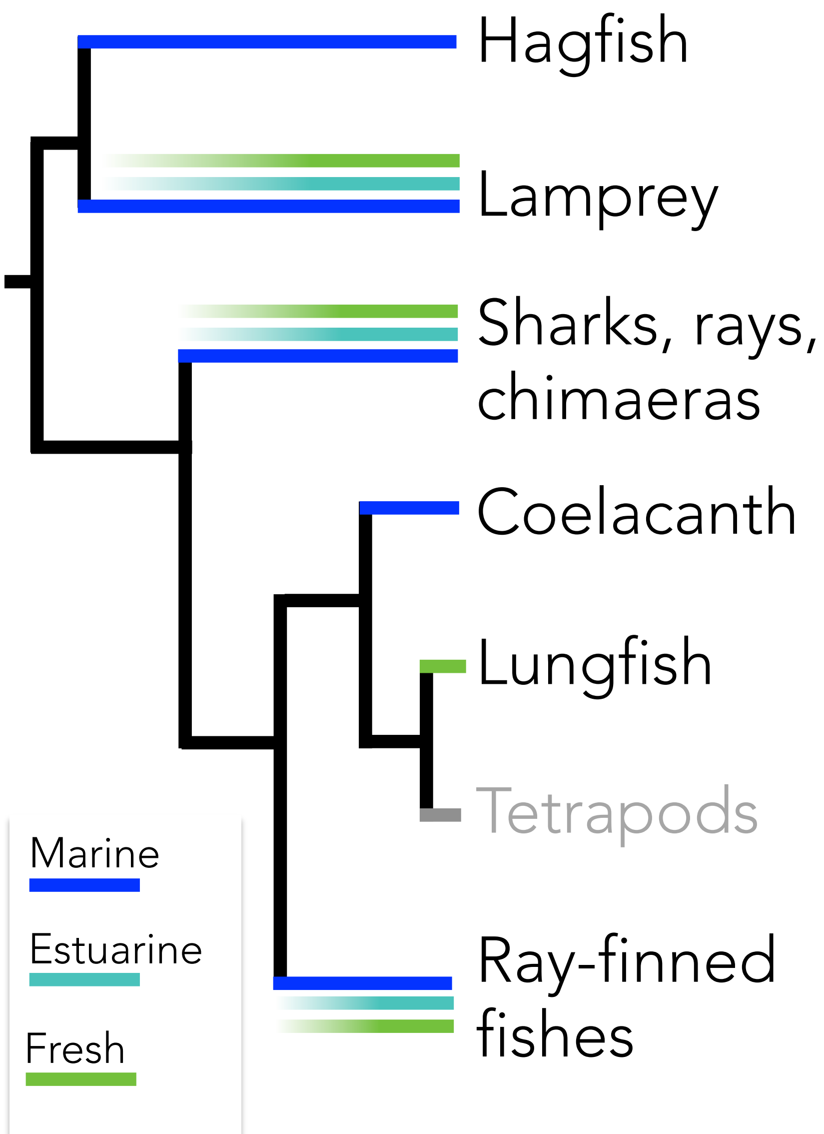



Stephen McCormick, USGS, U. Massachusetts Amherst

# Vertebrate phylogeny



# Distribution of osmotic niche and physiologies



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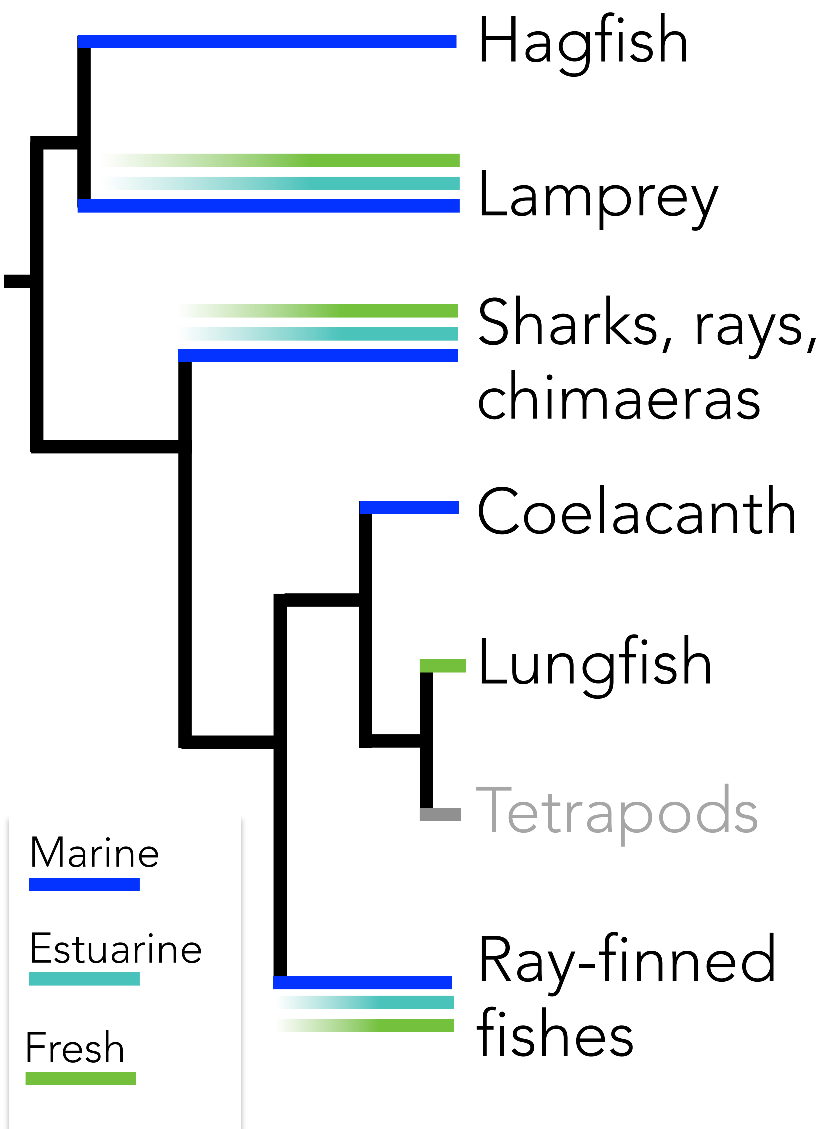
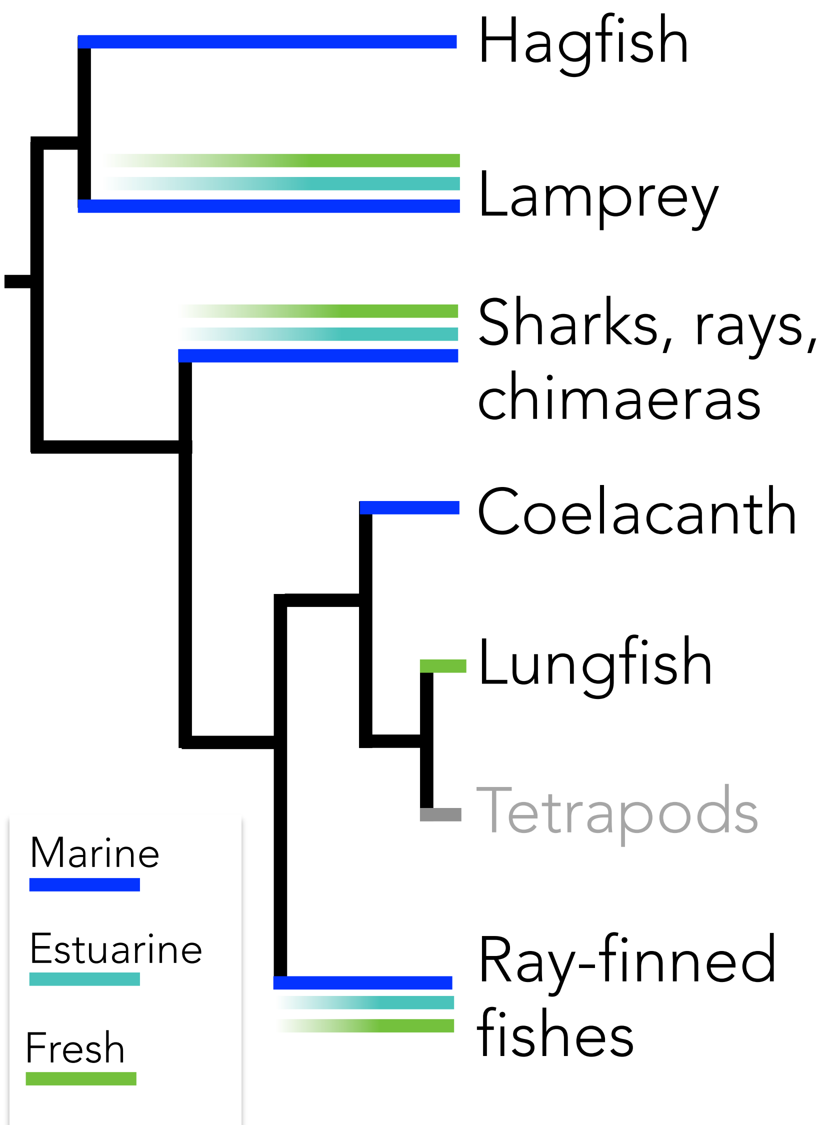


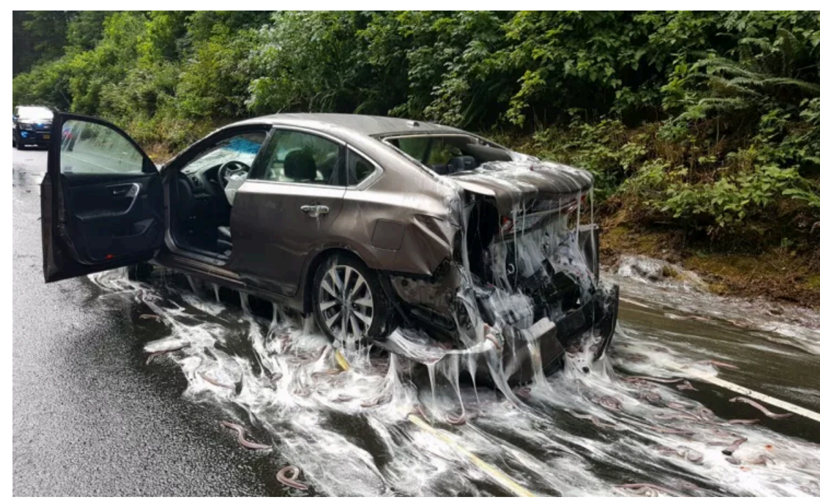

| Habitat |
|---|
| Marine |

# Distribution of osmotic niche and physiologies




**Habitat**

Marine



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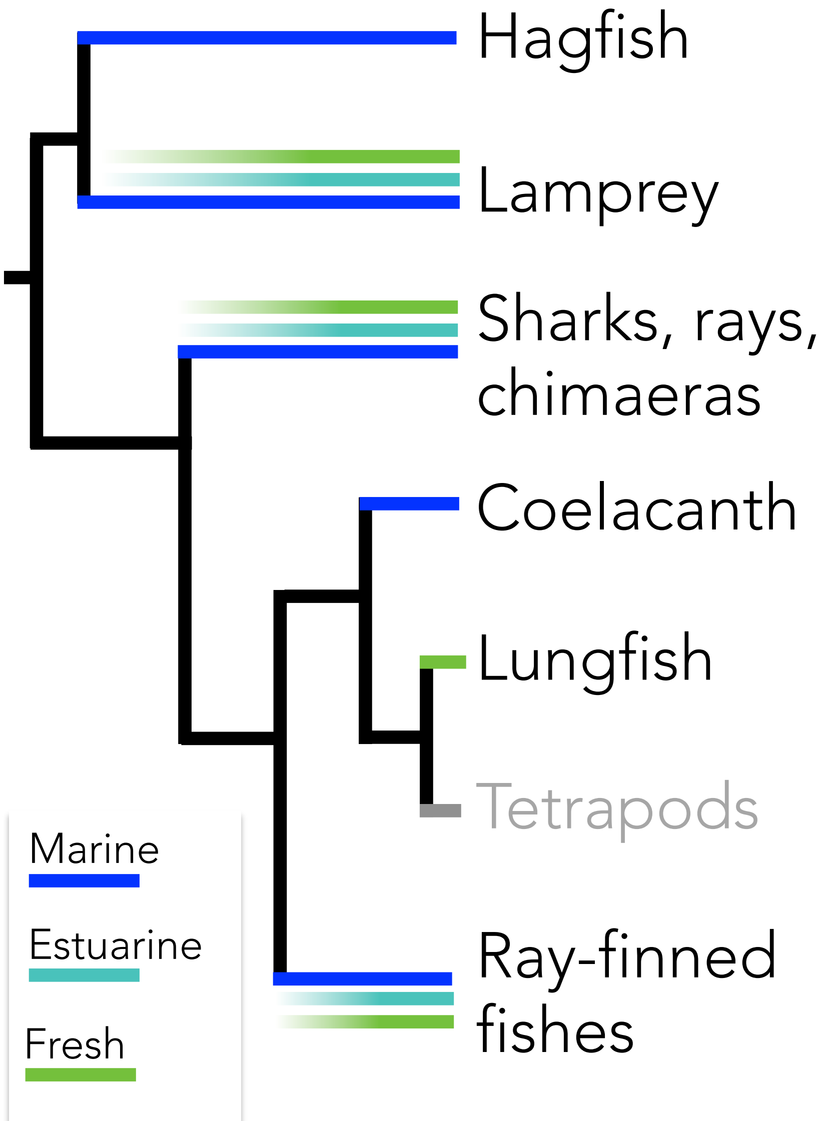


**Habitat**

Marine

M, E, F

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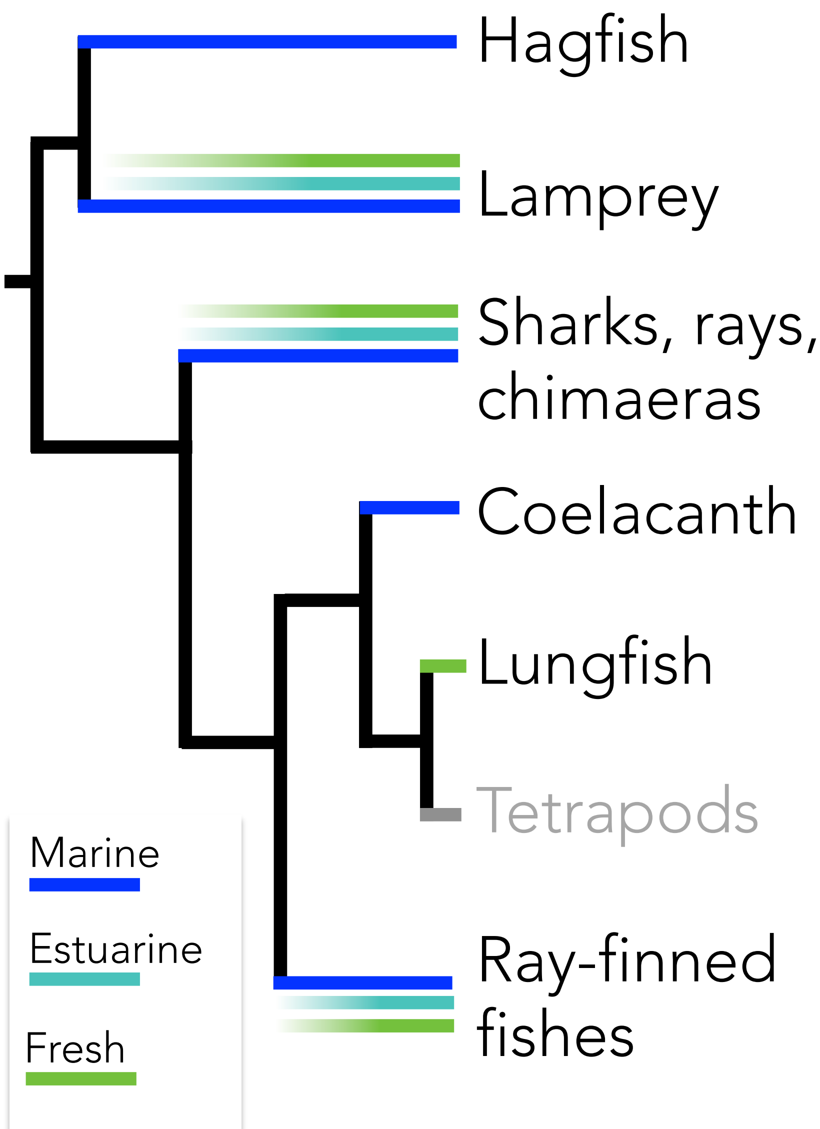
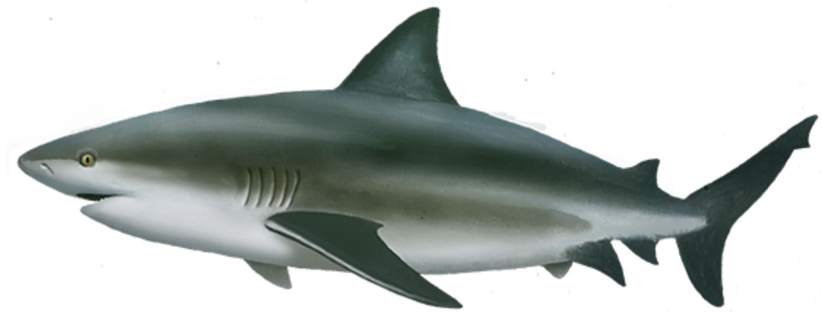



| Habitat |
| --- |
| Marine |
| M, E, F |
| M, E, F |



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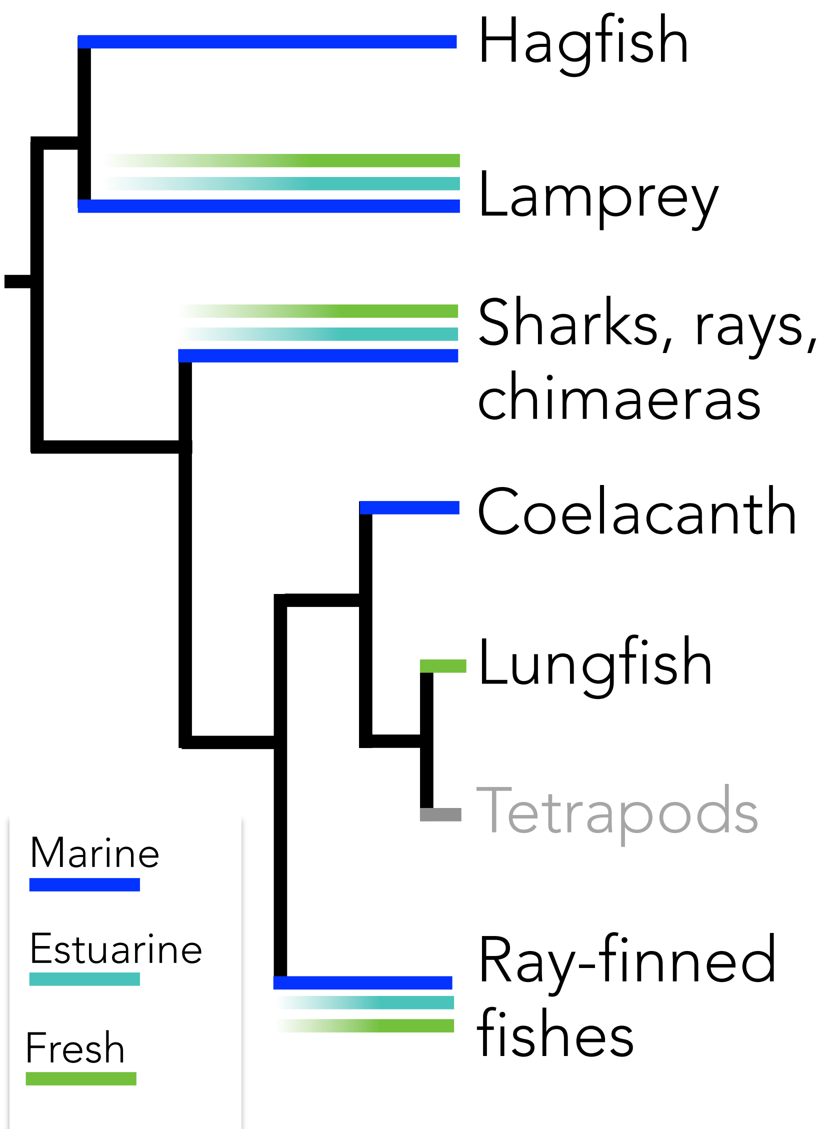


**Habitat**

Marine

M, E, F

M, E, F

M

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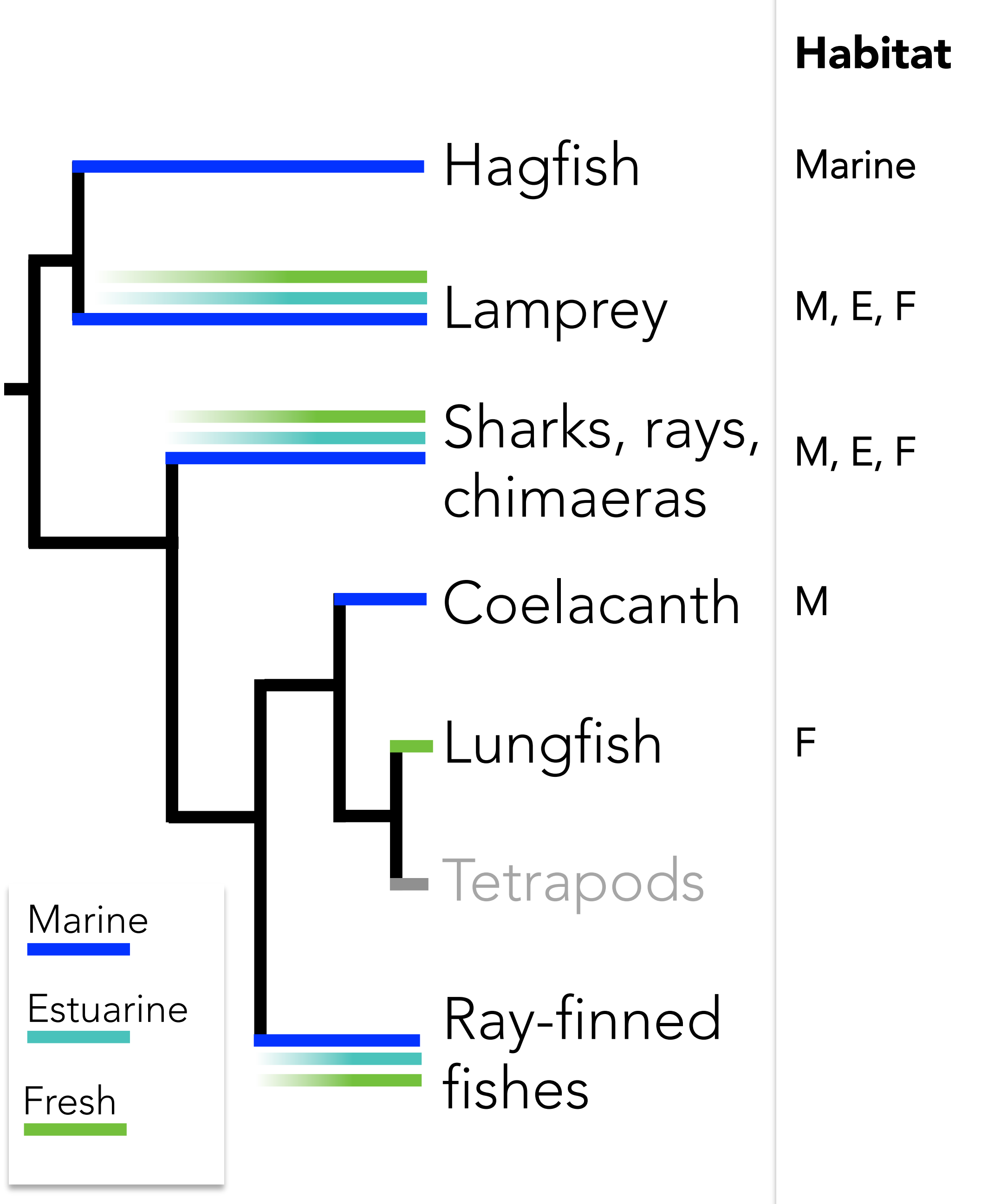


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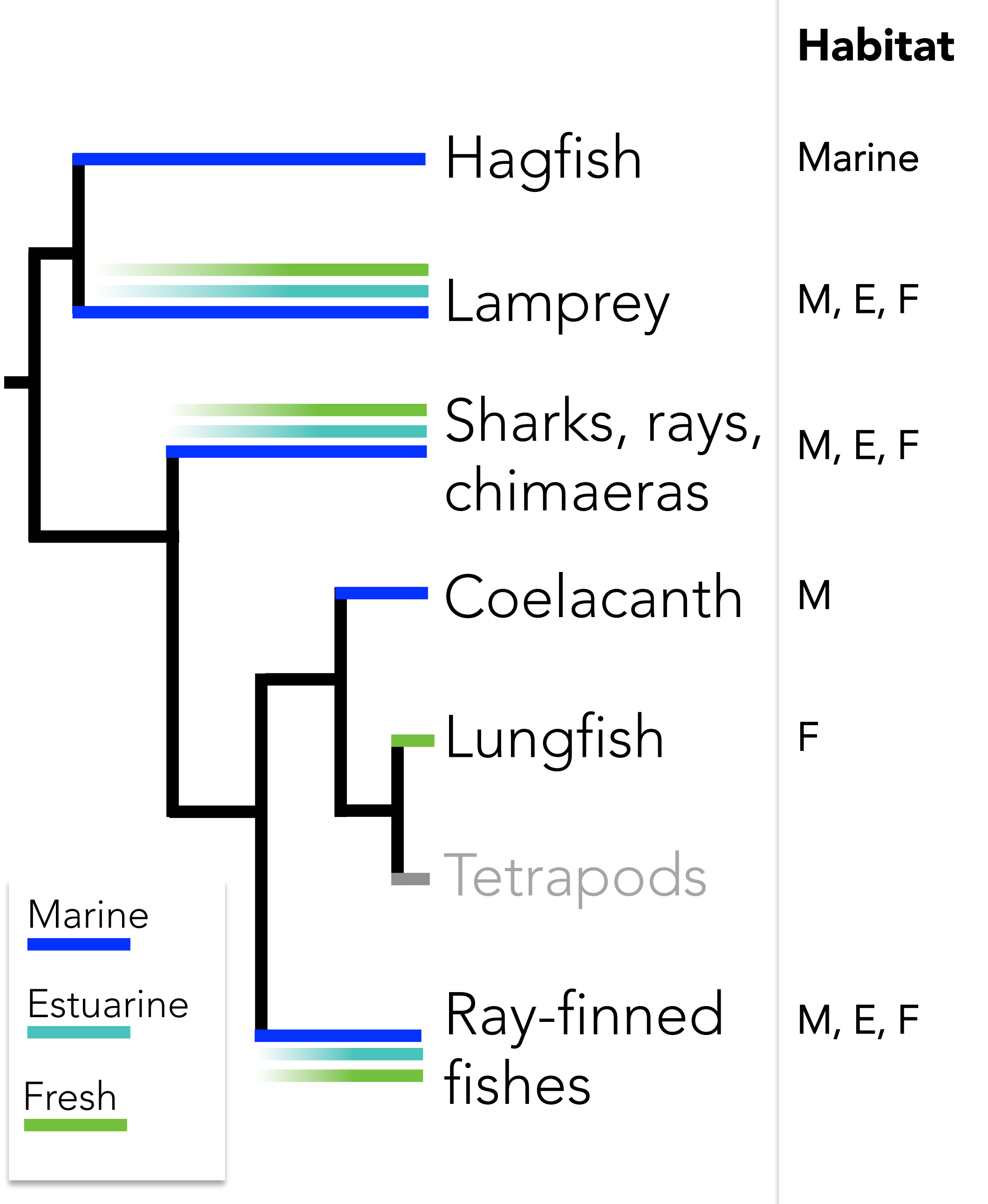


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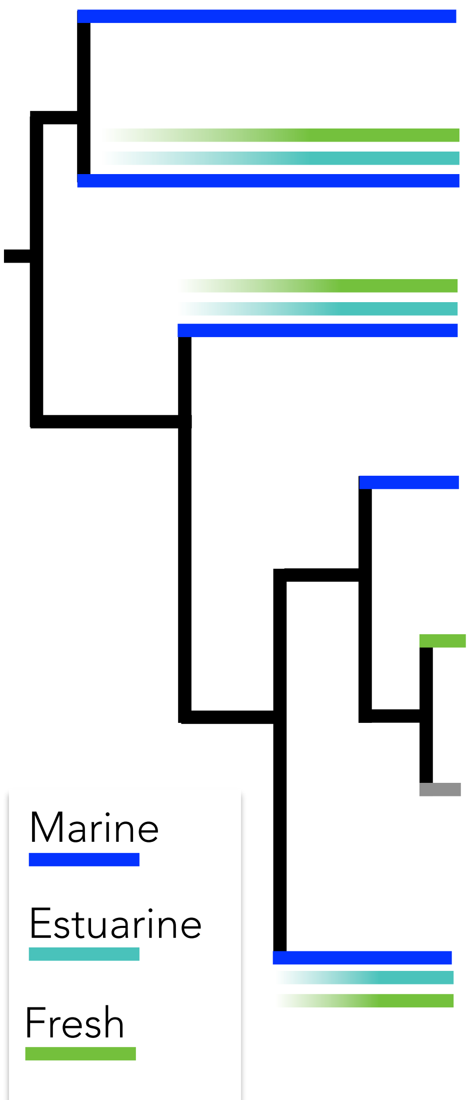
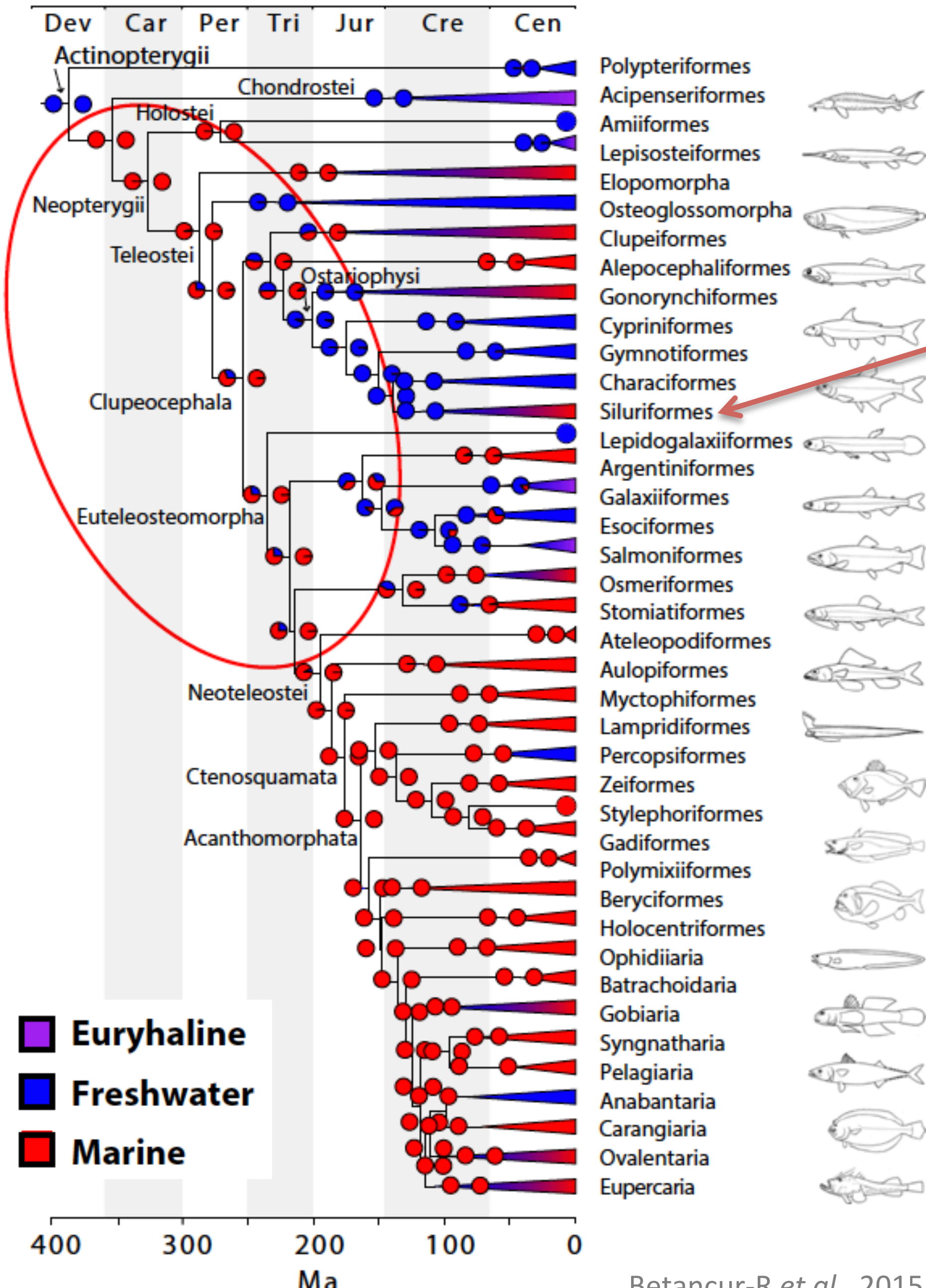



| | Habitat | Osmo... | Iono... |
|---|---|---|---|
| Hagfish | Marine | conform | conform |
| Lamprey | M, E, F | regulate | regulate |
| Sharks, rays, chimaeras | M, E, F | conform | regulate |
| | | urea | |
| Coelacanth | M | conform | regulate |
| | | urea | |
| Lungfish | F | regulate | regulate |
| Tetrapods | | | |
| Ray-finned fishes | M, E, F | regulate | regulate |

# Osmotic niche diversification in ray-finned fishes



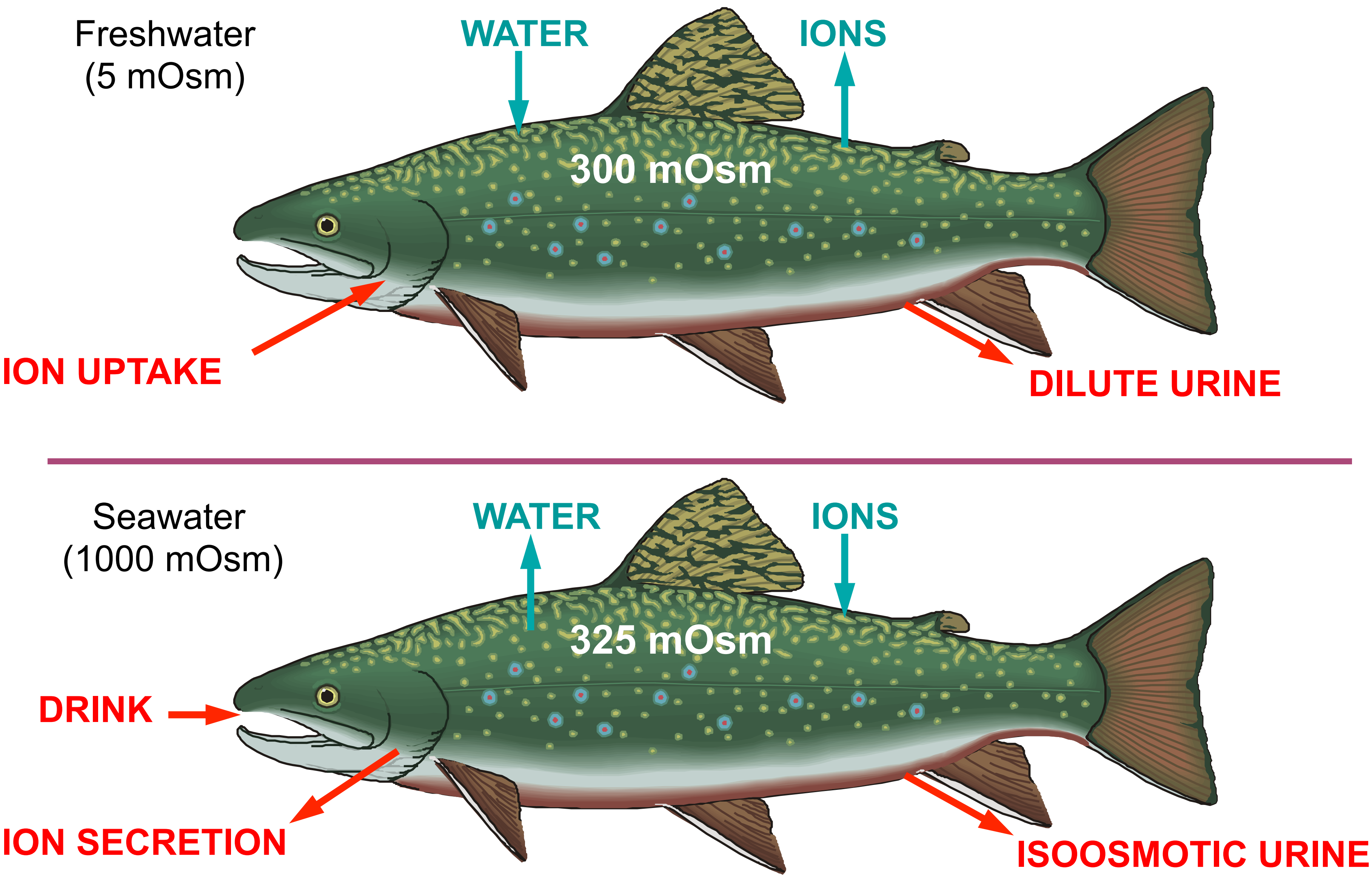

Betancur-R *et al.*, 2015

- Almost universally unidirectional (marine to fresh)
- Exceptions: ariid at plotosid catfish: several FW → SW transitions

*Bagre marinus*

- freshwater environments are refugia for ancient lineages that have been out-competed in marine environments.

# Osmoregulatory physiology of teleost fish

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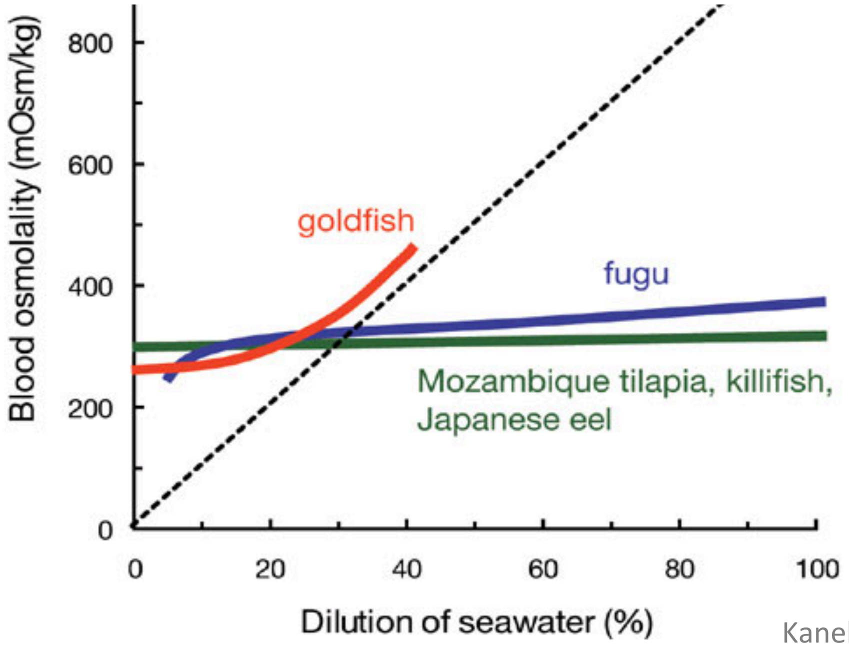
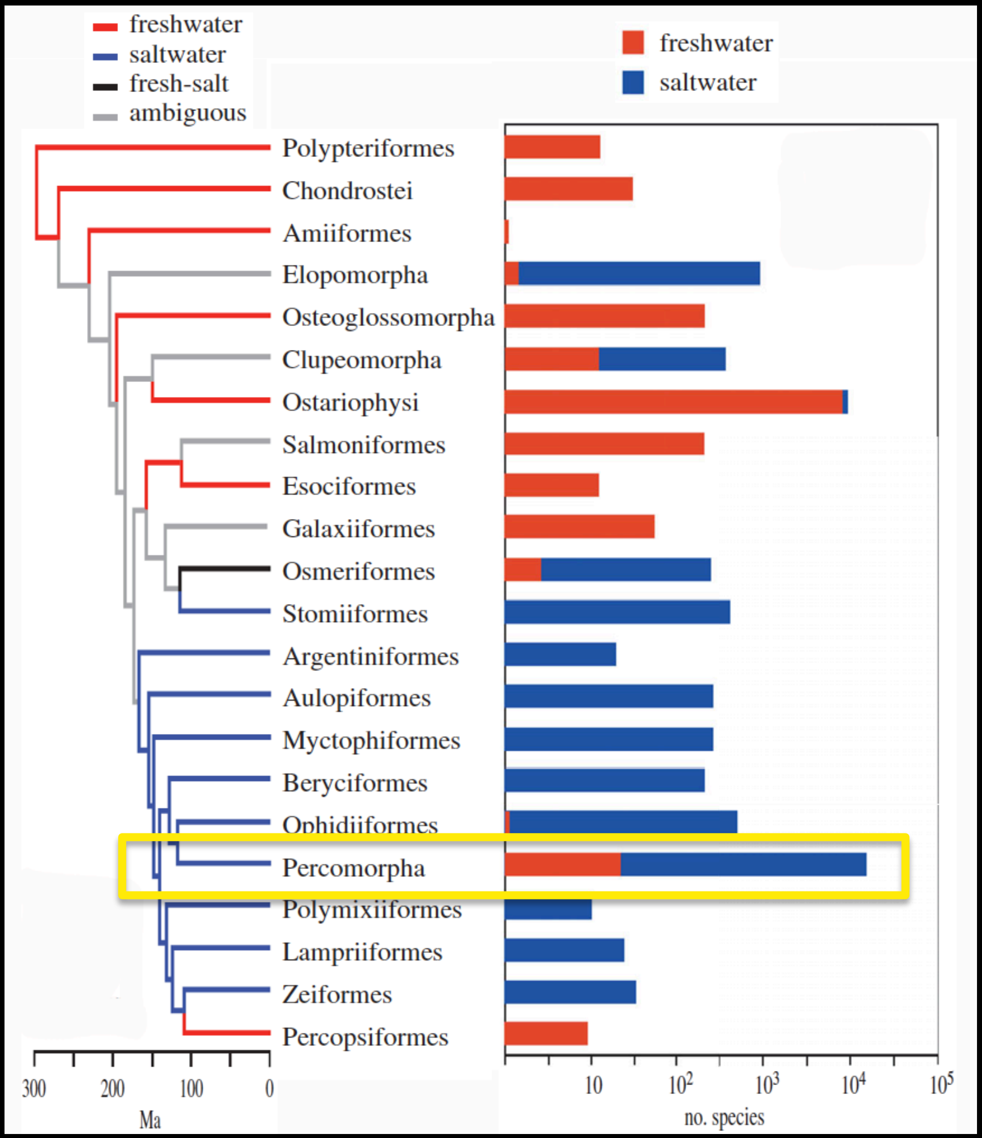
# Osmoregulatory physiology of teleost fish

## Stenohaline vs. Euryhaline



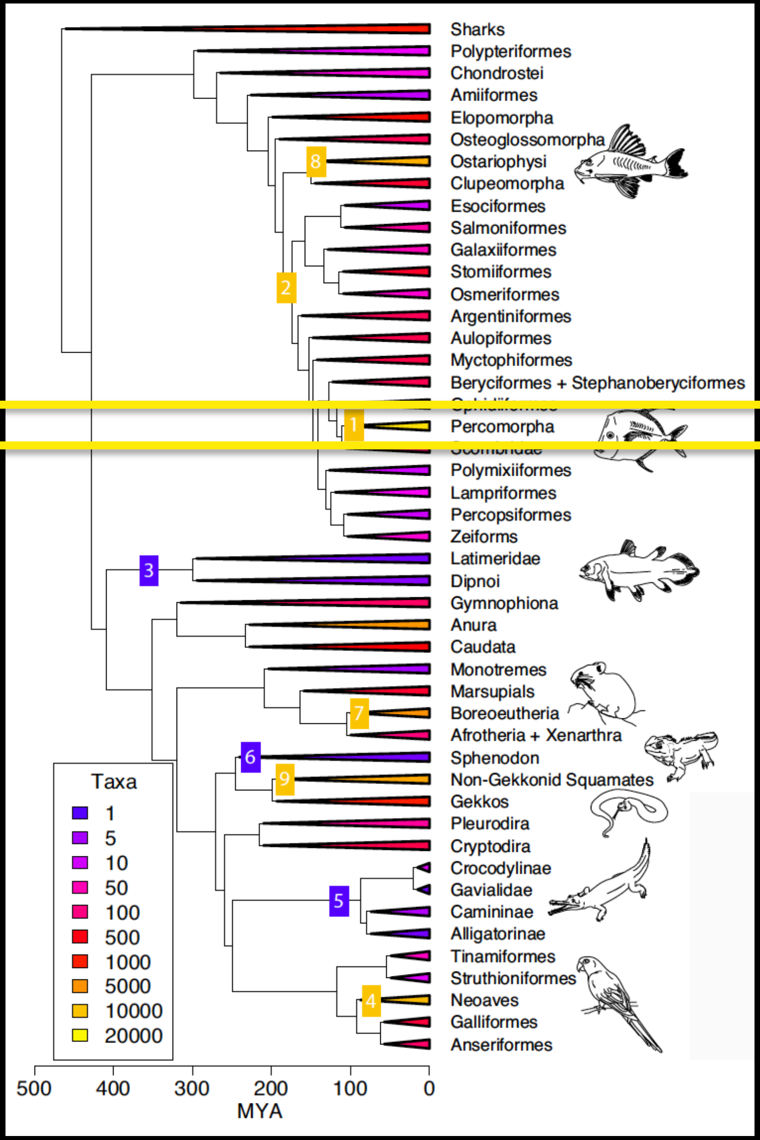

Kaneko et al., 2008

# Most large clades are exclusively marine or freshwater




Vega & Wiens 2012

# Percomorphs have highest speciation, most marine to FW transitions, most euryhaline sp.




Alfaro et al., 2009

# Marine to Freshwater:

Morphology

Physiology

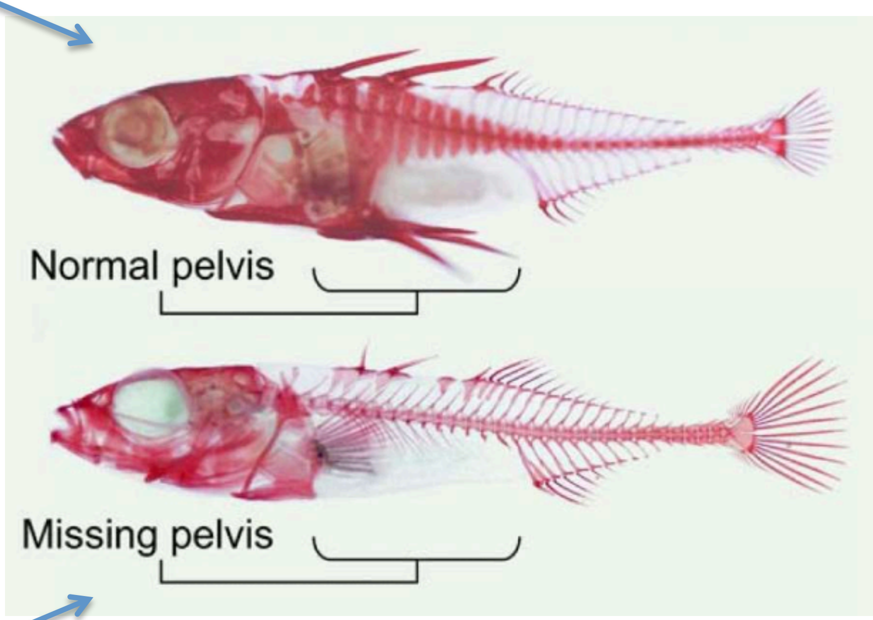
Microbiome?

# Marine to Freshwater: Morphology

Threespined stickleback (*Gasterosteus aculeatus*)

# Marine to Freshwater: Morphology

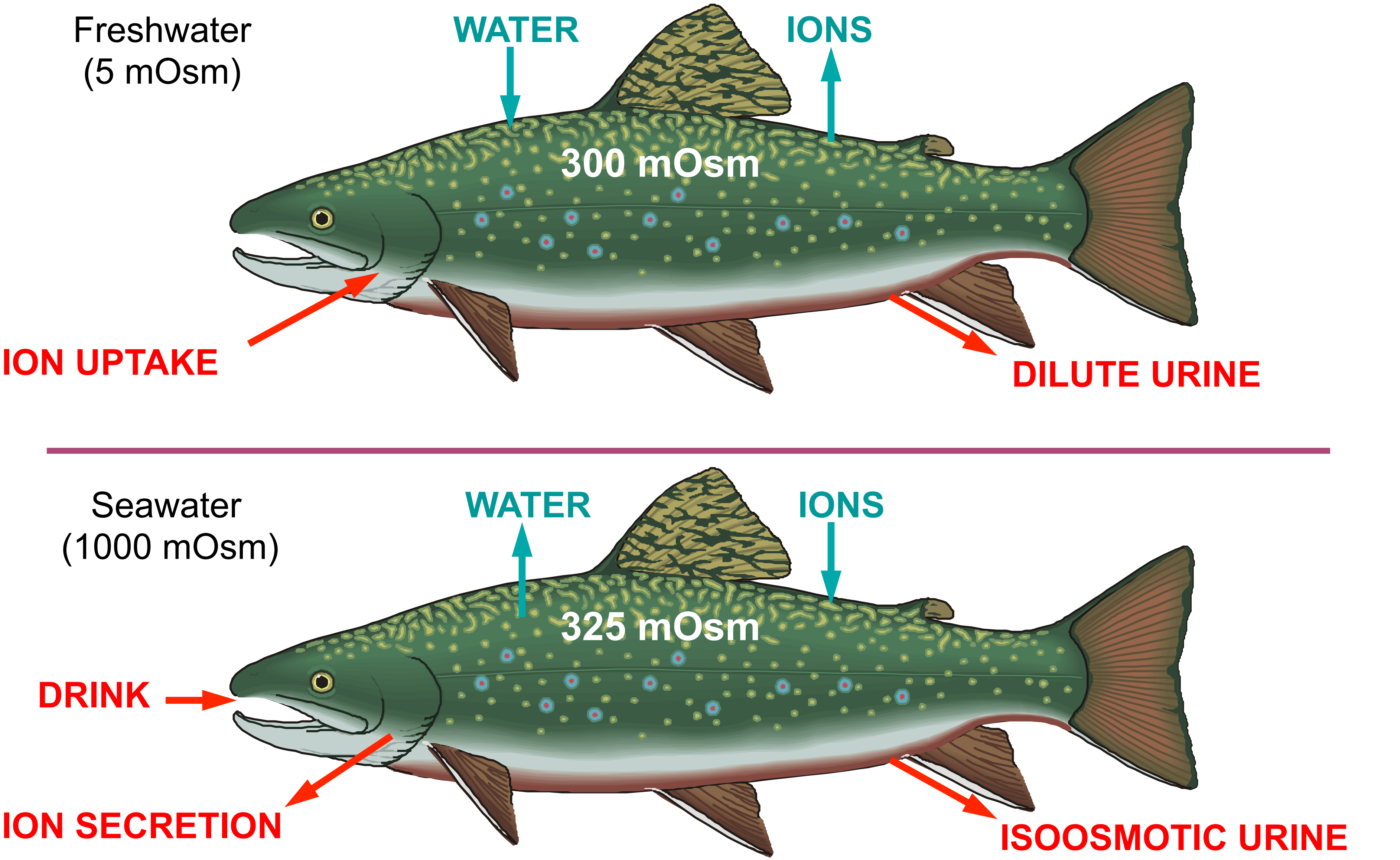
Marine stickleback




Freshwater stickleback

Photos: Michael Bell, Stony Brook U.; Mike Shapiro, U. of Utah

# Marine to Freshwater: Physiology

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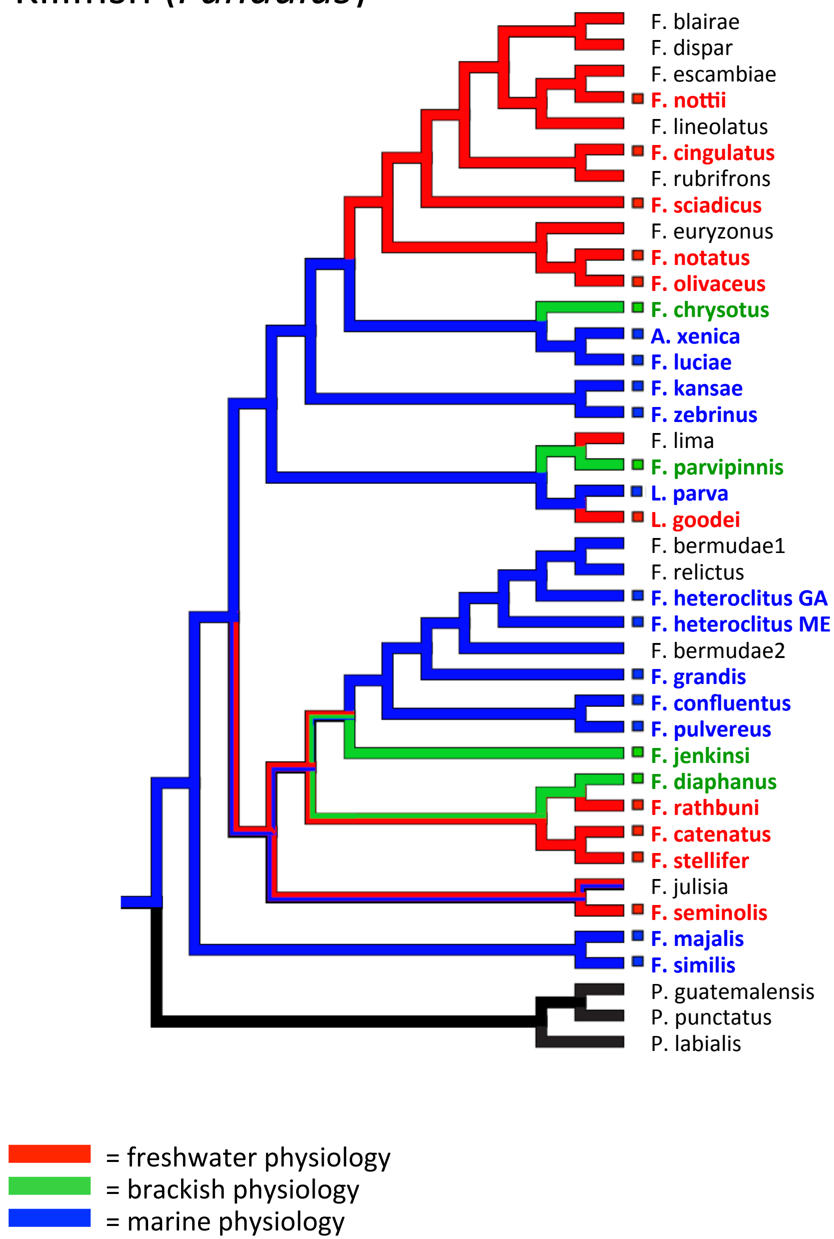
# Marine to Freshwater: Physiology

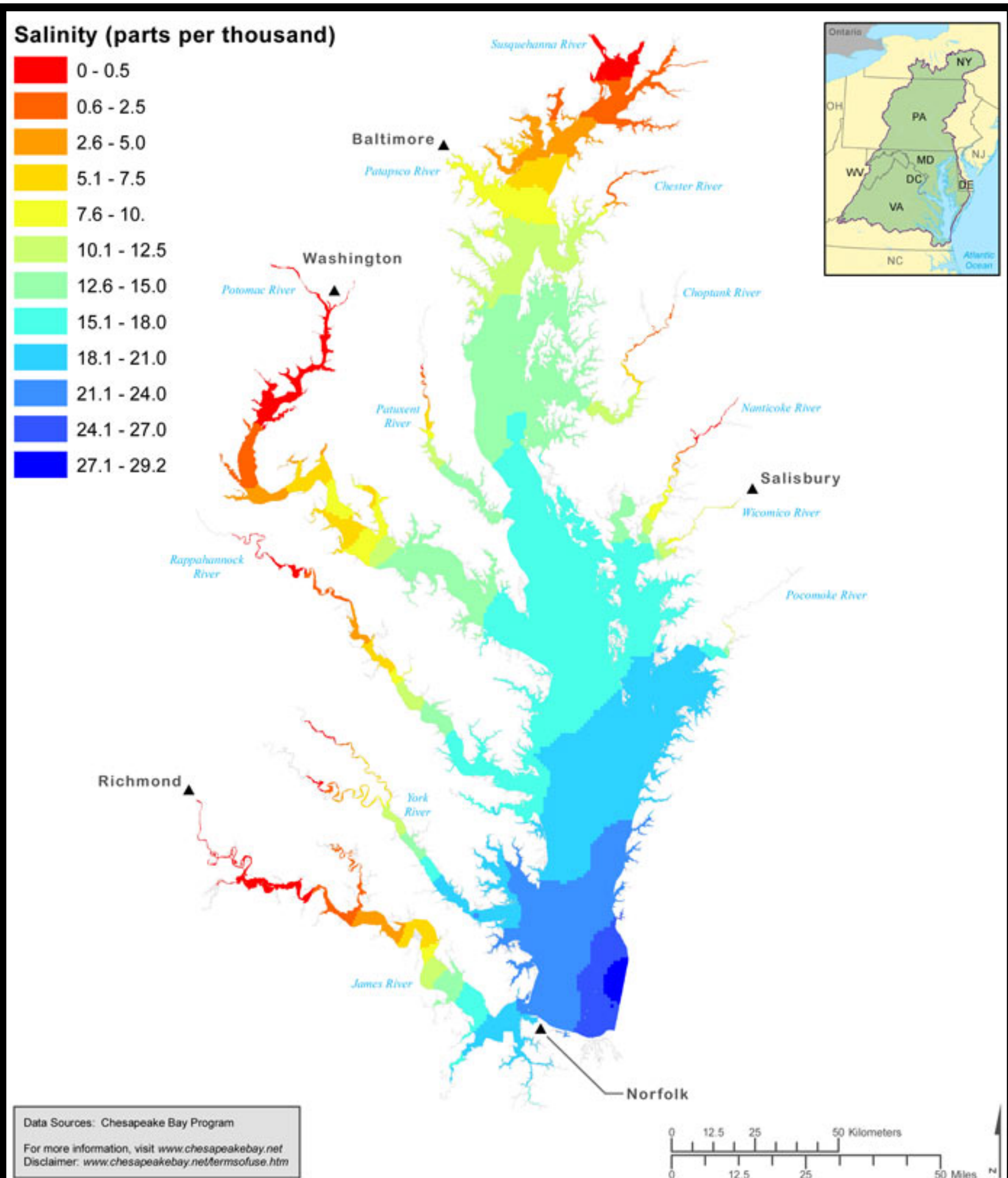
Killifish (*Fundulus*)

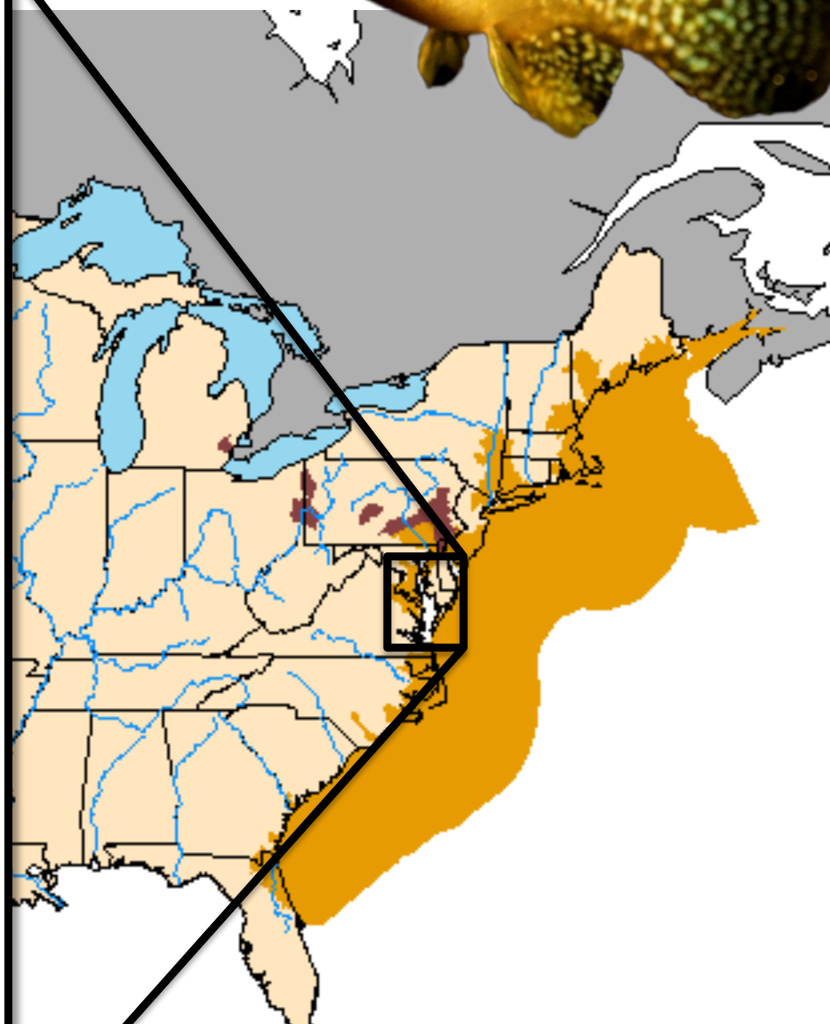



Whitehead, Evolution, 2010

# Marine to Freshwater: Physiology

Atlantic killifish (*Fundulus heteroclitus*)



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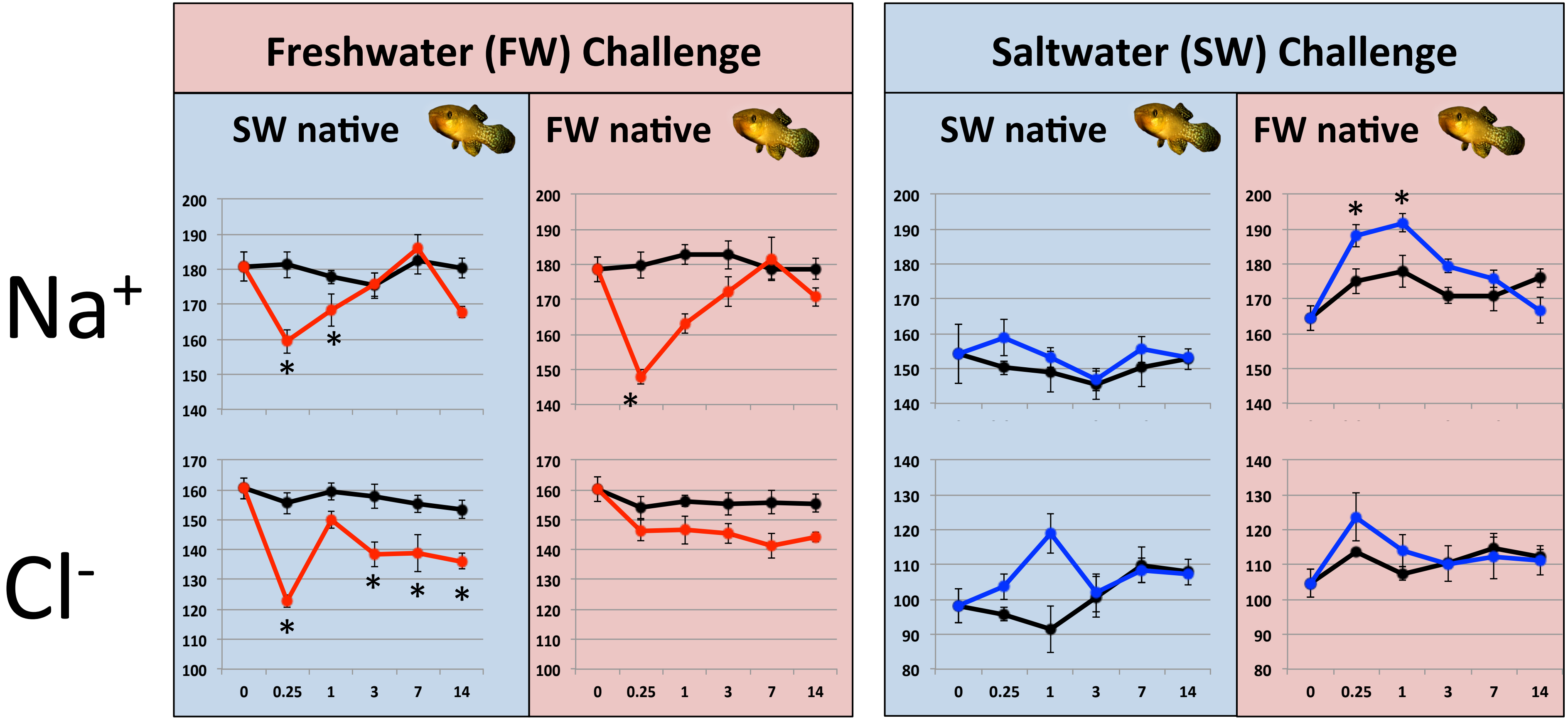


Brennan et al., 2015, JEB

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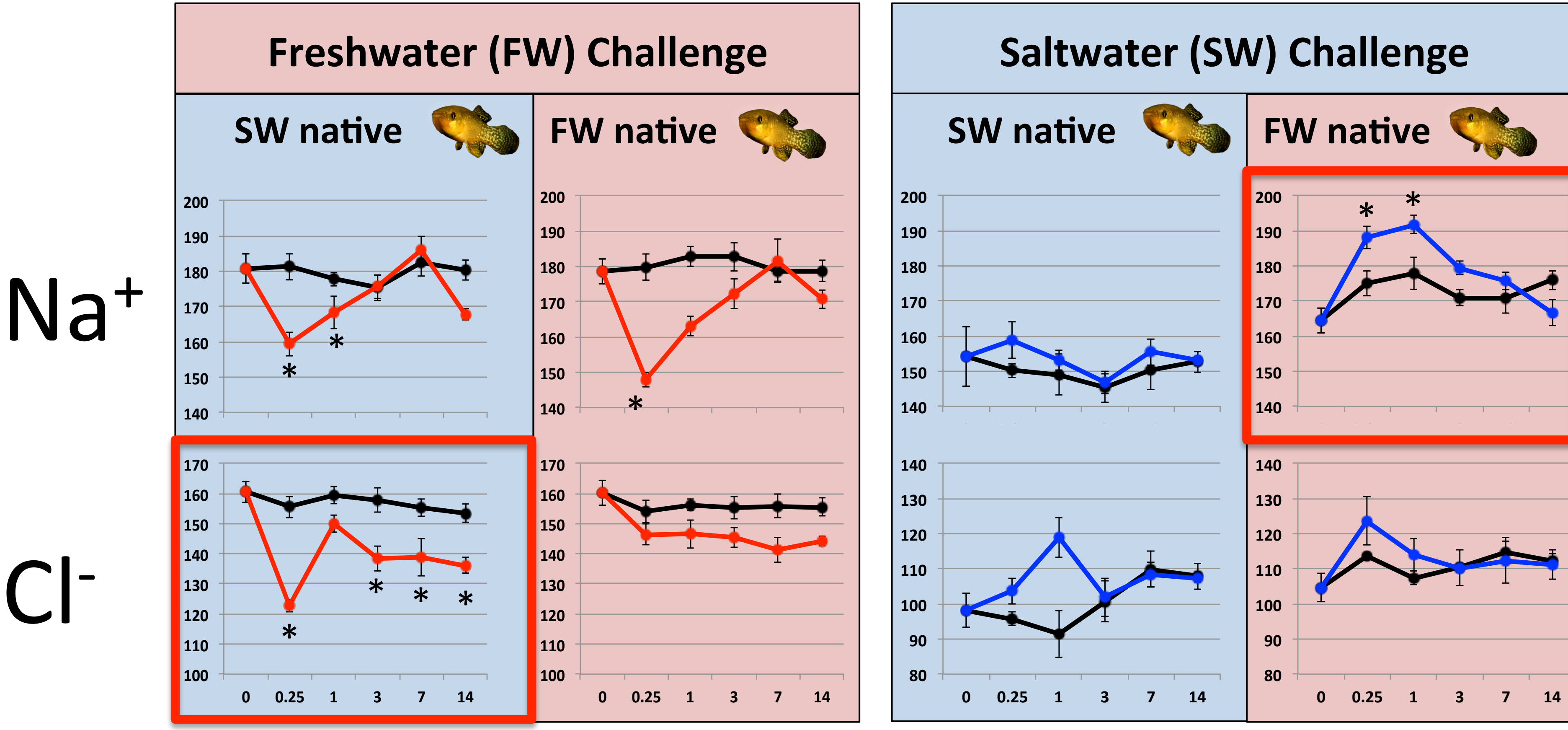


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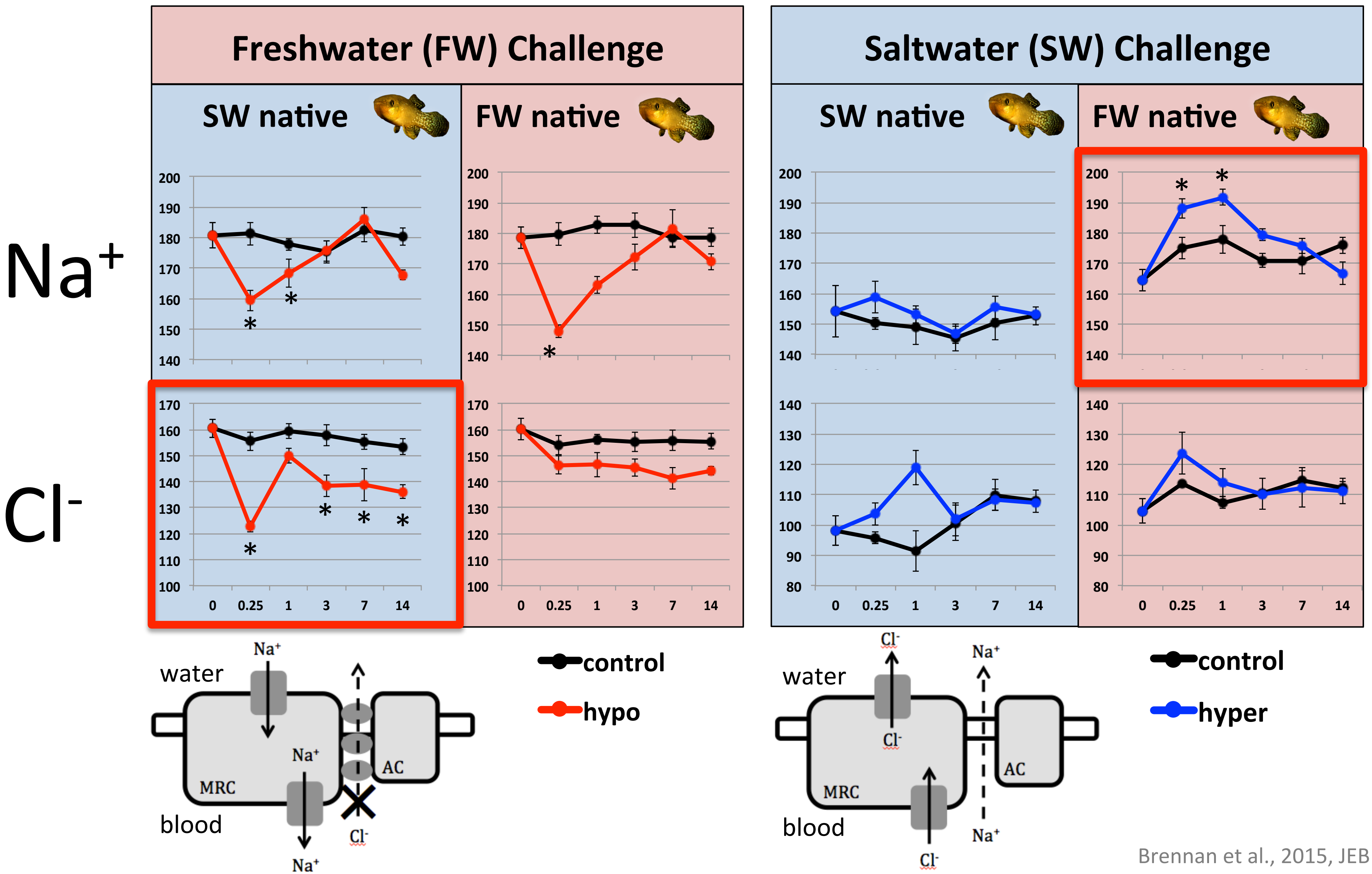


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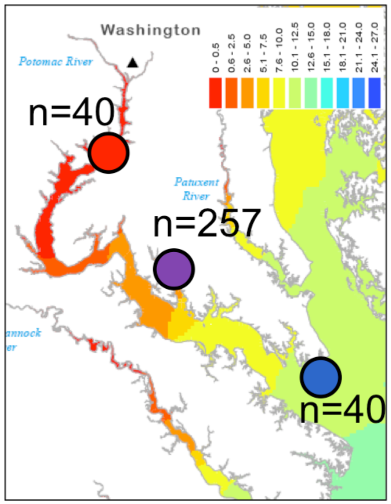
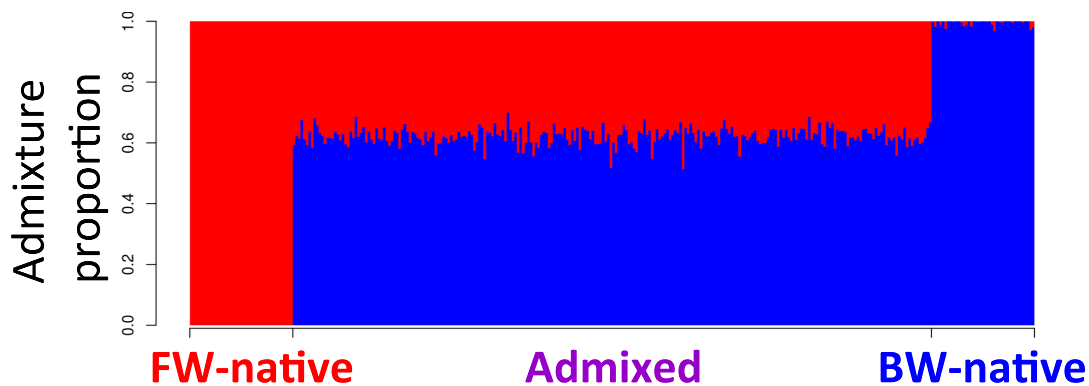
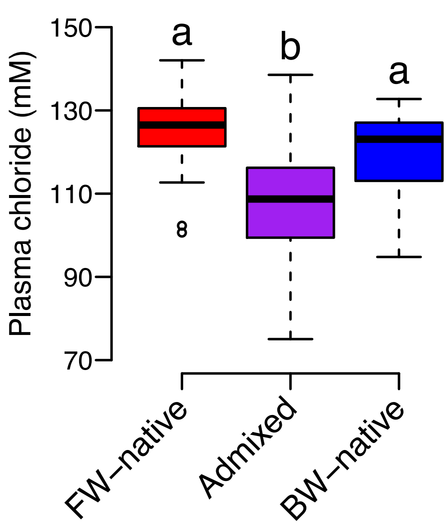


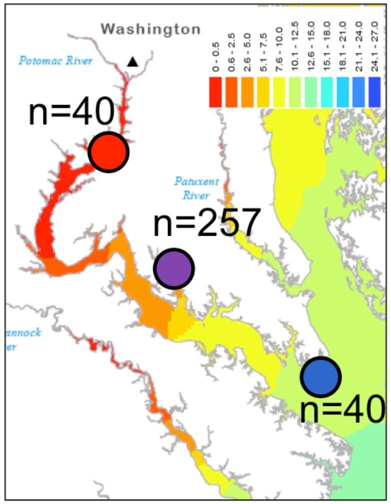



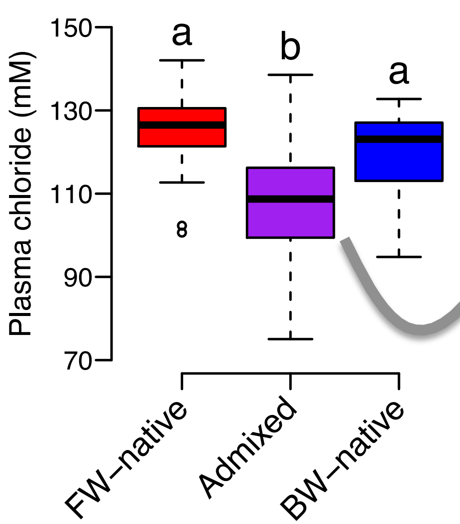




GWAS + Selection Scans

Brennan et al., 2018, MB&E

# Marine to Freshwater: Physiology




## GWAS:

**26 loci** account for **54%** of phenotypic variation

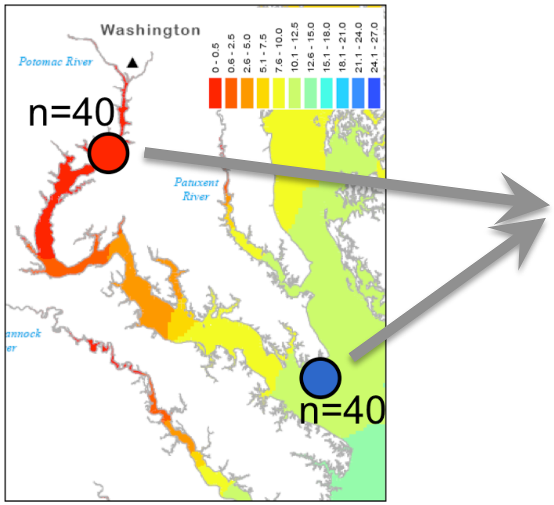
** Physiological regulation of chloride homeostasis is polygenic*

**Cell junction**: connexin, tricellulin, cadherins (2), cell adhesion molecule

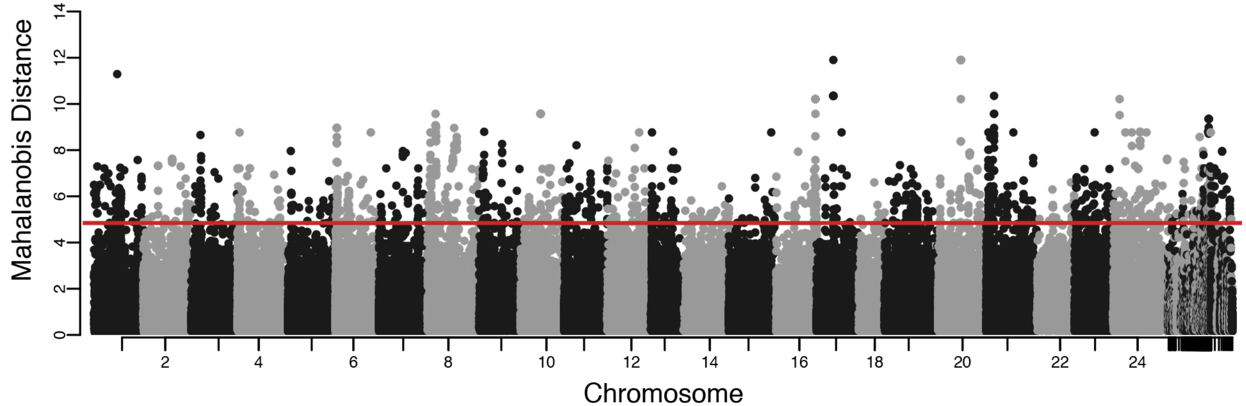
**Ion transport**: potassium channels (2), sodium bicarbonate transporter

Brennan et al., 2018, MB&E

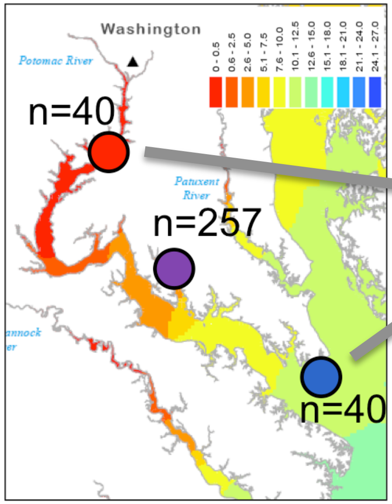
# Marine to Freshwater: Physiology



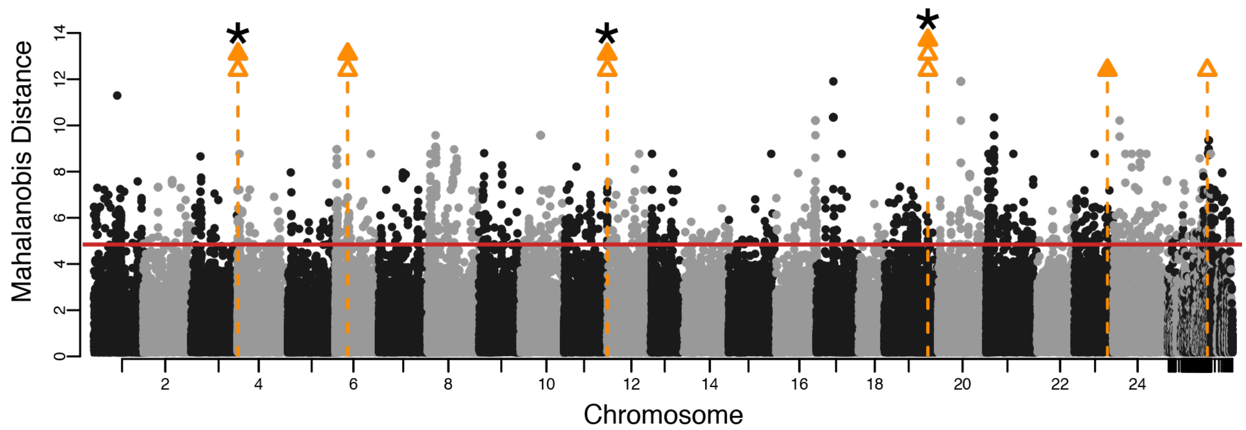

## Selection Scan



# Marine to Freshwater: Physiology




## Selection Scan + GWAS




Brennan et al., 2018, MB&E

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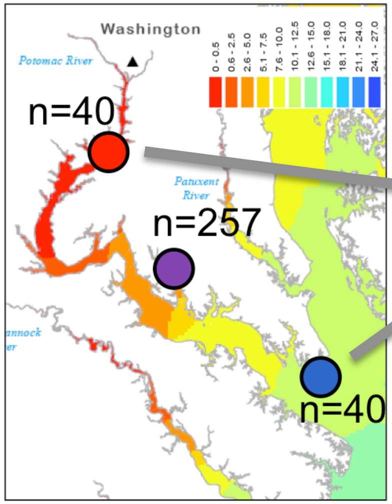


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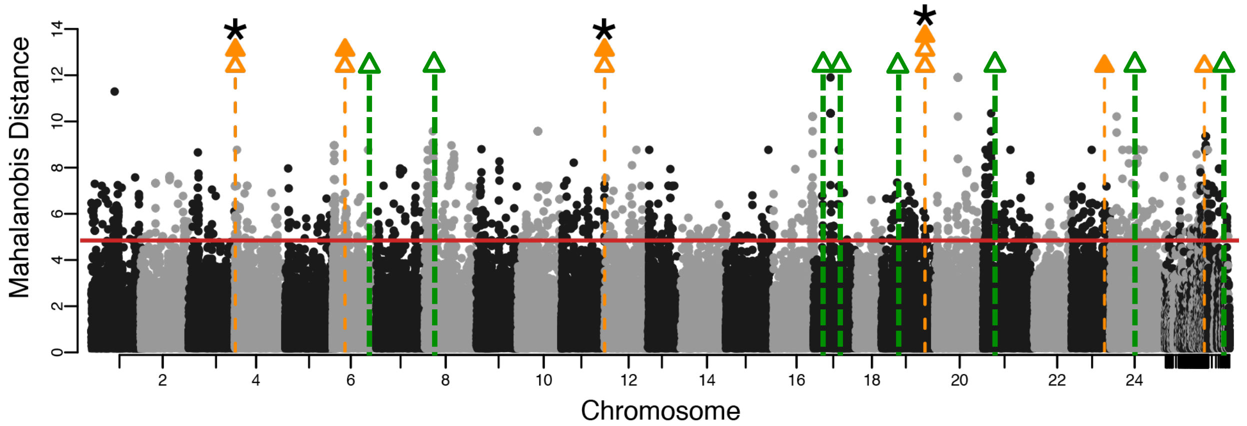
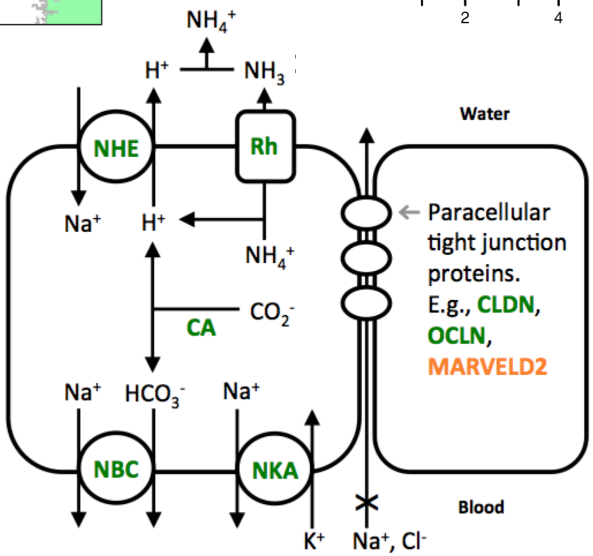



** Evolved sodium uptake metabolon?*

Brennan et al., 2018, MB&E

# Marine to Freshwater: Microbiome?

PNAS

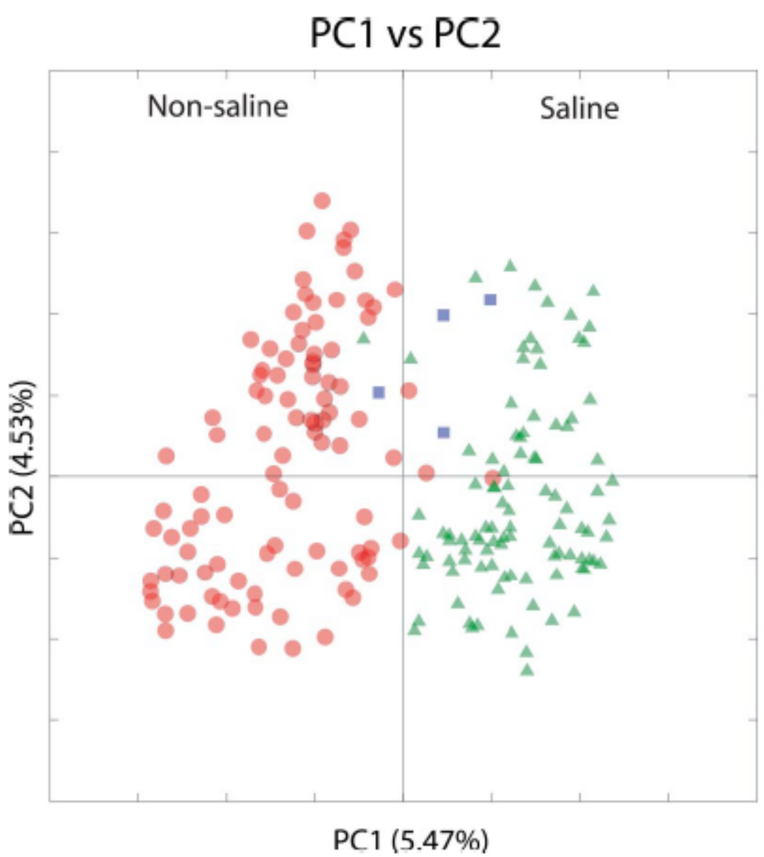
## Global patterns in bacterial diversity

Catherine A. Lozupone* and Rob Knight†‡

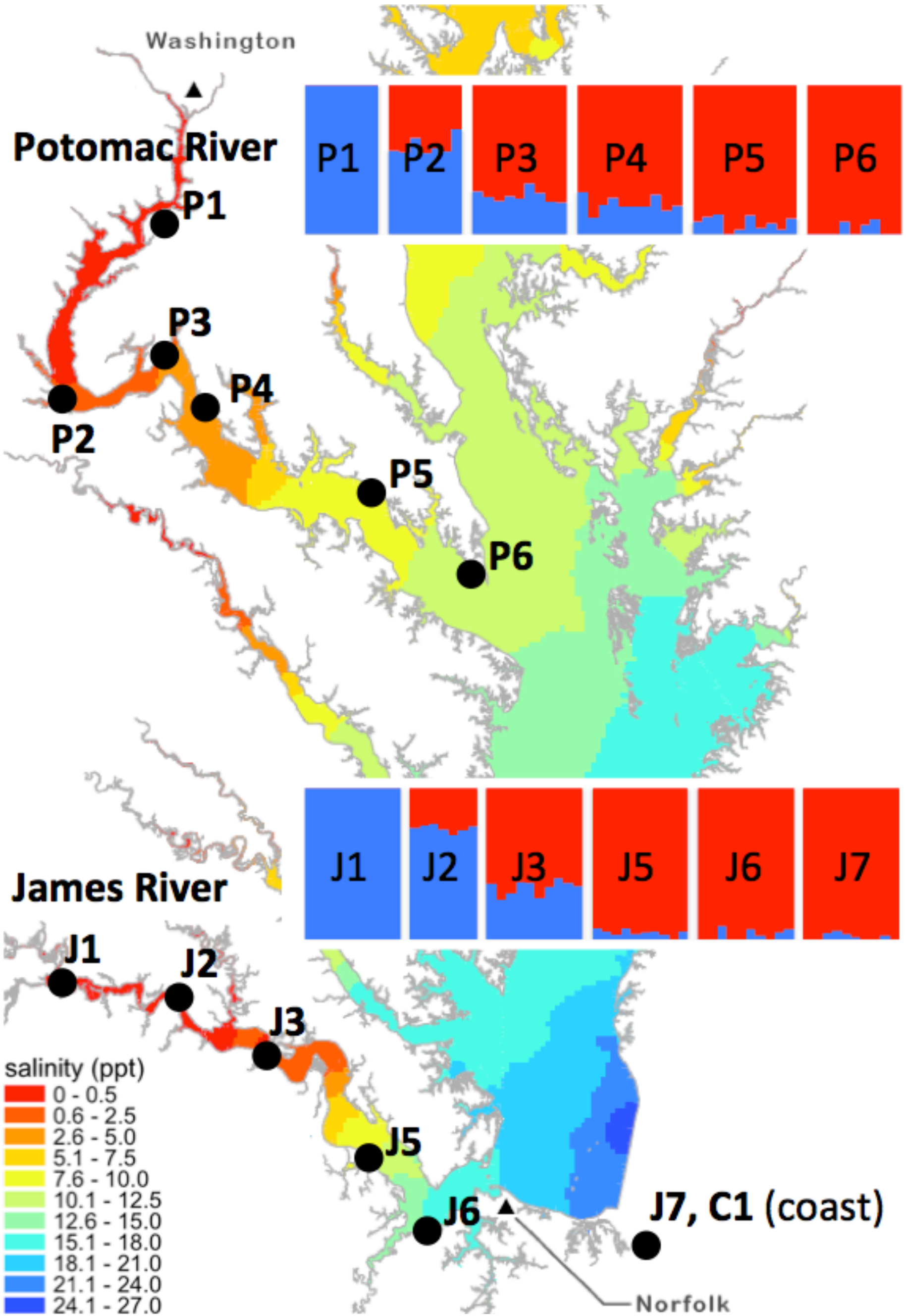
*Departments of Molecular, Cellular, and Developmental Biology and †Chemistry and Biochemistry, University of Colorado, Boulder, CO 80309

Edited by Norman R. Pace, University of Colorado, Boulder, CO, and approved May 29, 2007 (received for review December 22, 2006)

**Microbes are difficult to culture. Consequently, the primary source of information about a fundamental evolutionary topic, life's diversity, is the environmental distribution of gene sequences. We report the most comprehensive analysis of the environmental distribution of bacteria to date, based on 21,752 16S rRNA sequences compiled from 111 studies of diverse physical environments. We clustered the samples based on similarities in the phylogenetic lineages that they contain and found that, surprisingly, the major environmental determinant of microbial community composition is salinity rather than extremes of temperature, pH, or other physical and chemical factors represented in our samples. We find that sediments are more phylogenetically diverse than any other environment type. Surprisingly, soil, which has high species-level diversity, has below-average phylogenetic diversity. This work provides a framework for understanding the impact of environmental factors on bacterial evolution and for the direction of future sequencing efforts to discover new lineages.**



# Marine to Freshwater: Microbiome?




**Microbiome Sampling** (Sept 2014)

**Host** (10 fish per site, *F. heteroclitus* at all sites, congener *F. diaphanus* at freshwater site, congener *F. majalis* at marine site)

- Gill
- Intestine
- Feces

**Environment**

- Water
- Sediment

*F. diaphanus*

- freshwater

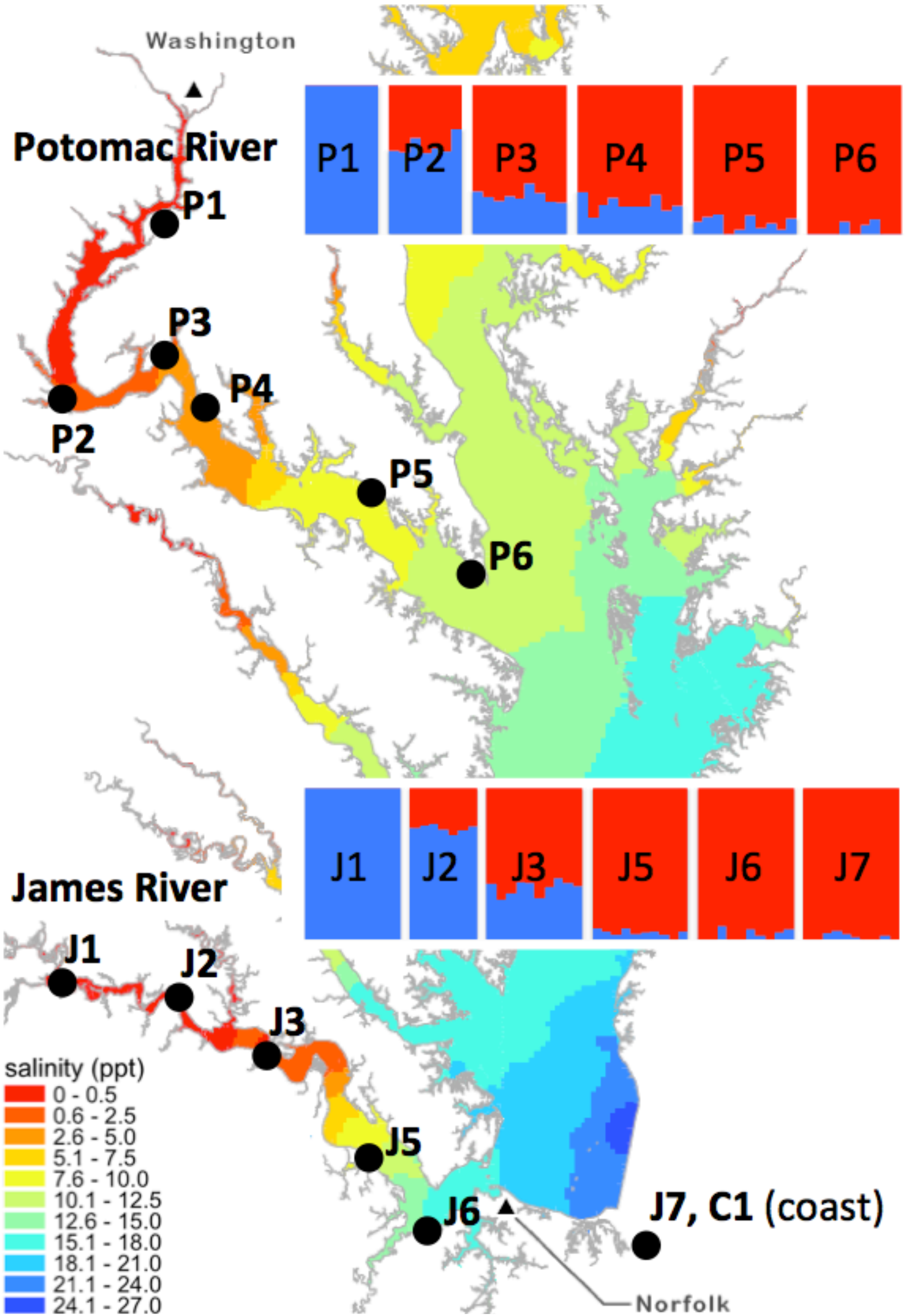
*F. heteroclitus*

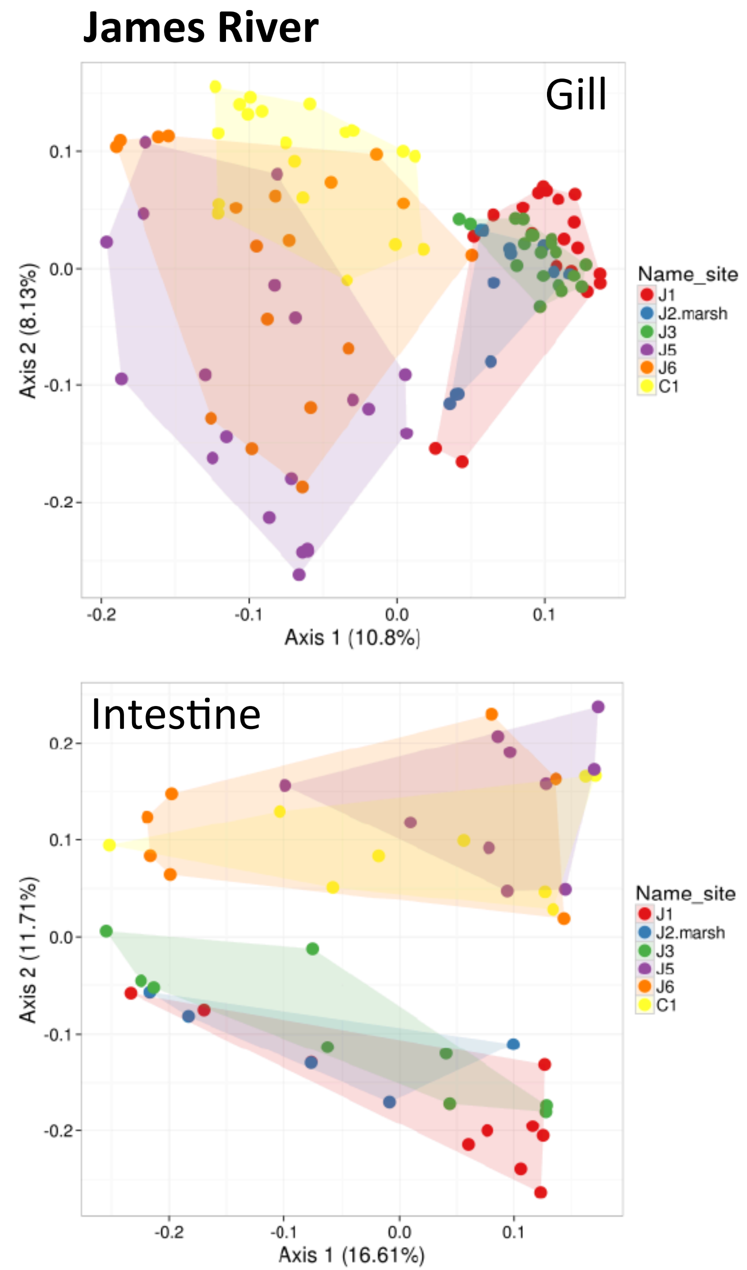
- euryhaline

*F. majalis*

- marine

# Marine to Freshwater: Microbiome?



# Conclusions:

- Adaptation from marine to freshwater environments is important for generating the unprecedented phyletic diversity of fishes
- Much of the molecular machinery that underlies osmoregulation is ancient
- Transitions are highly asymmetric: almost universally from marine to fresh
- Euryhaline estuarine species may be important for seeding marine to fresh transitions
- Osmoregulation is a trait underlain by many genes
- Genetic variation that is associated with osmoregulatory abilities is evolving along salinity gradients
- Other traits evolve during marine to freshwater transitions, including morphology and perhaps microbiome associations.