

Repeated evolution following habitat transitions from marine to freshwater

Dr. Antoine Fraimout
May 9th 2023



Main questions

Can populations respond adaptively to habitat changes and can we predict these adaptive changes?

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Is evolution predictable?

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Is evolution predictable?

Do adaptive phenotypes evolve repeatedly in response to the same environmental change?

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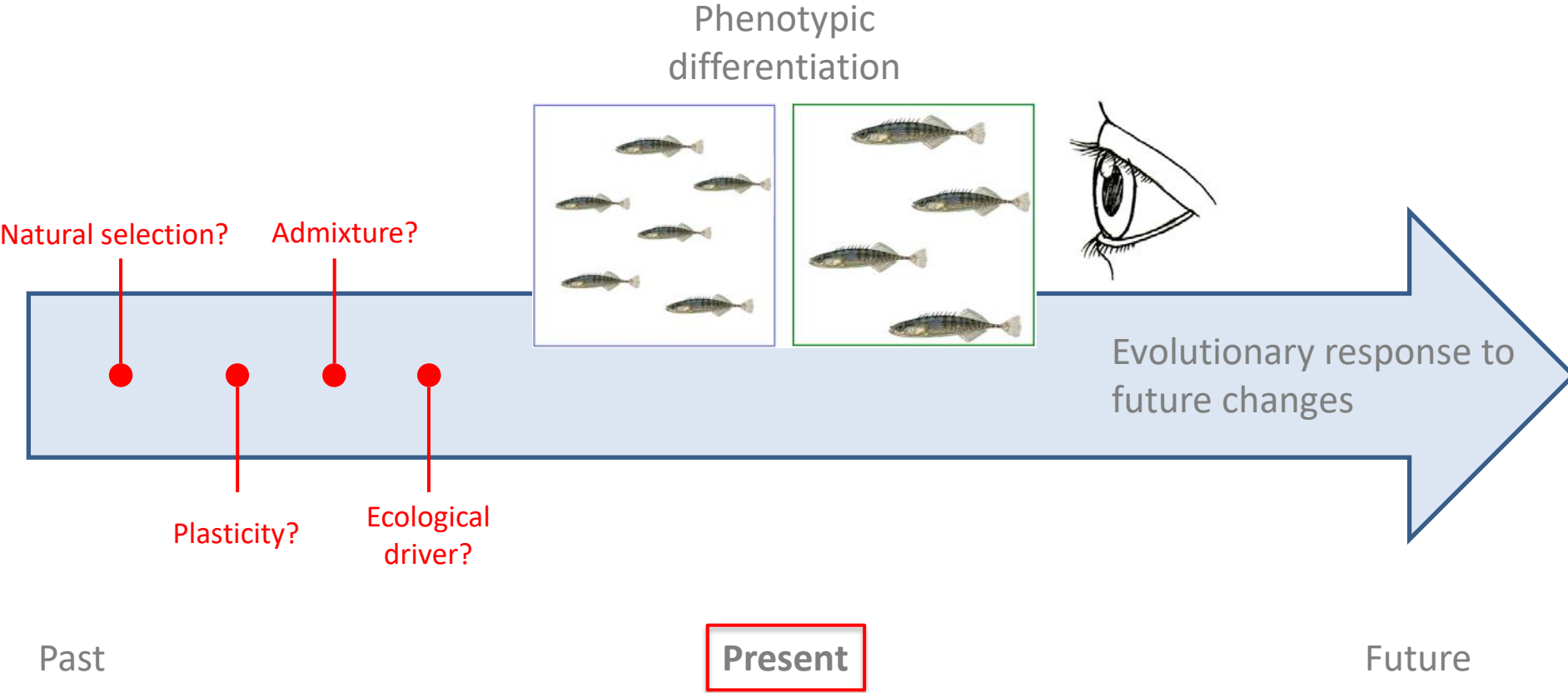
Can populations respond adaptively to habitat changes and can we predict these adaptive changes?

Is evolution predictable?

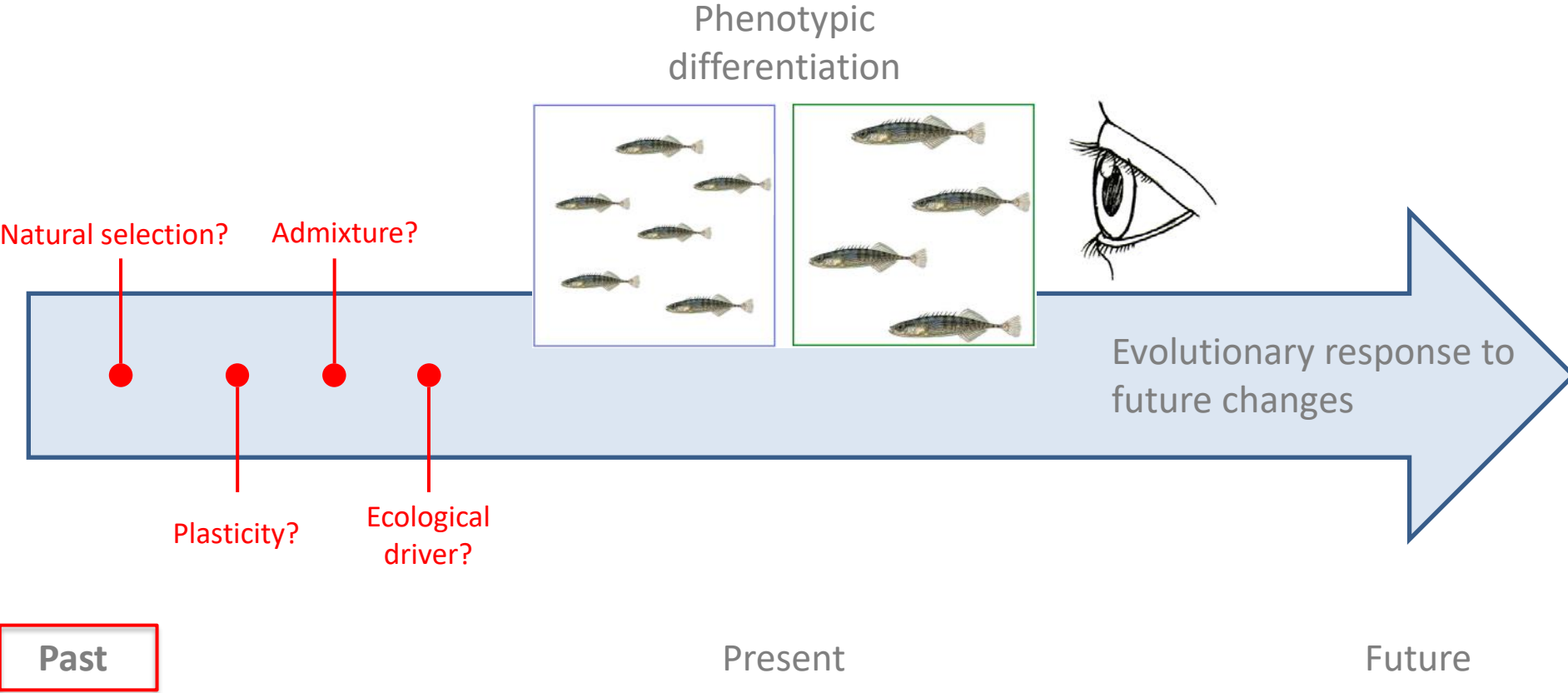
Do adaptive phenotypes evolve repeatedly in response to the same environmental change?

Testimony for evolution by natural selection

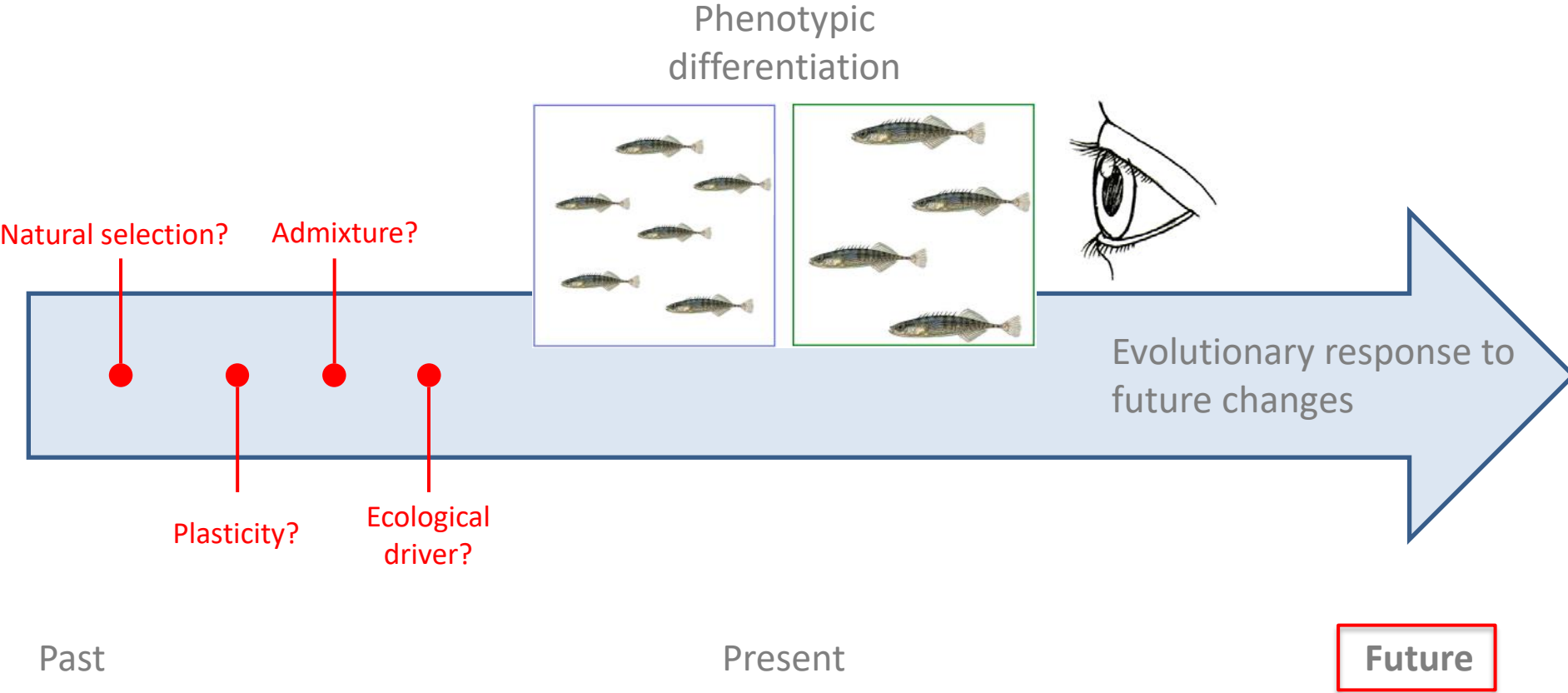
Experimental quantitative genetics approach



Experimental quantitative genetics approach



Experimental quantitative genetics approach



Habitat transitions

Environmental, demographic and selective changes



Photo: A. Fraimout

Baltic Sea (Pori, Finland)

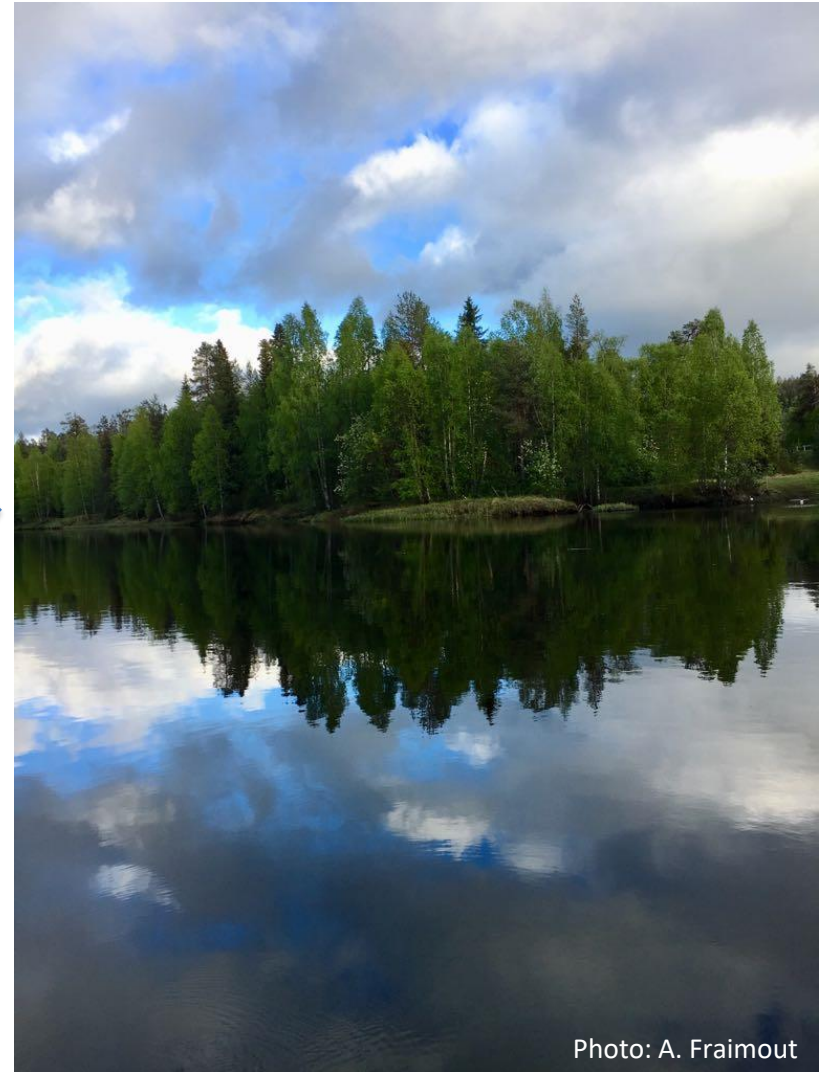
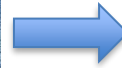


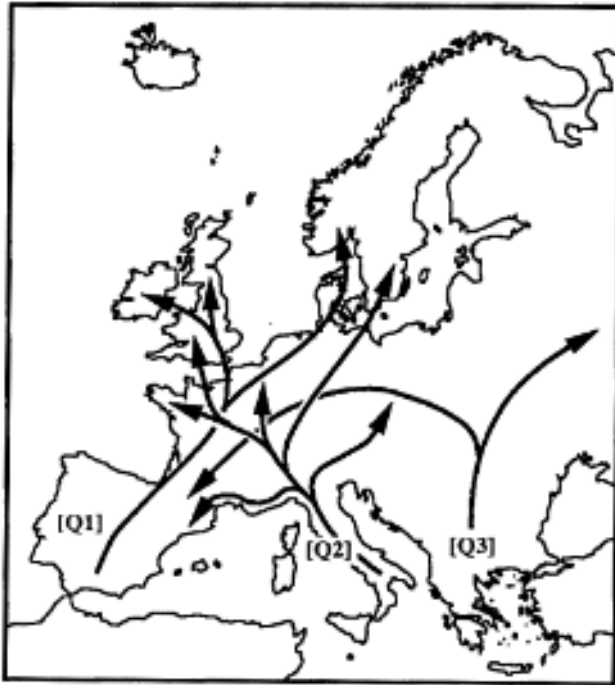
Photo: A. Fraimout

Oulanka river (Kuusamo, Finland)

Habitat transitions

Multiple independent colonization events

Quercus sp. (white oaks)

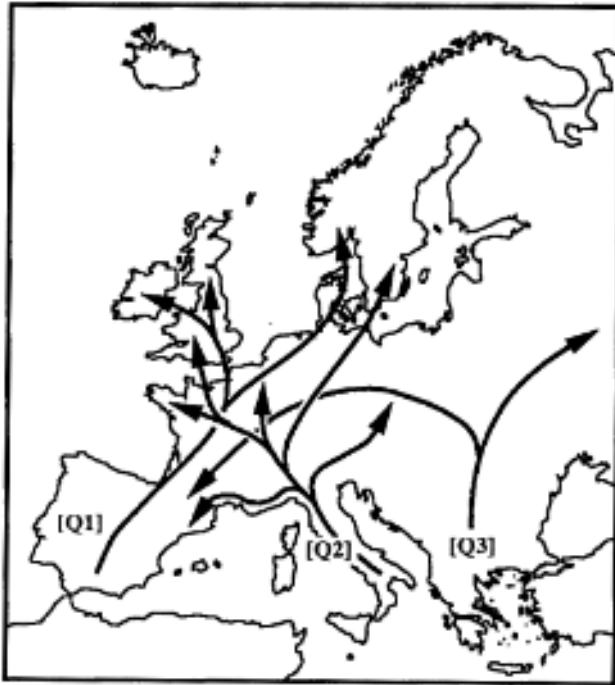


Post-glacial colonization
(Taberlet *et al.* 1998)

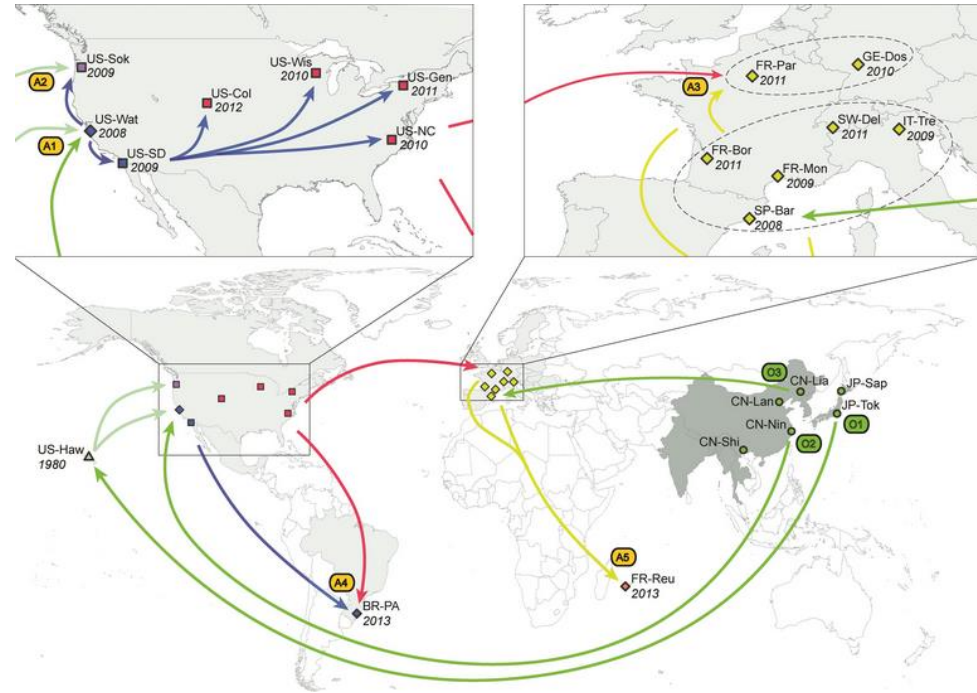
Habitat transitions

Multiple independent colonization events

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Post-glacial colonization
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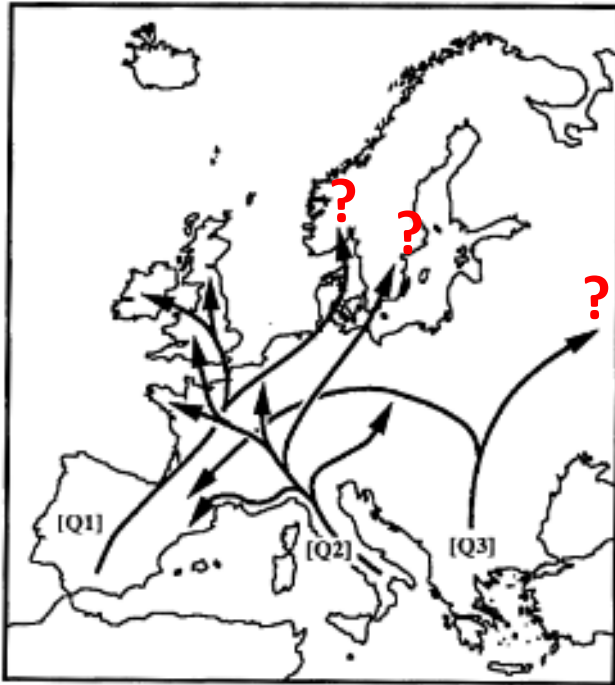


Biological invasions
(Frainout *et al.* 2017)

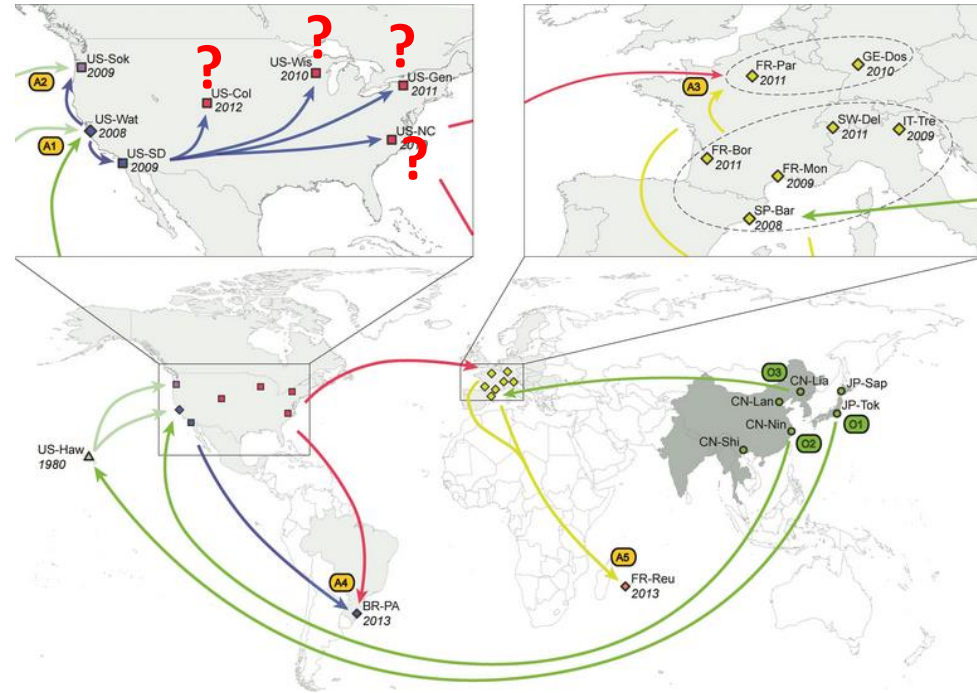
Habitat transitions

Multiple independent colonization events

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Post-glacial colonization
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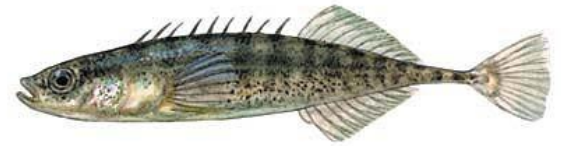


Biological invasions
(Frainout *et al.* 2017)

Outline

Part I : Repeated evolution following post-glacial colonization of freshwater by nine-spined sticklebacks

- Parallel evolution of behaviour
- (non)Parallel evolution?

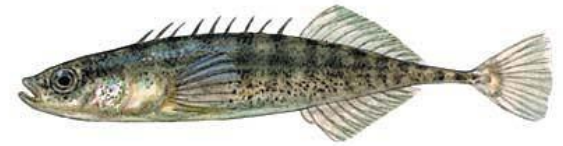


Pungitius pungitius

Outline

Part I : Repeated evolution following post-glacial colonization of freshwater by nine-spined sticklebacks

- Parallel evolution of behaviour
- (non)Parallel evolution?



Pungitius pungitius

Part II : Repeated evolution following multiple invasions of freshwater by copepods

- Genetic bases of salinity adaptation



Eurytemora affinis

Glossary

Repeated evolution: same evolutionary output occurring multiple times

Glossary

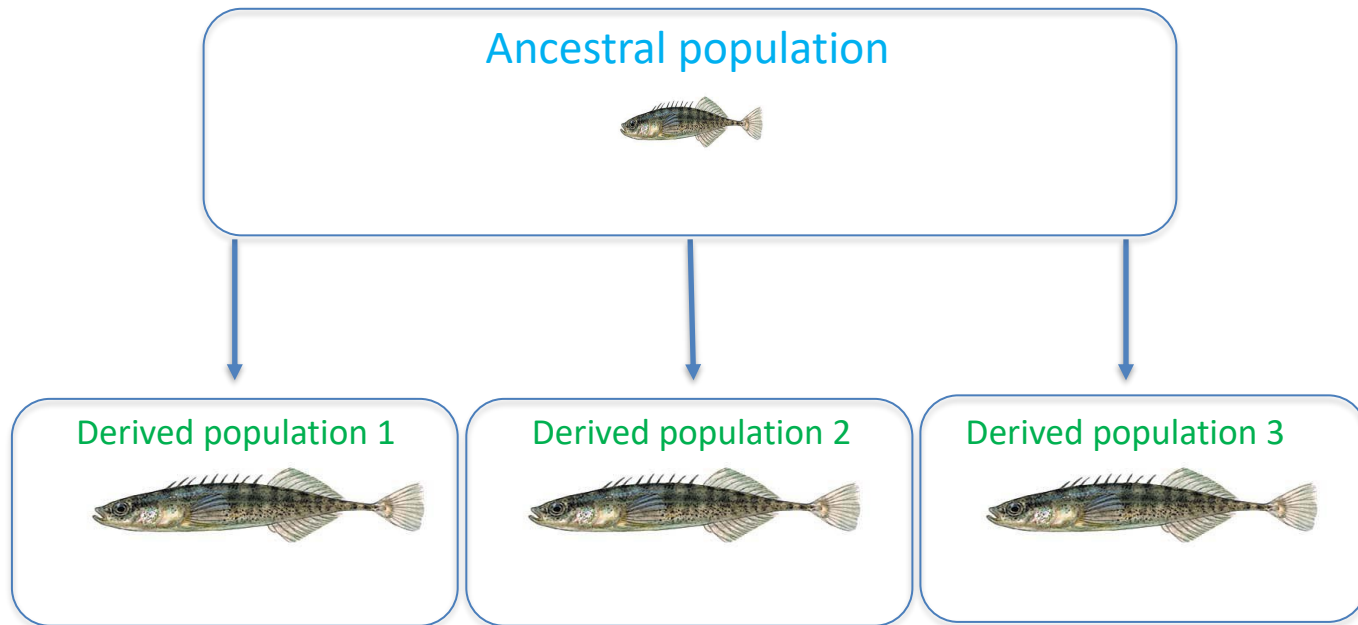
Repeated evolution: same evolutionary output occurring multiple times

Parallel phenotypic evolution: evolution of similar phenotypes between multiple populations of the same species

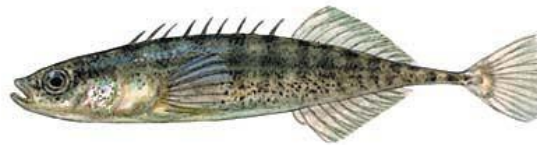
Glossary

Repeated evolution: same evolutionary output occurring multiple times

Parallel phenotypic evolution: evolution of similar phenotypes between multiple populations of the same species



Part I : Repeated evolution following post-glacial colonization of freshwater by nine-spined sticklebacks



UNIVERSITY OF HELSINKI



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I – The nine-spined stickleback

(a)

Three-spined stickleback



● Freshwater

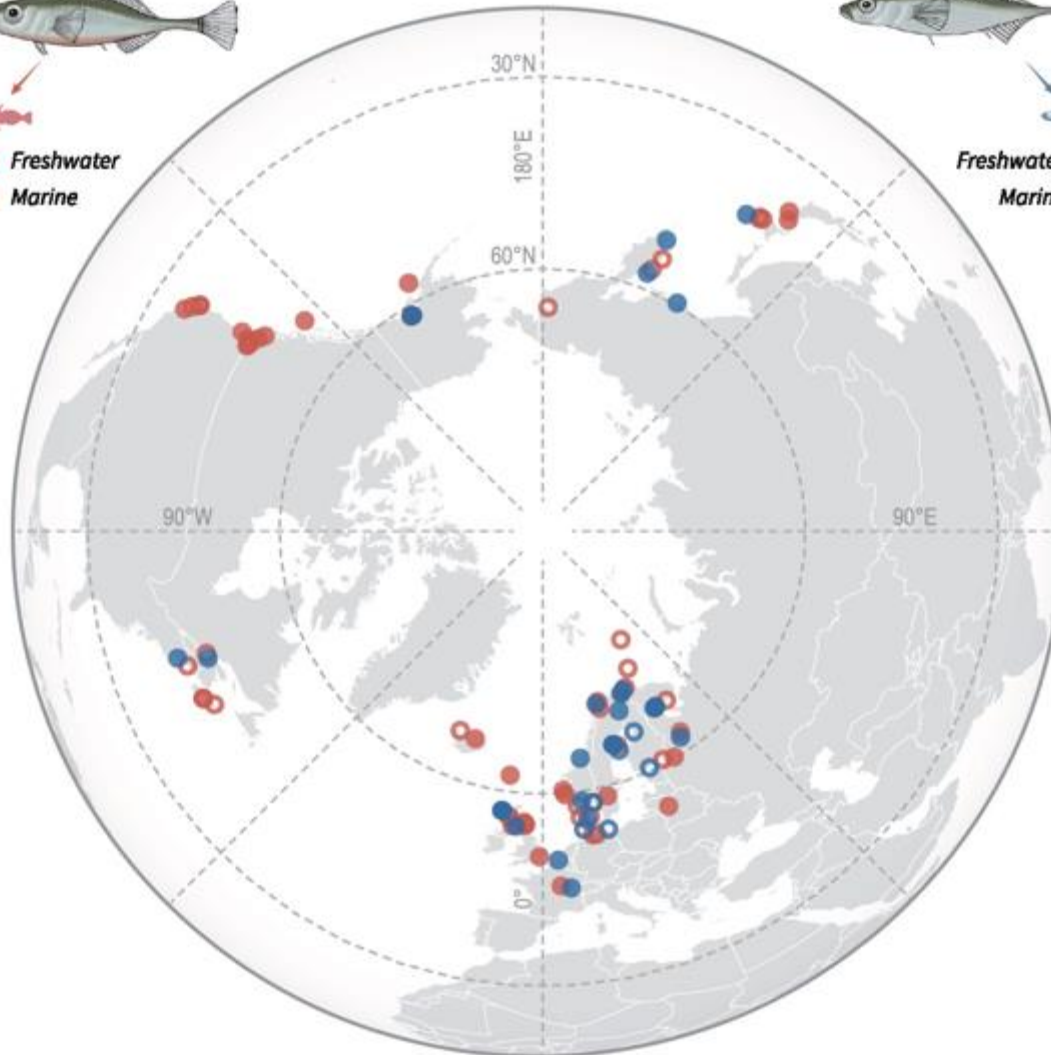
○ Marine

Nine-spined stickleback



● Freshwater

○ Marine



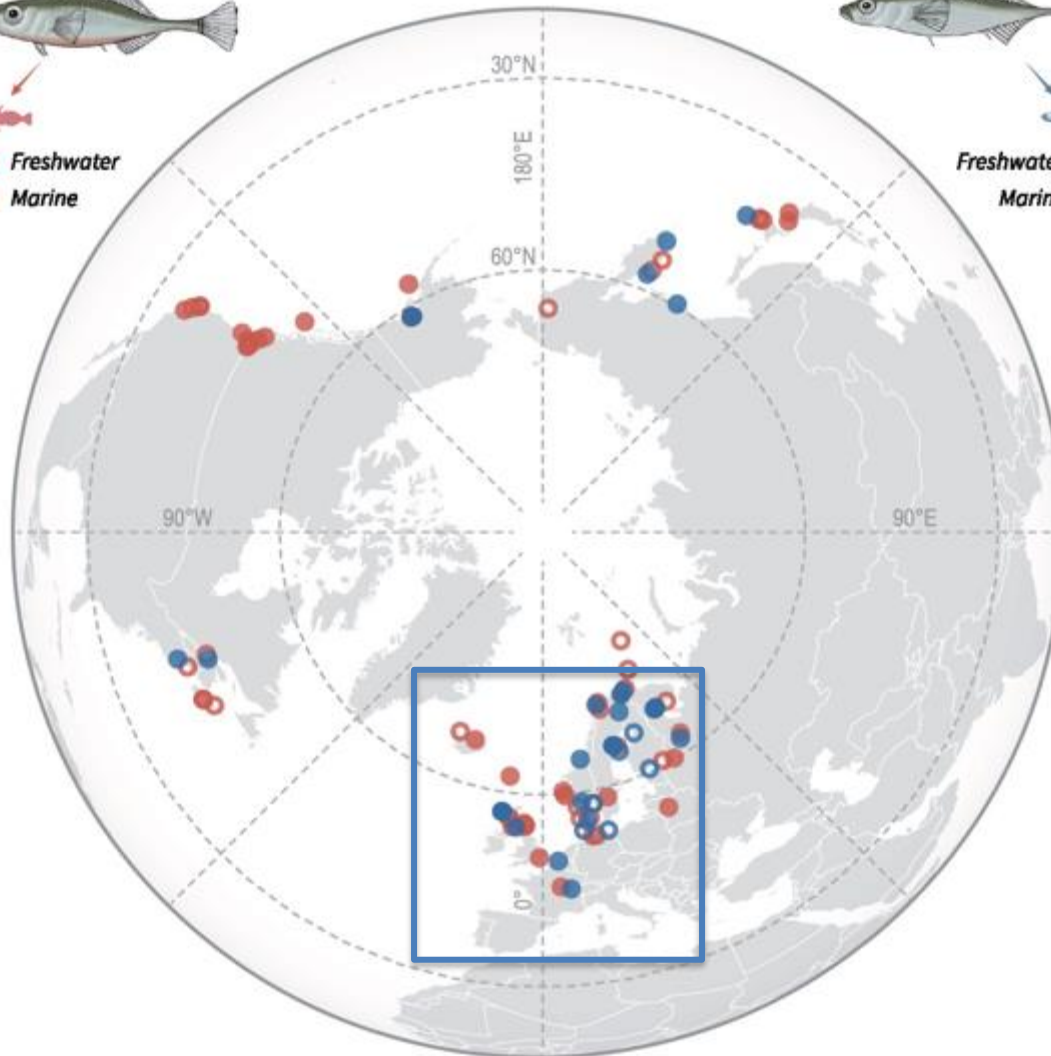
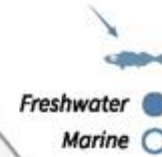
I – The nine-spined stickleback

(a)

Three-spined stickleback



Nine-spined stickleback

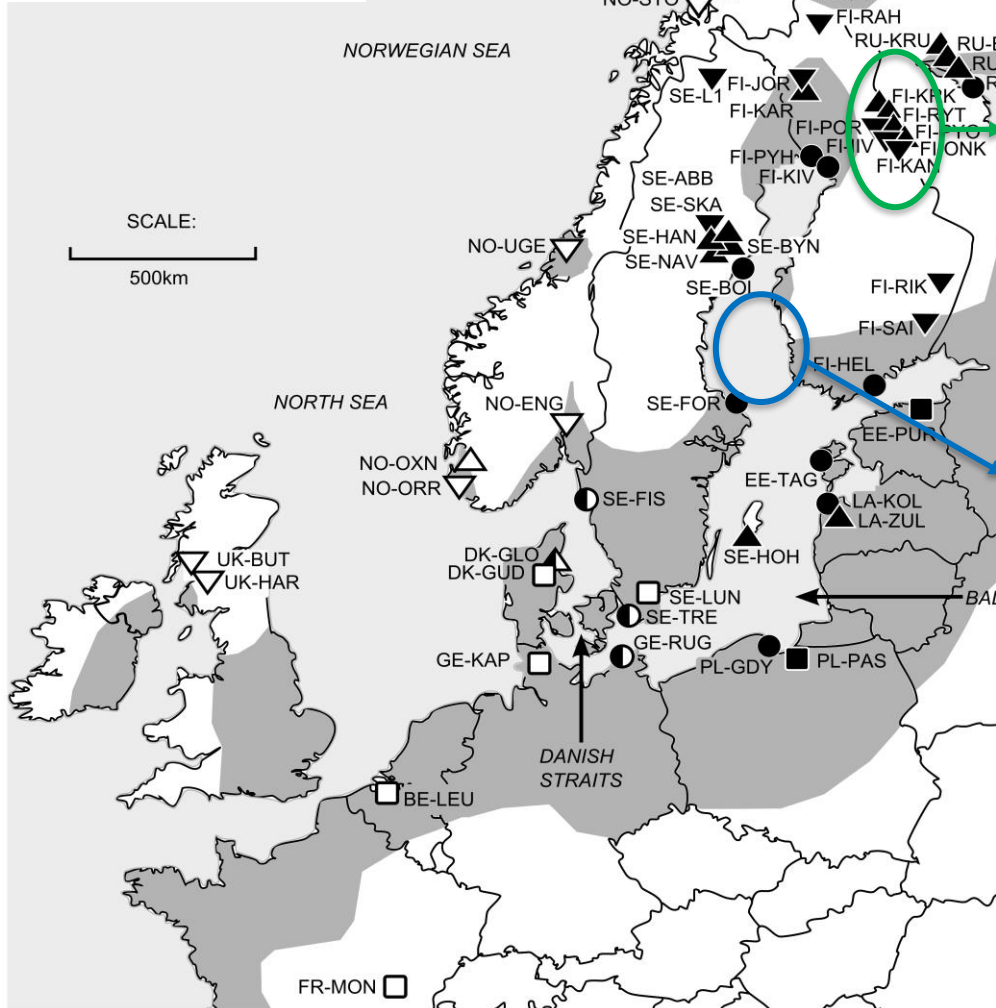


I – Habitat transition

▲ Freshwater pond



Pungitius pungitius



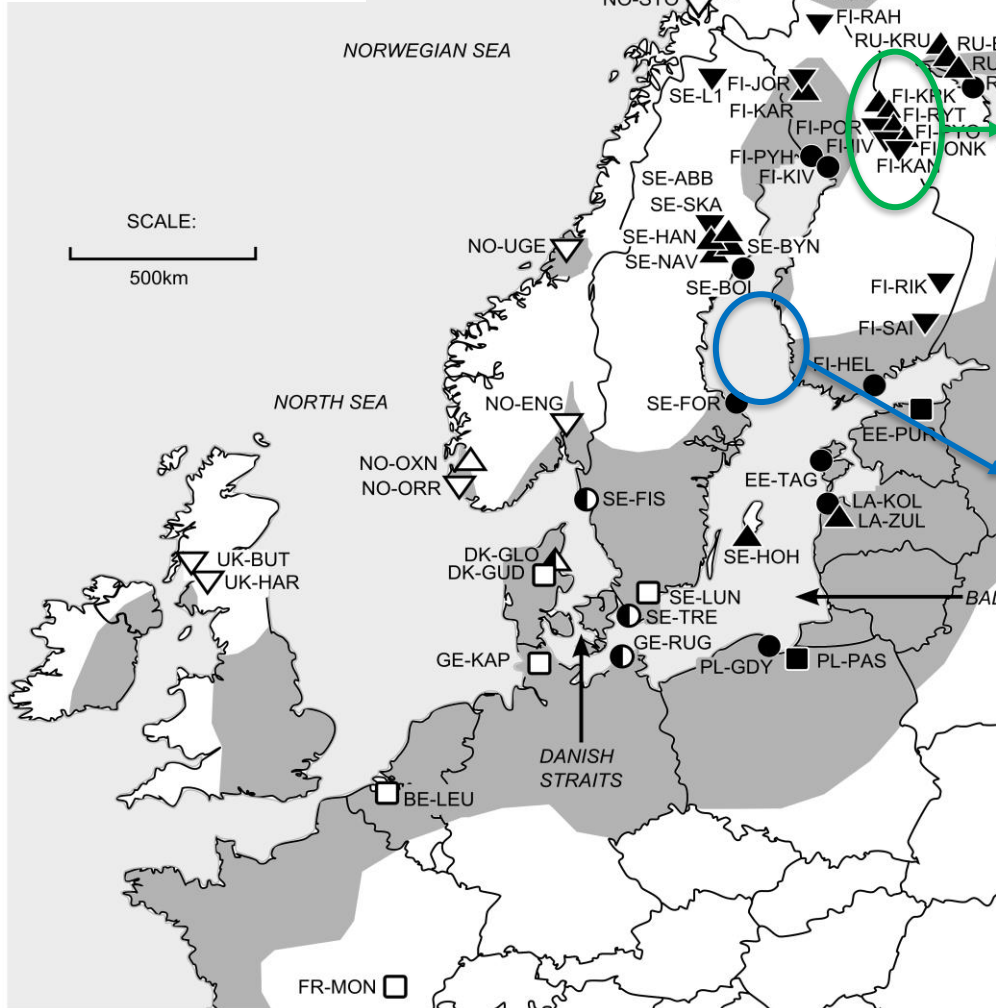
● Marine habitat



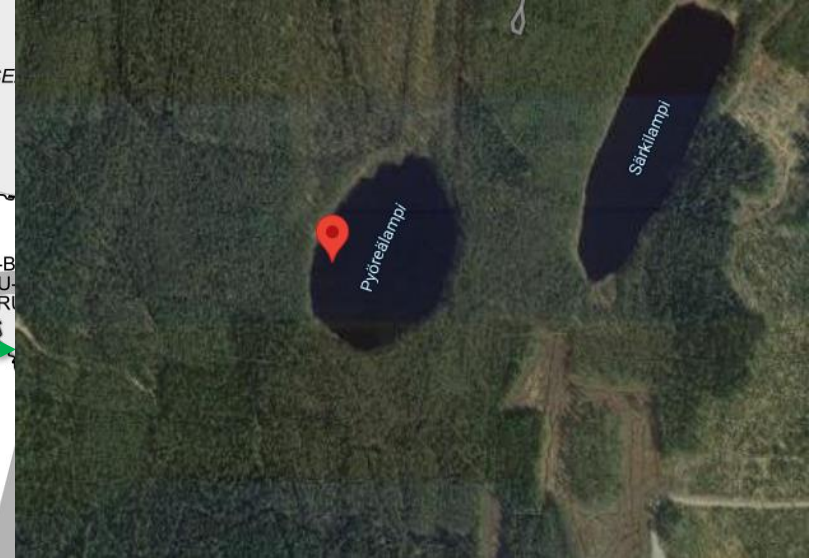
I – Habitat transition



Pungitius pungitius



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● Marine habitat

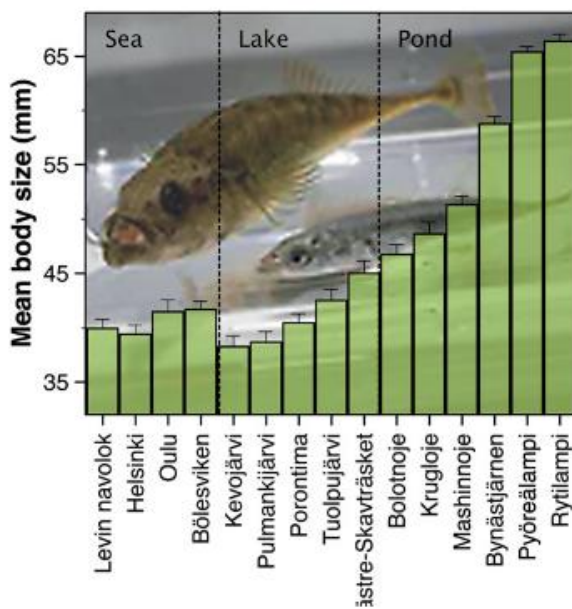


Photo: A. Fraimout

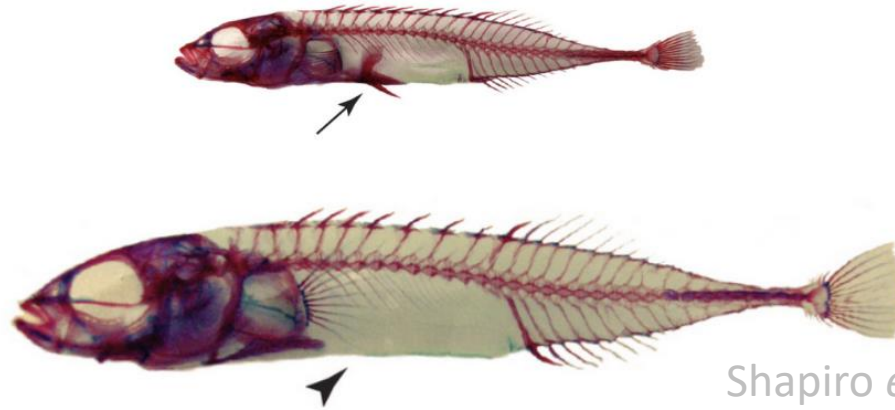
I – Repeated phenotypic evolution



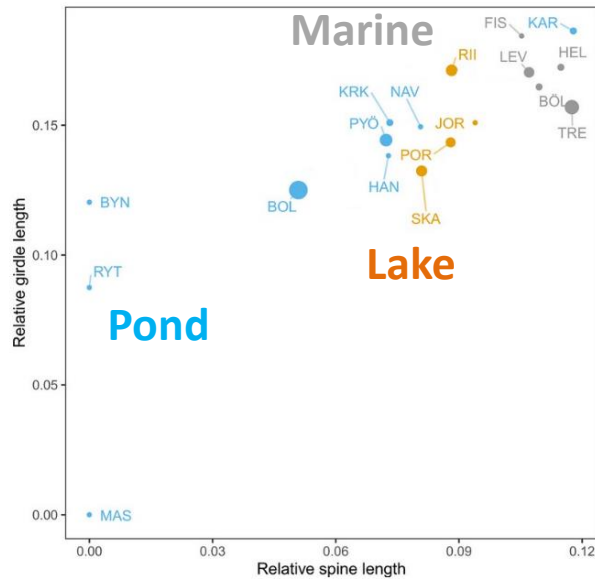
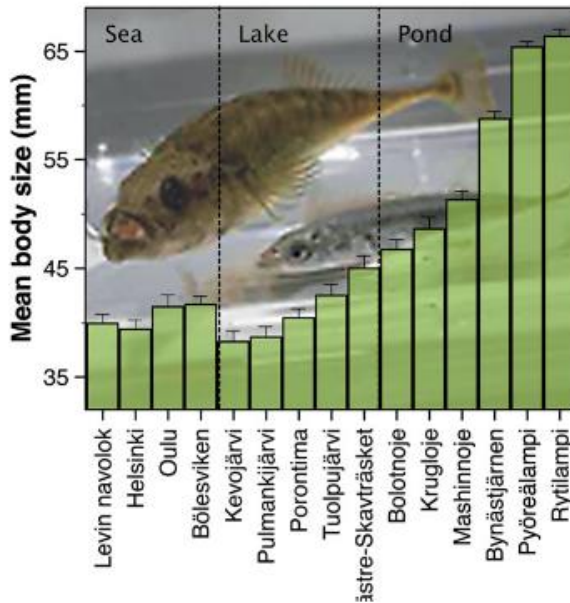
I – Repeated phenotypic evolution



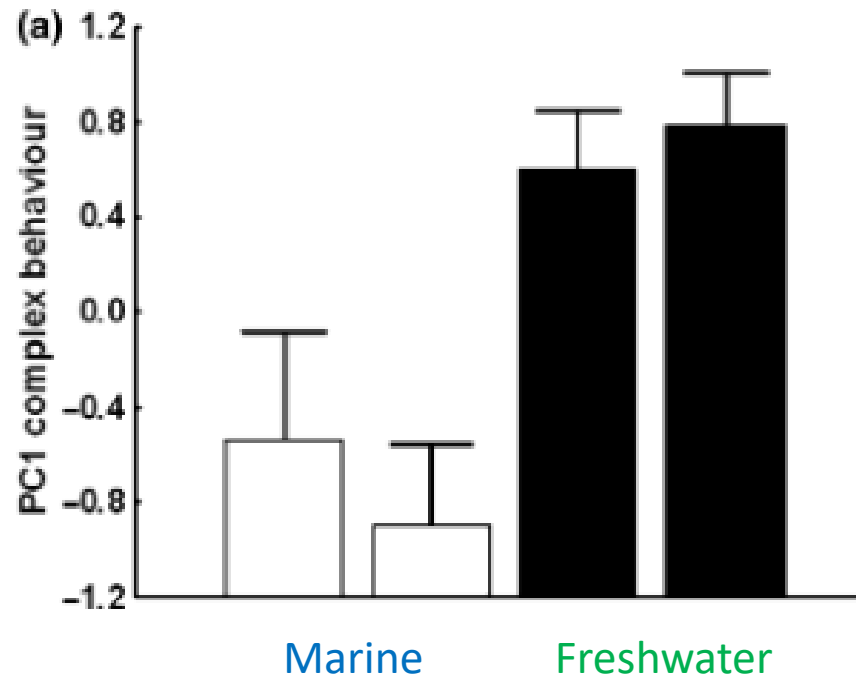
I – Repeated phenotypic evolution



Shapiro *et al.* (2009)



I – Repeated phenotypic evolution



Common garden experiment showed **marine** individuals are **shy and peaceful**, while **pond** individuals are **bold and aggressive**

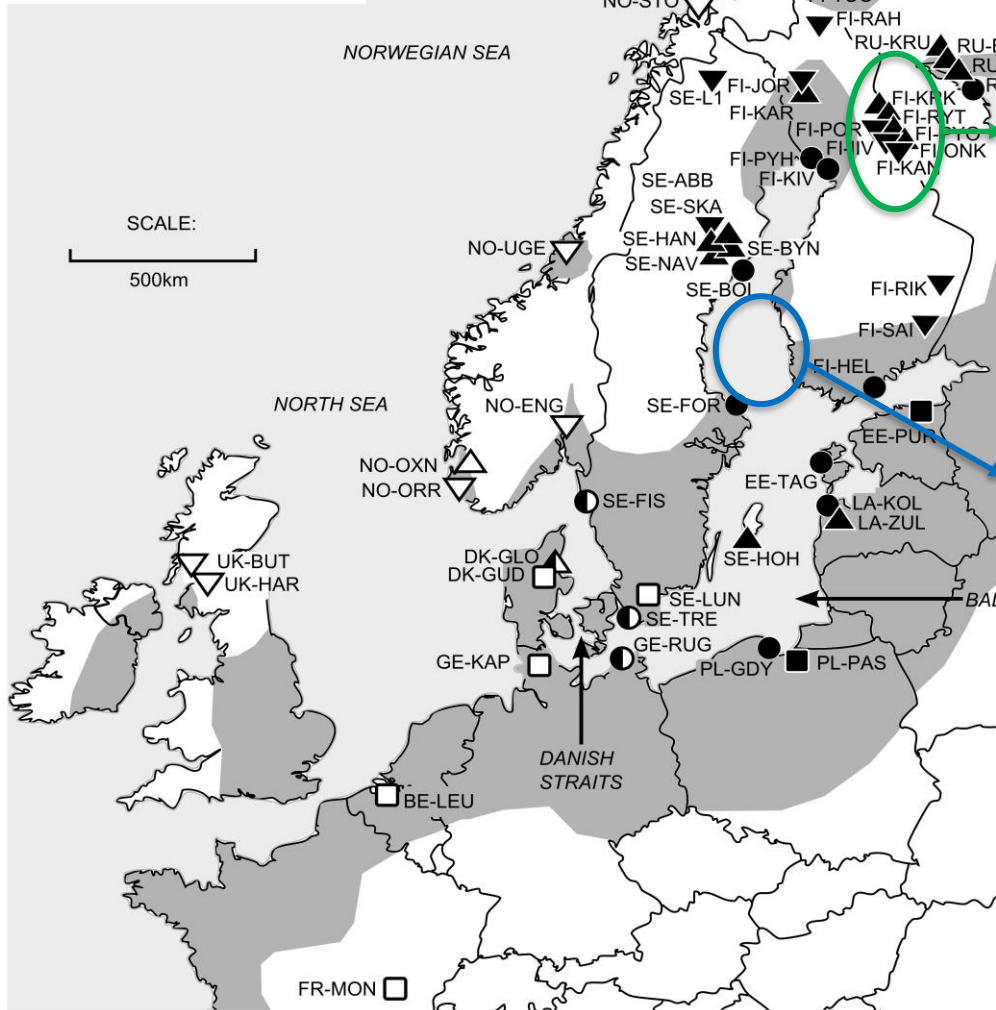
What drove behaviour evolution in freshwater *P. pungitius*?

I – Habitat differentiation

▲ Freshwater pond



Pungitius pungitius



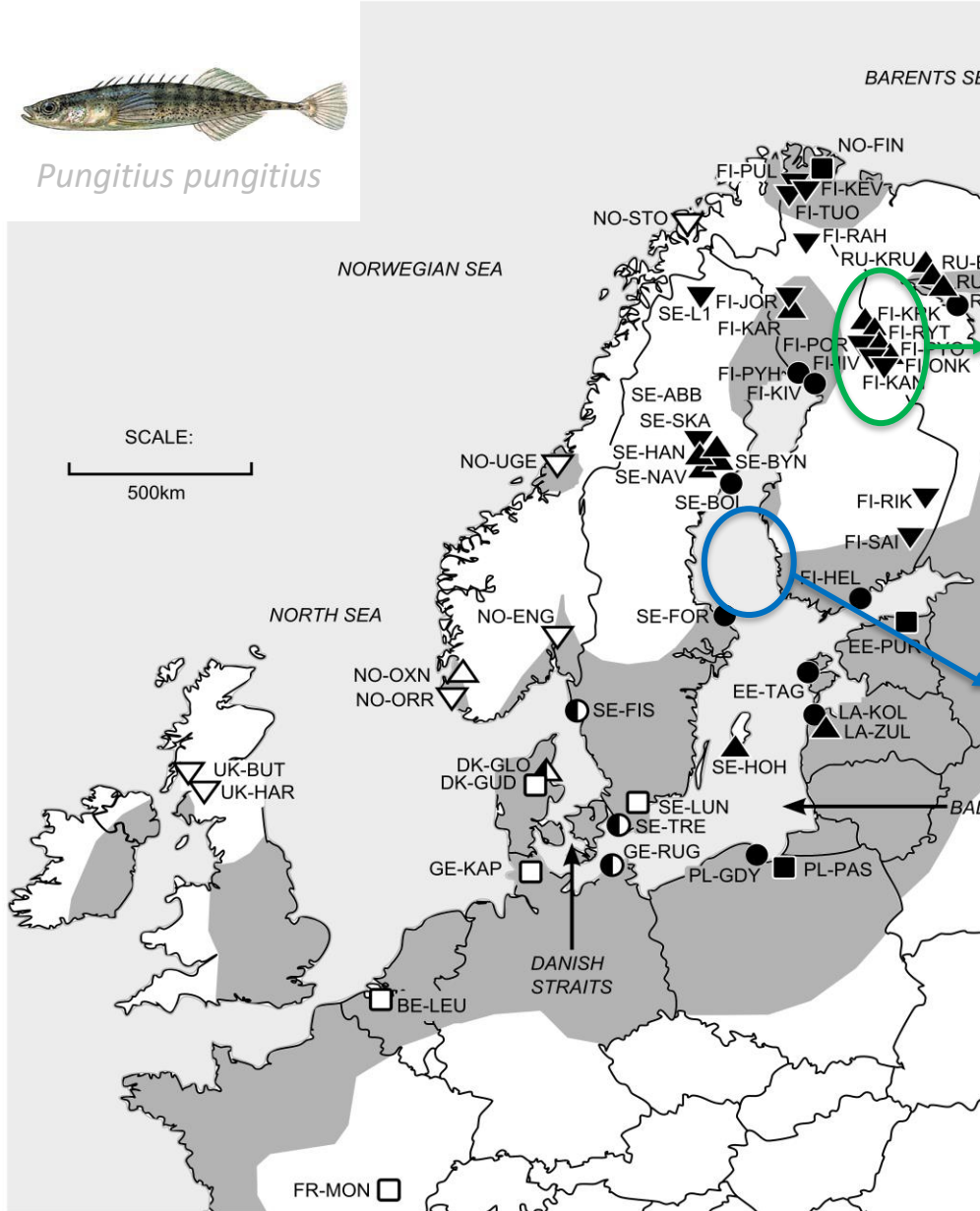
● Marine habitat



I – Habitat differentiation



Pungitius pungitius



▲ Freshwater pond



● Marine habitat



I – Research question

Did predation release drive repeated evolution of behaviour in *P. pungitius*?

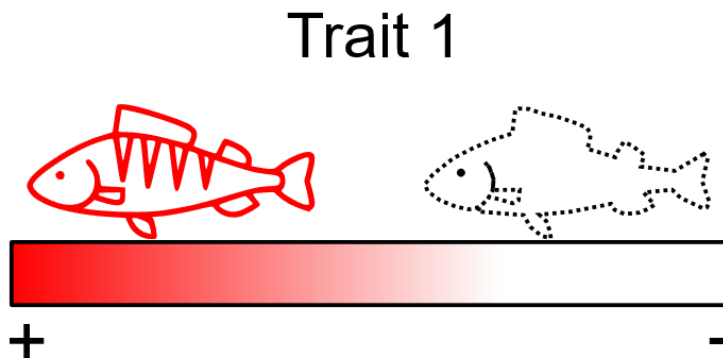
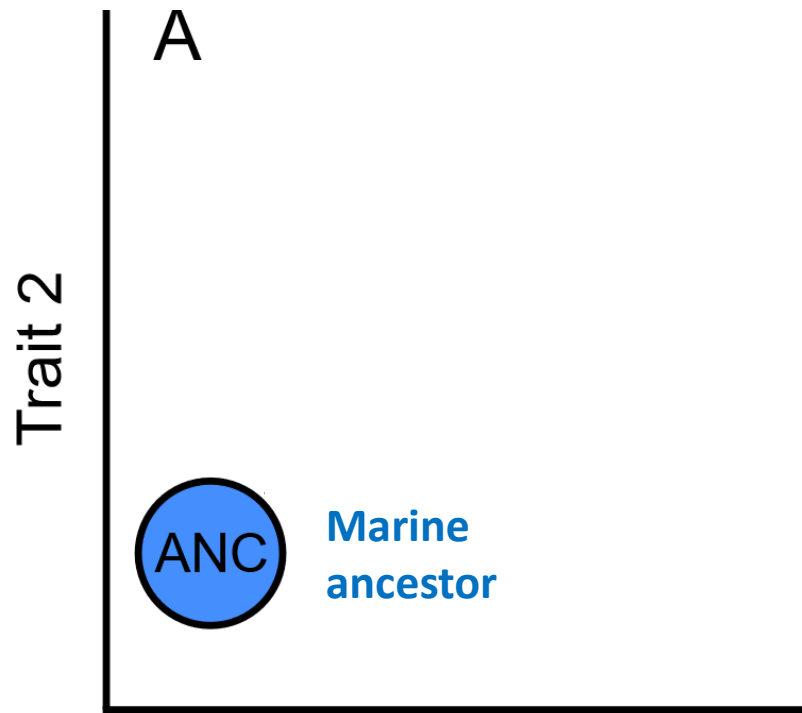
I – Research question

Did predation release drive repeated evolution of behaviour in *P. pungitius*?

Did behaviour evolve in parallel among freshwater populations?

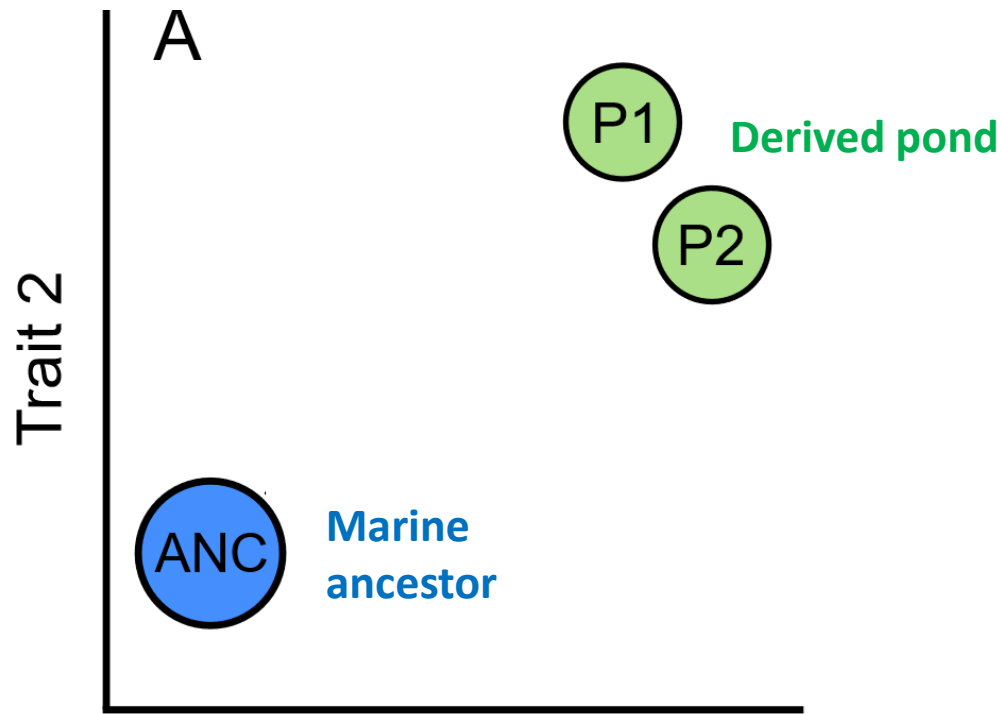
I – A geometric approach to parallel evolution

I – Theory

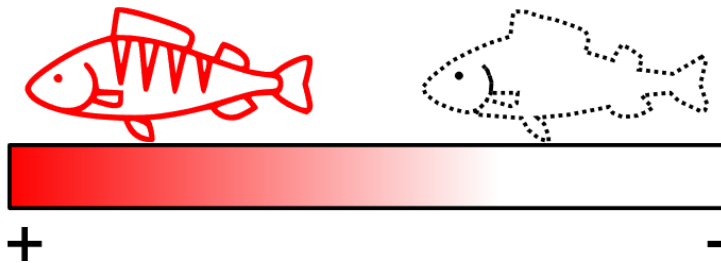


**High predation
pressure**

I – Theory

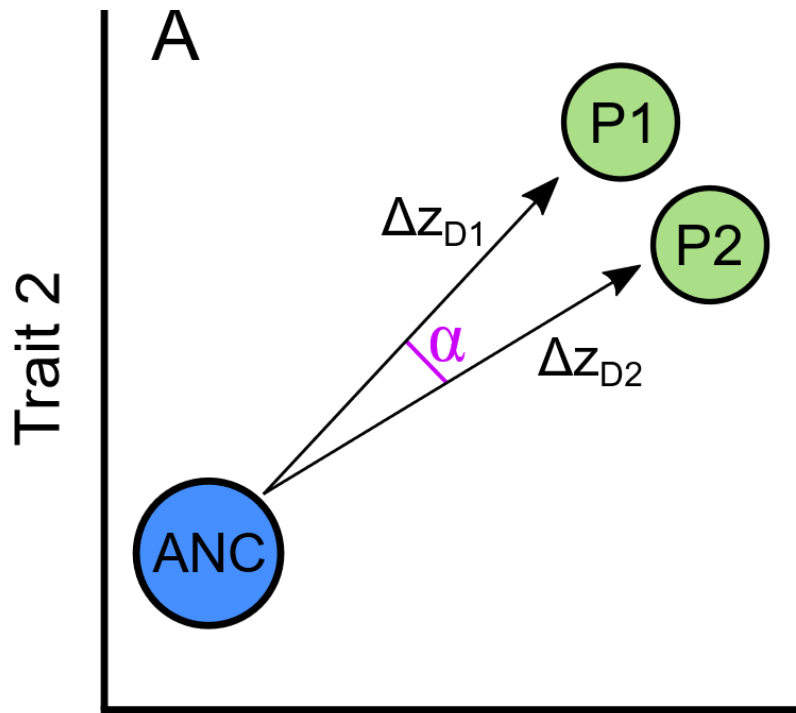


Trait 1

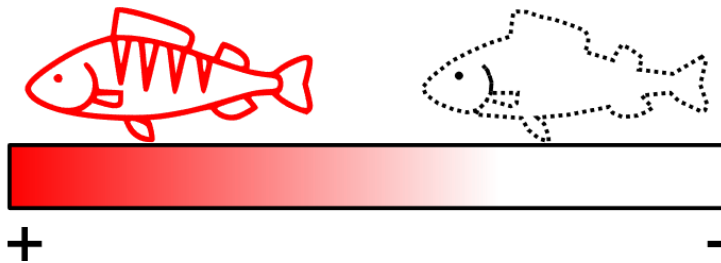


Low predation pressure

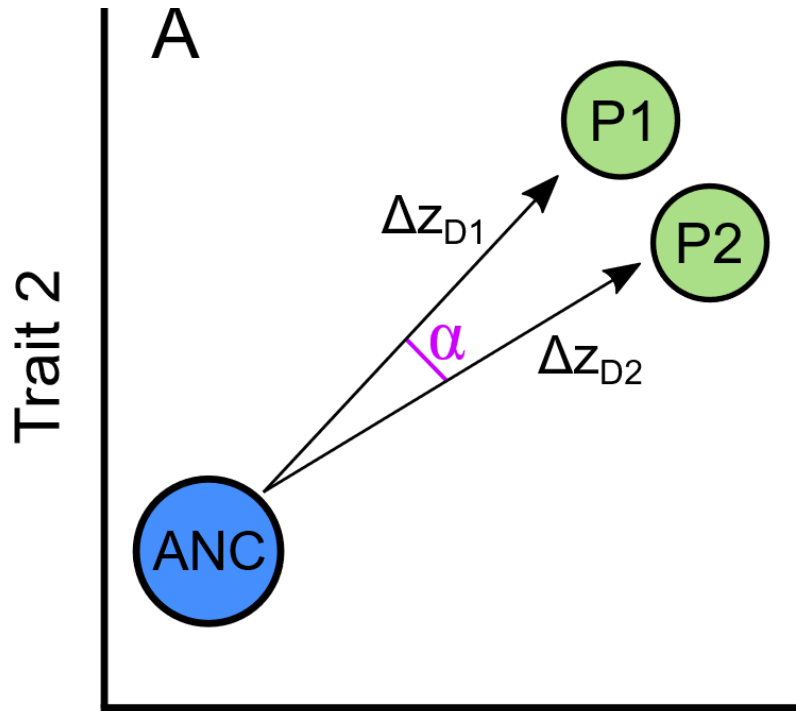
I – Theory



Δz_D = vector of phenotypic divergence

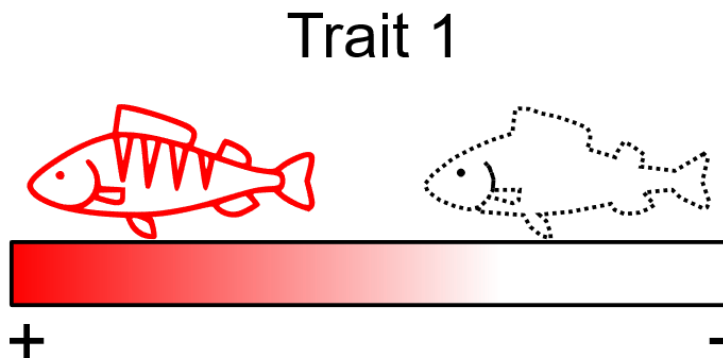


I – Theory

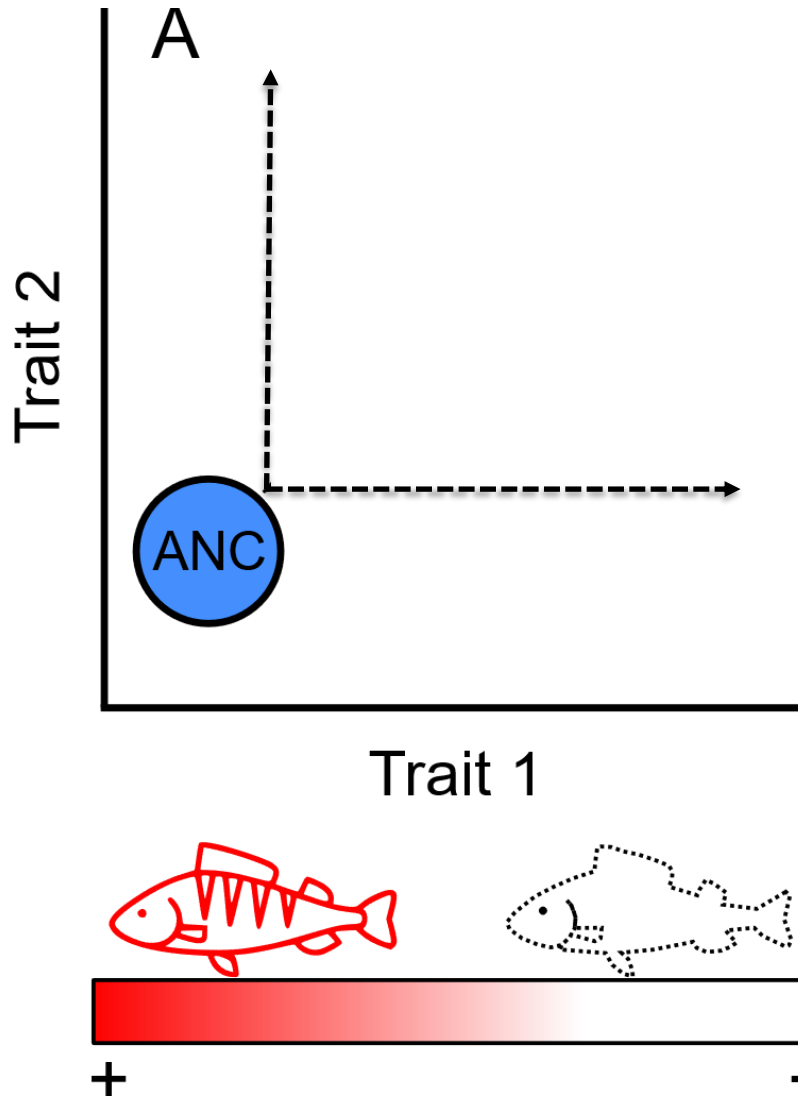


Δz_D = vector of phenotypic divergence

α = angle between divergence vectors



I – Theory

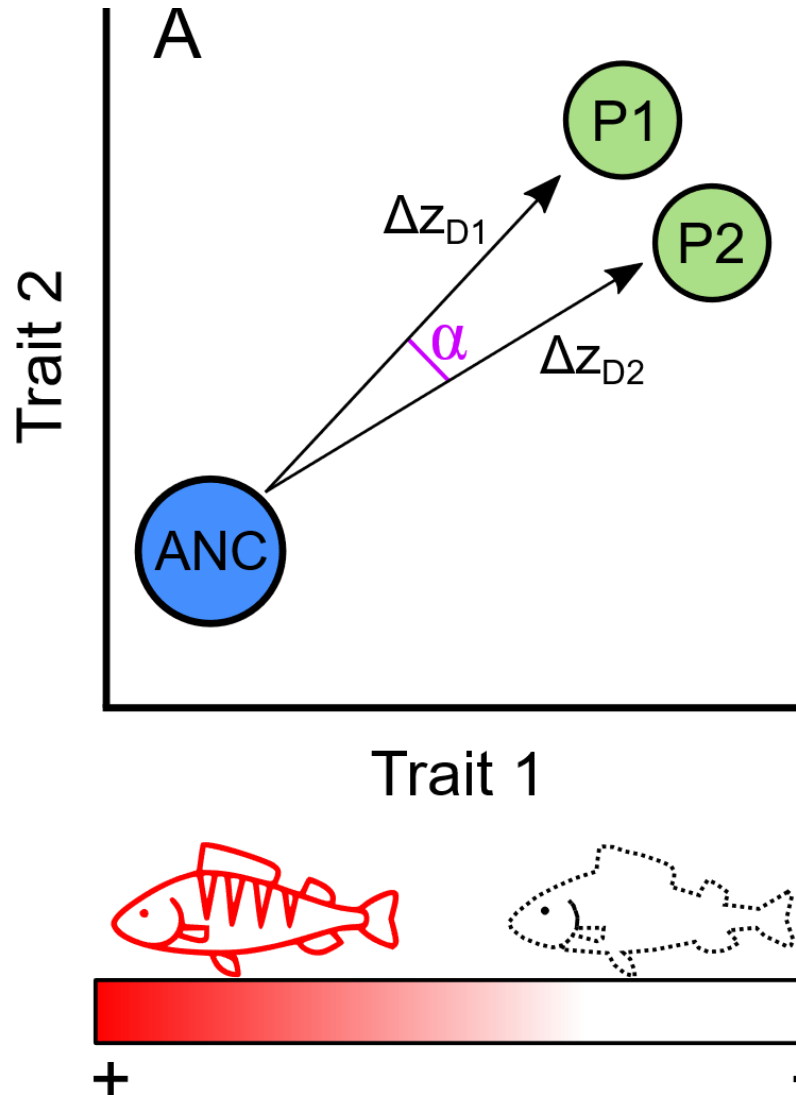


Δz_D = vector of phenotypic divergence

α = angle between divergence vectors

$H_0: \alpha = 90^\circ \rightarrow$ phenotypic evolution in random directions

I – Theory



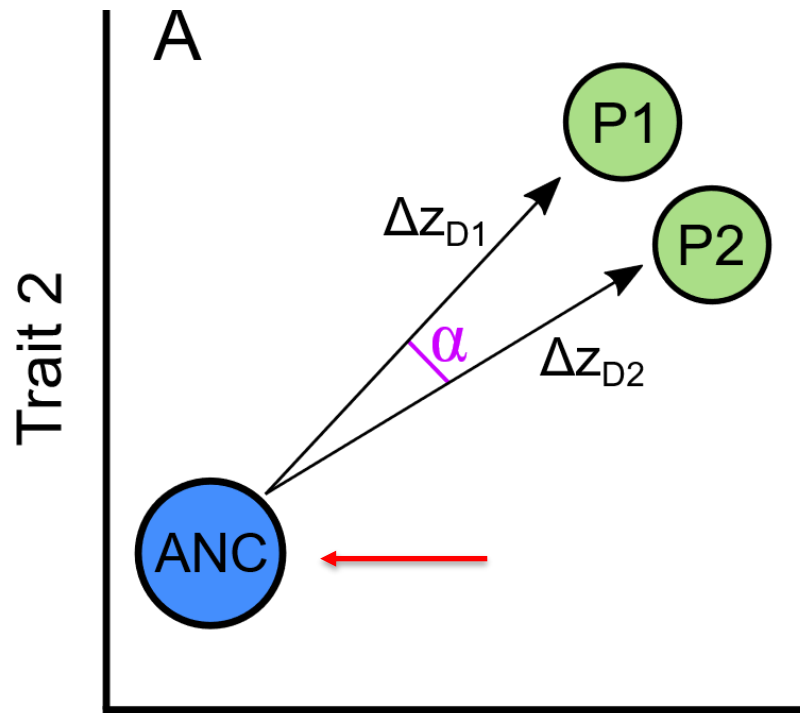
Δz_D = vector of phenotypic divergence

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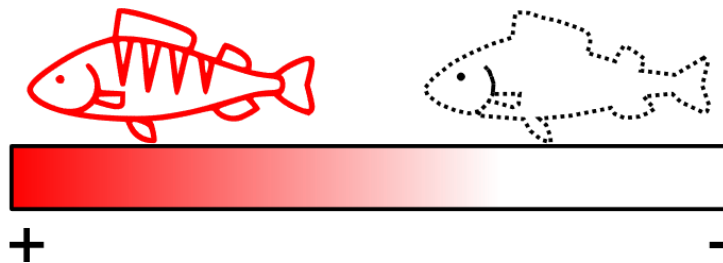
H_0 : $\alpha = 90^\circ$ → phenotypic evolution in random directions

H_1 : $\alpha = 0^\circ$ → parallel evolution

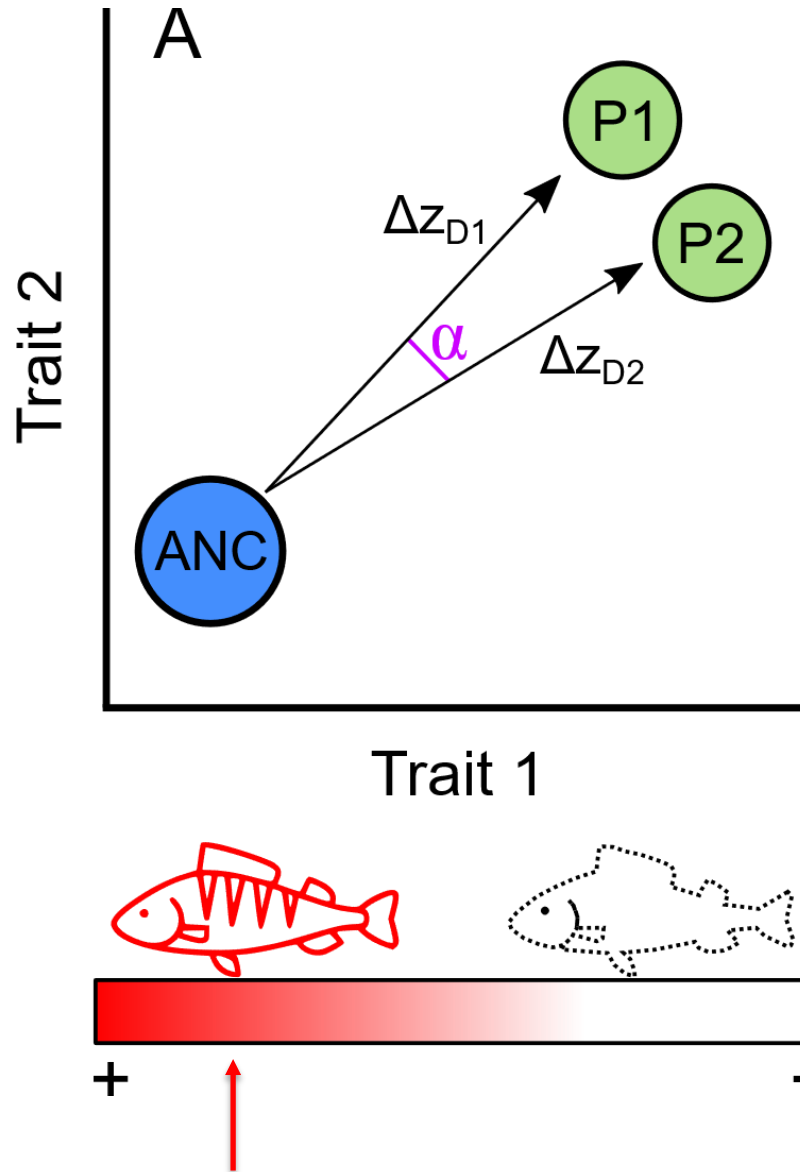
I – Practice



Sample [marine ancestors](#)

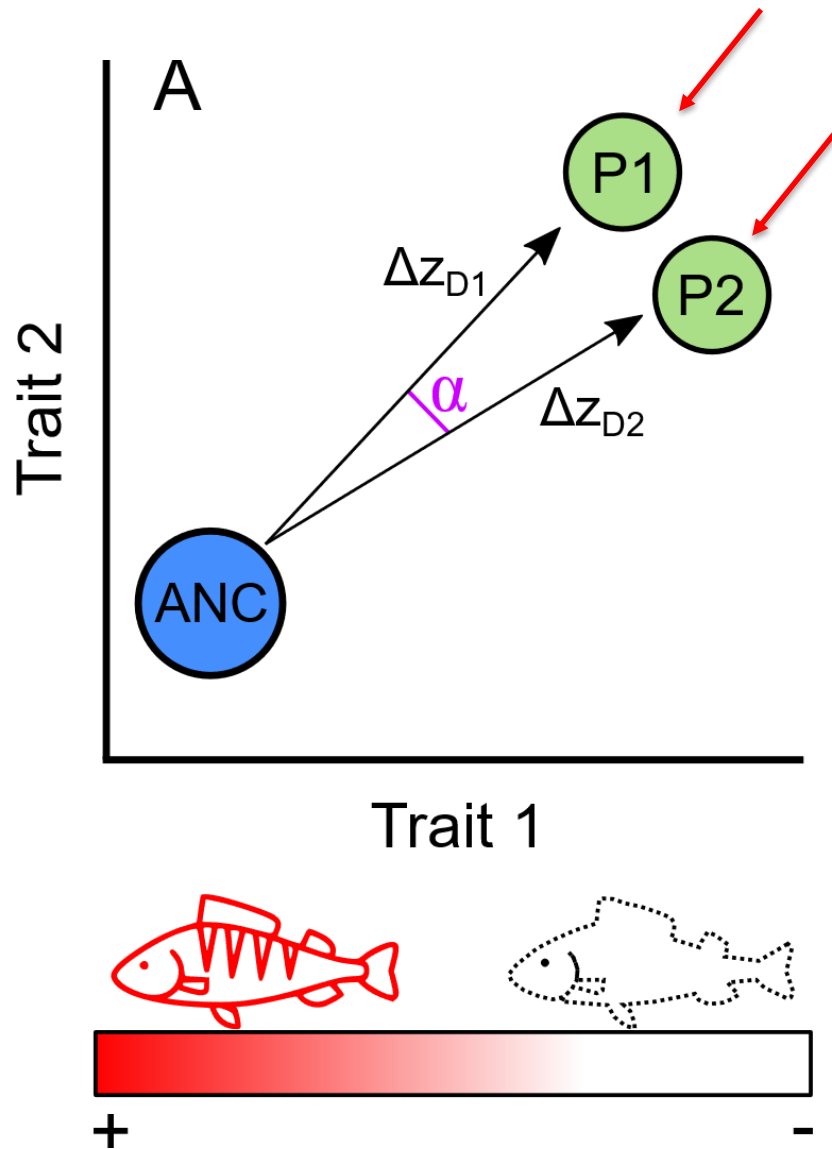


I – Practice



Sample [marine ancestors](#)
Experimental tests of behaviour
under predation risk

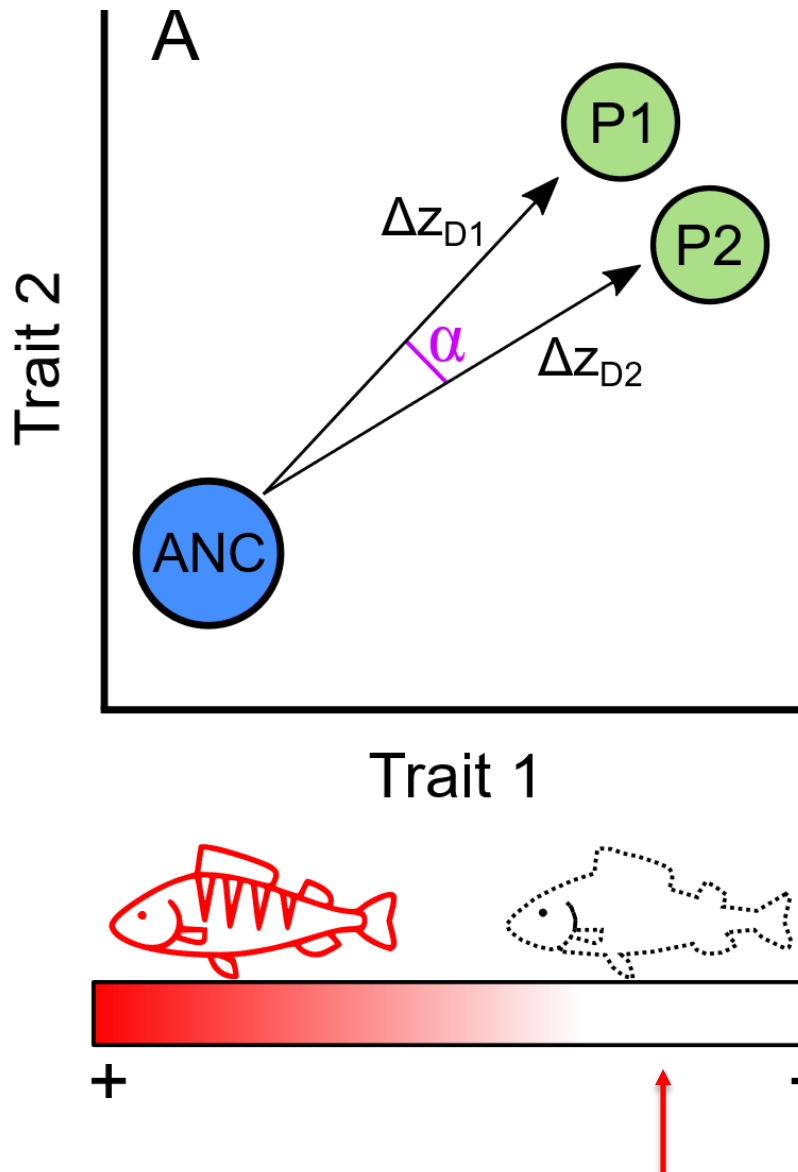
I – Practice



Sample **marine ancestors**
Experimental tests of behaviour
under predation risk

Sample replicate **freshwater**
populations

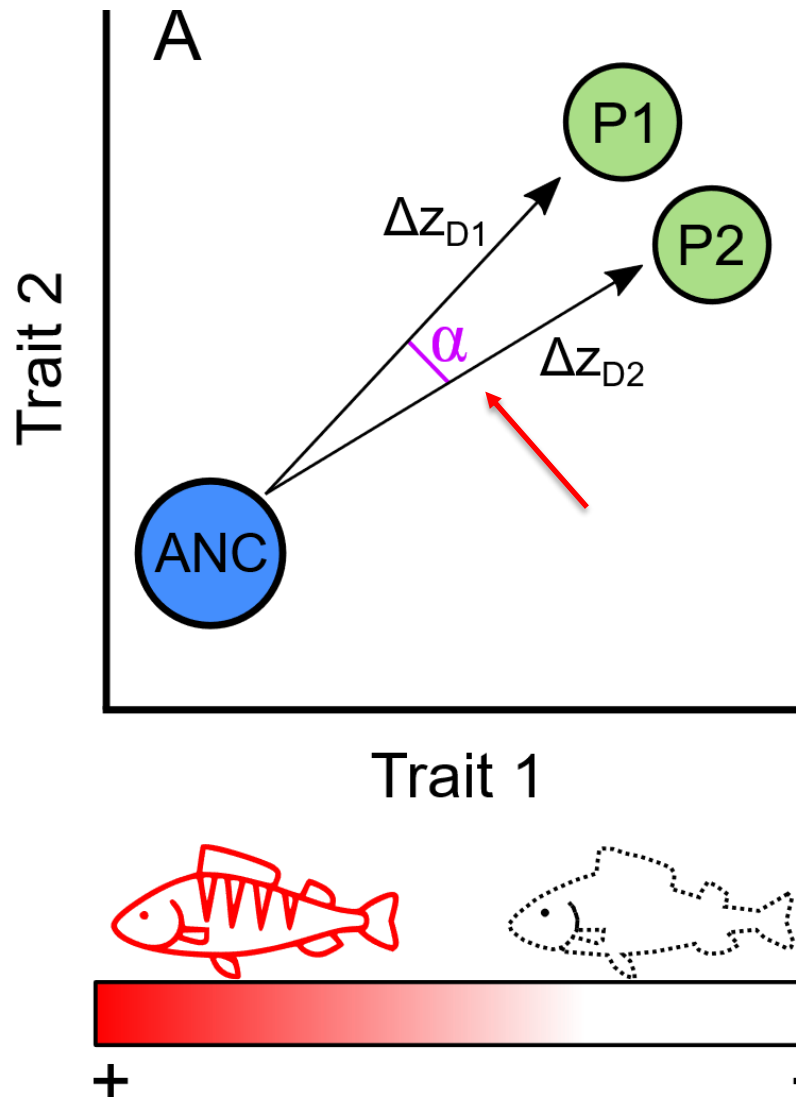
I – Practice



Sample **marine ancestors**
Experimental tests of behaviour
under predation risk

Sample replicate **freshwater populations**
Experimental tests of behaviour
without predation

I – Practice

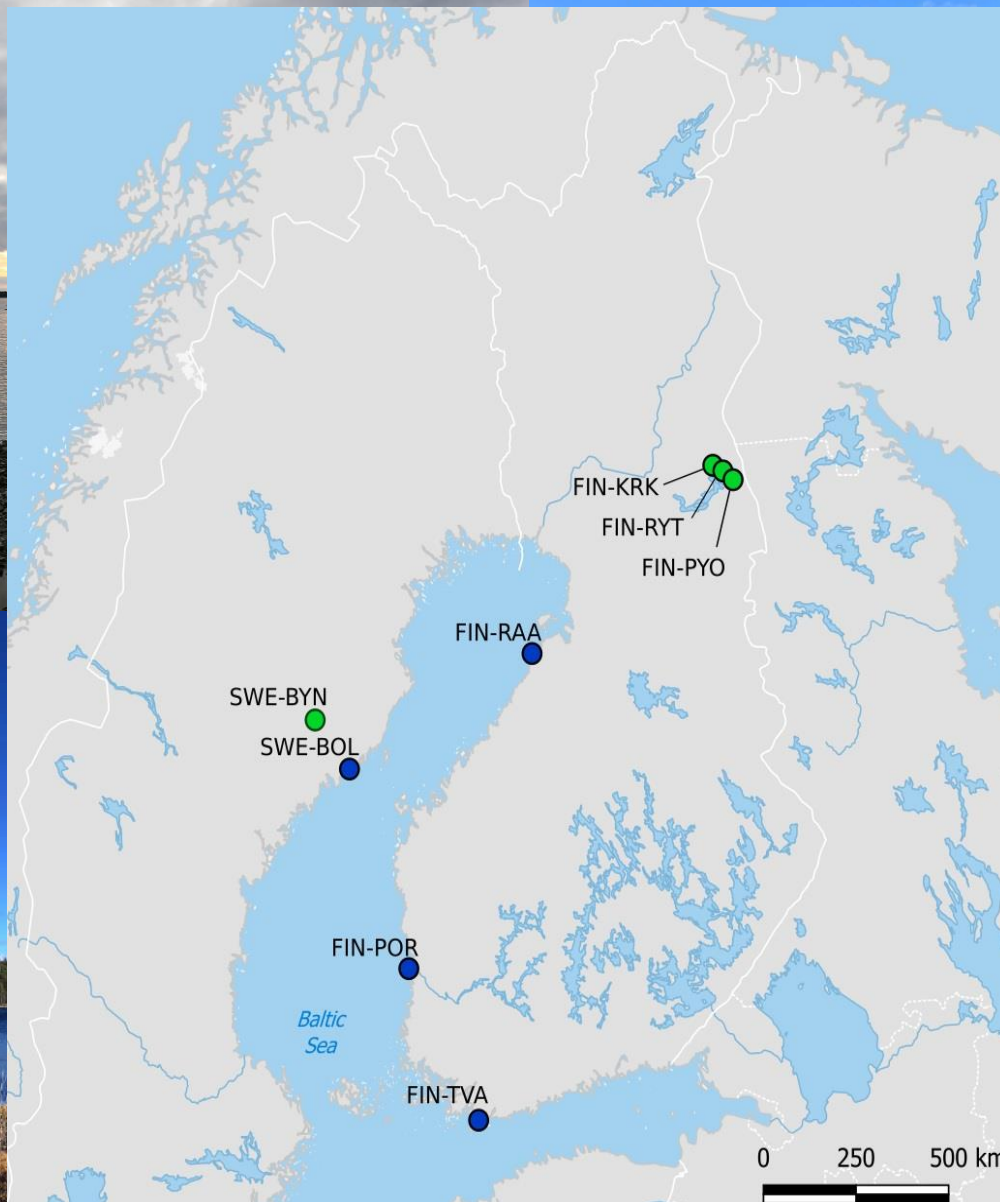


Sample **marine ancestors**
Experimental tests of behaviour
under predation risk

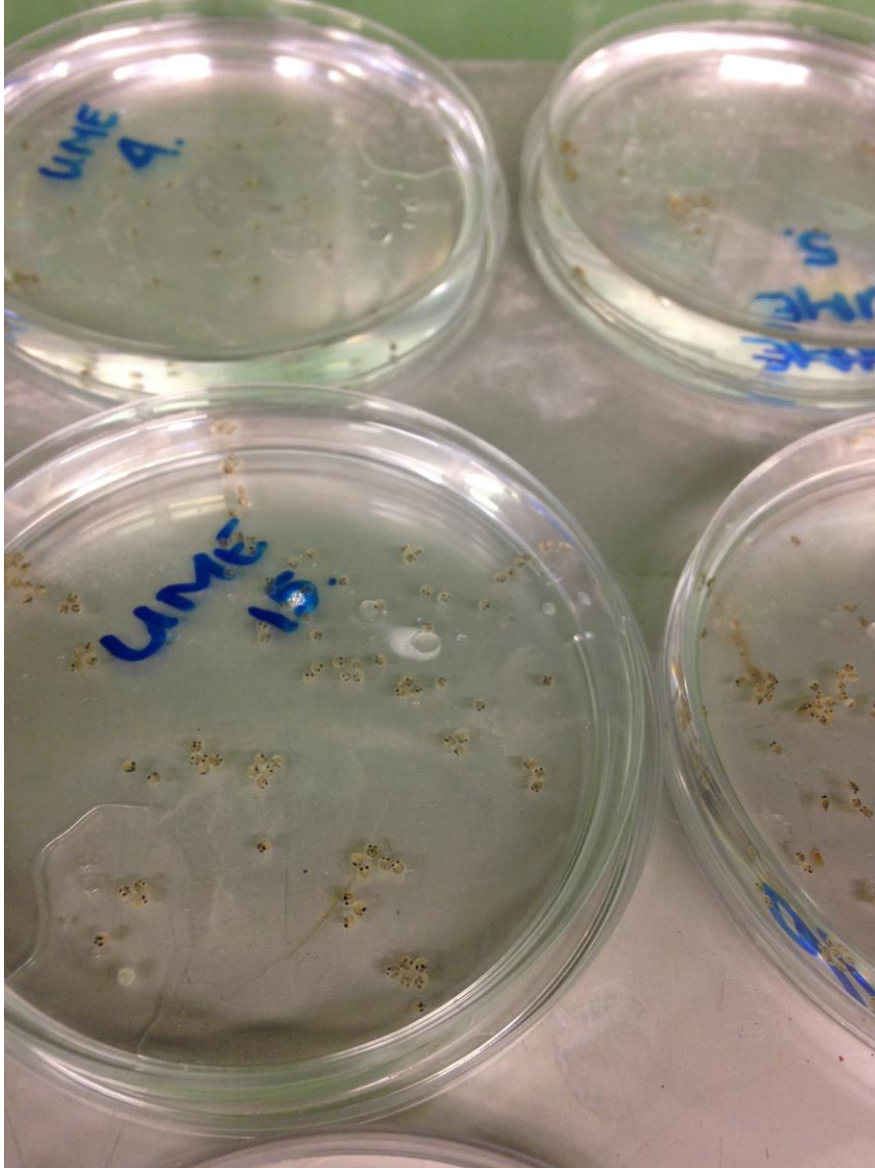
Sample replicate **freshwater populations**
Experimental tests of behaviour
without predation

Calculate α between phenotypic divergence vectors





I – Common garden rearing



In vitro fertilization



Rearing in controlled tanks

I – Common garden rearing

Reduced effects of environmental variance on phenotypic variance



Rearing in controlled tanks

I – Common garden rearing

Reduced effects of environmental variance on phenotypic variance

Measure genetically based differences among populations



Rearing in controlled tanks

I – Common garden rearing

Reduced effects of environmental variance on phenotypic variance

Measure genetically based differences among populations

Individuals phenotyped at the same age



Rearing in controlled tanks

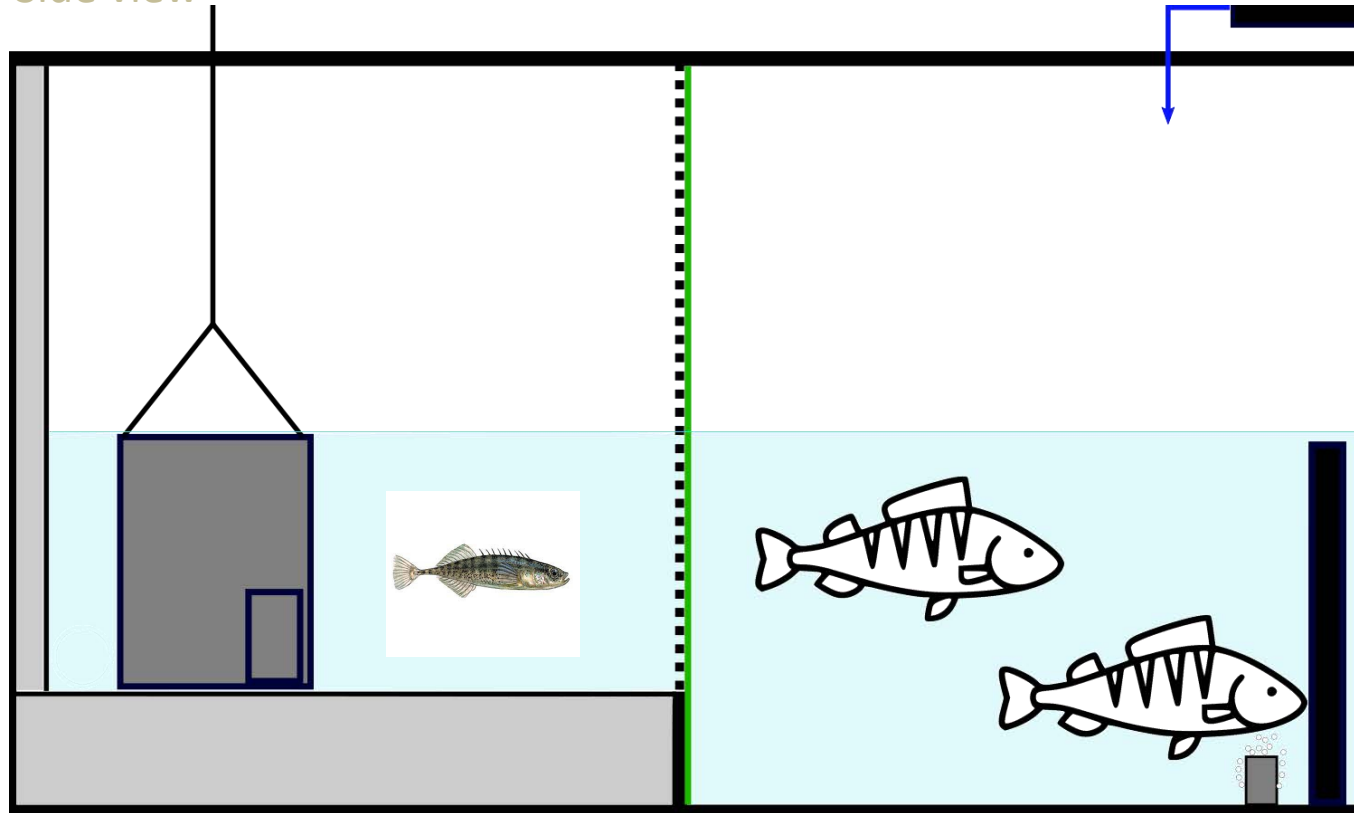
I – Experimental setup



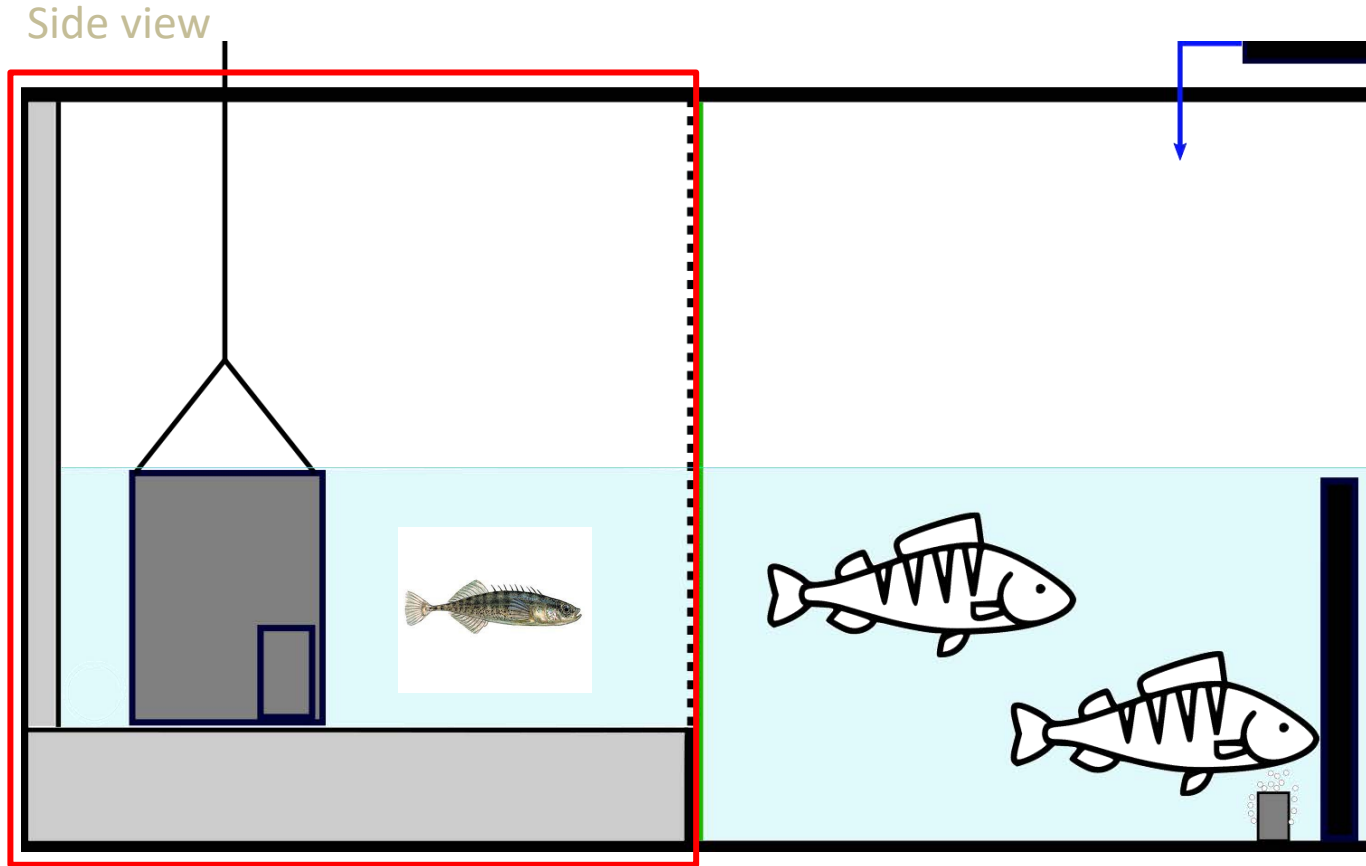
Elisa Päiviö, MSc

I – Experimental setup

Side view

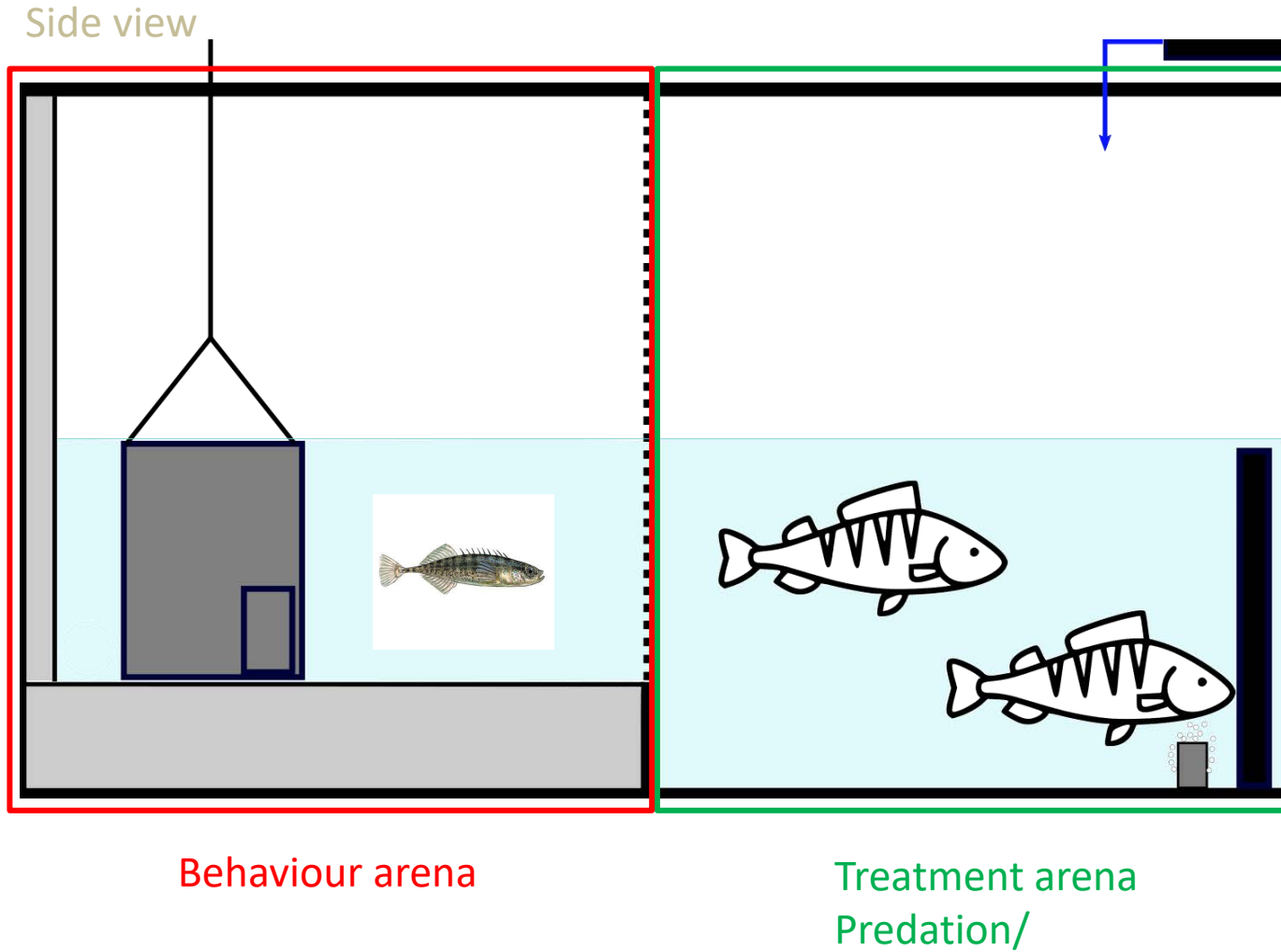


I – Experimental setup

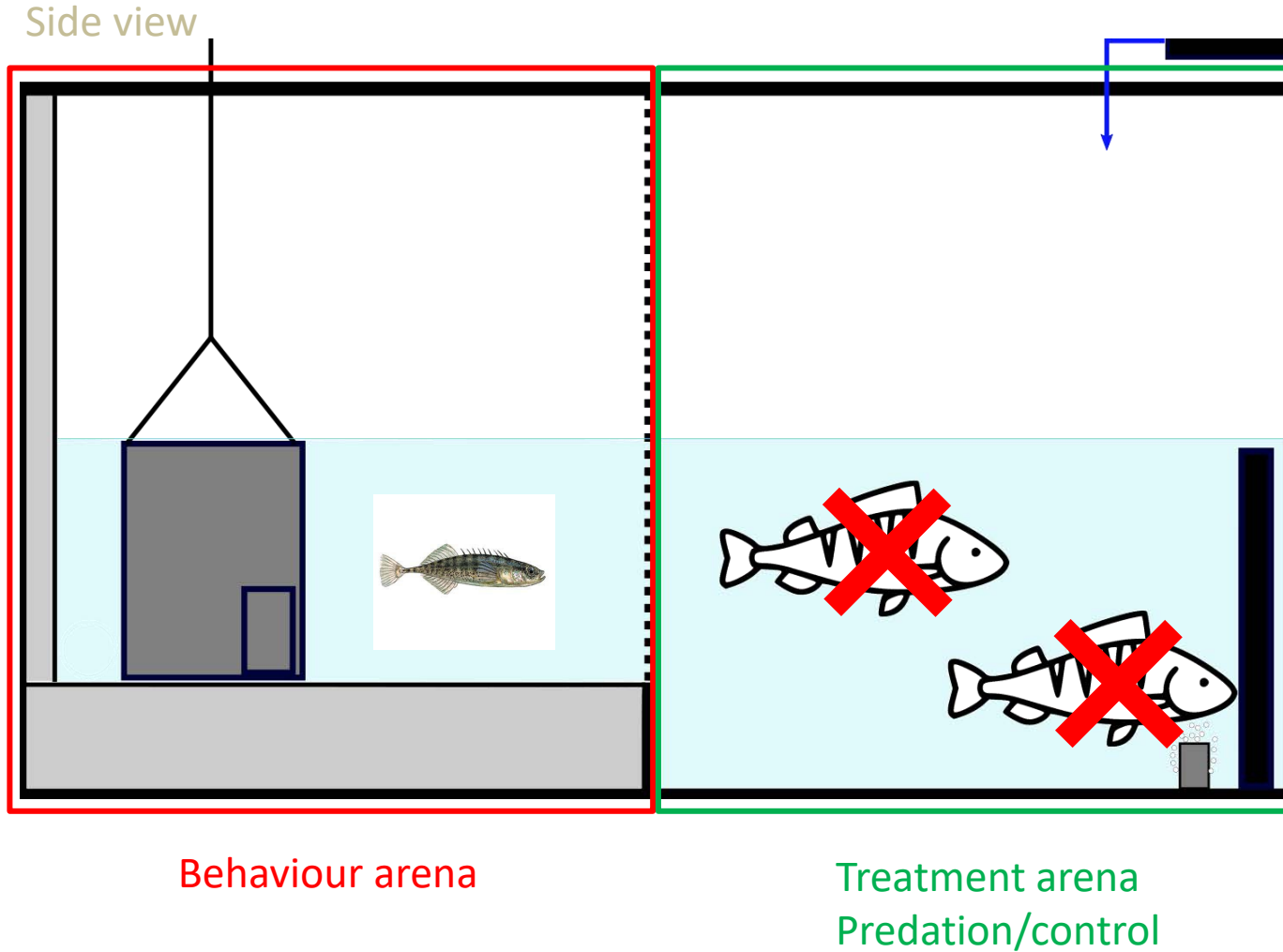


Behaviour arena

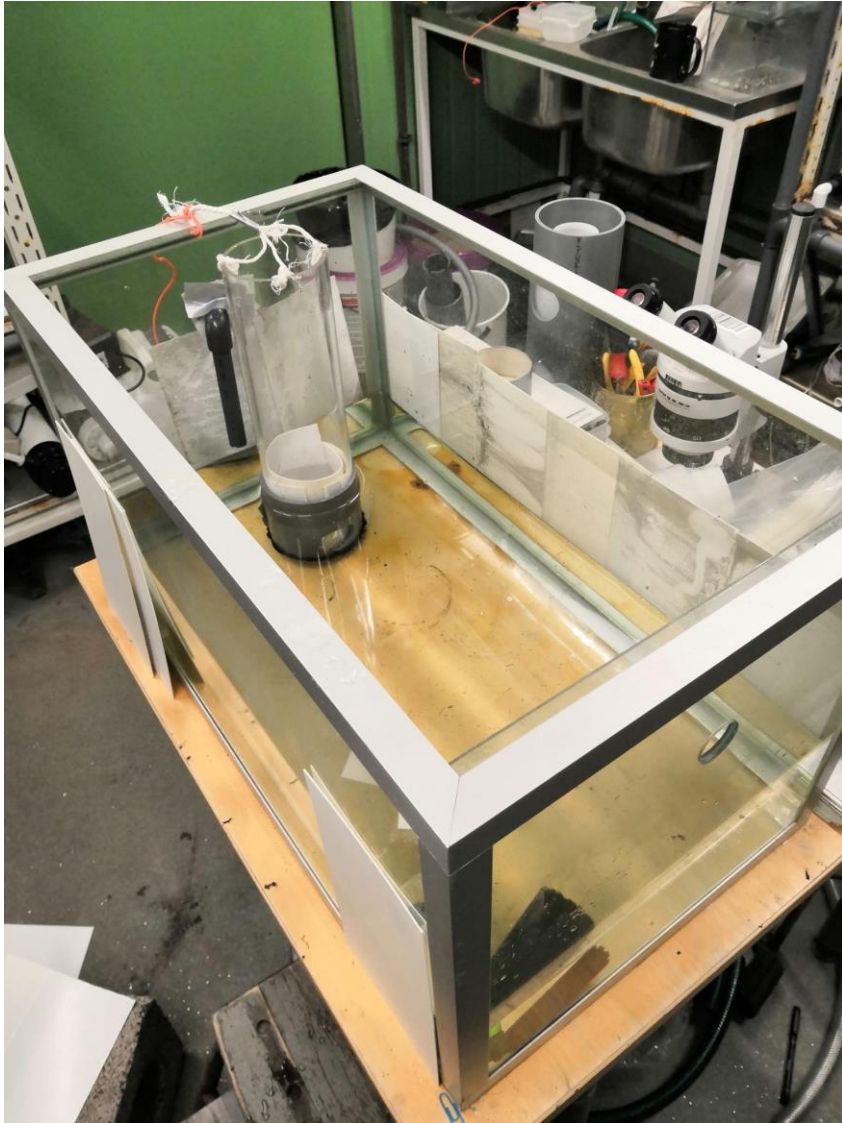
I – Experimental setup



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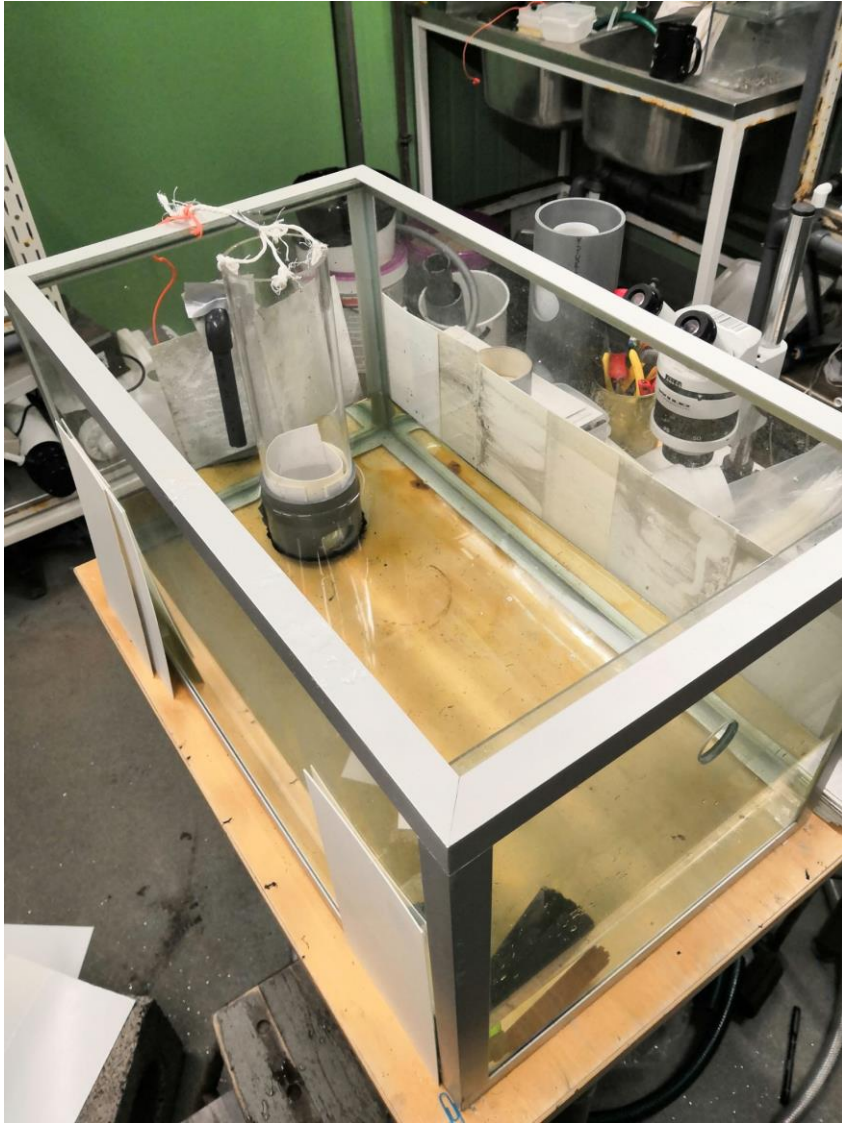


I – Experimental setup



Strictly identical between treatments

I – Experimental setup

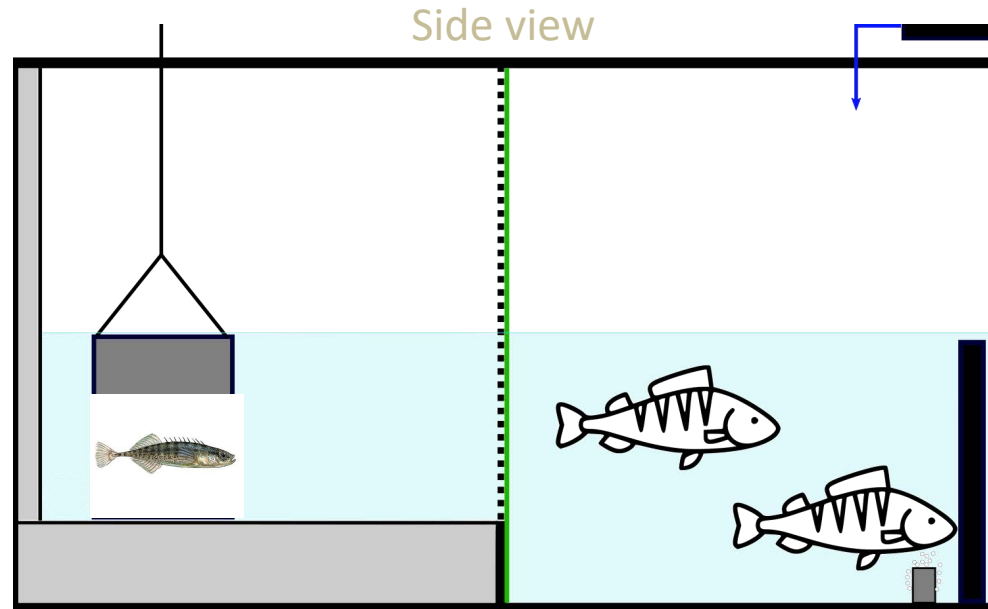


Strictly identical between treatments

I – Behavioural tests: exploration and foraging

Exploration

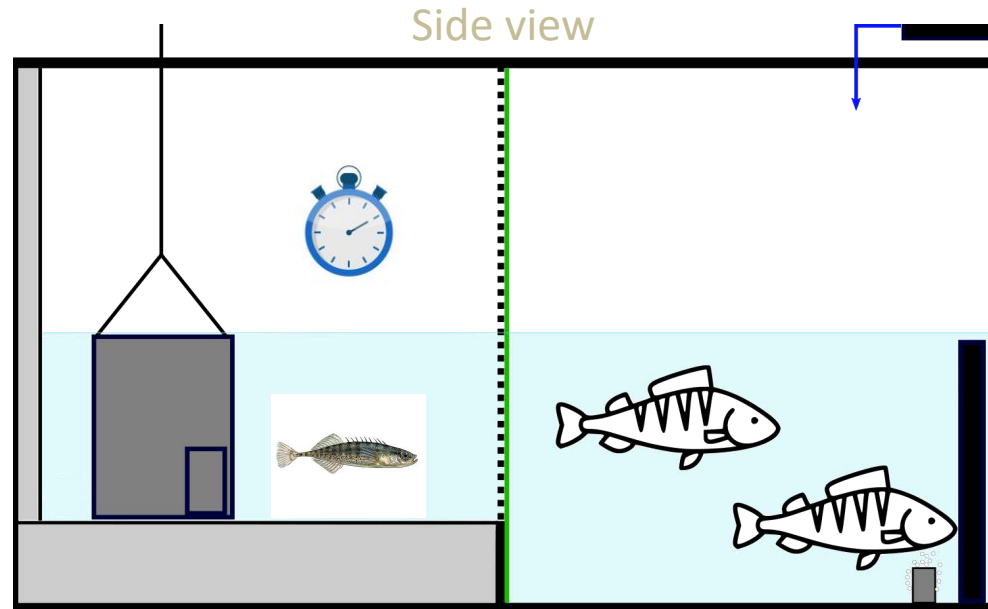
Latency to exit refuge and start exploring



I – Behavioural tests: exploration and foraging

Exploration

Latency to exit refuge and start exploring

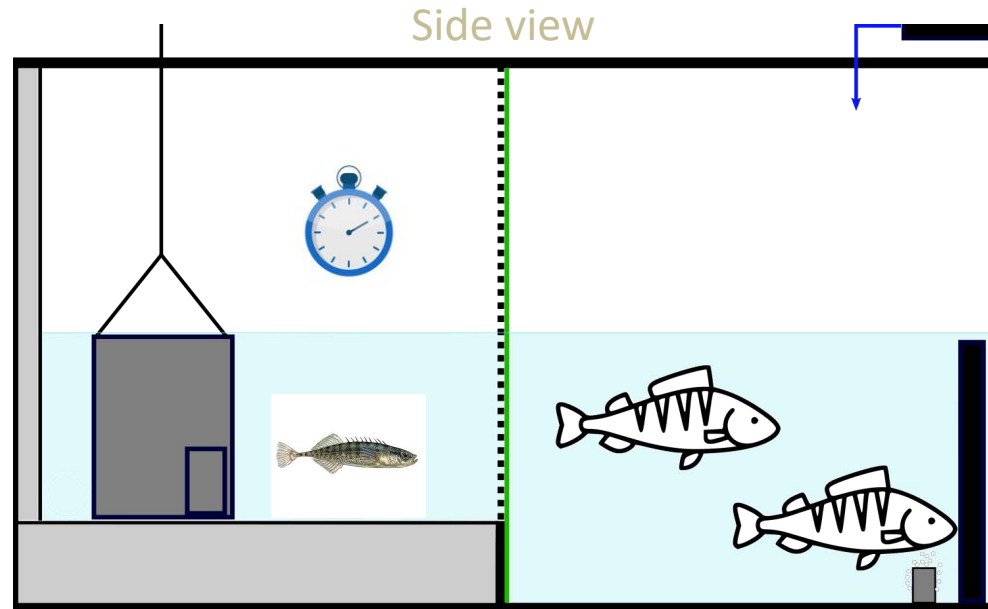


I – Behavioural tests: exploration and foraging

Exploration

Latency to exit refuge and start exploring

Time spent in the open area
(activity time)

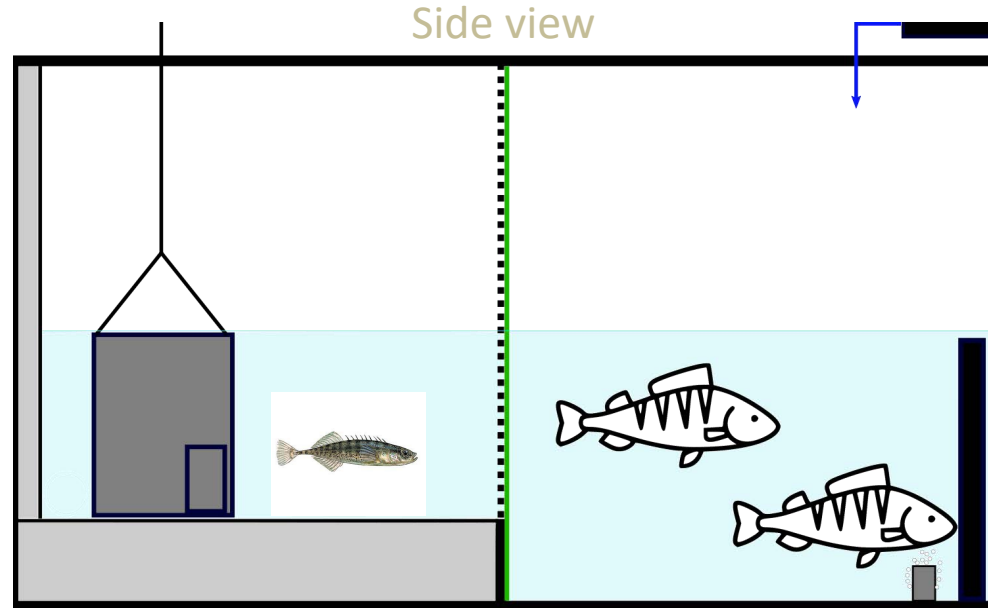


I – Behavioural tests: exploration and foraging

Exploration

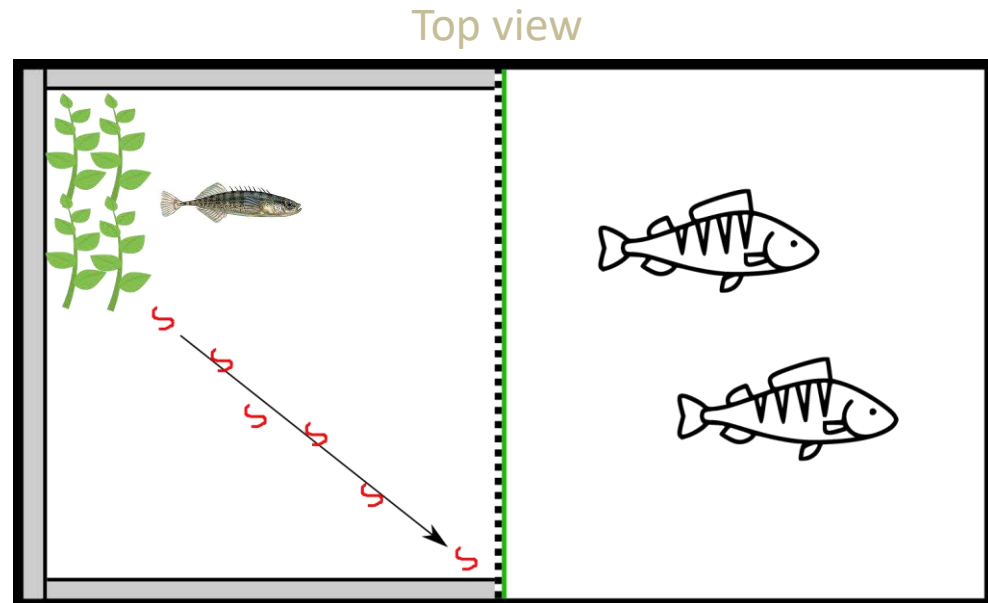
Latency to exit refuge and start exploring

Time spent in the open area
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Foraging

Latency to start feeding

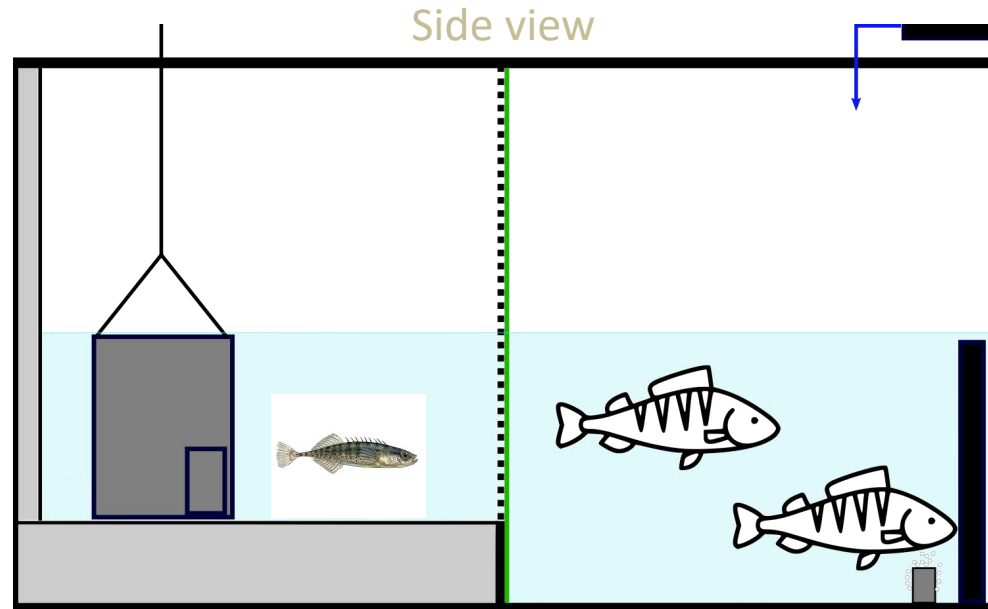


I – Behavioural tests: exploration and foraging

Exploration

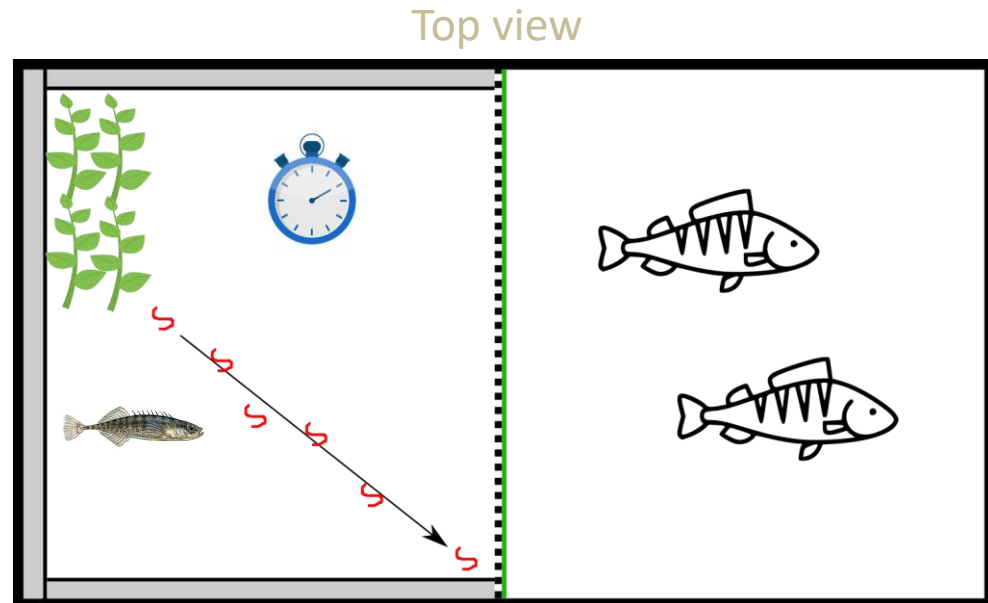
Latency to exit refuge and start exploring

Time spent in the open area
(activity time)



Foraging

Latency to start feeding

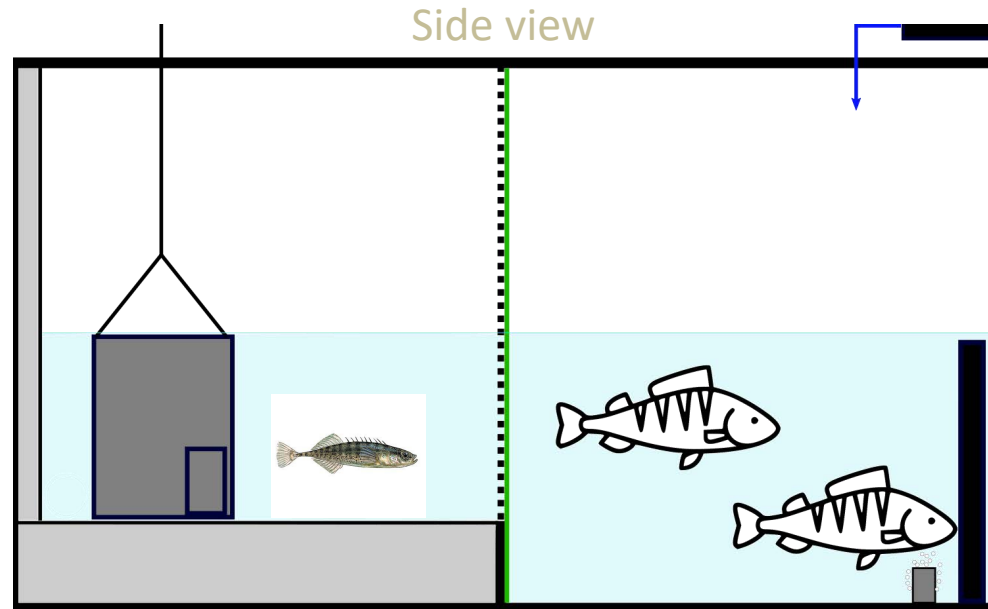


I – Behavioural tests: exploration and foraging

Exploration

Latency to exit refuge and start exploring

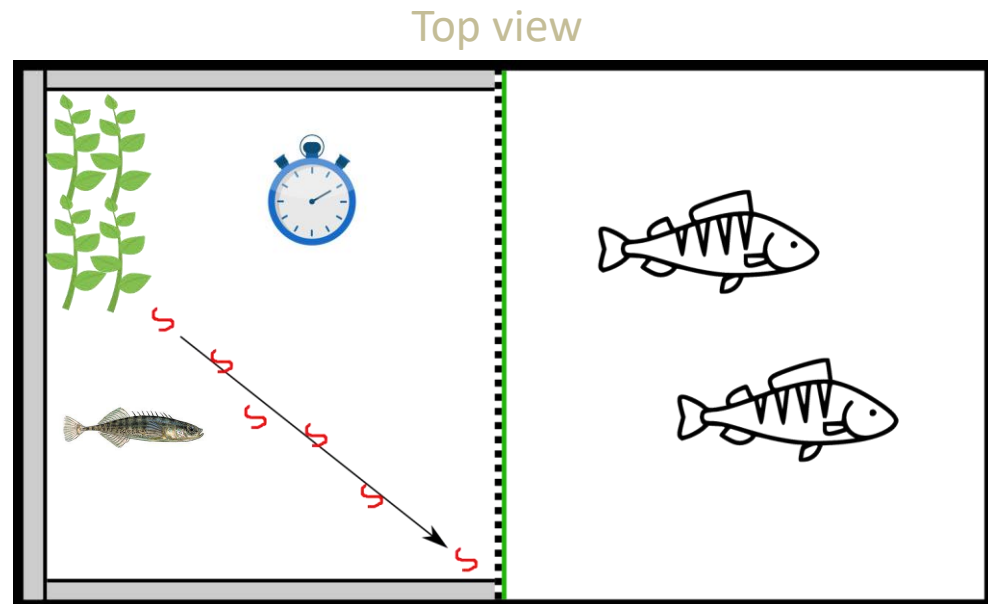
Time spent in the open area
(activity time)



Foraging

Latency to start feeding

Number of food intakes



I – Data summary

8 populations (4 ponds/4 marine)

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5-10 F1 full-sib family per population

I – Data summary

8 populations (4 ponds/4 marine)

5-10 F1 full-sib family per population

465 individuals

I – Data summary

8 populations (4 ponds/4 marine)

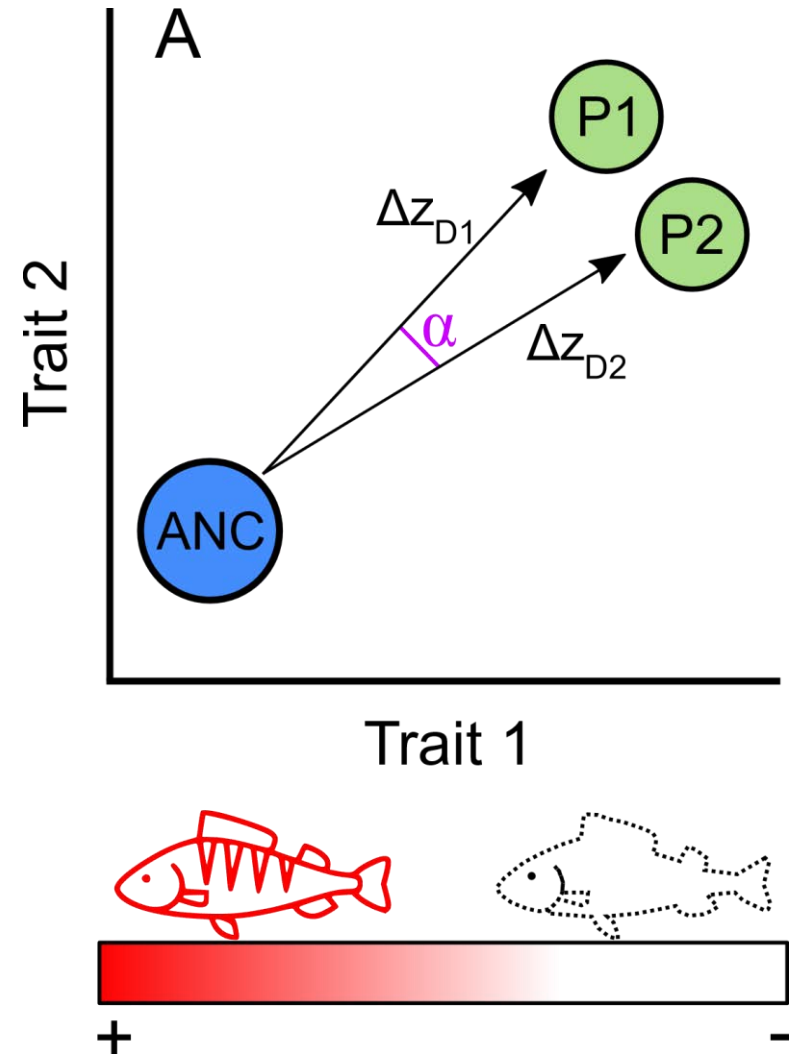
5-10 F1 full-sib family per population

465 individuals

4 behaviour traits

I – Analyses

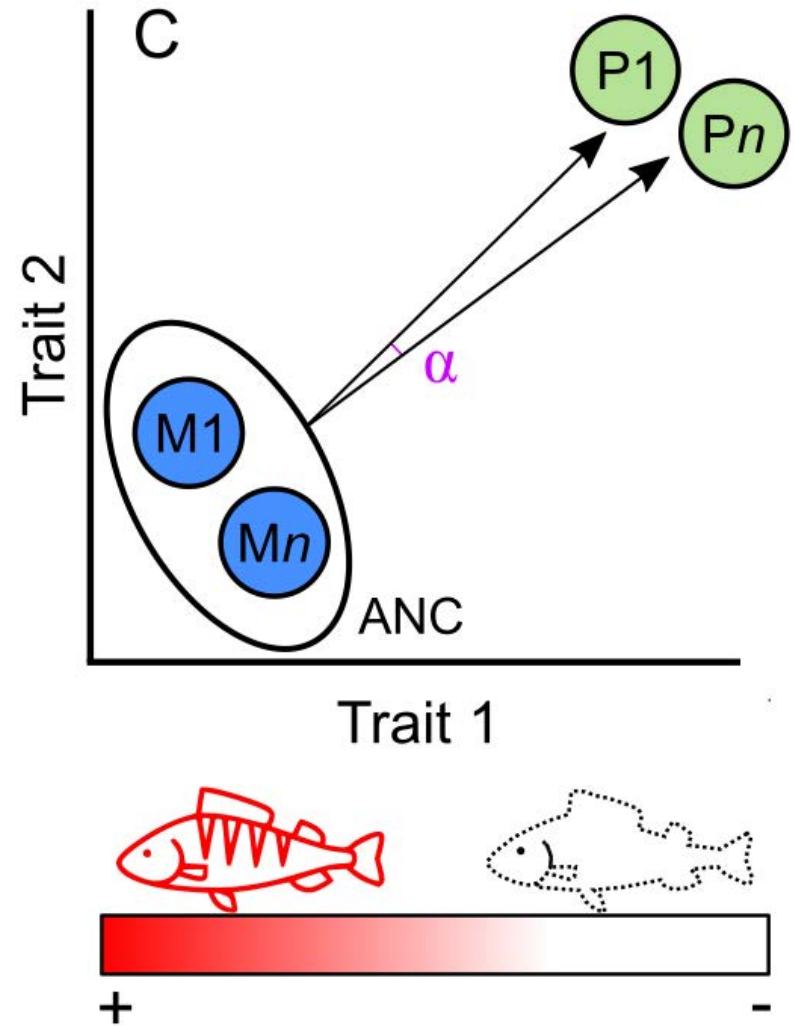
Phenotypic vectors of evolutionary divergence (Z_D) estimated from the difference in mean multivariate phenotype between **ancestral** and **derived** populations



I – Analyses

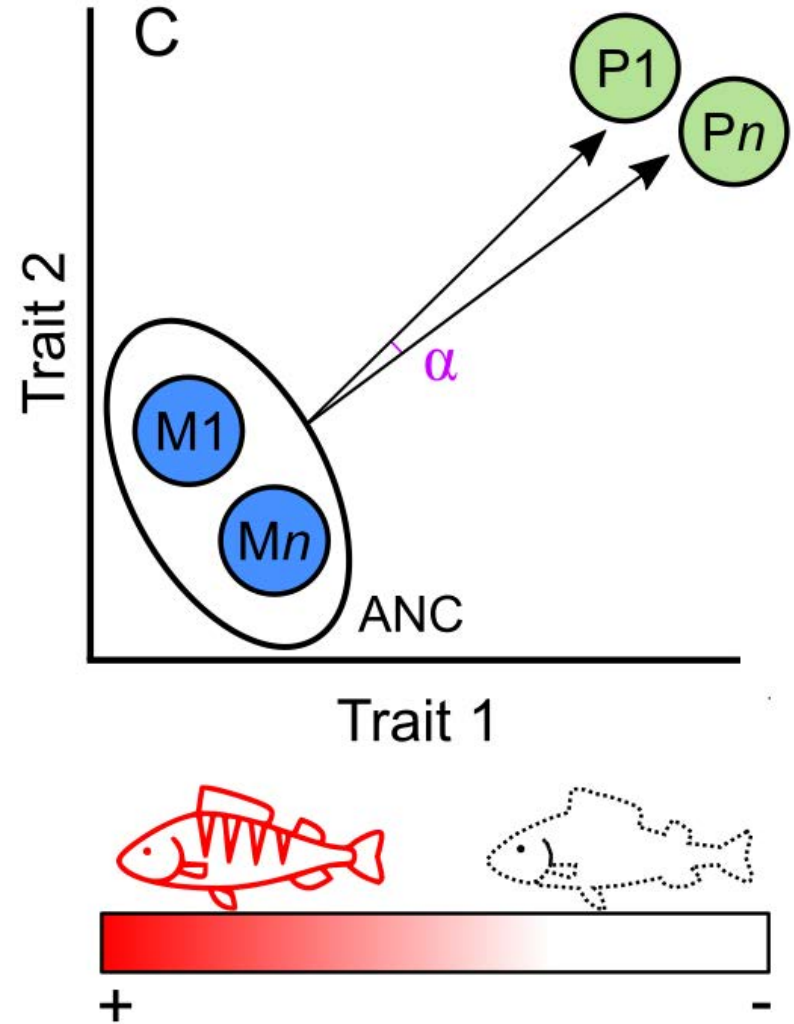
Ancestor = marine populations in predation treatment

Derived = pond populations in control treatment



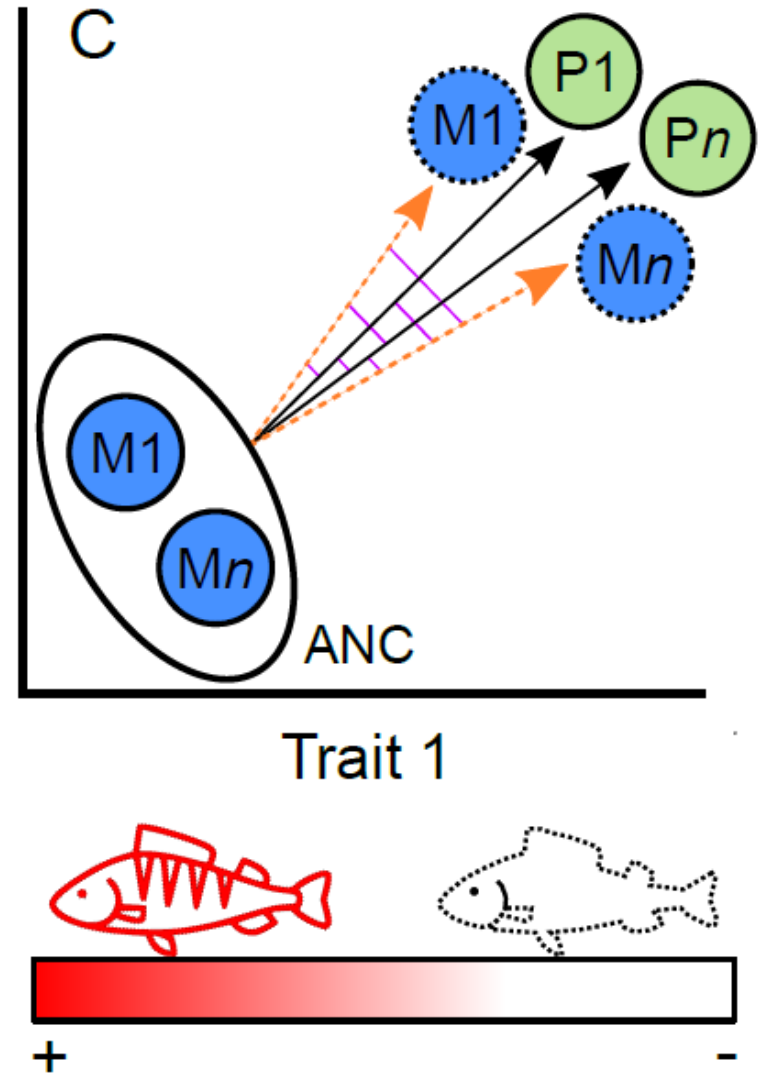
I – Analyses

Estimation of **angles** between vectors to determine whether **evolution** occurred in **parallel**



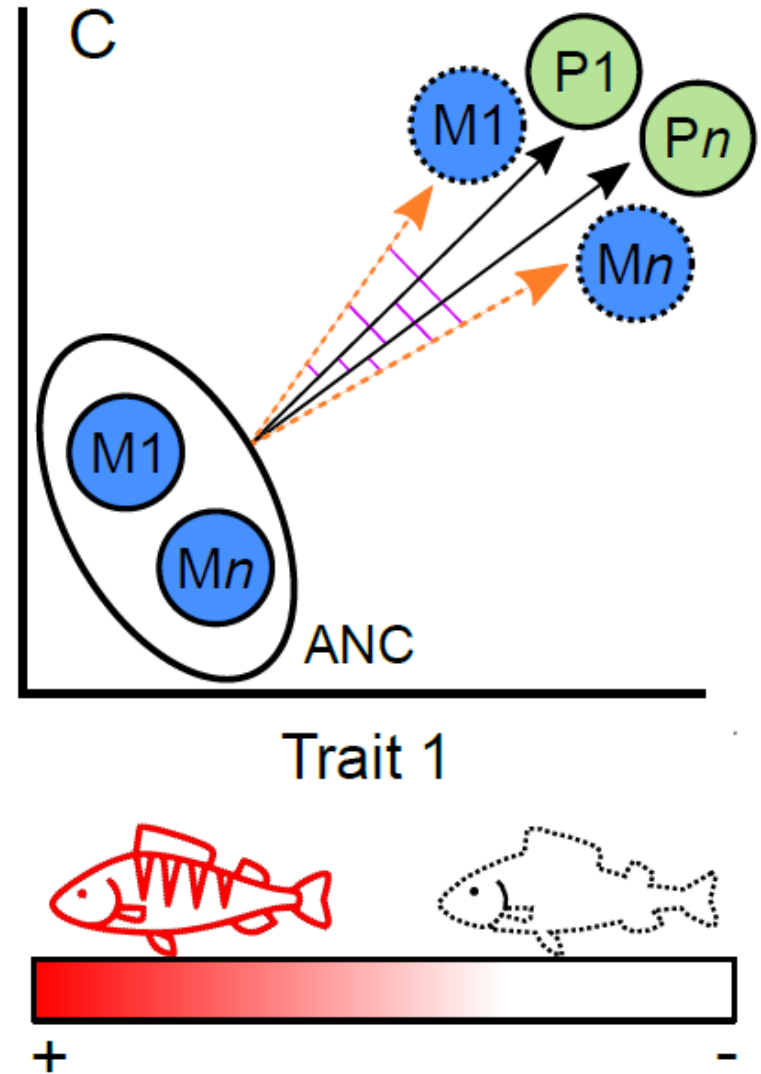
I – Analyses

Phenotypic **vectors of plasticity** estimated from the **difference** in **mean phenotype** between **hypothetical ancestor** and **marine** populations in **control** treatment

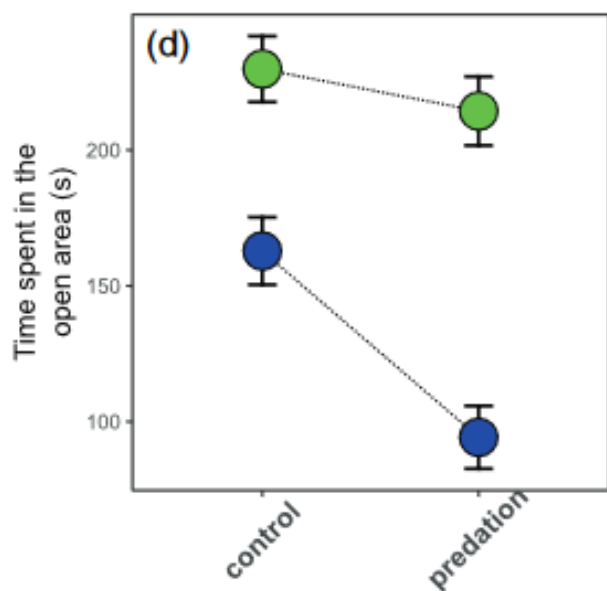
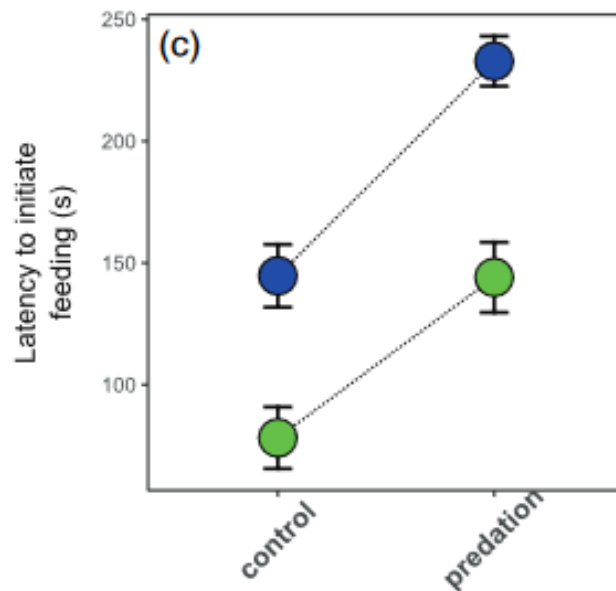
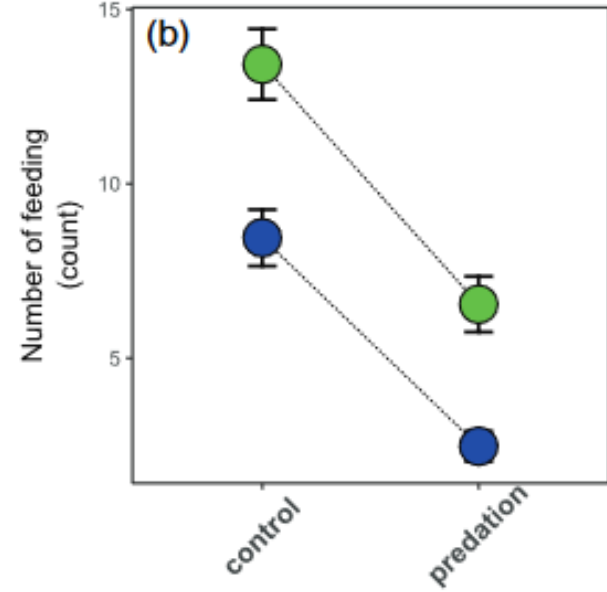
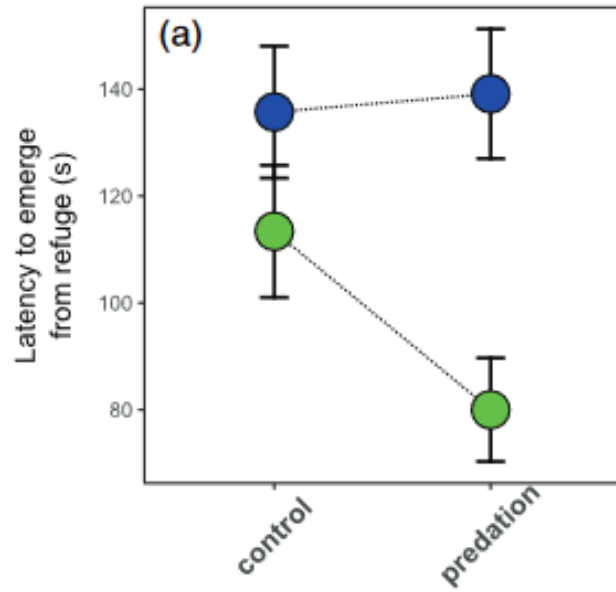


I – Analyses

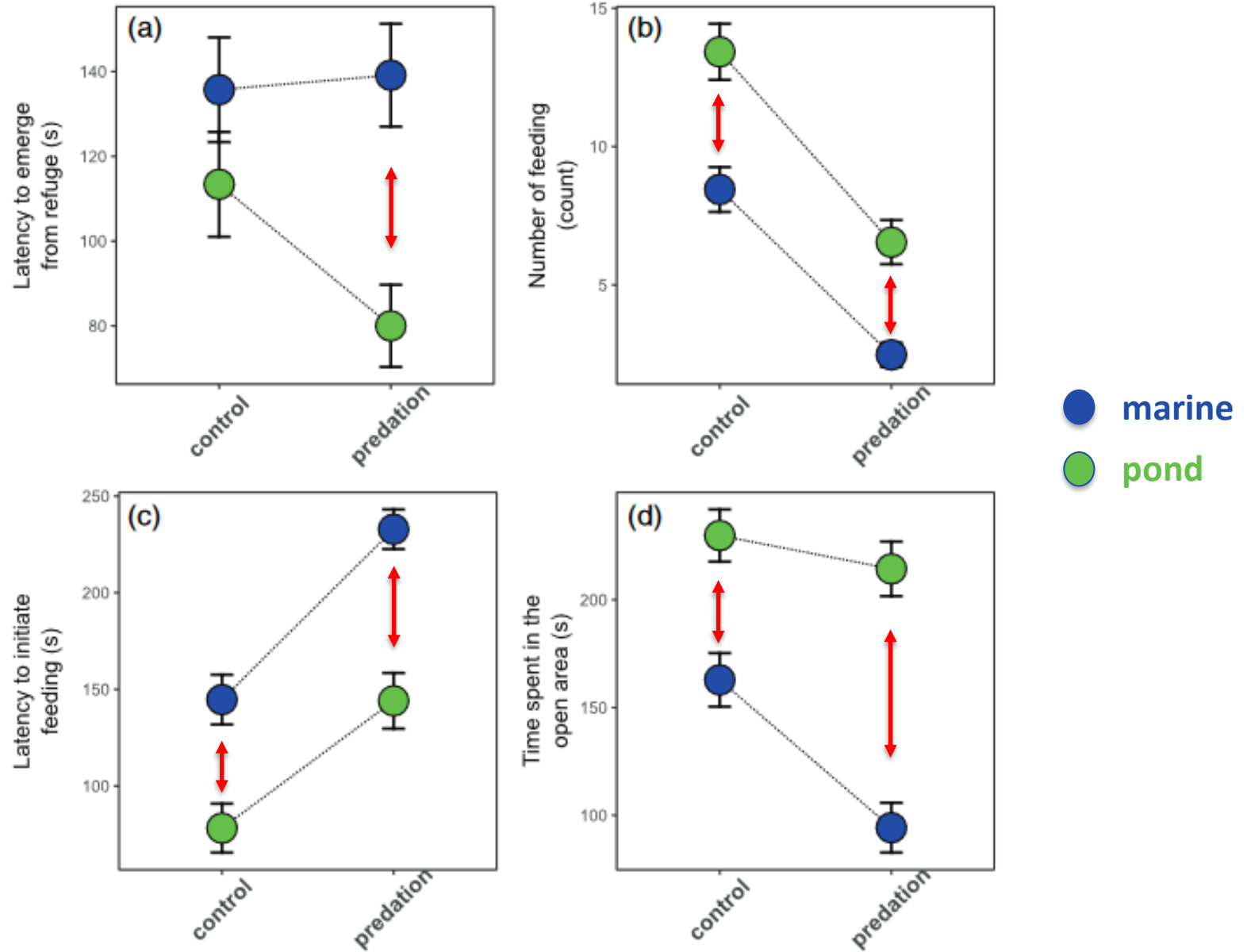
Estimation of **angles** between **divergence** and **plasticity** vectors to determine whether **plasticity to relaxed predation** drove evolution of behaviour



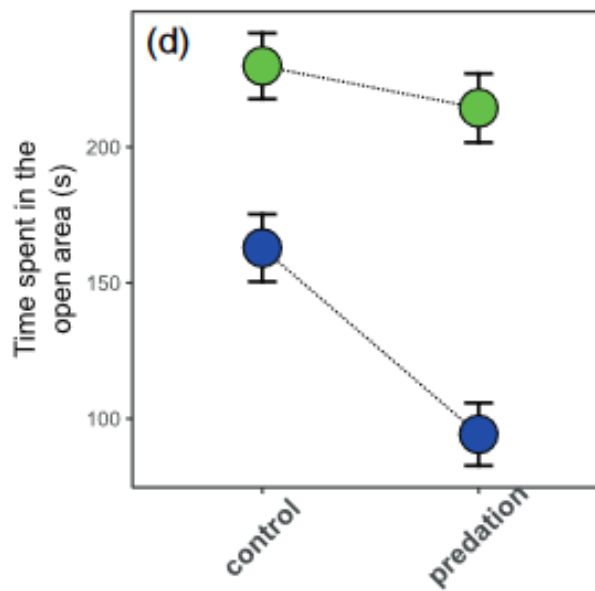
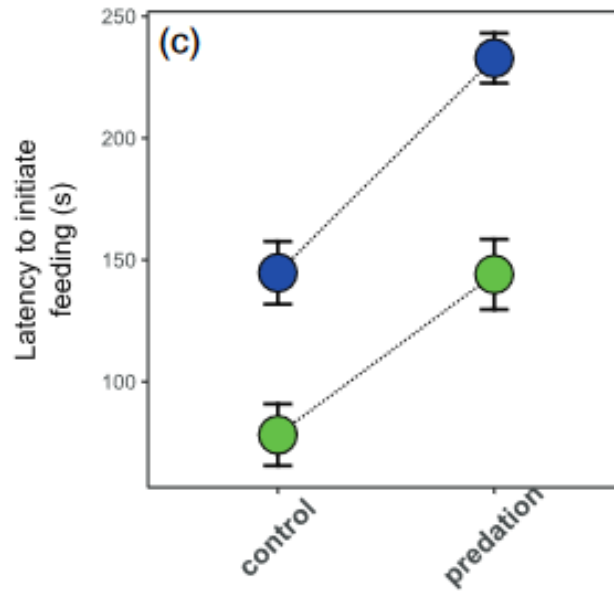
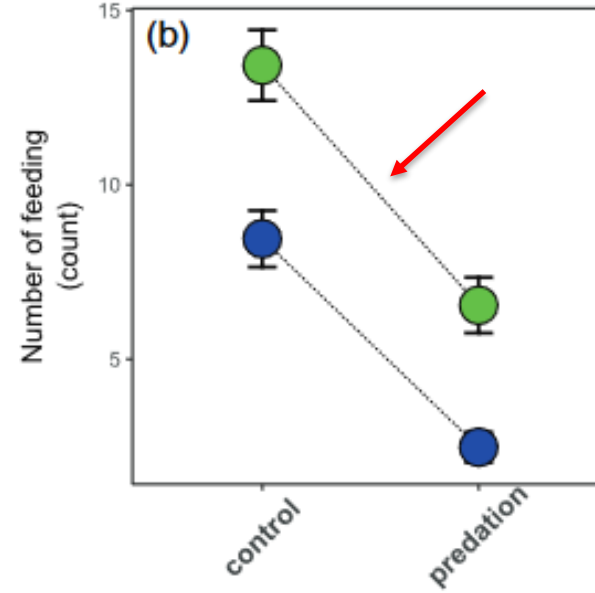
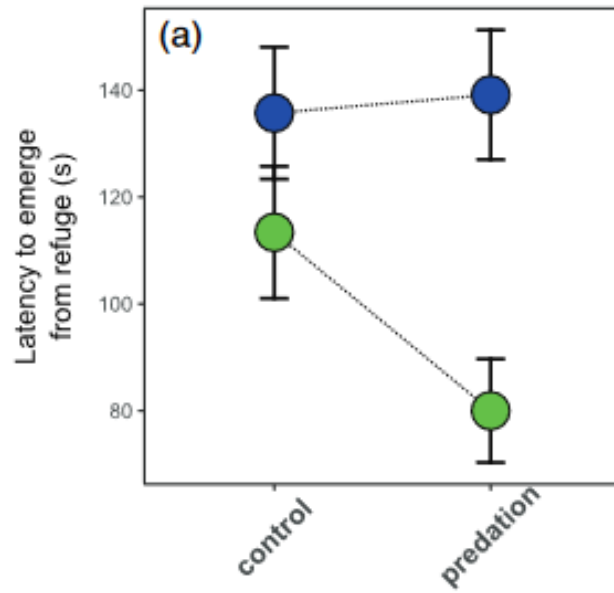
I – Results



I – Results: habitat effect

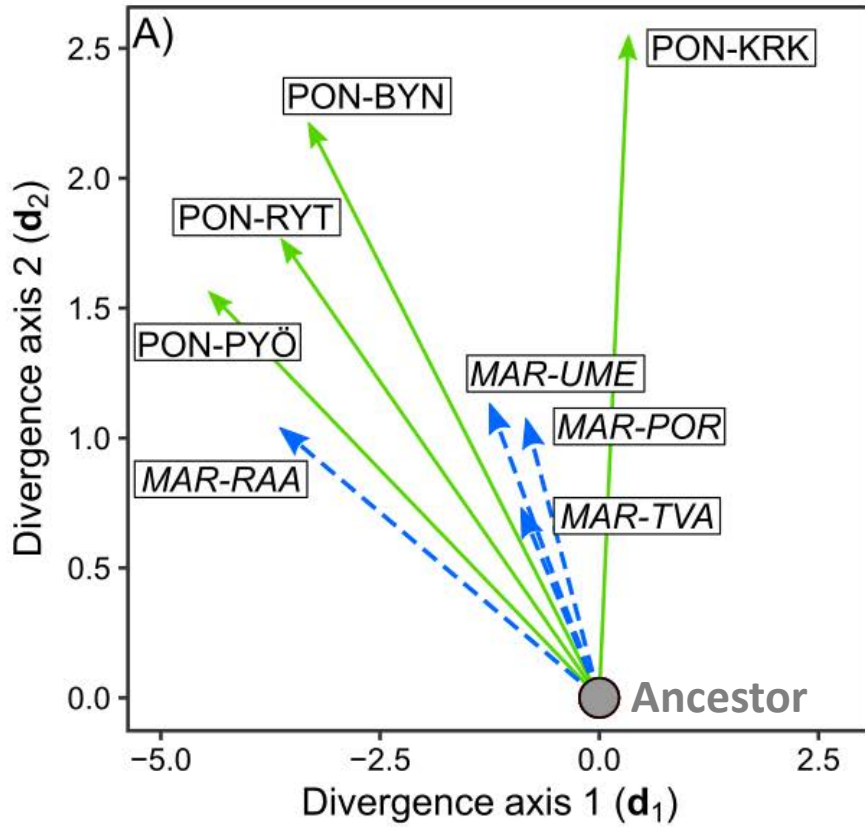


I – Results: treatment effect

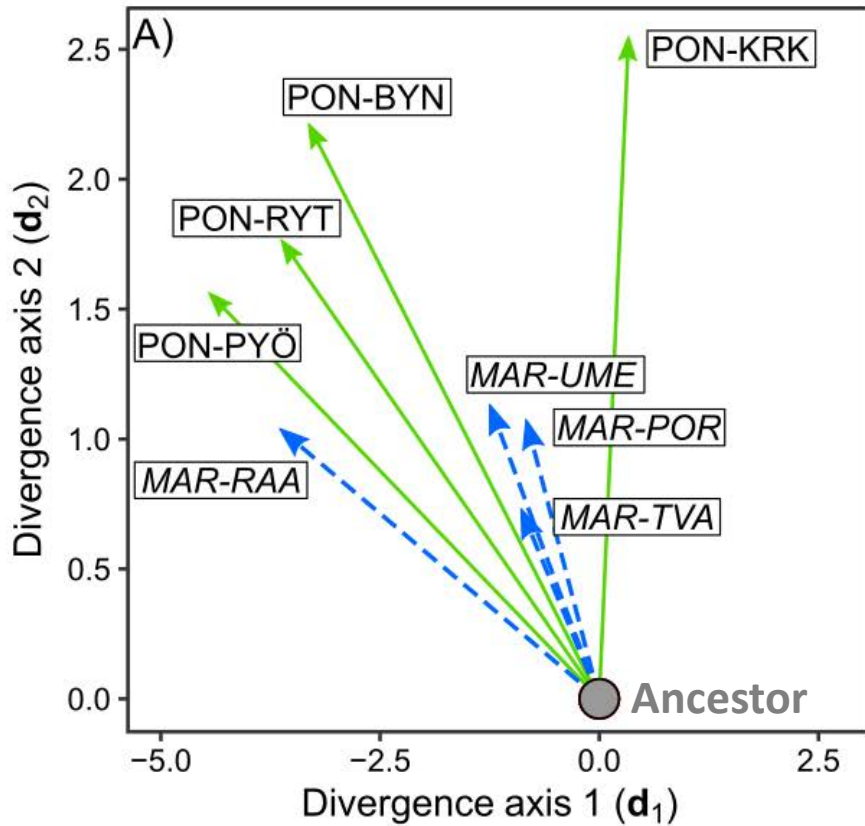


● marine
● pond

I – Results



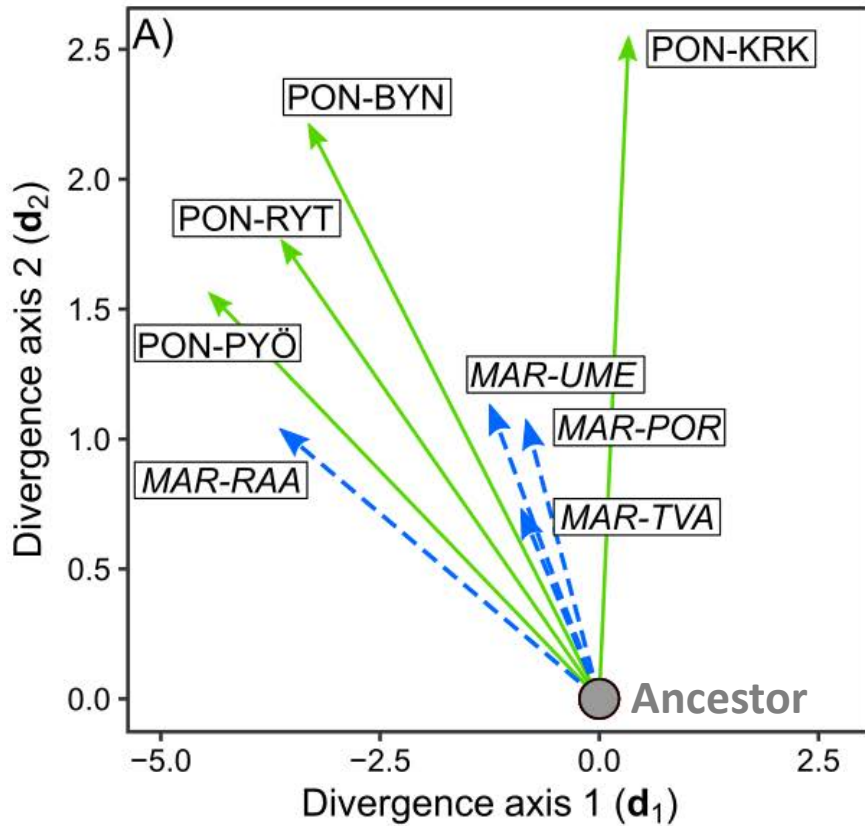
I – Results



Divergence vectors

- > difference between pond and ancestral marine

I – Results



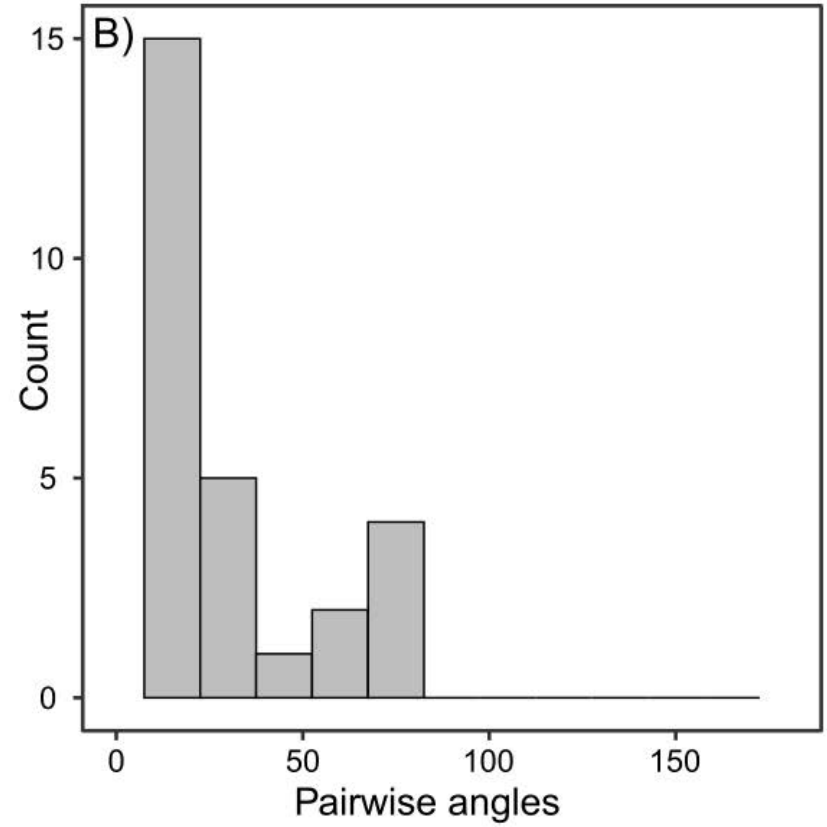
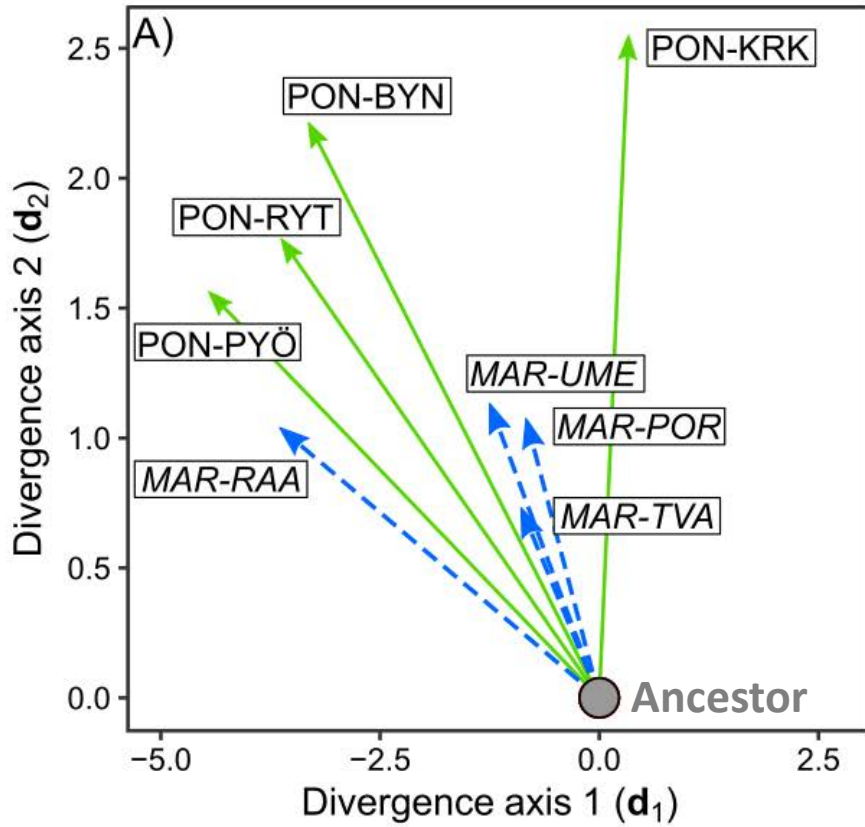
Divergence vectors

- > difference between pond and ancestral marine

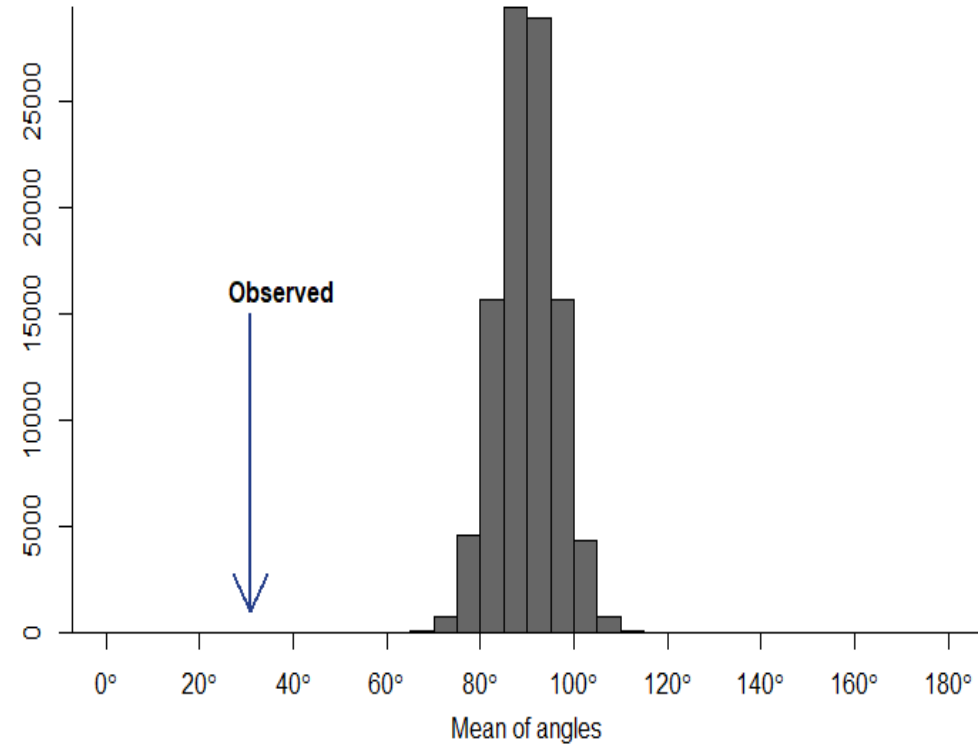
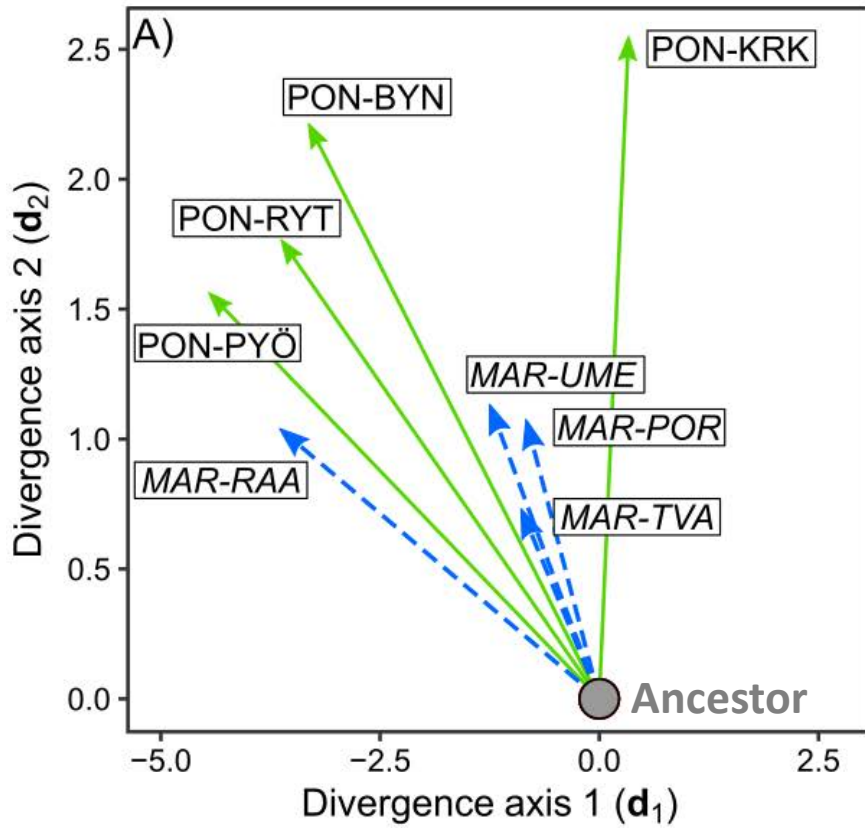
Plasticity vectors

- > difference between marine in control and ancestral marine

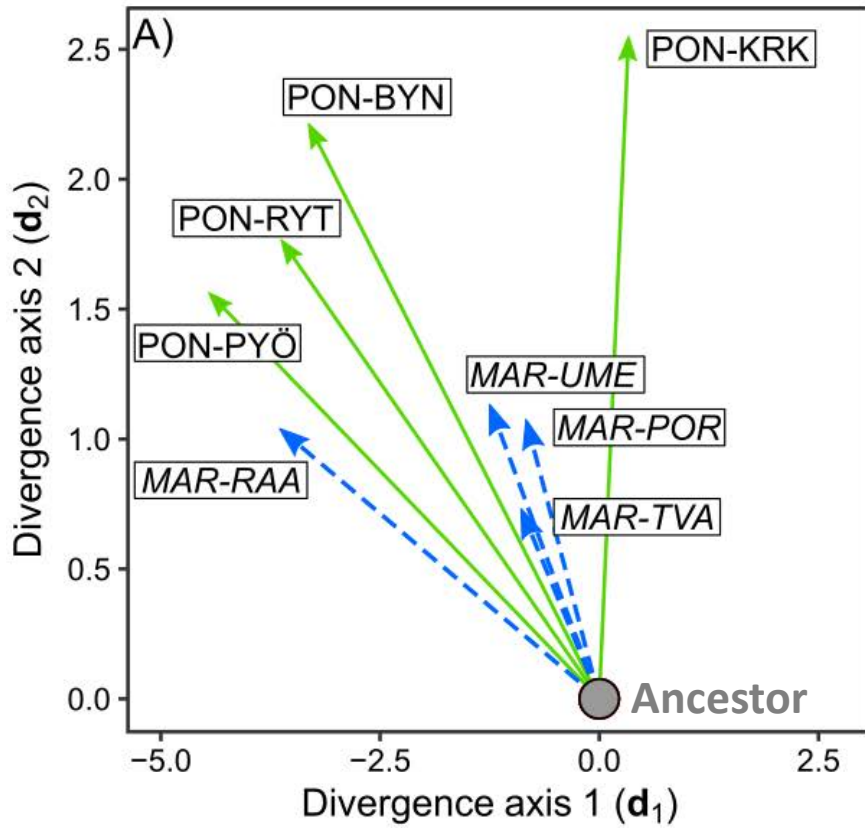
I – Results



I – Results

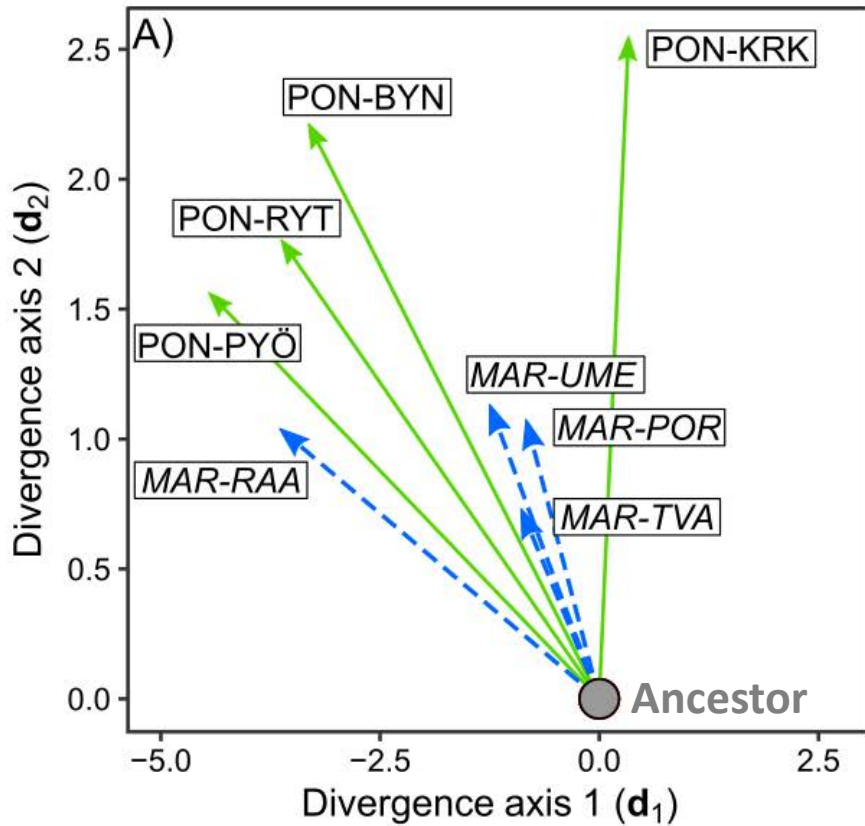


I – Results



Alignment between divergence vectors

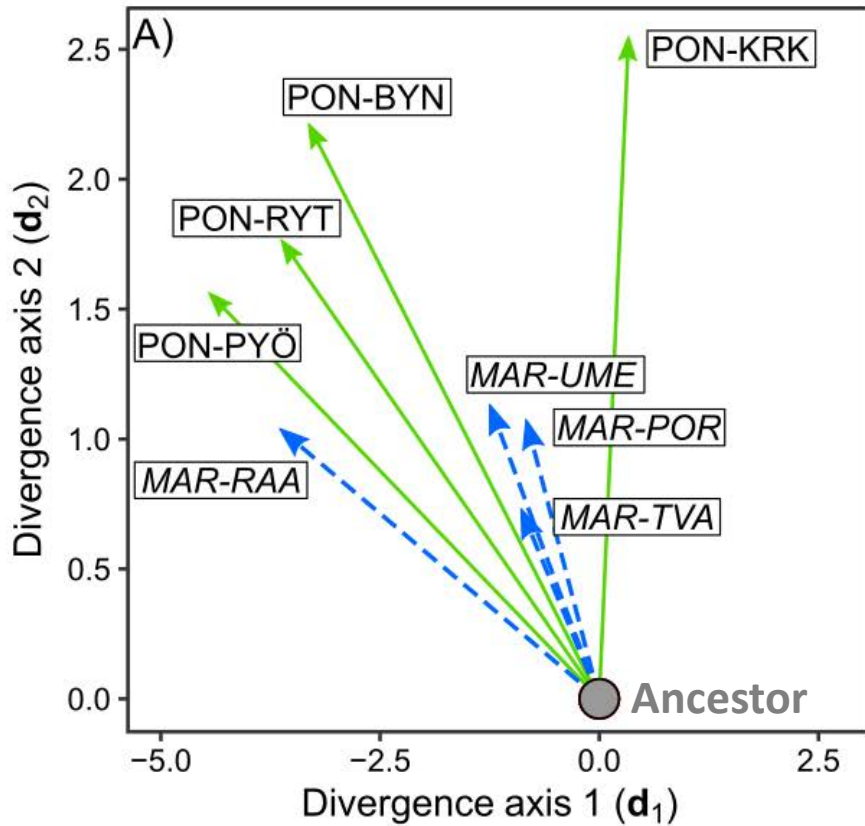
I – Results



Alignment between divergence vectors

Parallel evolution of complex behavior

I – Results

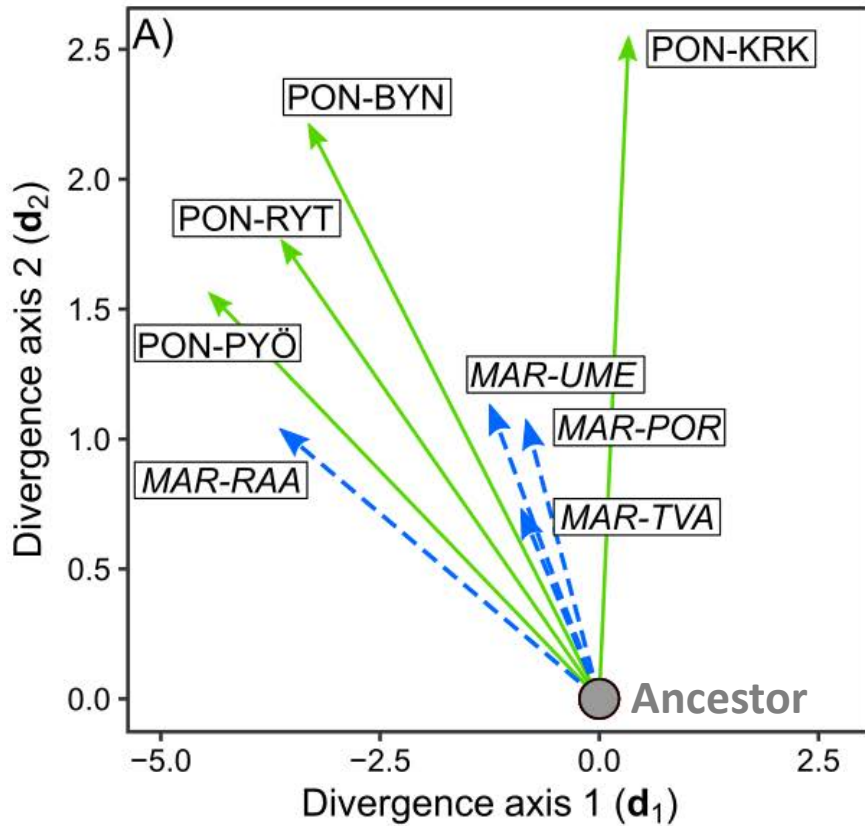


Alignment between divergence vectors

Parallel evolution of complex behavior

Alignment between plasticity vectors

I – Results



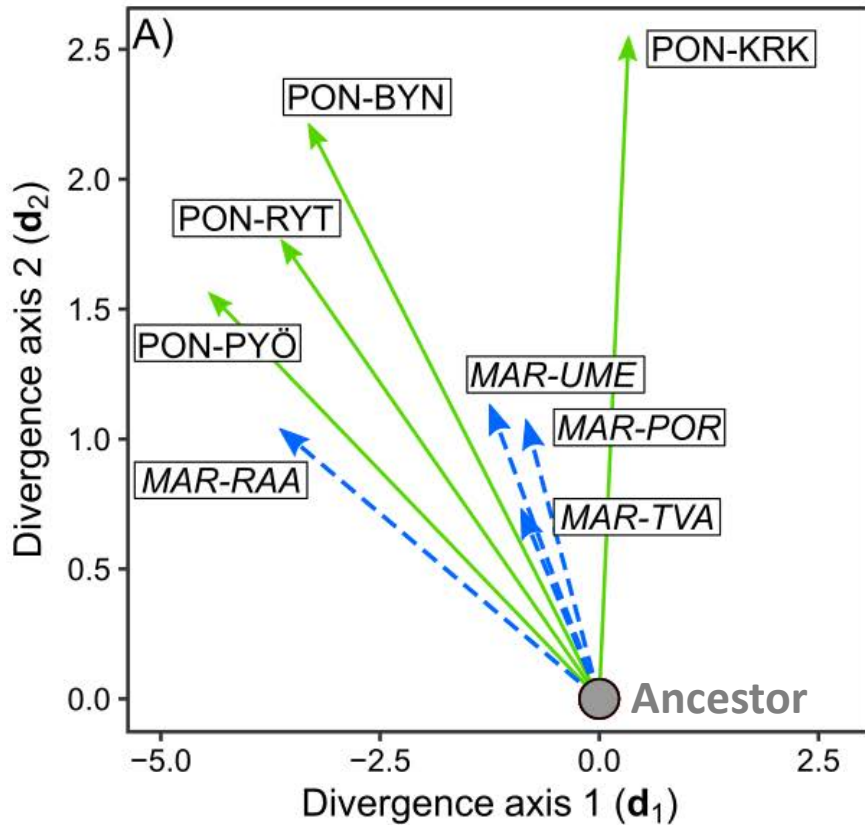
Alignment between divergence vectors

Parallel evolution of complex behavior

Alignment between plasticity vectors

Shared plastic response to predation release

I – Results



Alignment between divergence vectors

Parallel evolution of complex behavior

Alignment between plasticity vectors

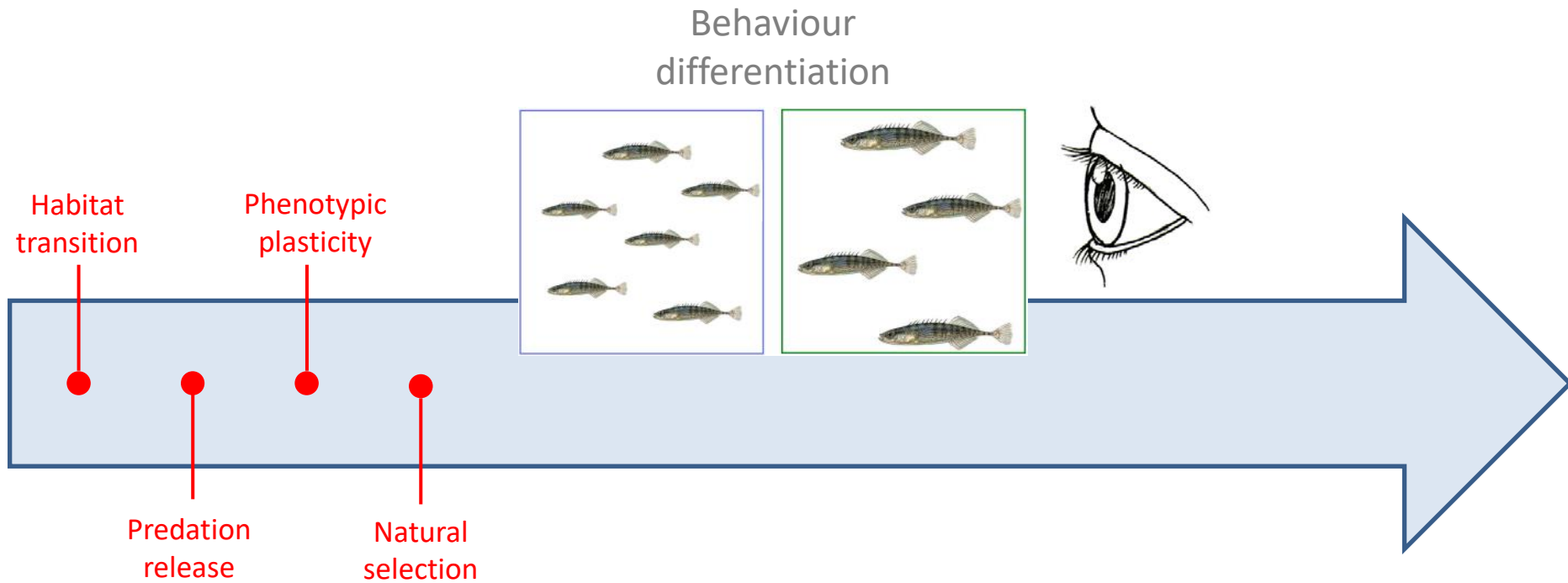
Shared plastic response to predation release

Alignment between divergence and plasticity vectors

Predation is the ecological driver of repeated evolution

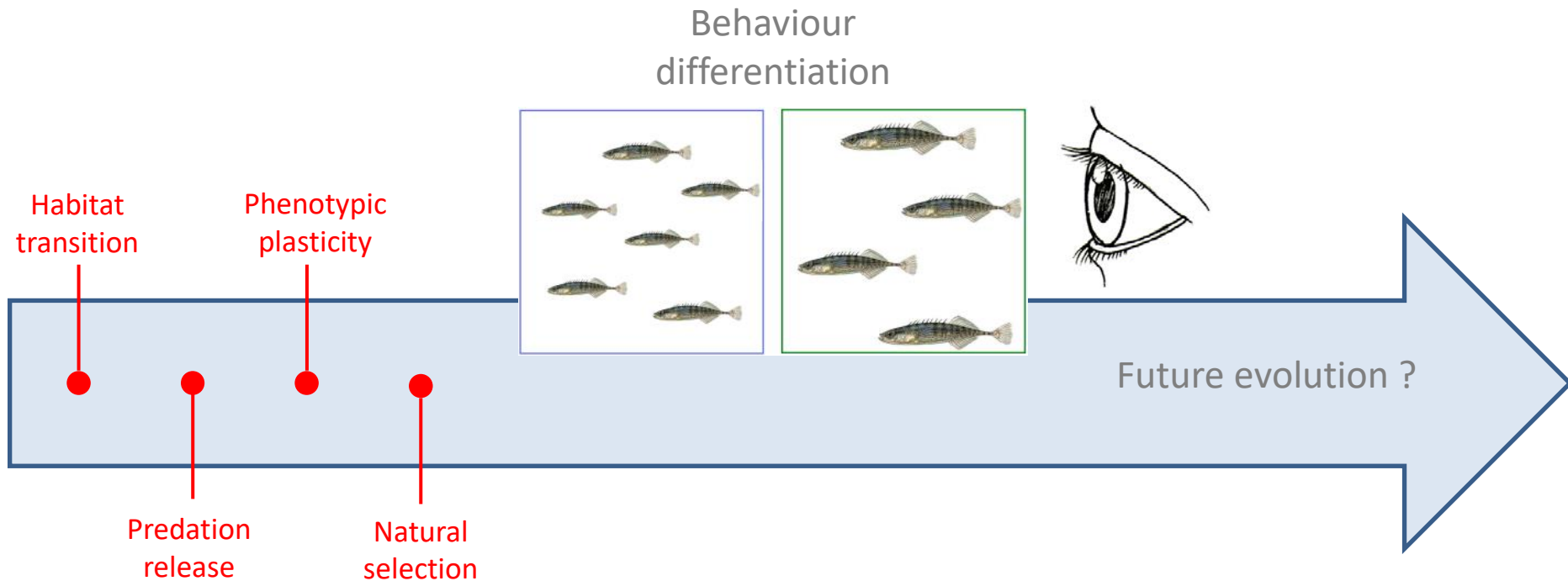
I – Conclusions

Relaxed risk of predation drove parallel evolution of nine-spined stickleback behavior



I – Conclusions

Relaxed risk of predation drove parallel evolution of nine-spined stickleback behavior



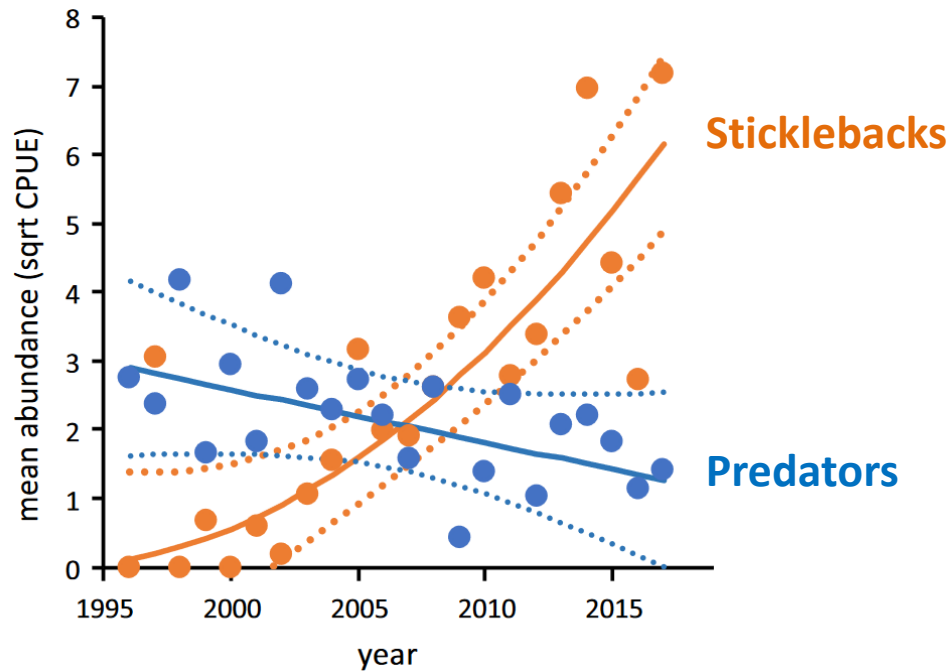
I – Future evolution?

Review

Past and Current Trends of Coastal Predatory Fish in the Baltic Sea with a Focus on Perch, Pike, and Pikeperch

Jens Olsson

Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Coastal Research
Skolgatan 6, 74242 Öregrund, Sweden; Jens.Olsson@slu.se; Tel.: +46-(0)104784144



Eriksson *et al.* 2021

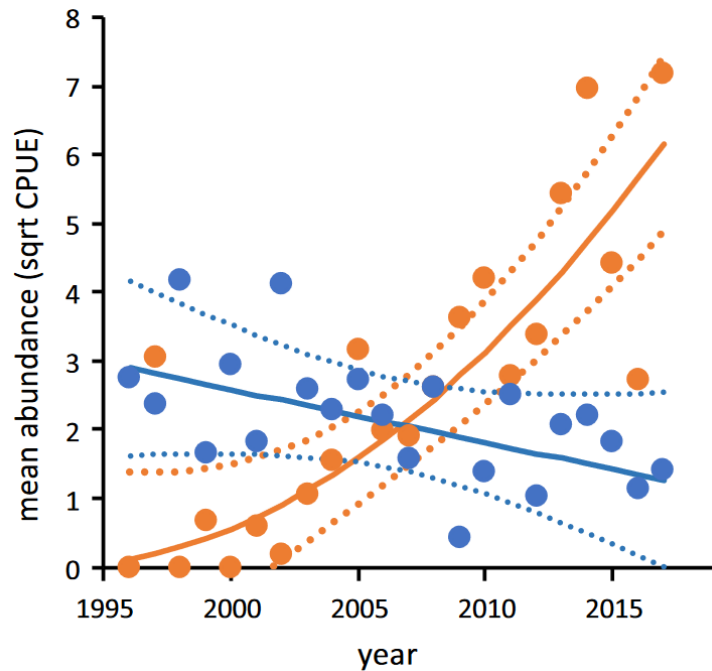
I – Future evolution?

Review

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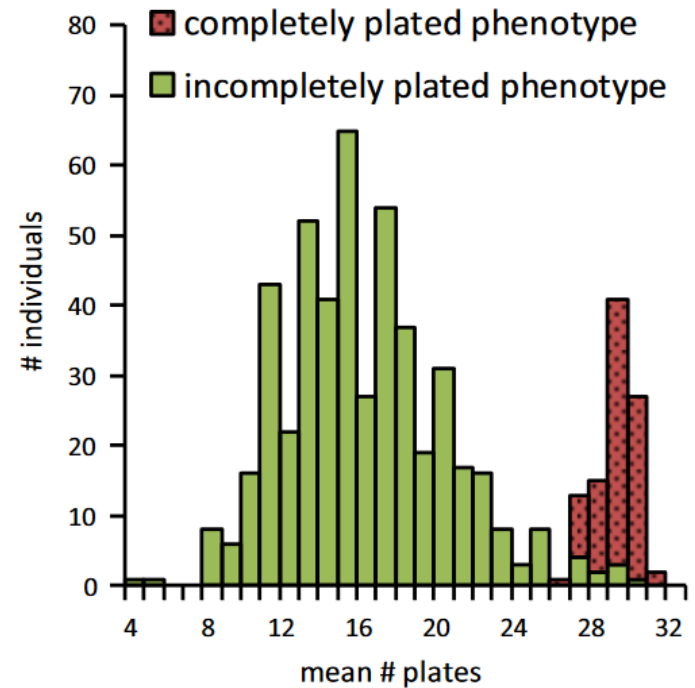
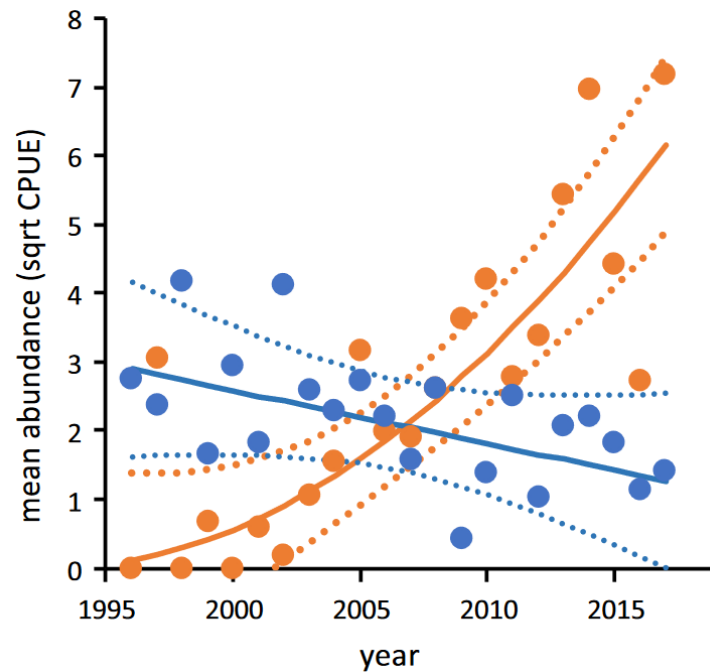


Emergence of freshwater phenotypes in the sea?

I – Future evolution?

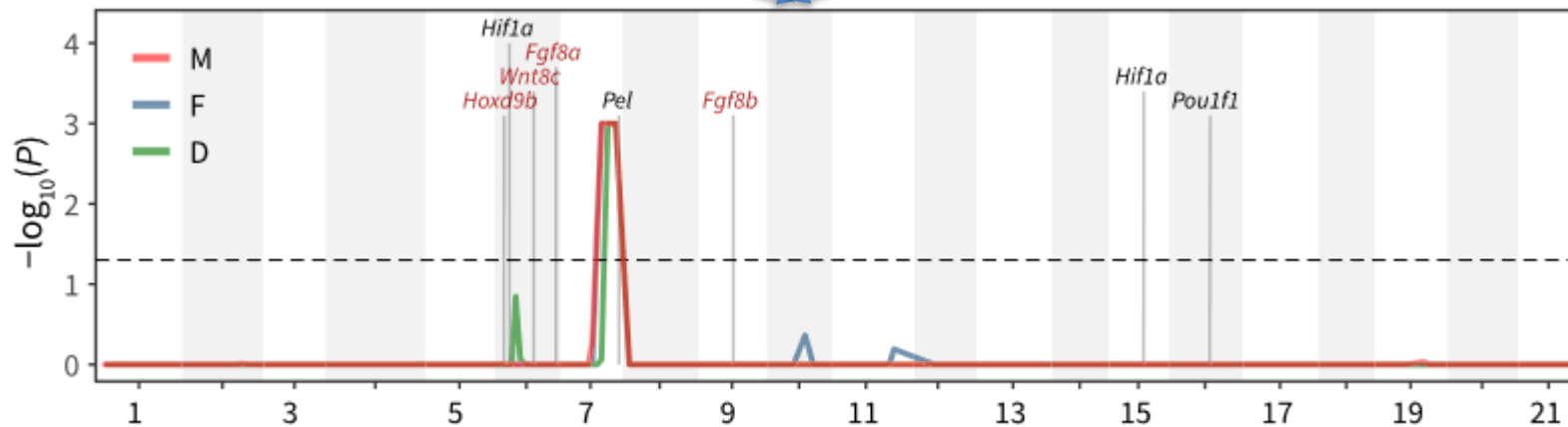
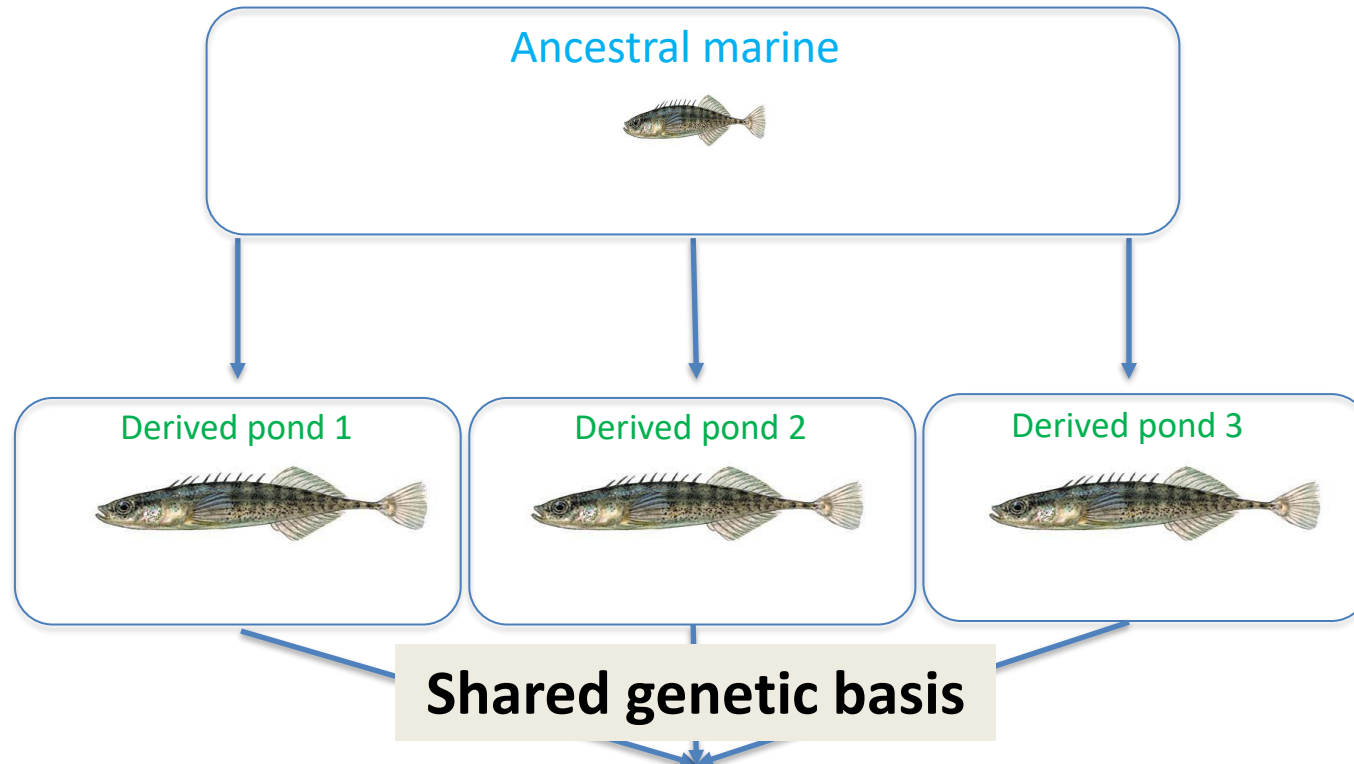
Habitat segregation of plate phenotypes in a rapidly expanding population of three-spined stickleback

BRITAS KLEMENS ERIKSSON ^{1,†} CASEY YANOS,¹ SARAH J. BOURLAT,² SERENA DONADI ³
MICHAEL C. FONTAINE,^{4,5} JOAKIM P. HANSEN,⁶ EGLÉ JAKUBAVIČIŪTĖ,⁷ KARINE KIRAGOSYAN,¹
MARTINE E. MAAN,¹ JUHA MERILÄ,^{8,9} ÅSA N. AUSTIN,¹⁰ JENS OLSSON,³ KATRIN REISS,¹¹ GÖRAN SUNDBLAD,³
ULF BERGSTRÖM,³ AND JOHAN S. EKLÖF¹⁰



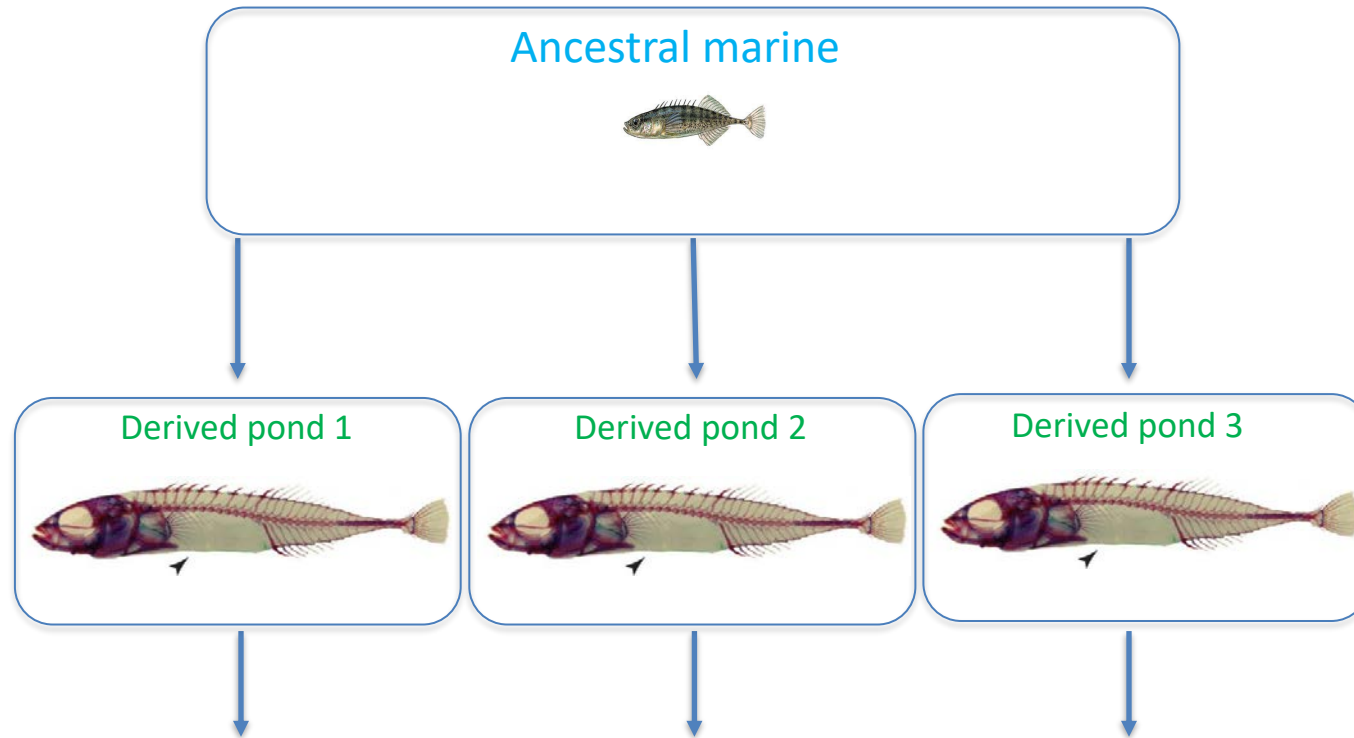
Is evolution predictable?

Is evolution **always** predictable?

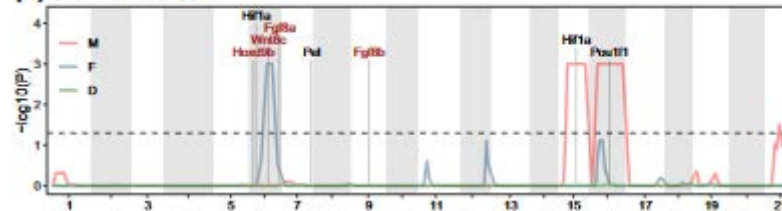


(non)parallel genetic evolution

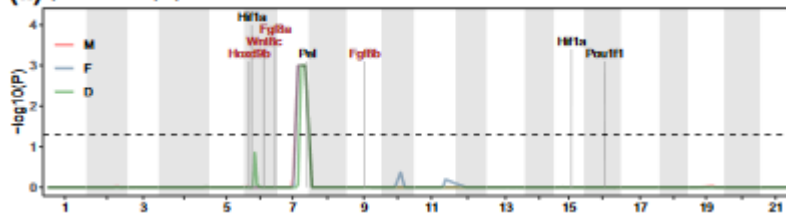
Kemppainen *et al.* 2021



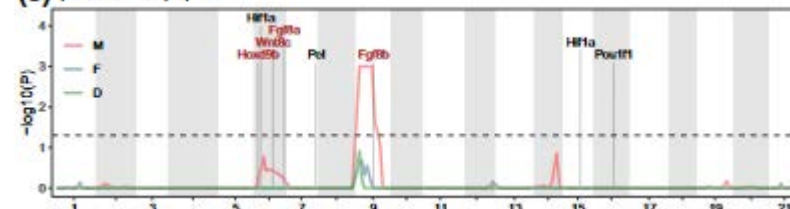
(c) | HEL x BYN | Spine



(a) | HEL x RYT | Spine



(e) | HEL x PYÖ | Spine



(non) parallel genetic evolution

« Multiple paths to the same destination »
- Yamakasi & Kitano 2021

(non) parallel genetic evolution

ARTICLE

Received 2 Jun 2014 | Accepted 8 Sep 2014 | Published 27 Oct 2014

DOI: 10.1038/ncomms6168

Parallel evolution of Nicaraguan crater lake cichlid fishes via non-parallel routes

Kathryn R. Elmer^{1,2}, Shaohua Fan¹, Henrik Kusche^{1,3}, Maria Luise Spreitzer^{1,3}, Andreas F. Kautt^{1,3}, Paolo Franchini¹ & Axel Meyer^{1,3}

Genetic population structure constrains local adaptation in sticklebacks

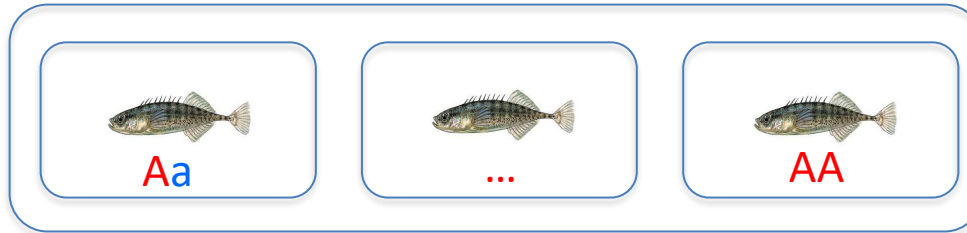
Petri Kemppainen¹  | Zitong Li^{1,2}  | Pasi Rastas^{1,3} | Ari Löytynoja³  |
Bohao Fang¹  | Jing Yang^{1,4} | Baocheng Guo⁵  | Takahito Shikano¹ | Juha Merilä^{1,6} 

Distinct Patterns of Selective Sweep and Polygenic Adaptation in Evolve and Resequencing Studies

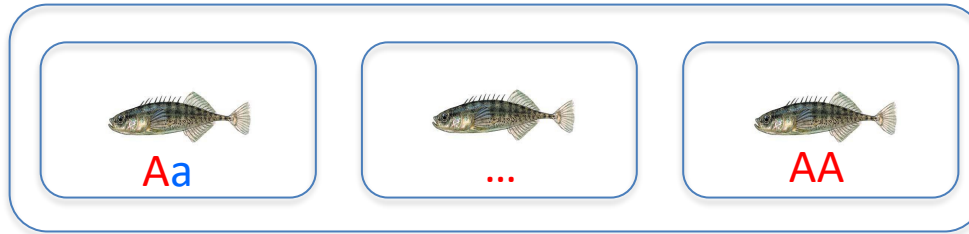
Neda Barghi, Christian Schlötterer 

When is evolution predictable?

Genetic population structure in the sea

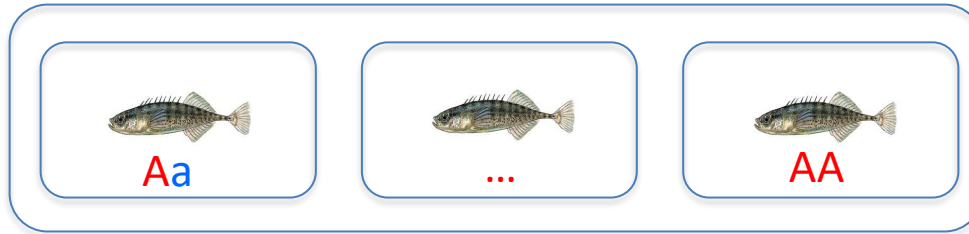


Genetic population structure in the sea



Selection on heterogeneous pool of standing genetic variation

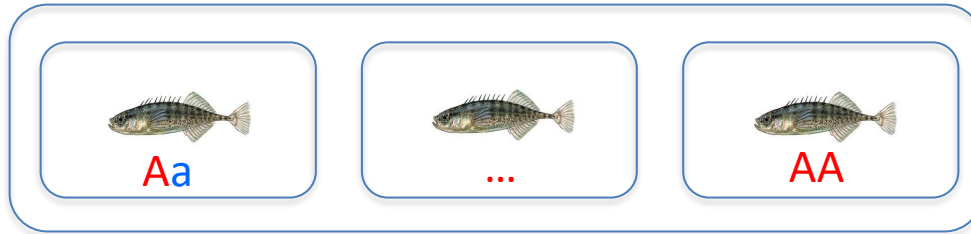
Genetic population structure in the sea



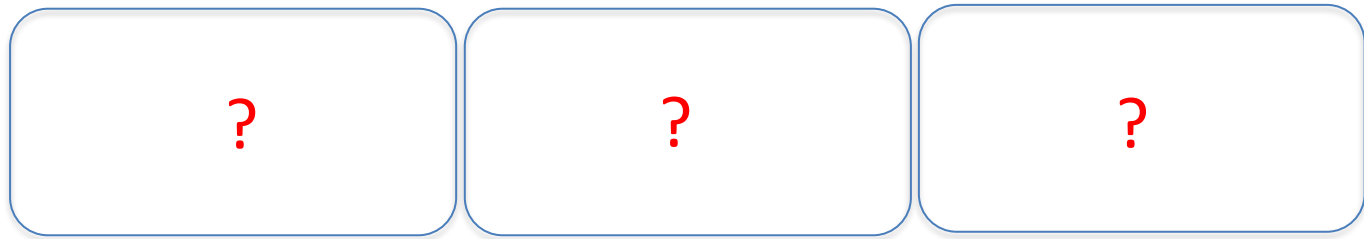
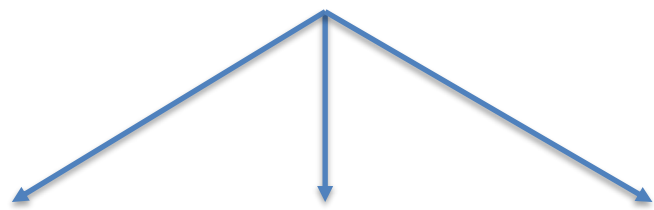
Selection on heterogeneous pool of standing genetic variation



Genetic heterogeneity in the ancestral population



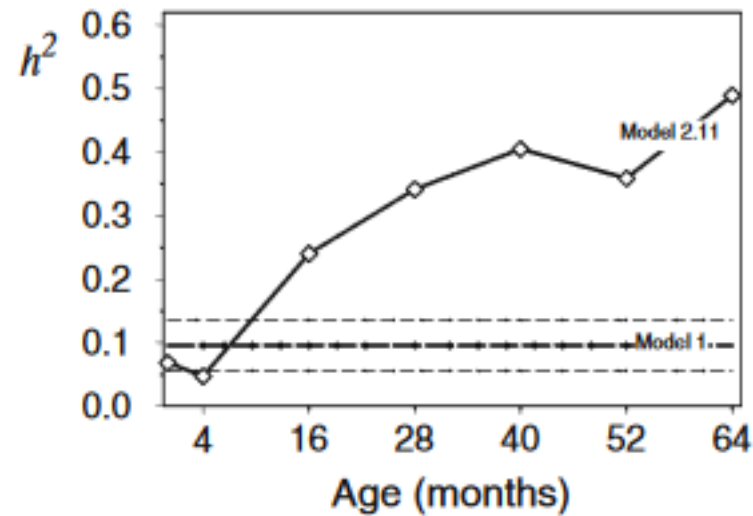
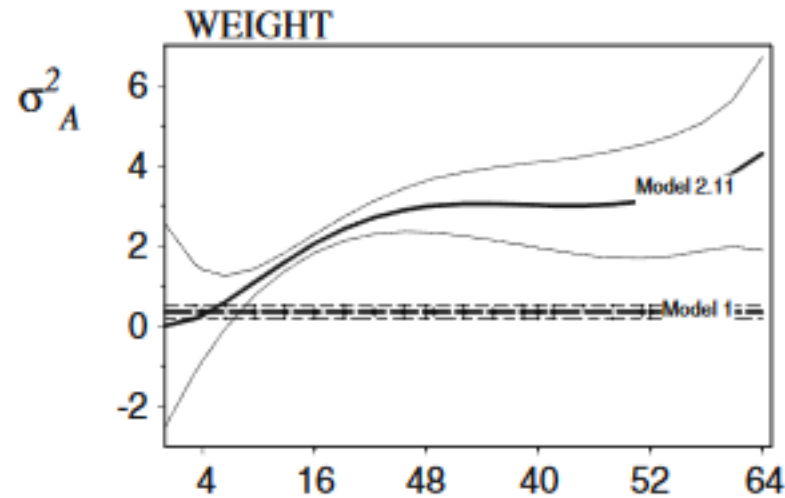
Selection on heterogeneous pool of standing genetic variation



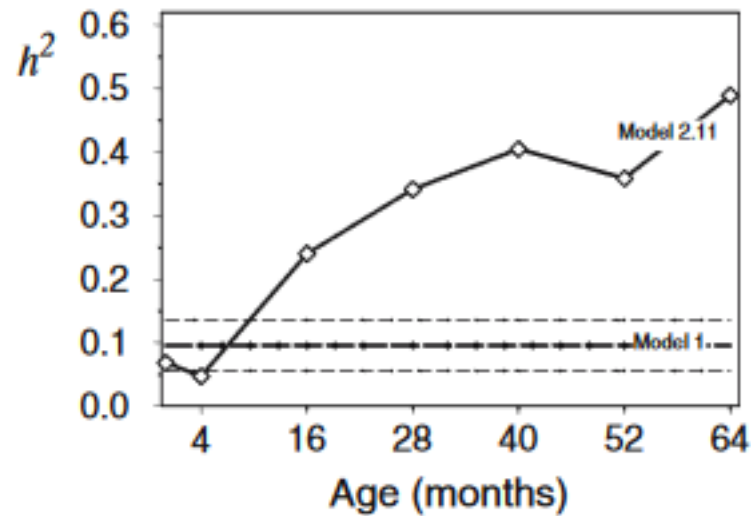
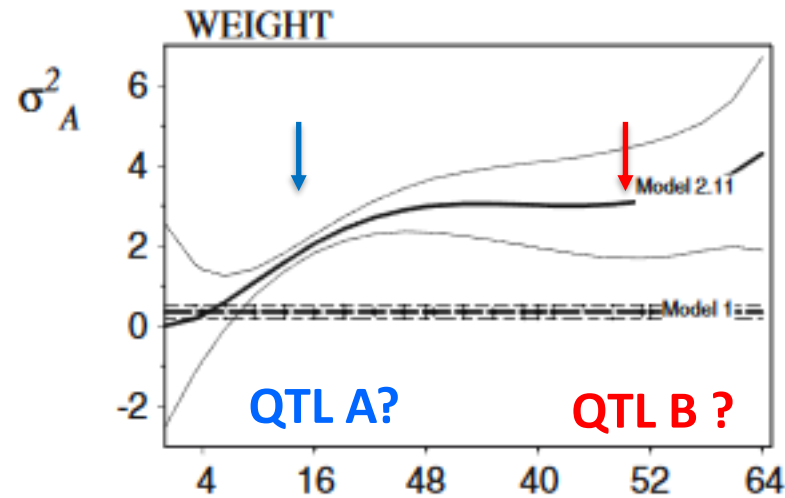
**Heterogeneous genetic variation decreases likelihood
of parallel evolution**

II - Investigating sources of non parallel evolution

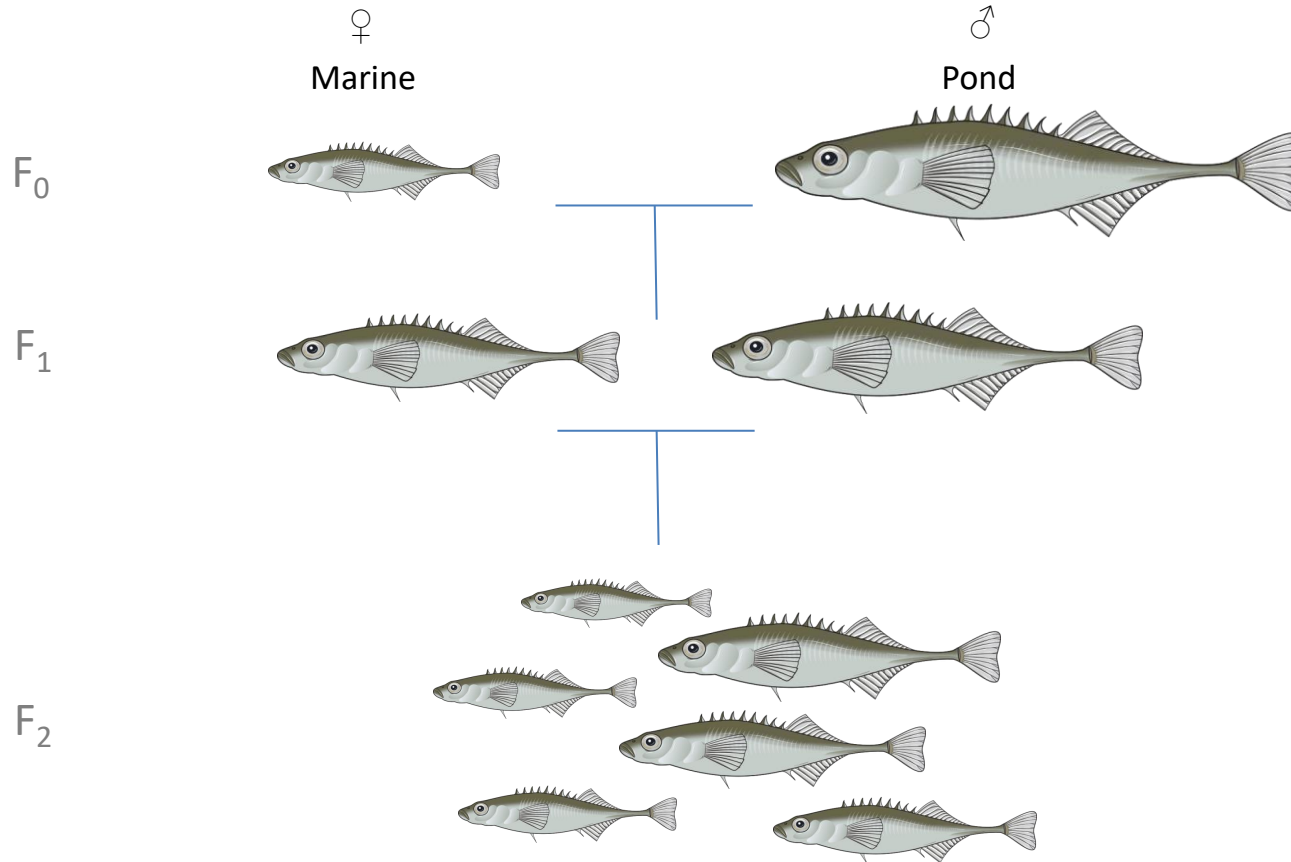
II - Investigating sources of non parallel evolution



II - Investigating sources of non parallel evolution

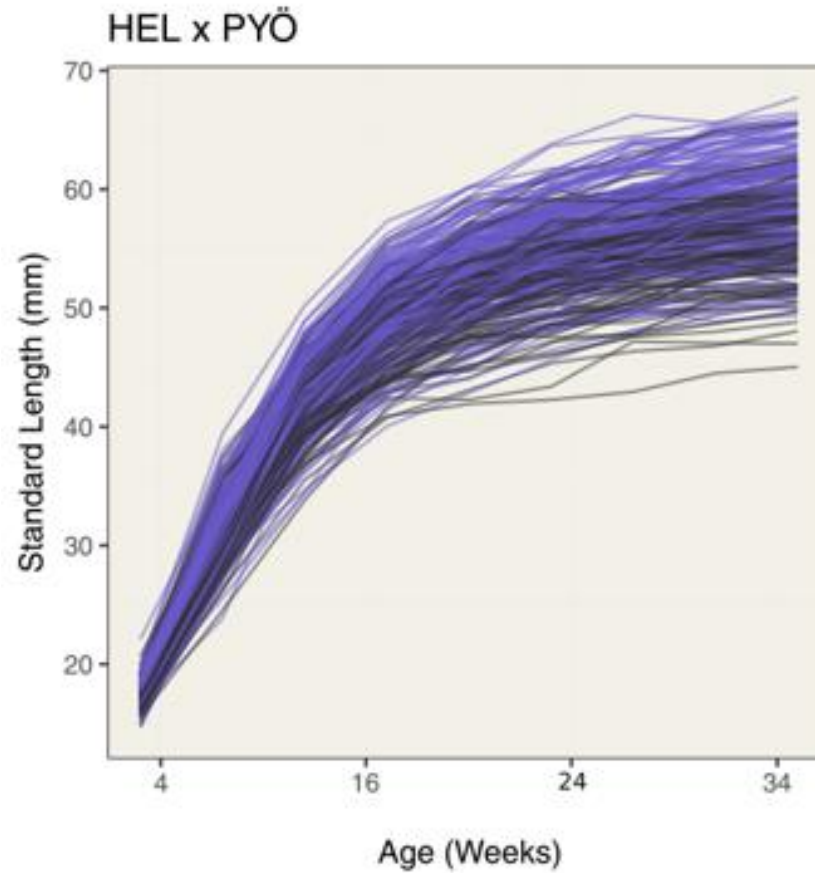


II – Quantitative genetics of body size: QTL mapping

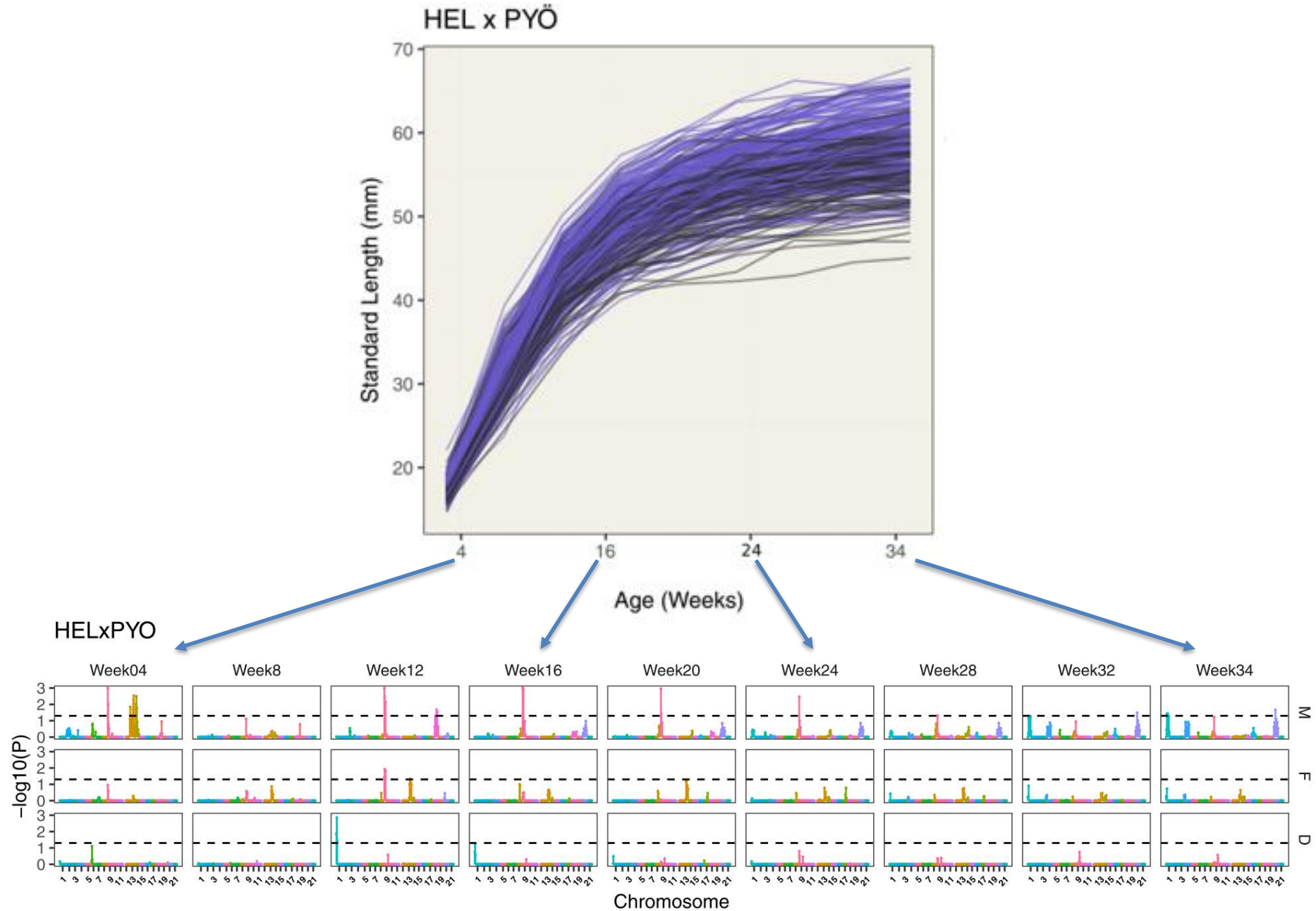


Inter-population F₂ QTL cross

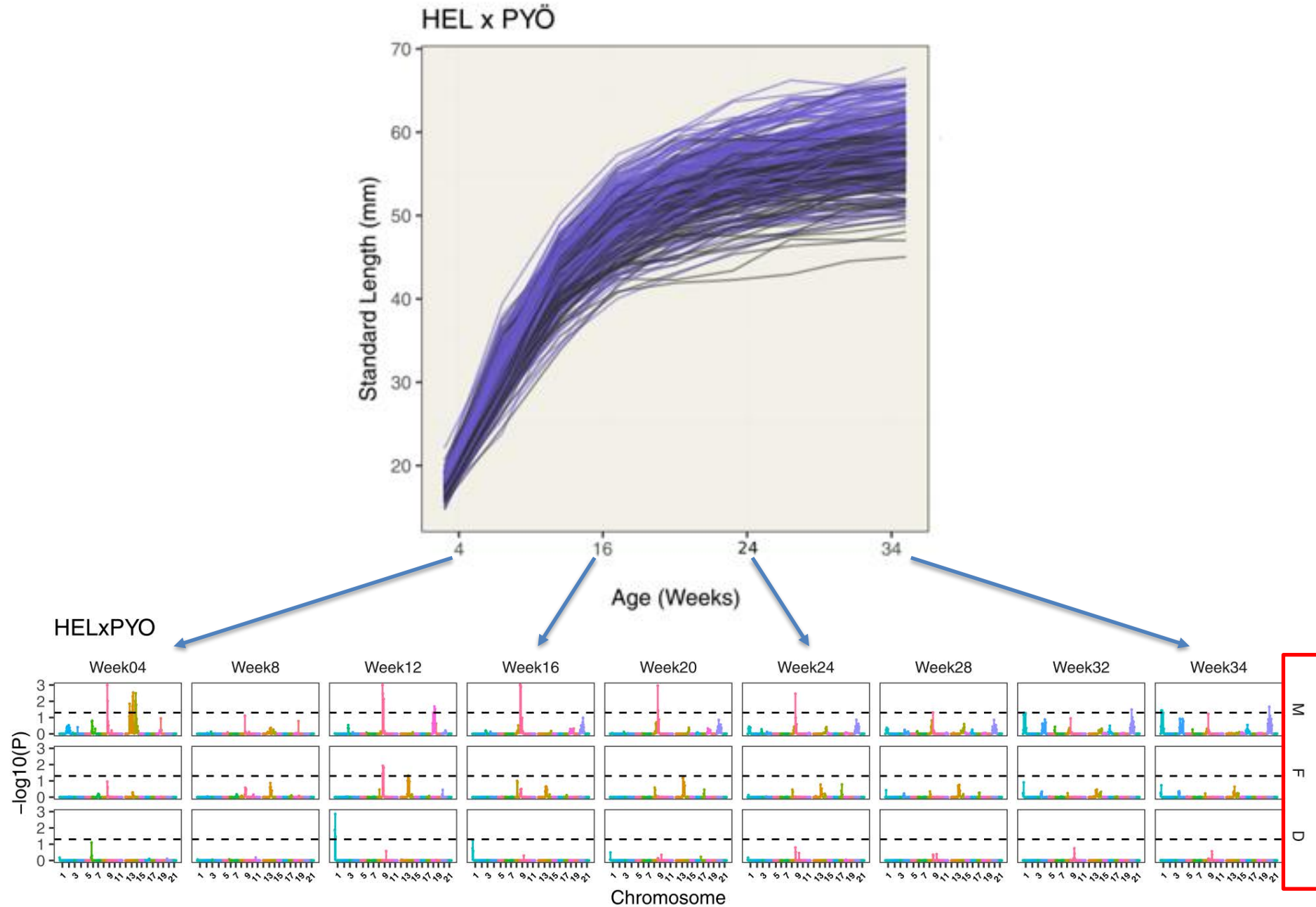
II – Quantitative genetics of body size: QTL mapping



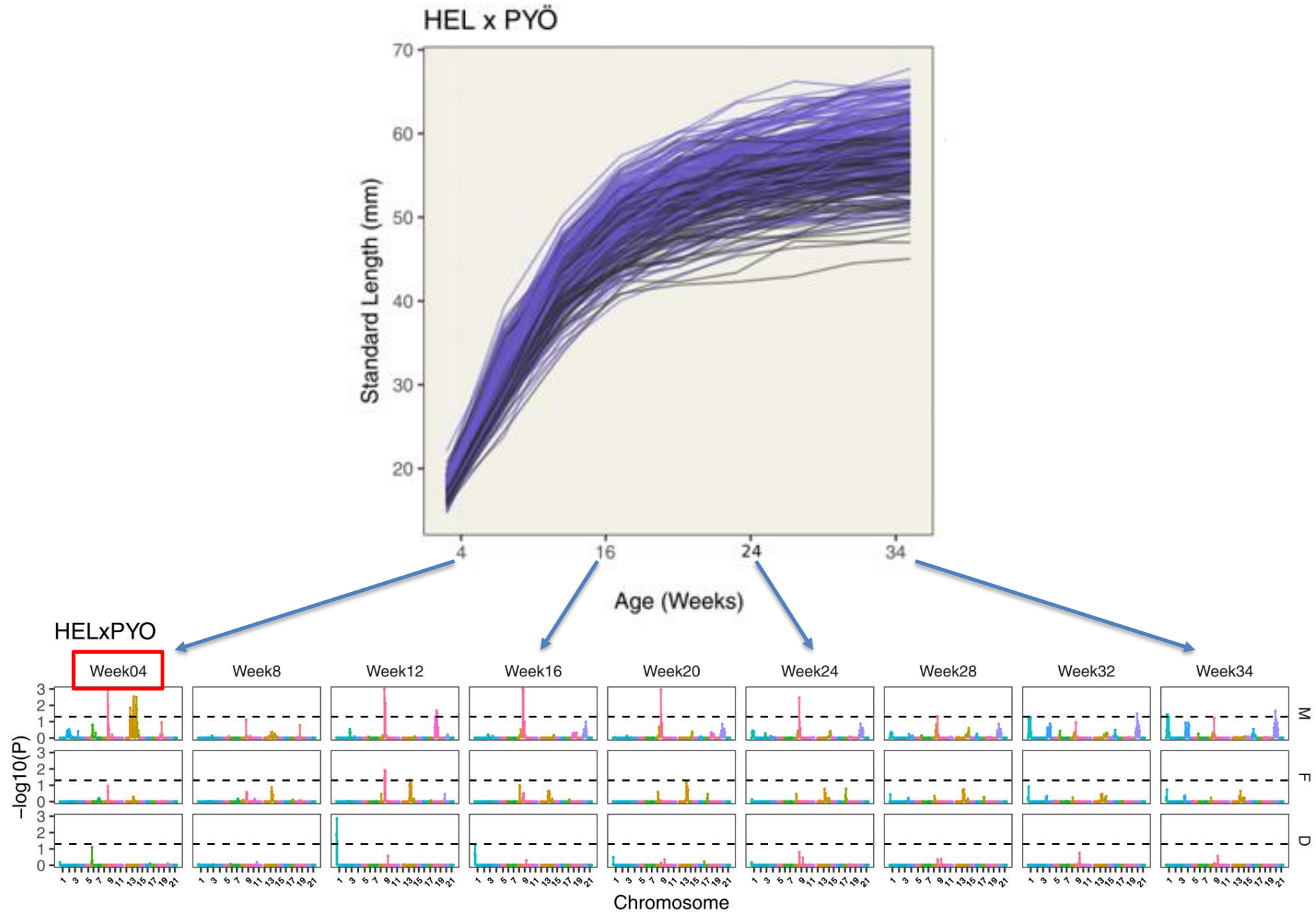
II – Quantitative genetics of body size: QTL mapping



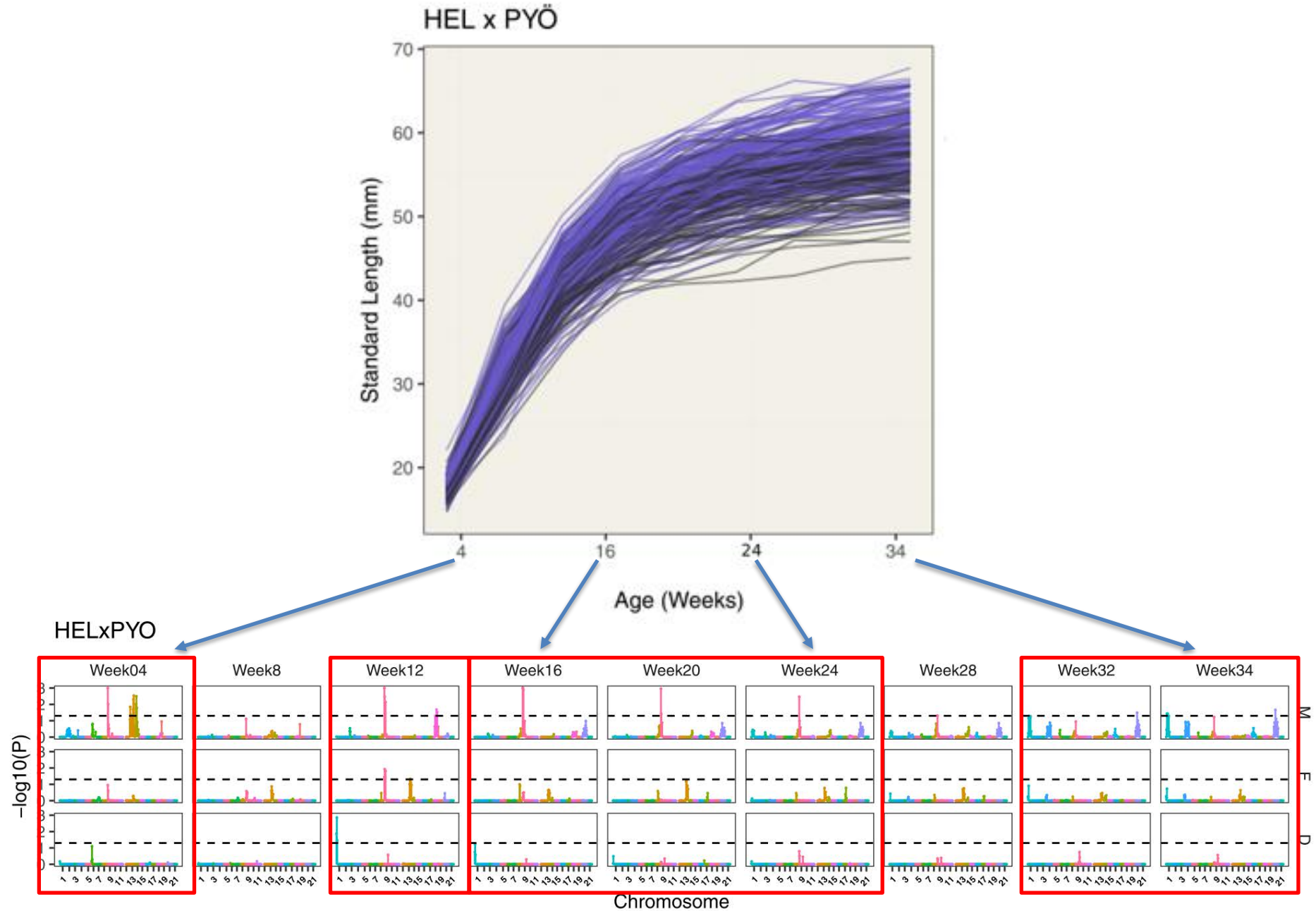
II – Quantitative genetics of body size: QTL mapping



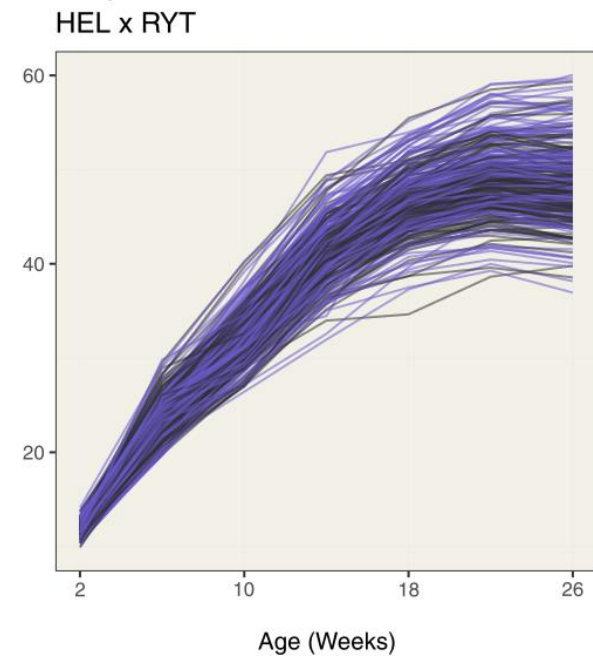
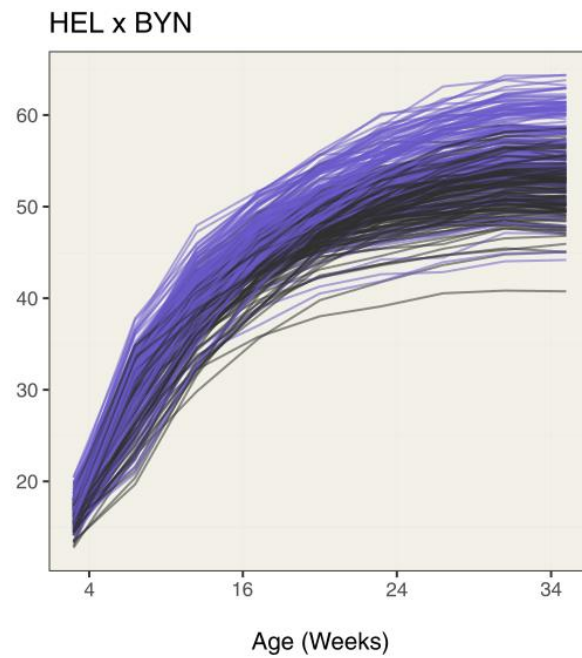
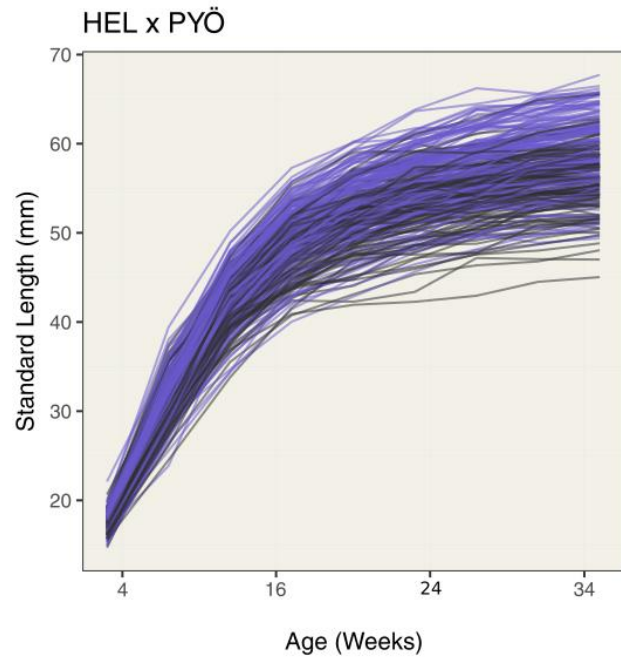
II – Quantitative genetics of body size: QTL mapping

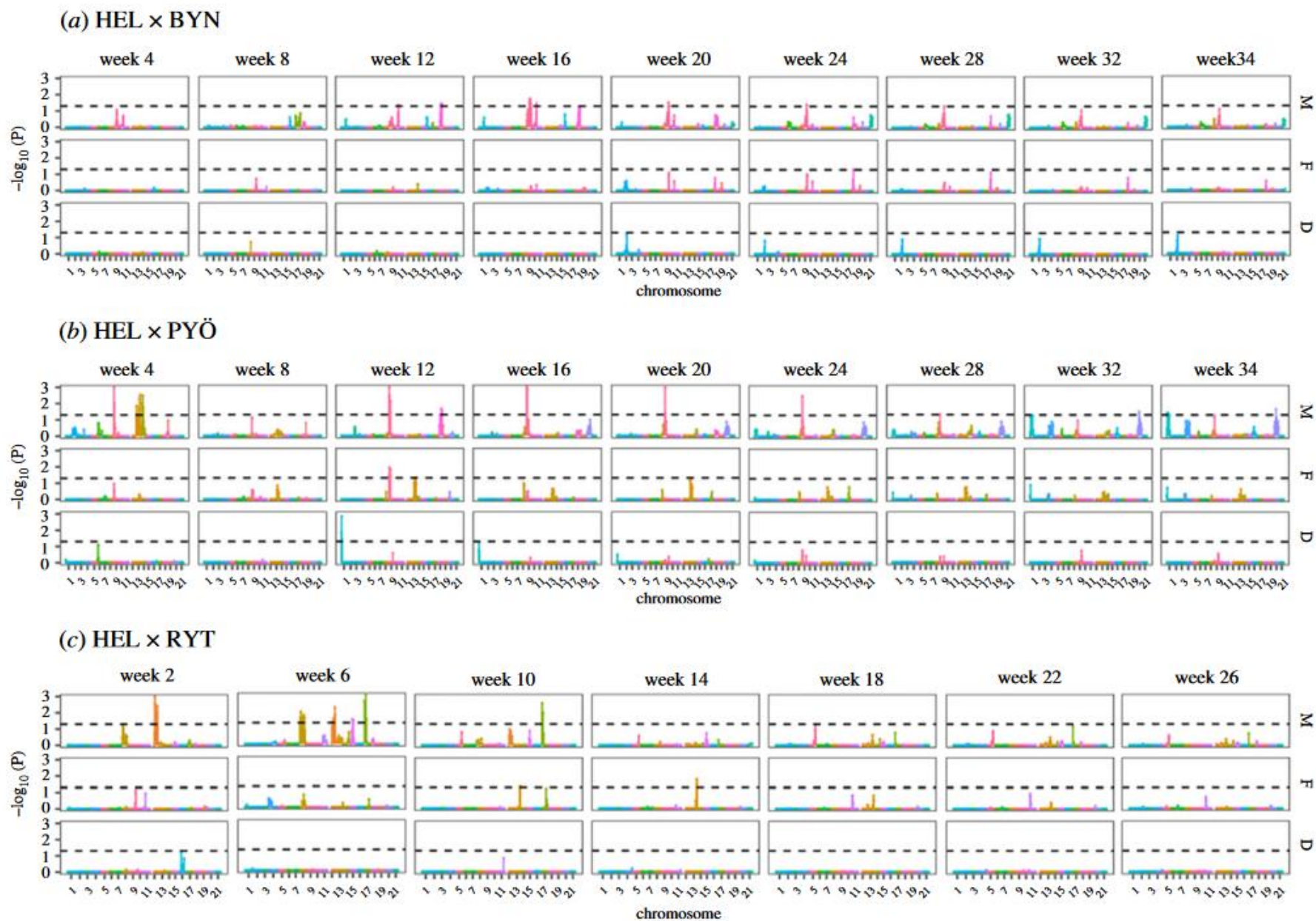


II – Quantitative genetics of body size: QTL mapping

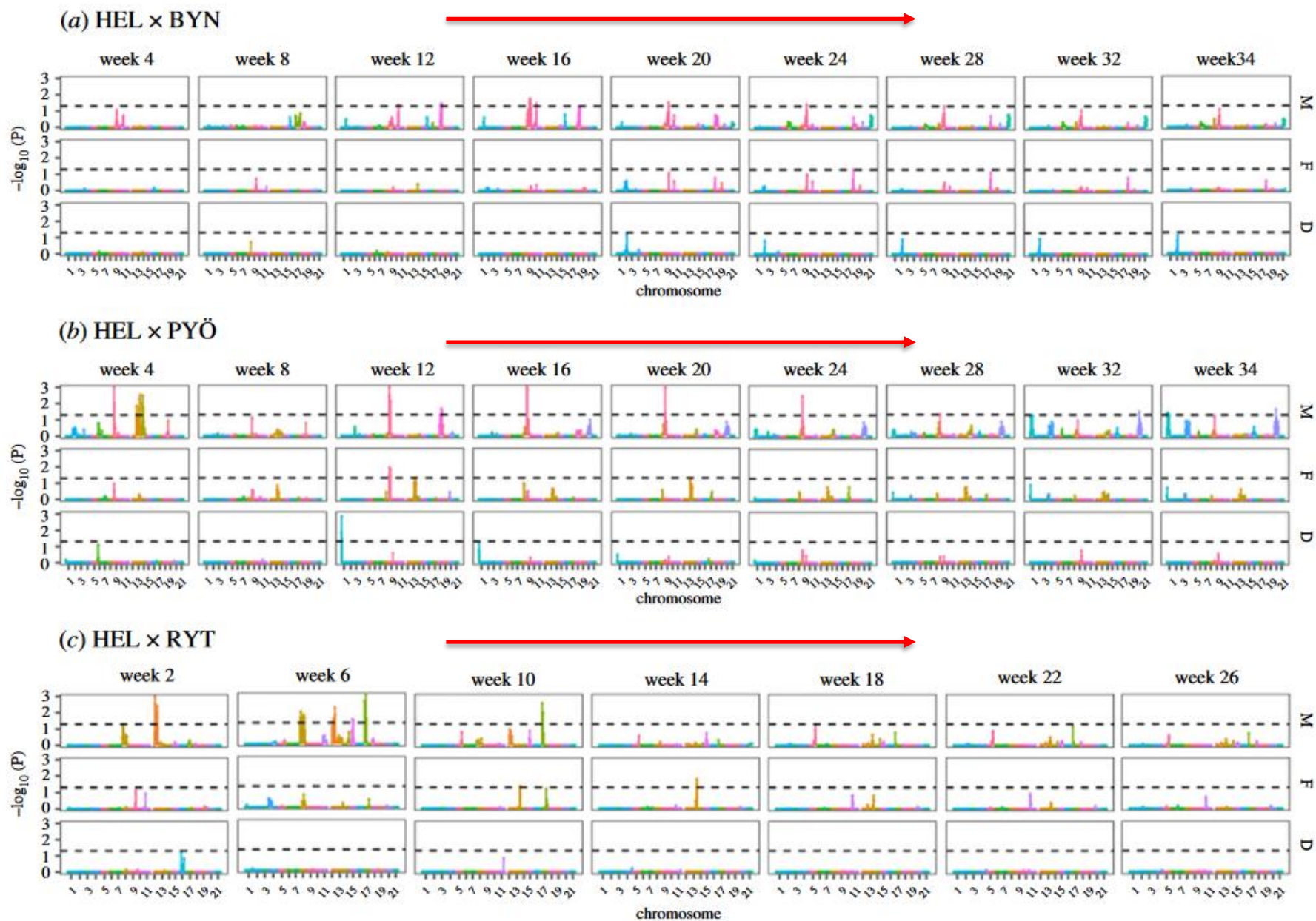


II – Quantitative genetics of body size: QTL mapping

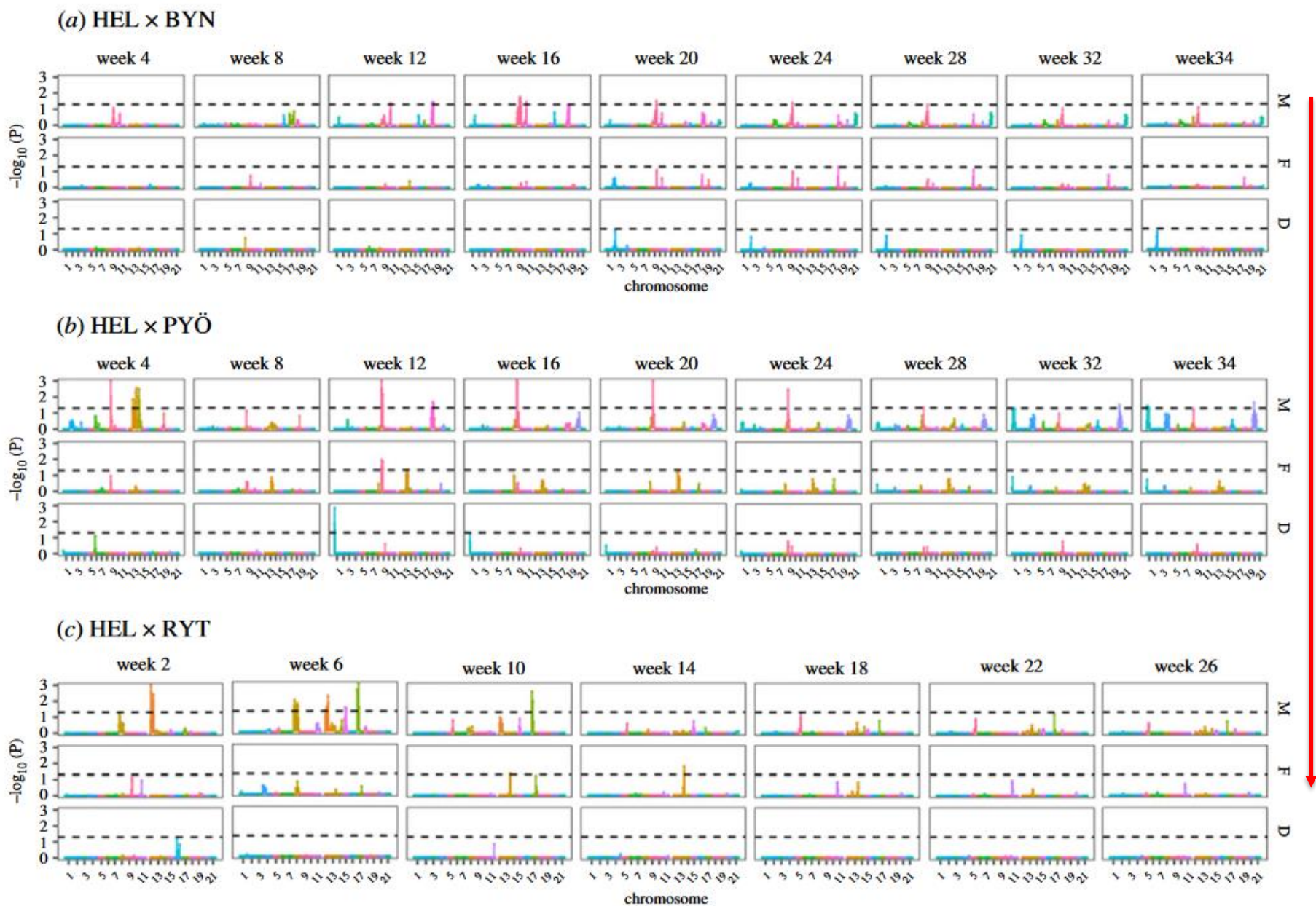




Age-specific genetic architecture

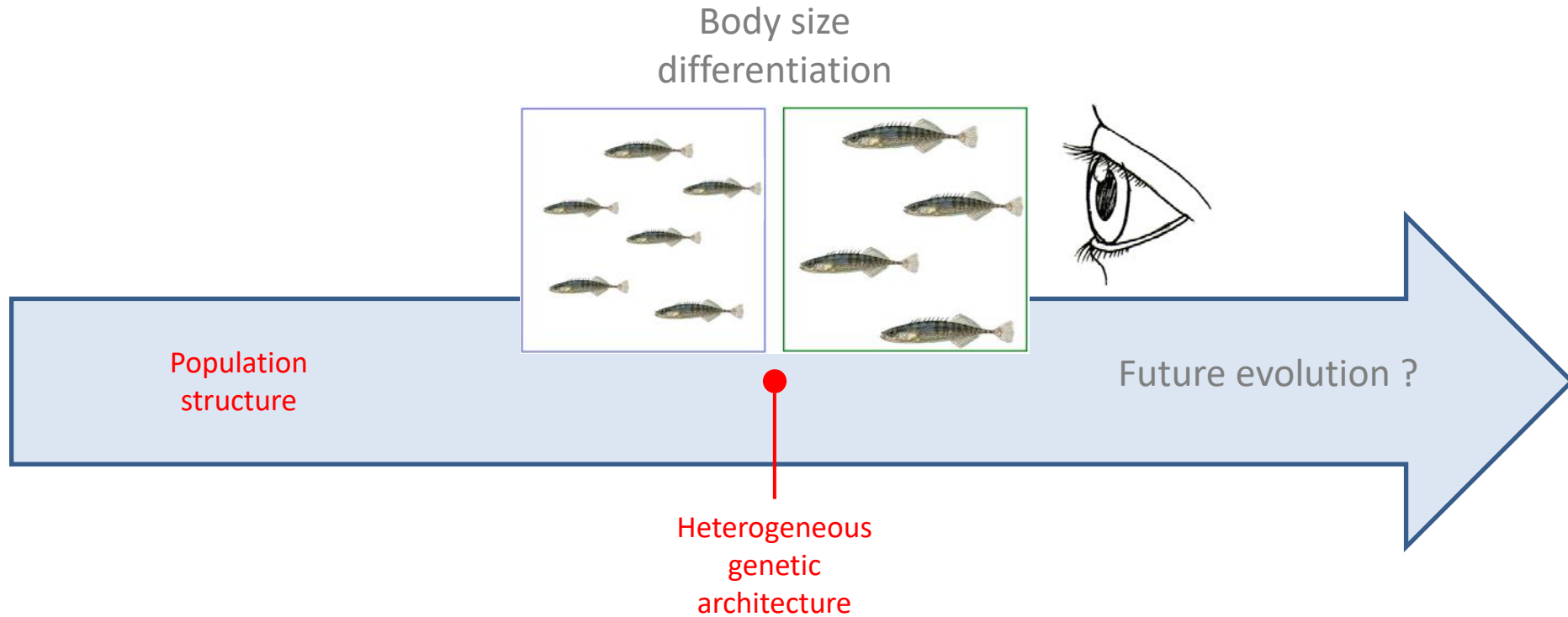


Population specific genetic architecture

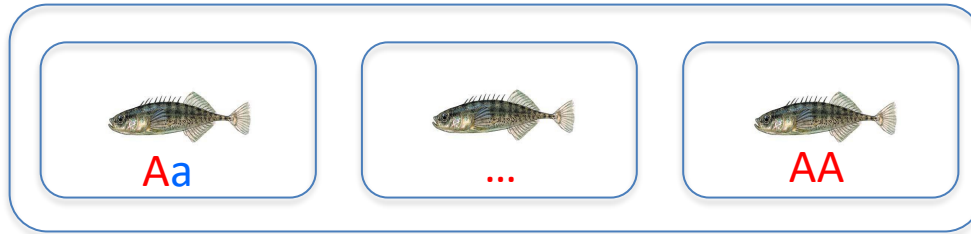


II – Conclusions

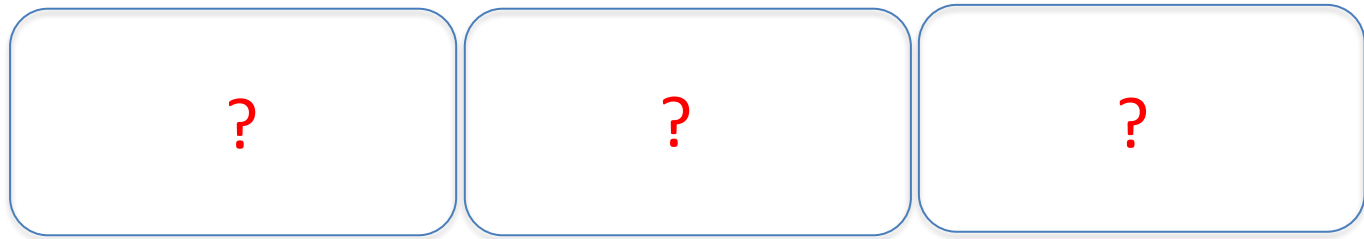
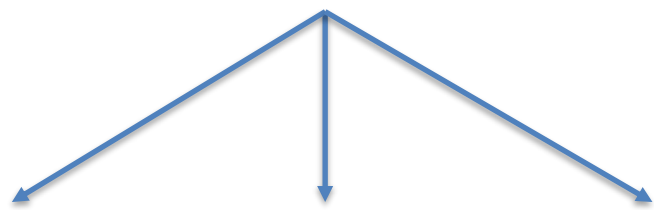
Age-specific genetic architecture of body size throughout ontogeny in nine-spined sticklebacks

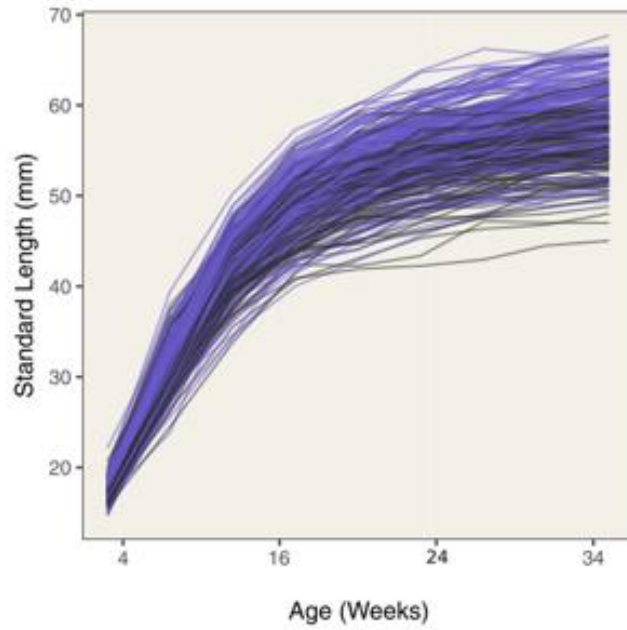


Genetic heterogeneity in the ancestral population

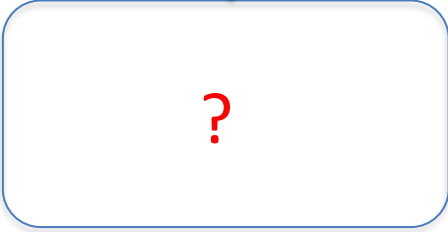
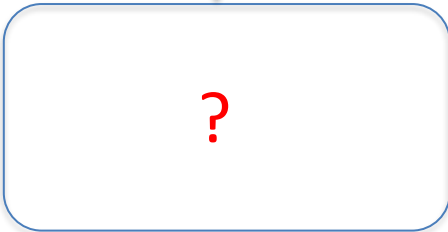
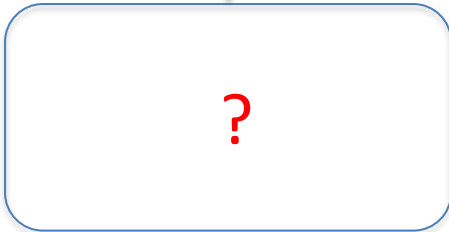


Selection on heterogeneous pool of standing genetic variation





Age-specific selection



Fisheries-Induced Evolution

Mikko Heino,^{1,2,3} Beatriz Díaz Pauli,¹
and Ulf Dieckmann³

¹Department of Biology and Hjort Centre for Marine Ecosystem Dynamics, University of Bergen, N-5020 Bergen, Norway; email: mikko.heino@uib.no

²Institute of Marine Research and Hjort Centre for Marine Ecosystem Dynamics, N-5817 Bergen, Norway

³Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria

ORIGINAL ARTICLE

Fisheries-induced neutral and adaptive evolution in exploited fish populations and consequences for their adaptive potential

Lise Marty,¹ Ulf Dieckmann² and Bruno Ernande^{1,2}

1 IFREMER, Laboratoire Ressources Halieutiques, Unité Halieutique Manche-Mer du Nord, Boulogne-sur-mer, France

2 IIASA, Evolution and Ecology Program, Laxenburg, Austria

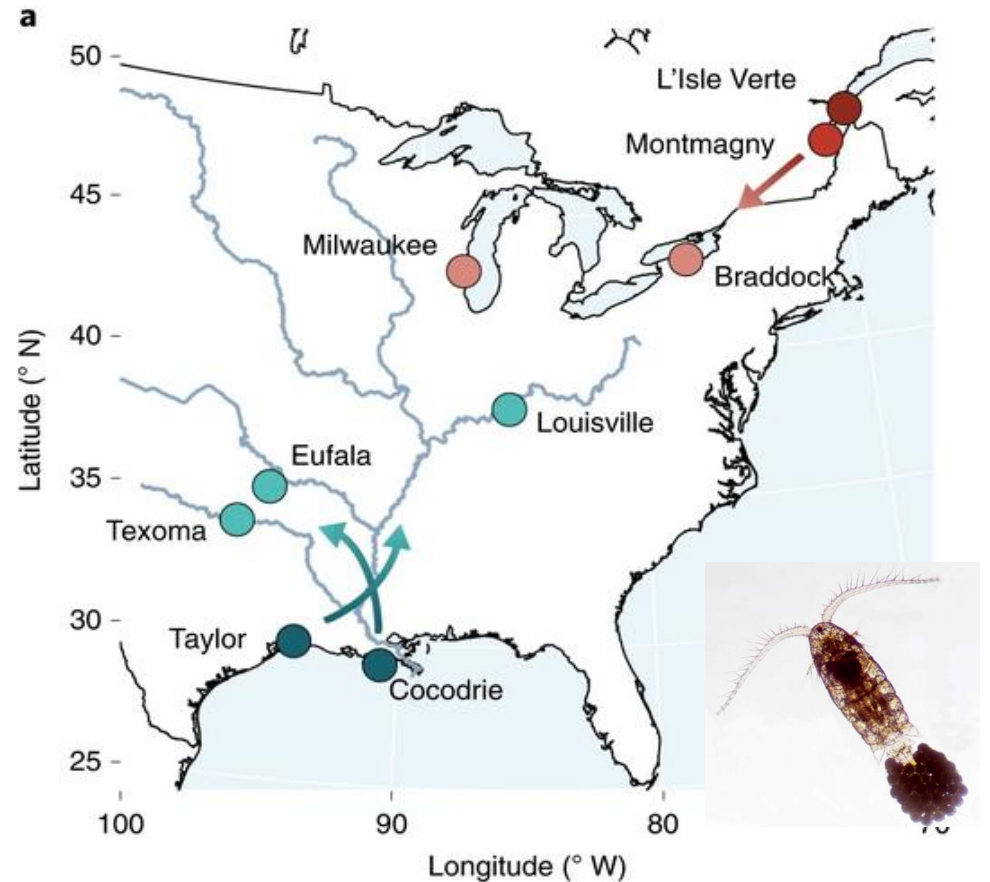
Part II : The genetic bases of repeated freshwater adaptation in copepods



II – Recent transition from marine to freshwater of *E. affinis*

Eurytemora affinis

Abundant marine planktonic species

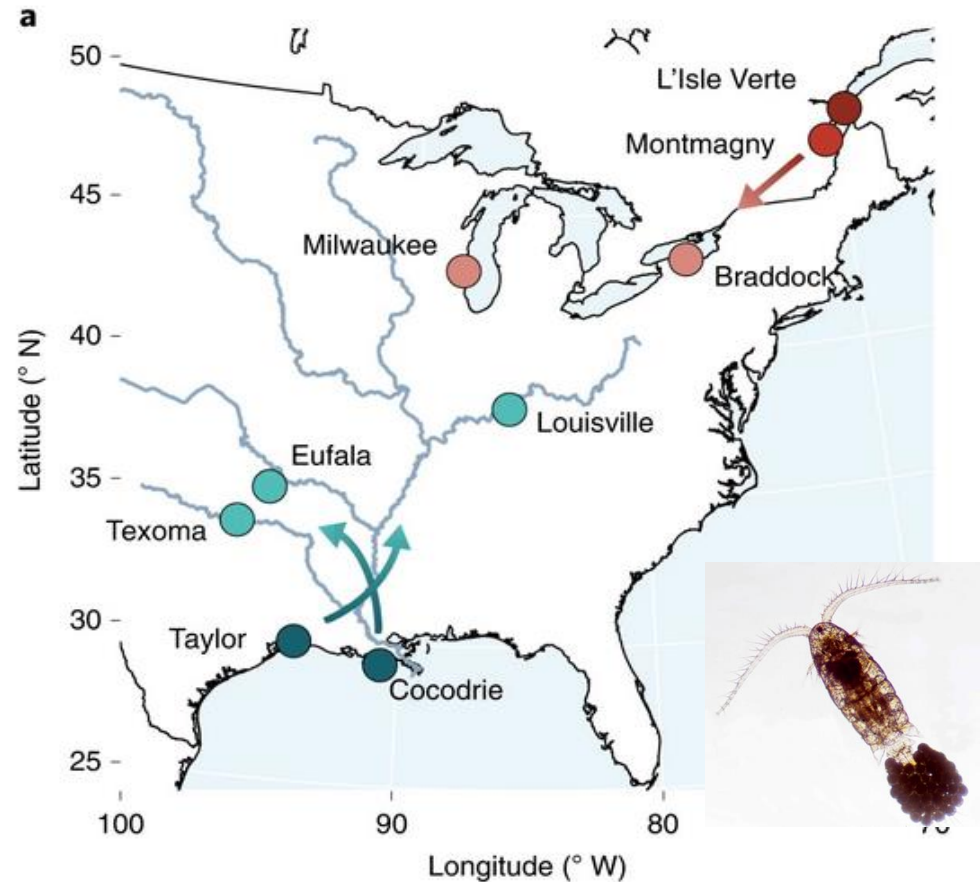


II – Recent transition from marine to freshwater of *E. affinis*

Eurytemora affinis

Abundant marine planktonic species

Transported with ballast waters to freshwater lakes



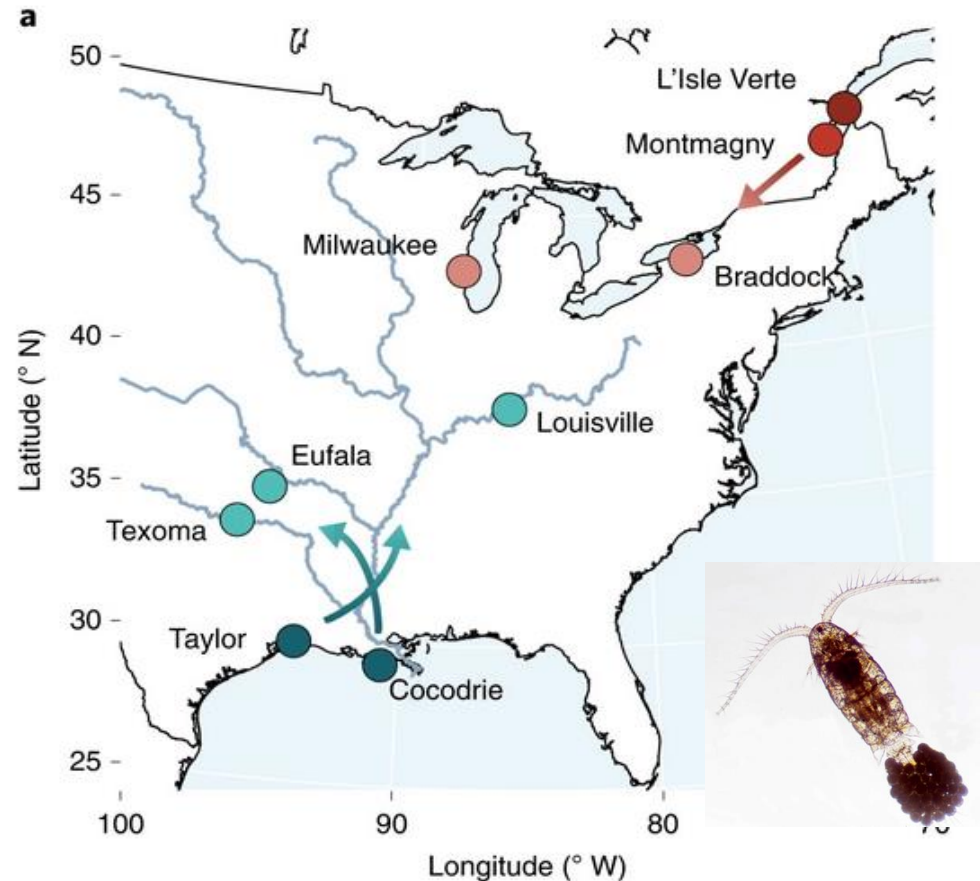
II – Recent transition from marine to freshwater of *E. affinis*

Eurytemora affinis

Abundant marine planktonic species

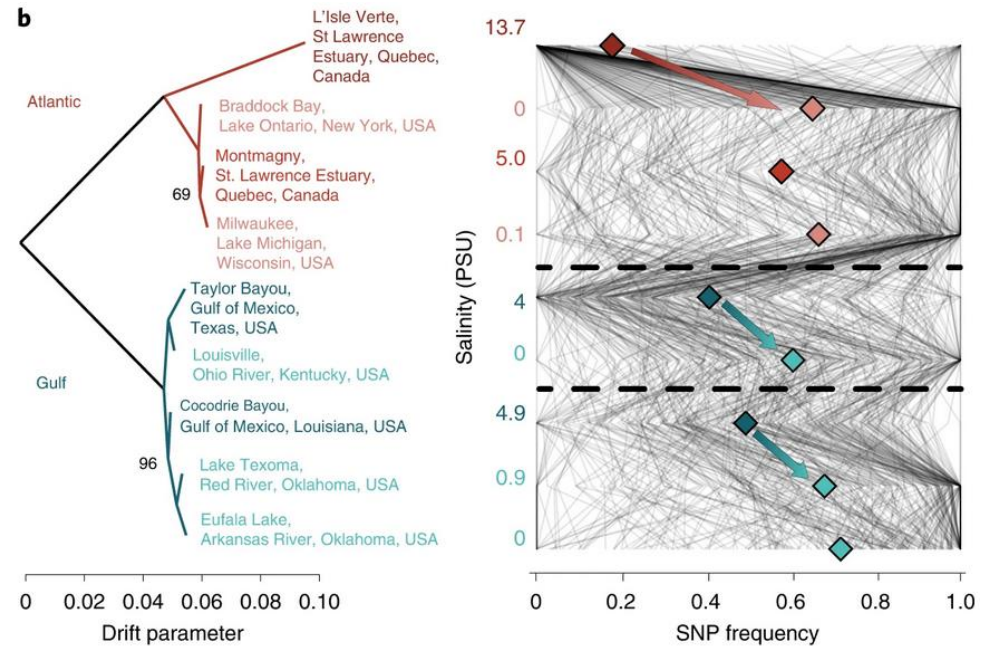
Transported with ballast waters to freshwater lakes

Adapted to freshwater in < 100 years



II – Recent transition from marine to freshwater of *E. affinis*

Balancing selection maintains genetic variation in the ancestral population

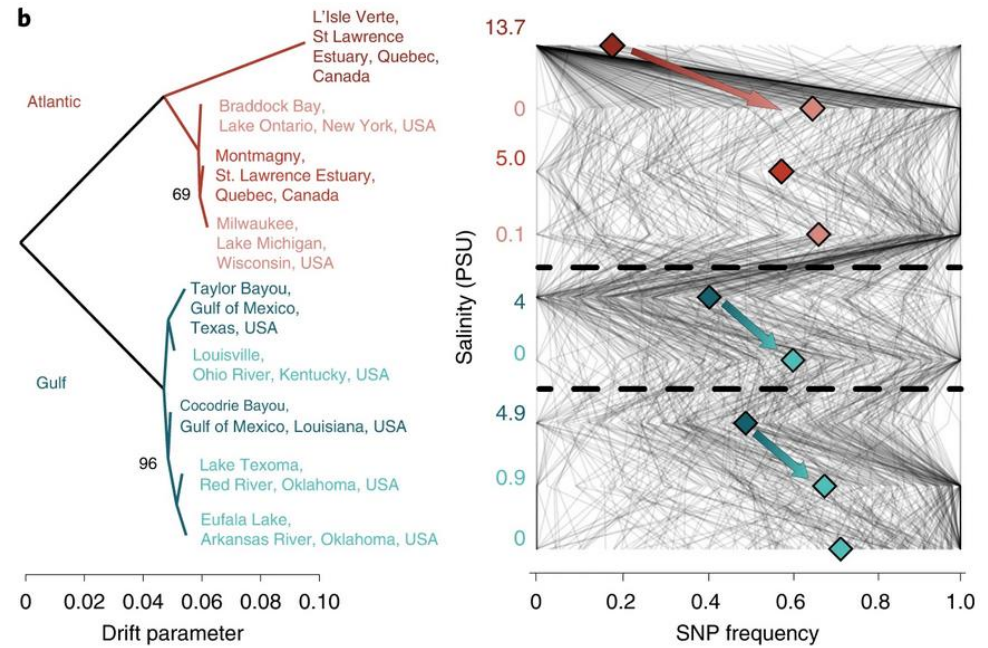


Stern & Lee 2020

II – Recent transition from marine to freshwater of *E. affinis*

Balancing selection maintains genetic variation in the ancestral population

Same SNPs increasing in frequency in parallel across lakes

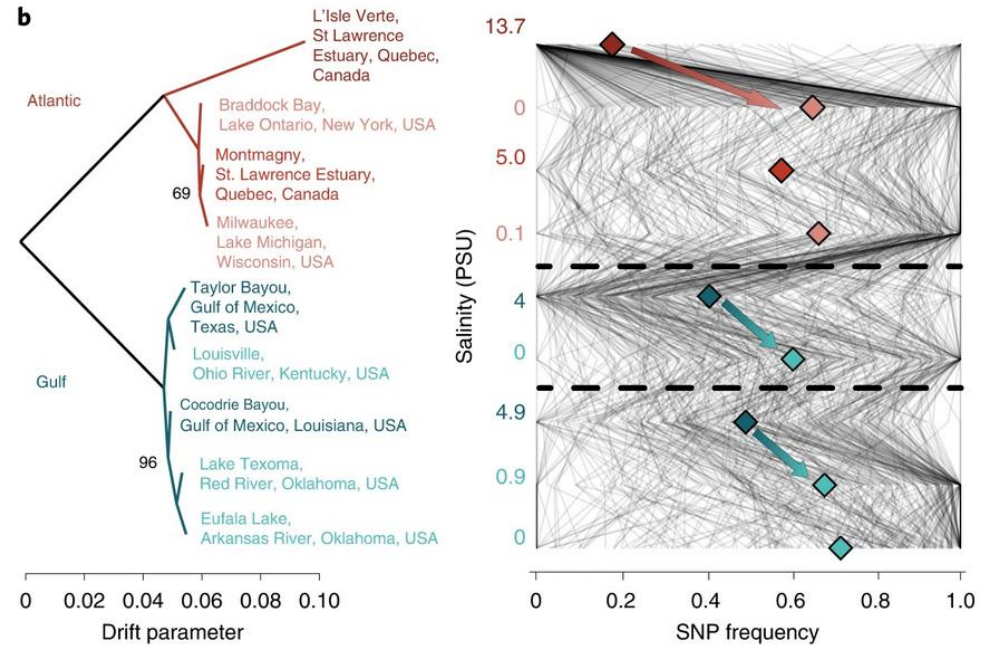
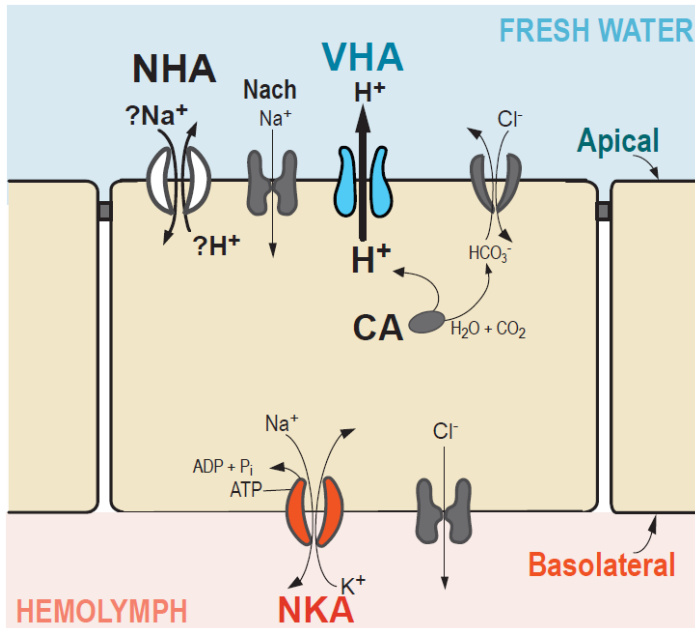


Stern & Lee 2020

II – Recent transition from marine to freshwater of *E. affinis*

Balancing selection maintains genetic variation in the ancestral population

Same SNPs increasing in frequency in parallel across lakes



Stern & Lee 2020

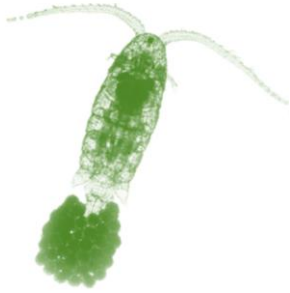
Located at ion-transporter genes

II – Research question

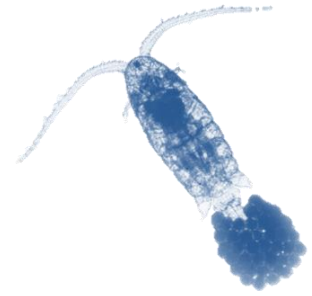
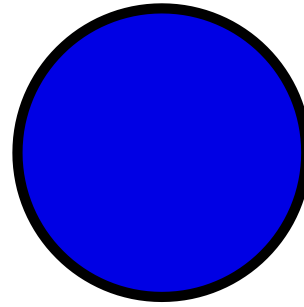
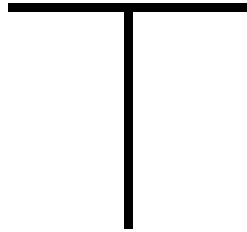
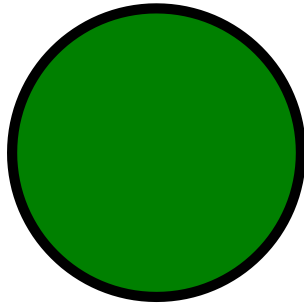
What are the fitness effects of ion-transporter alleles in different salinities ?

II – Experimental approach: genetic association study

II – A genetic association study

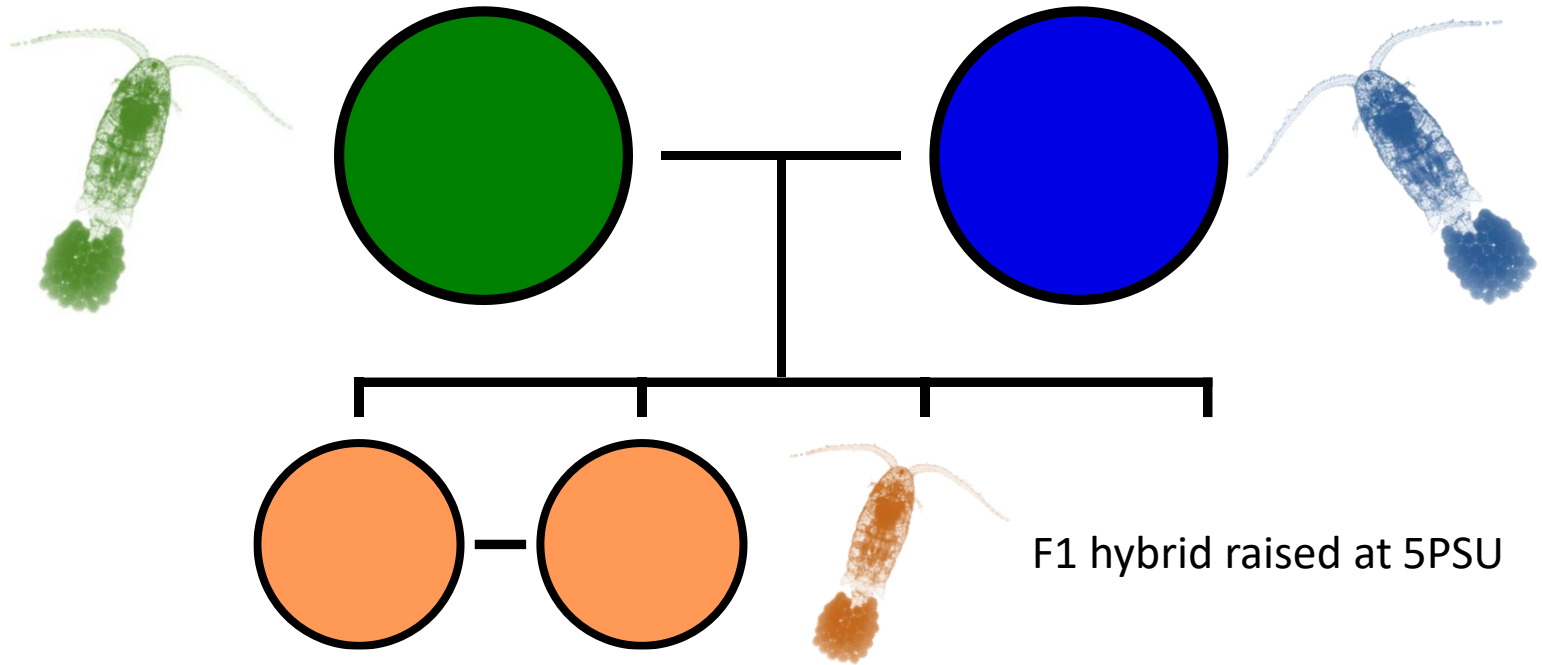


Wild Freshwater
Population
0PSU

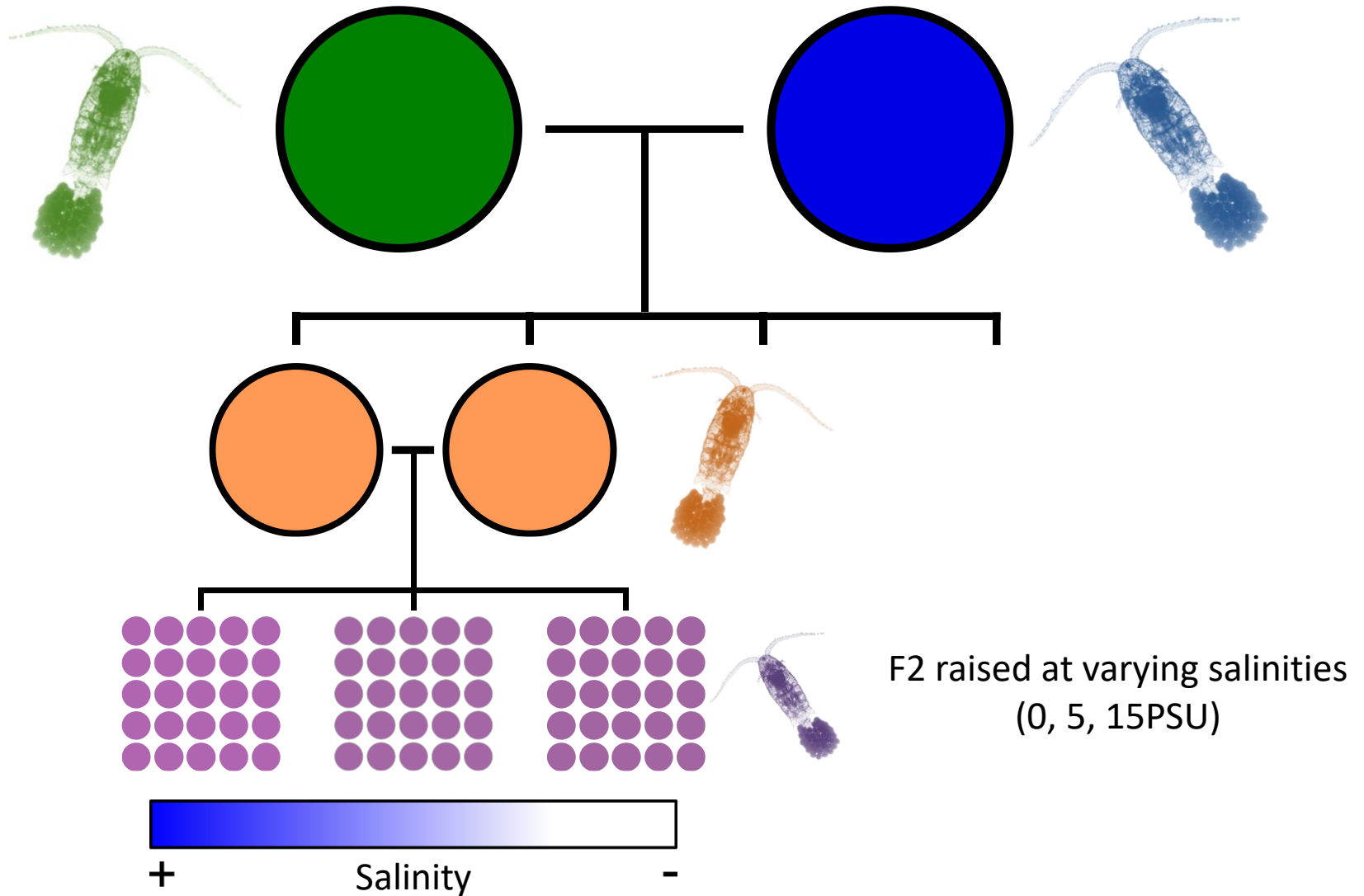


Inbred Saltwater
Population
15PSU

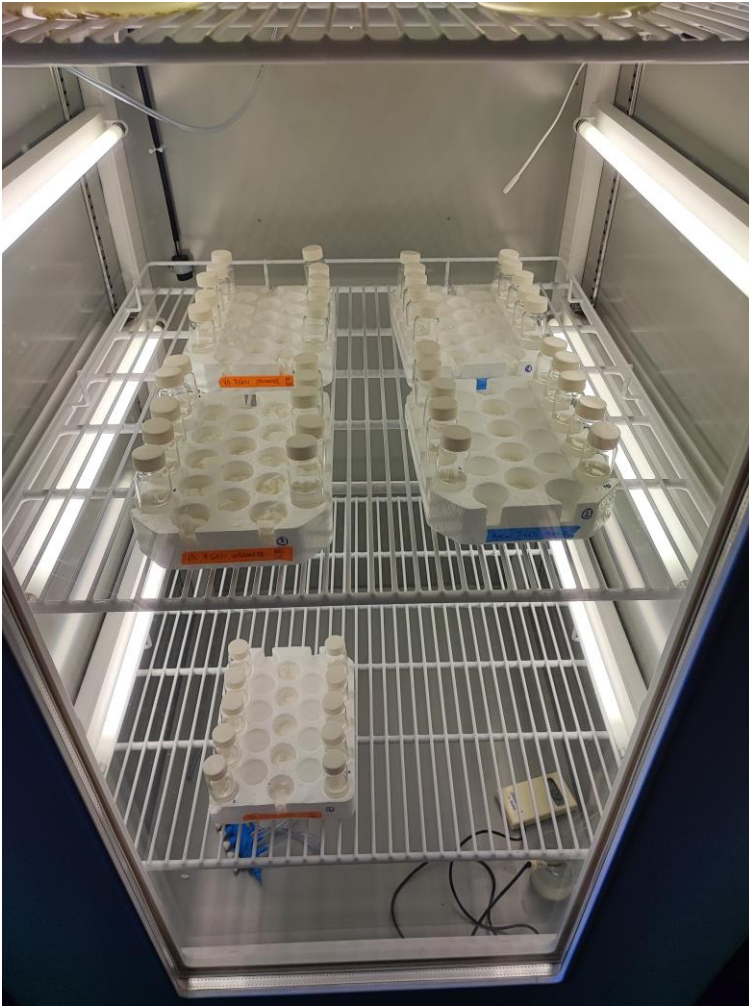
II – A genetic association study



II – A genetic association study

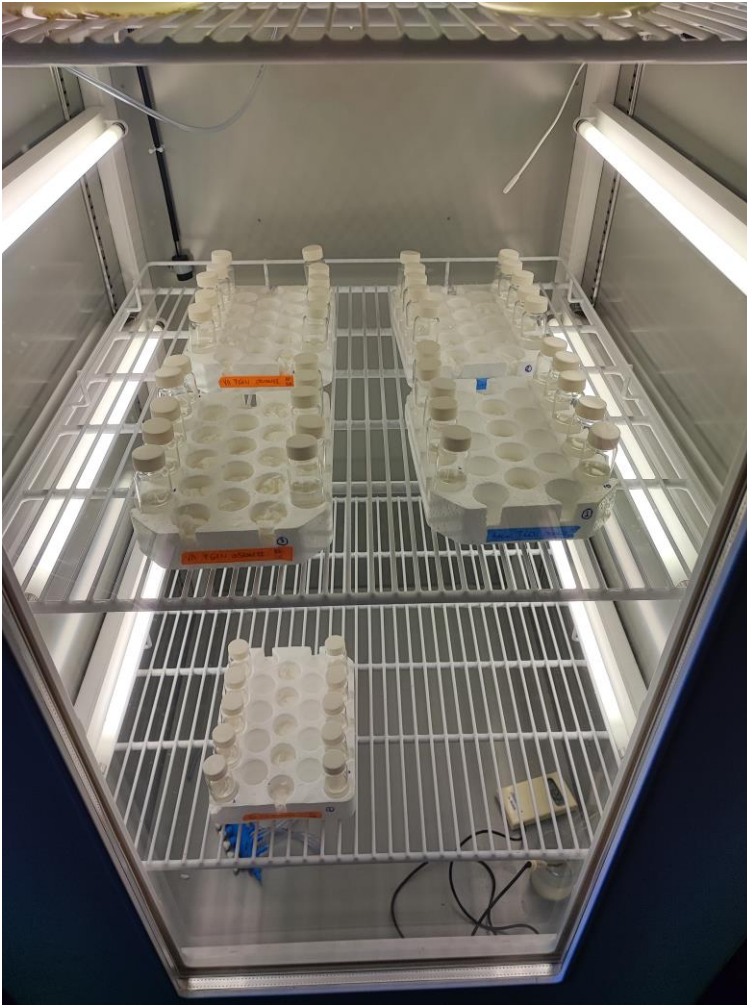


II – A genetic association study

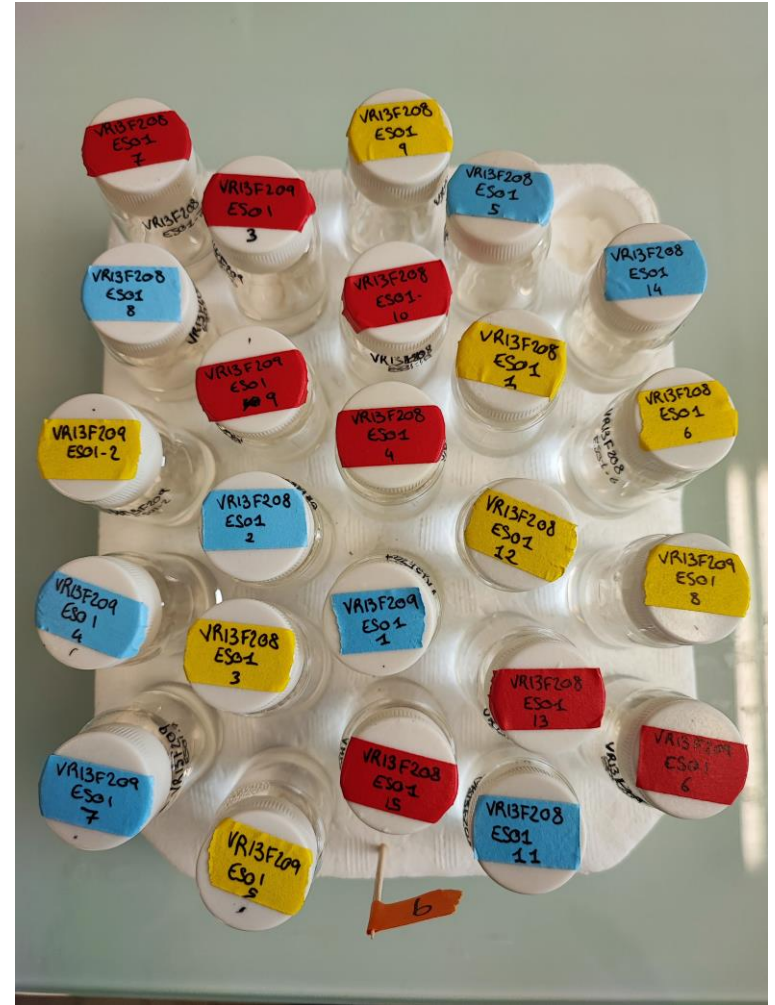


Controlled environment
incubators

II – A genetic association study

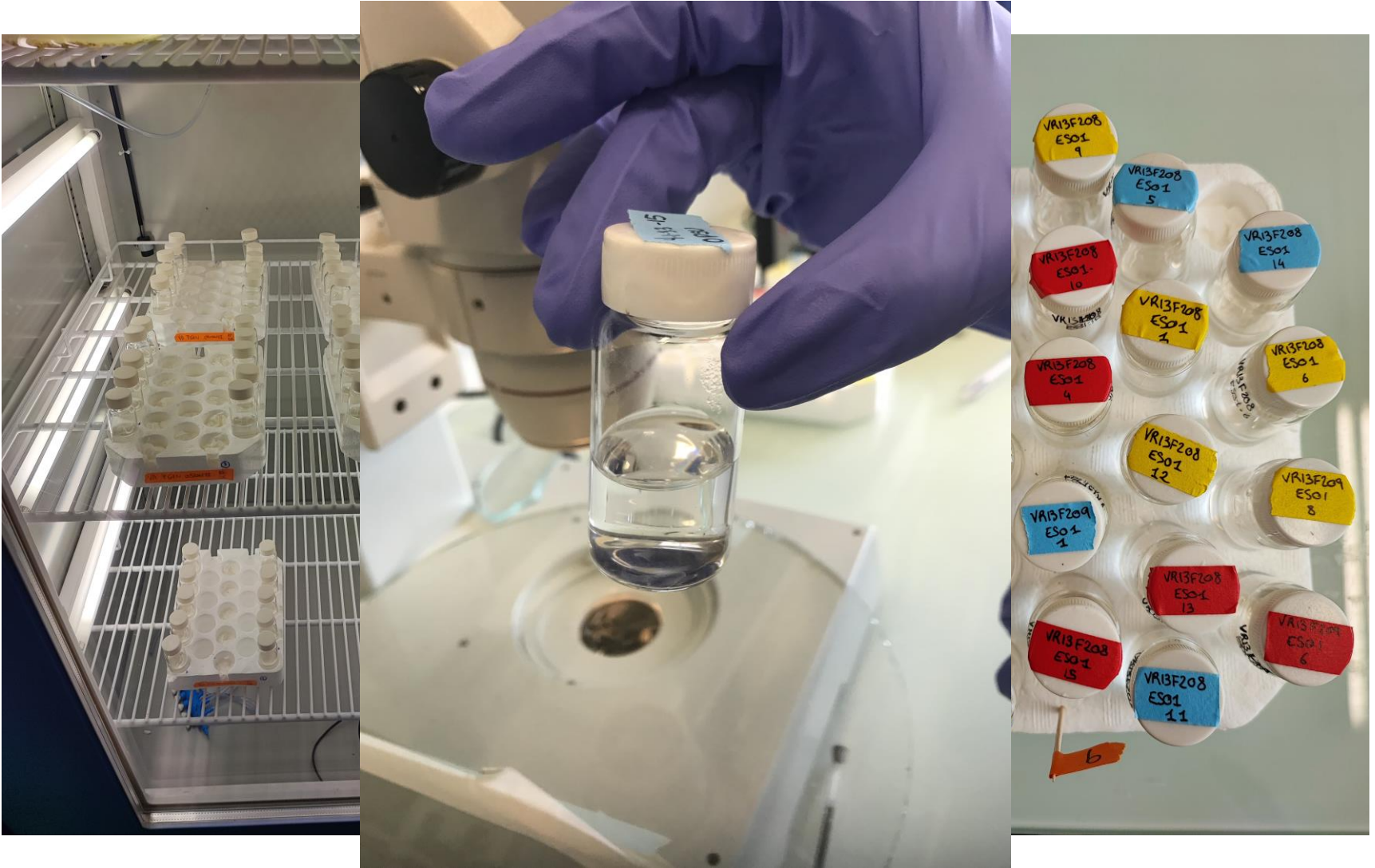


Controlled environment
incubators



Individual level salinity
treatments

II – A genetic association study



Daily record: life stage,
survival

II – Data summary

Data Block 1

387 F2 individuals

101 survivors



Teresa Popp
PhD candidate



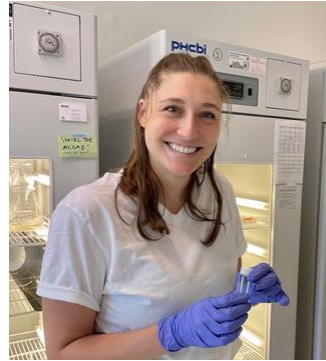
Benjamin Kleinerman
Lab technician

II – Data summary

Data Block 1

387 F2 individuals

101 survivors



Teresa Popp
PhD candidate



Benjamin Kleinerman
Lab technician

Data Block 2

514 F2 individuals

374 survivors

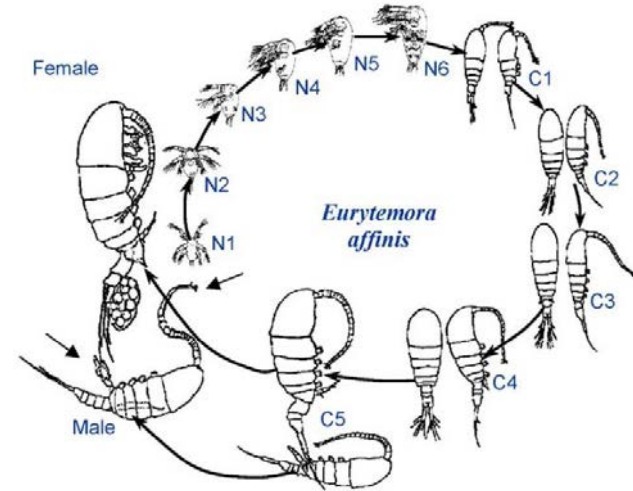


Estelle Dupré (M1) & Dorian Decamus (M2)

II – Data summary

Individual-level data on
fitness related traits

Development time

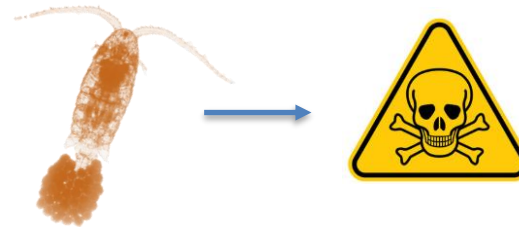


II – Data summary

Individual-level data on
fitness related traits

Development time

Survival rate



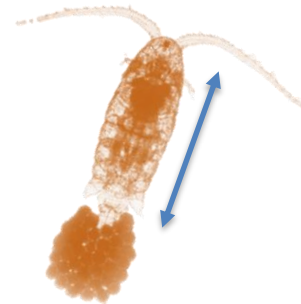
II – Data summary

Individual-level data on
fitness related traits

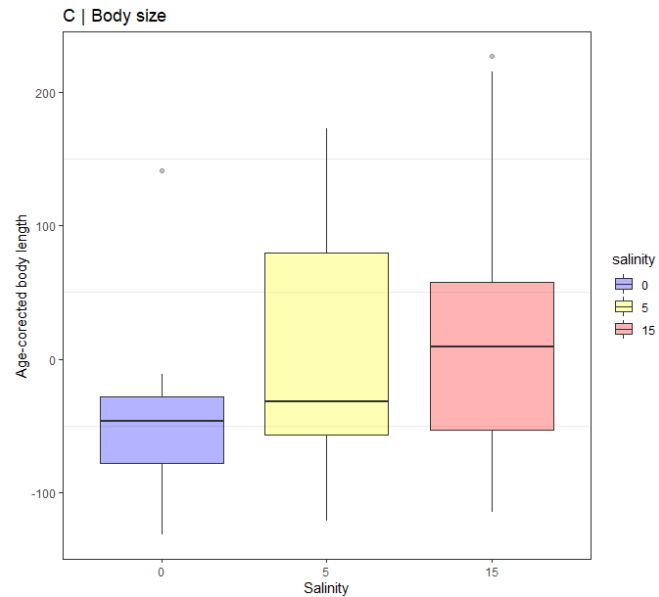
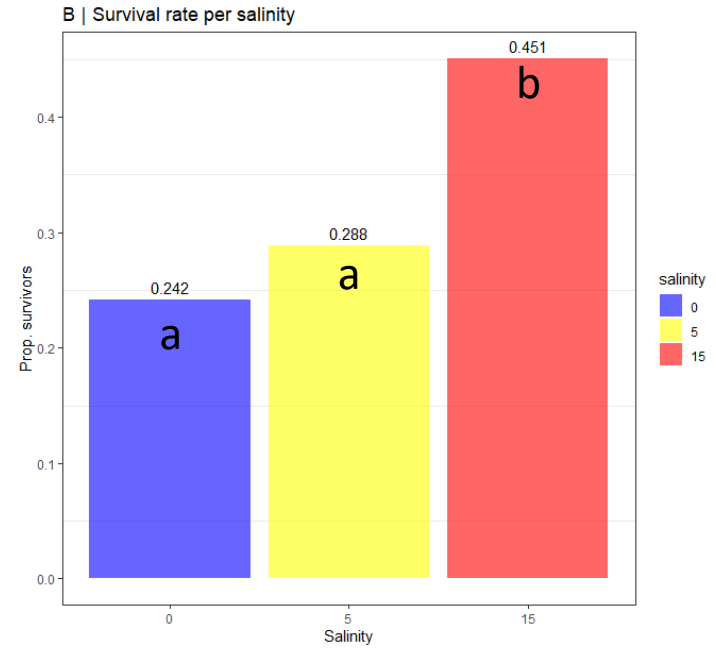
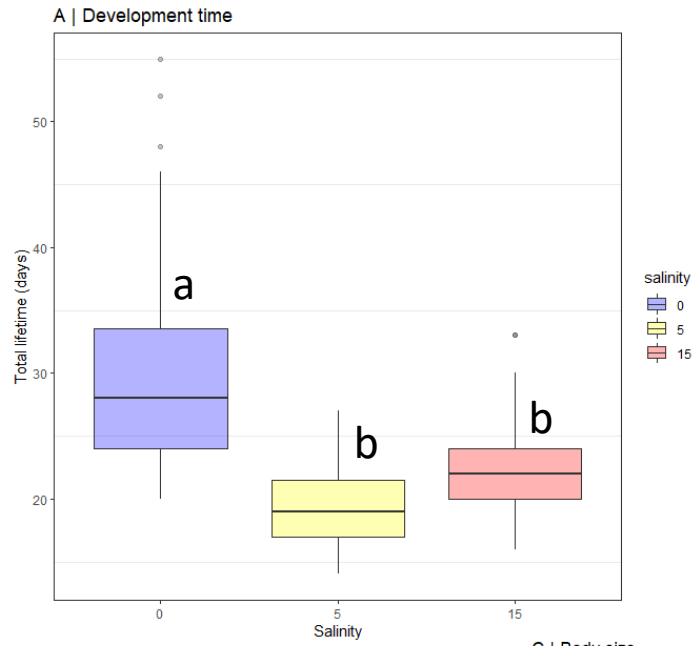
Development time

Survival rate

Body size

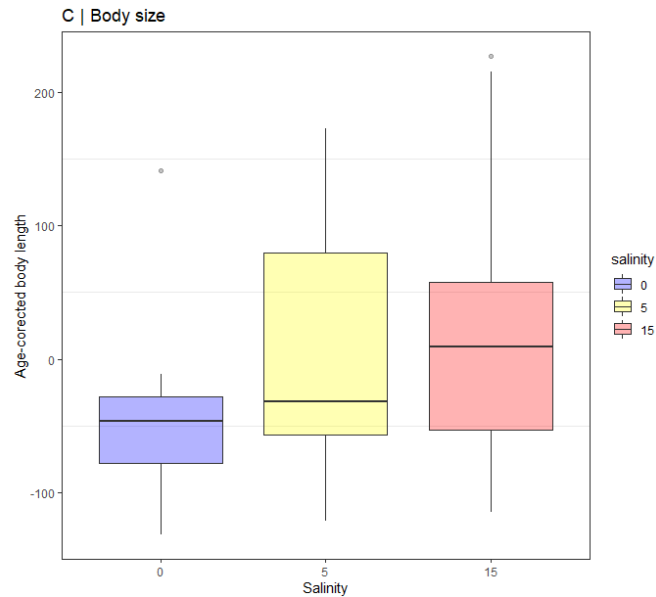
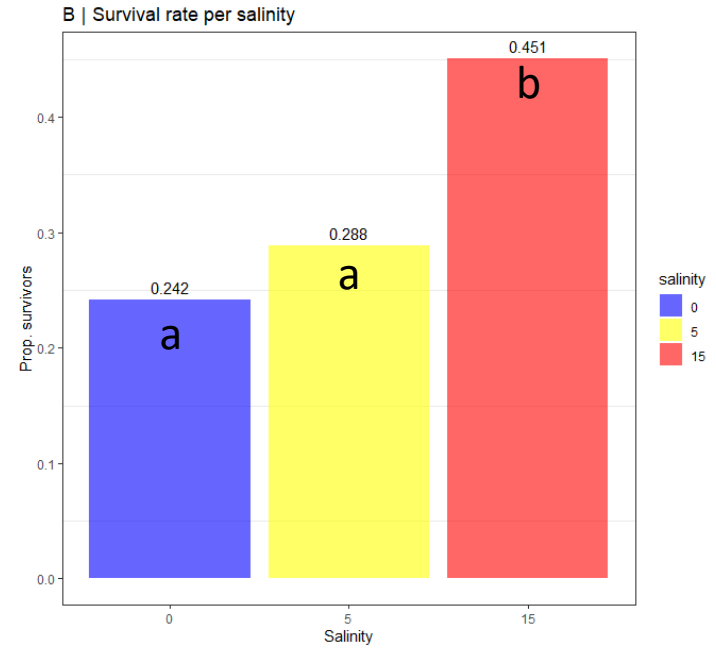
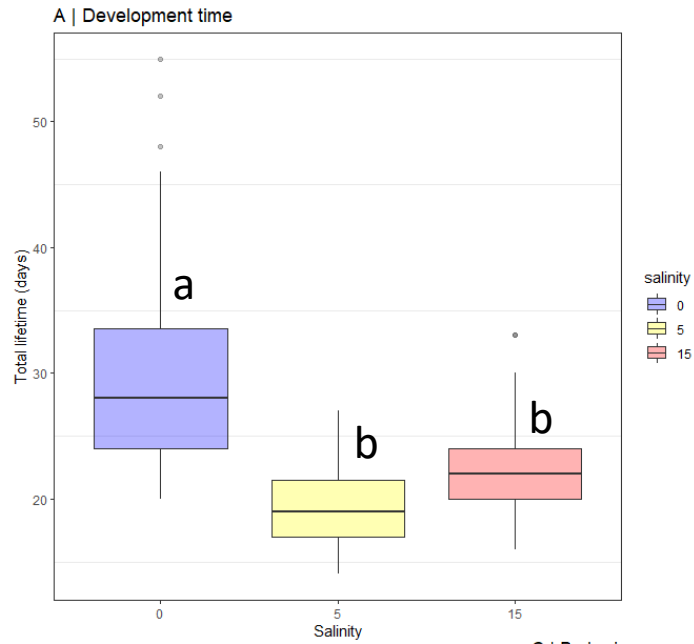


II – Preliminary results block 1



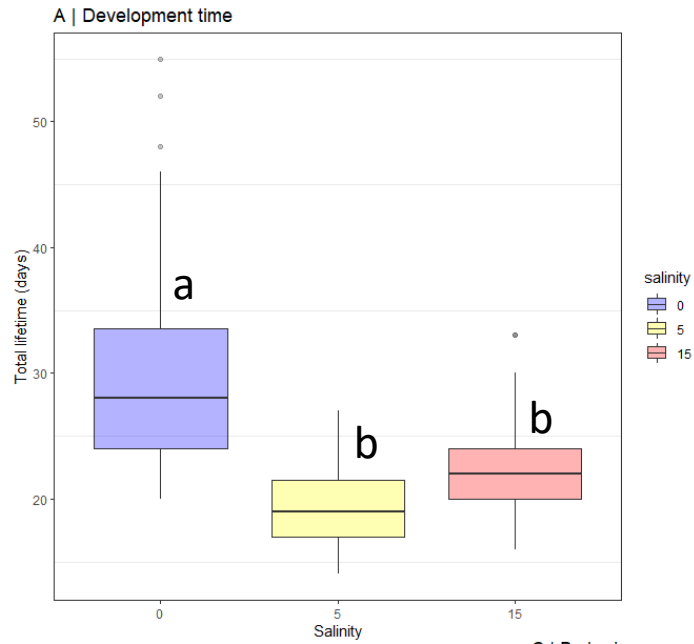
II – Preliminary results block 1

Slower development time in freshwater

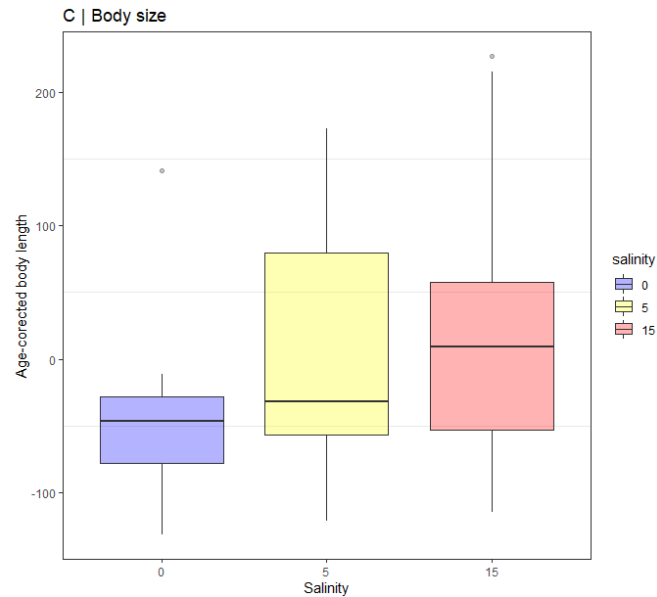
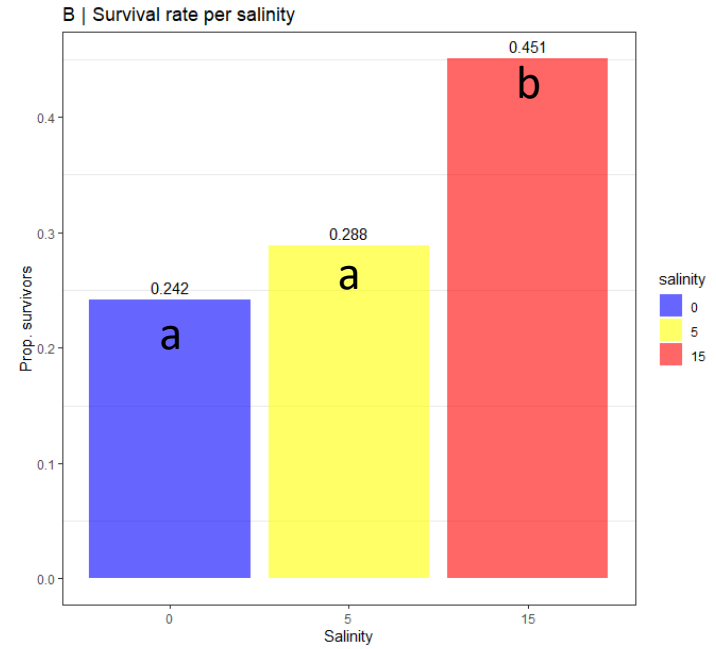


II – Preliminary results block 1

Slower development time in freshwater

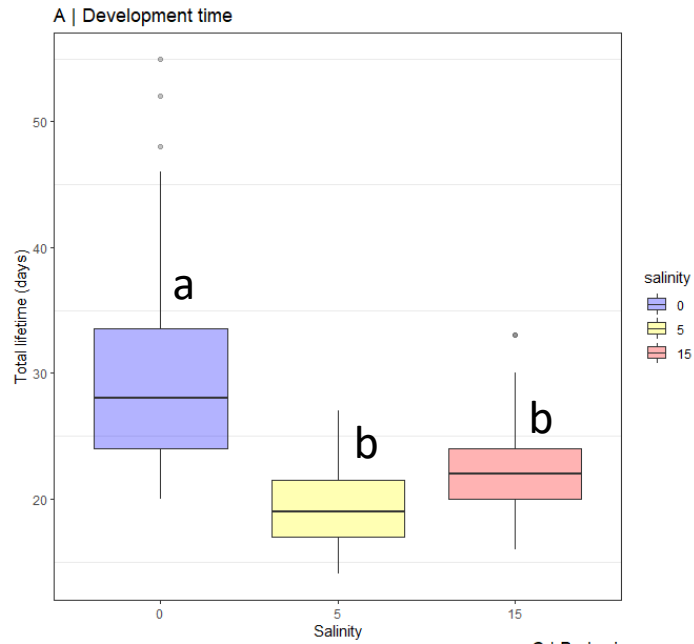


Higher mortality rate in freshwater

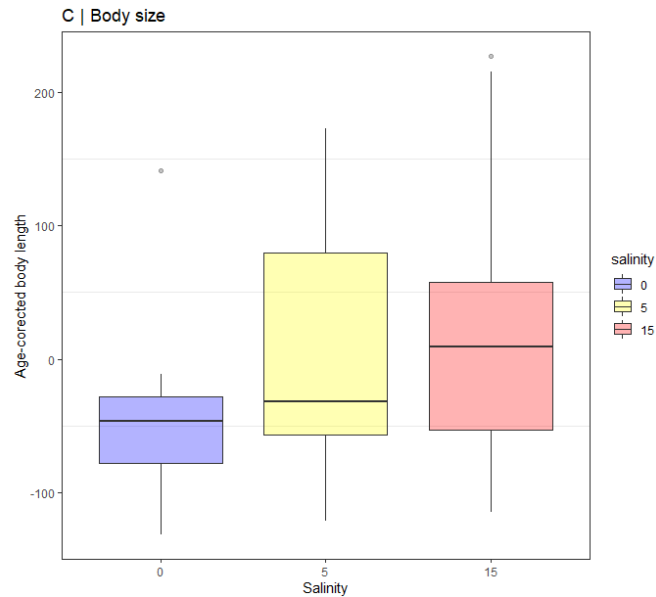
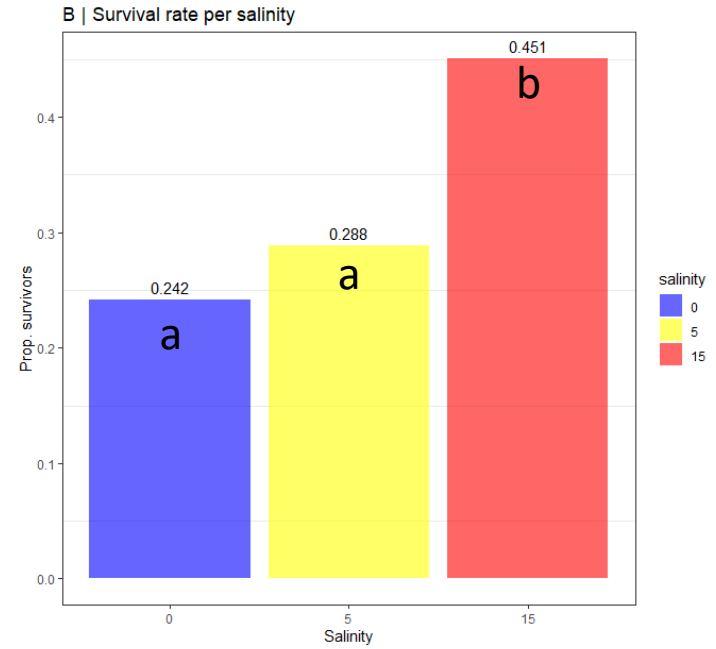


II – Preliminary results block 1

Slower development time in freshwater

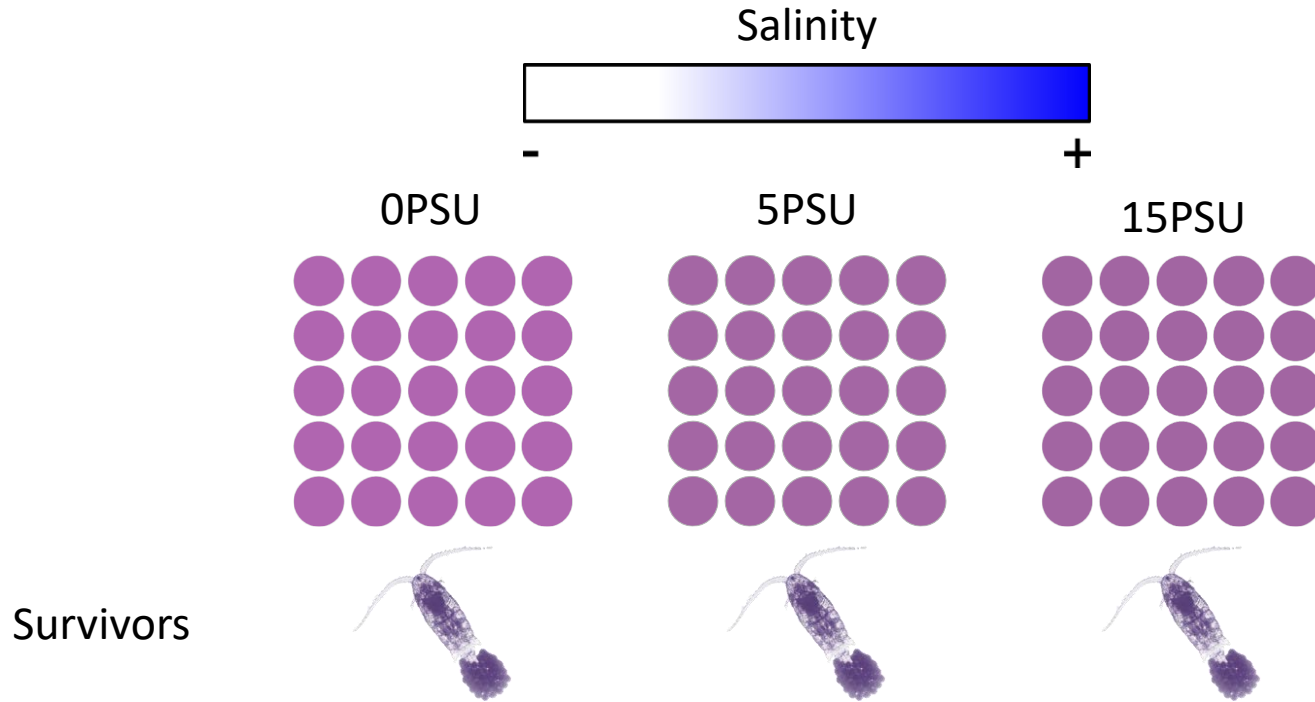


Higher mortality rate in freshwater

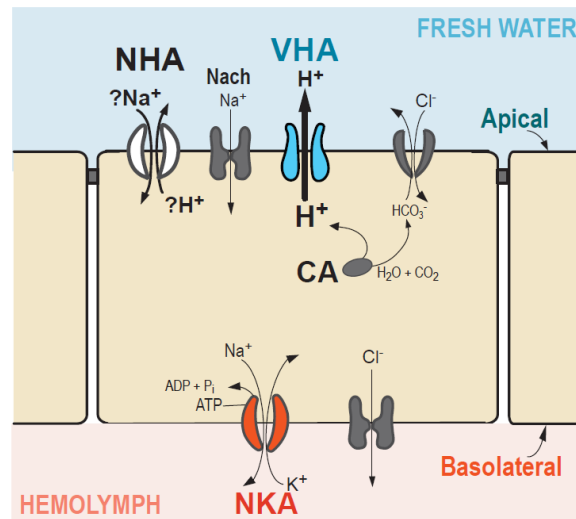


**Smaller size in freshwater
(NS)**

II – Genotyping at candidate loci

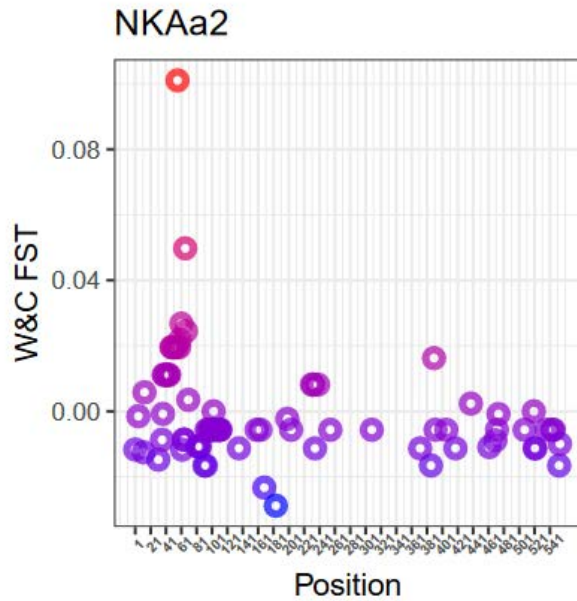
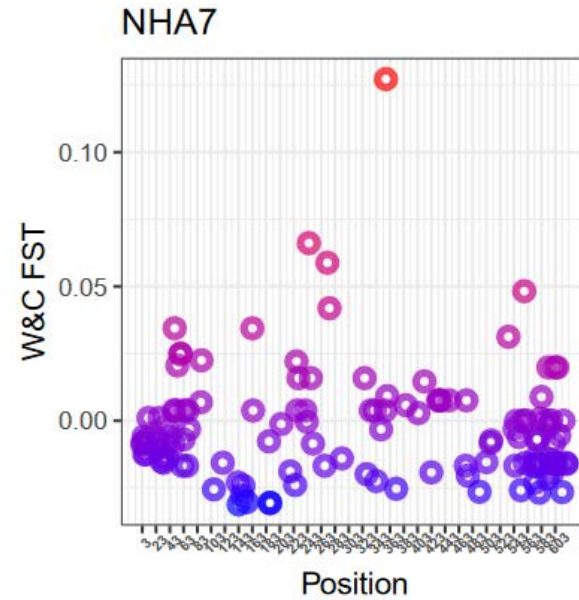
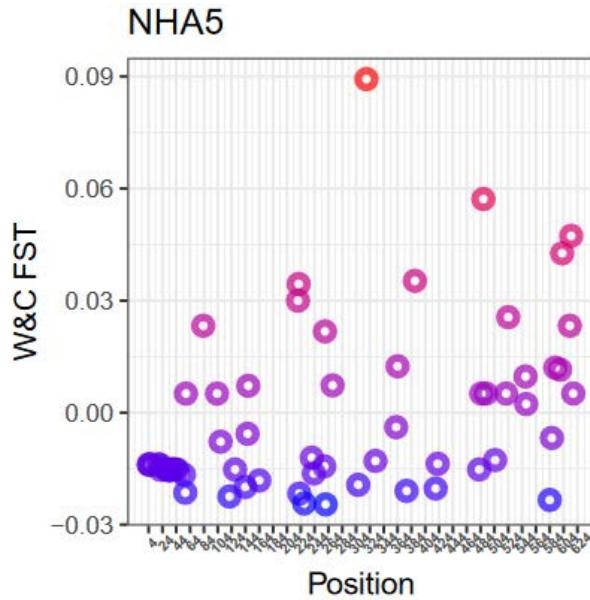


Individual-level data:
genotype at candidate
genes



NHA5
NHA7
NKAA2

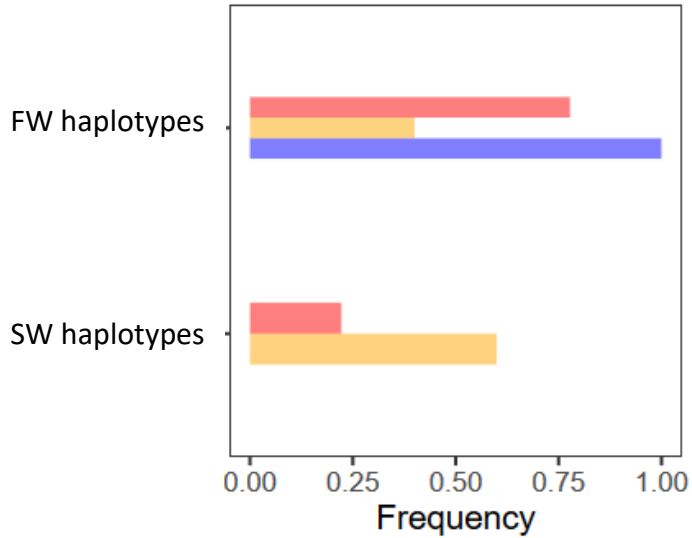
II – Preliminary results block 1



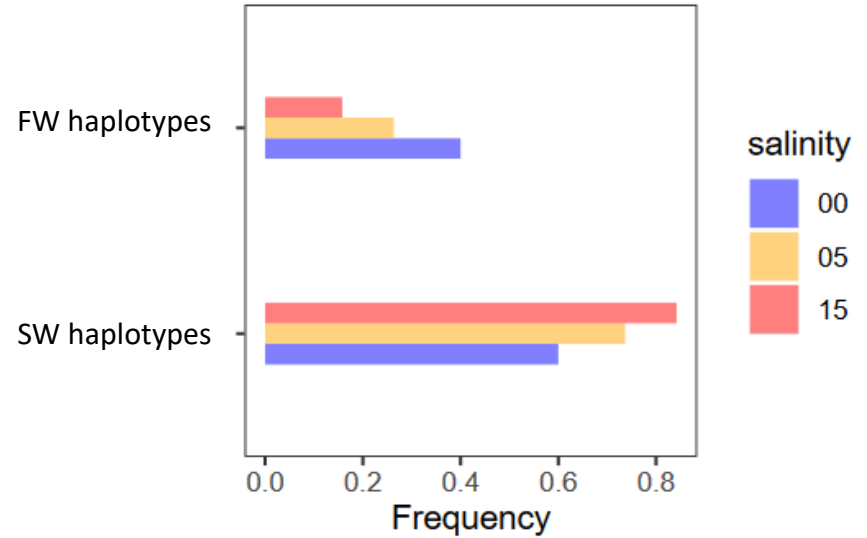
Genetic differentiation between survivors of salt- and fresh-water treatment

II – Preliminary results block 1

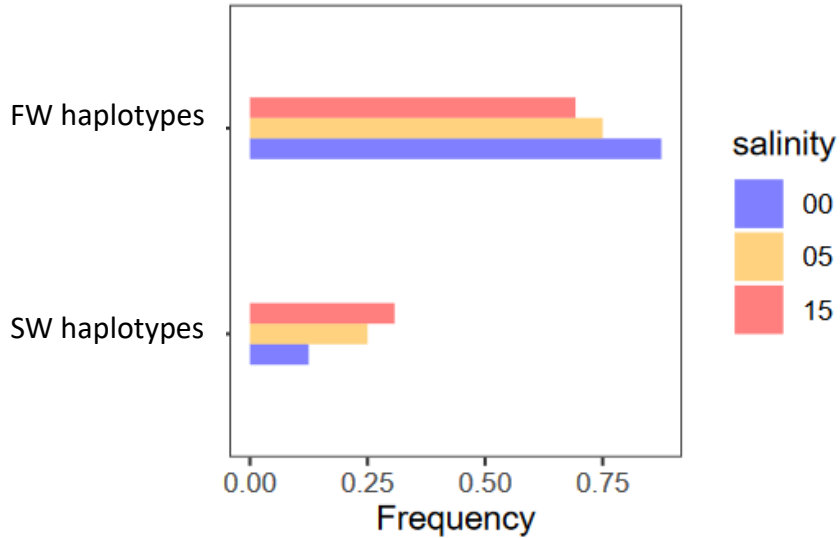
NHA5



NHA7

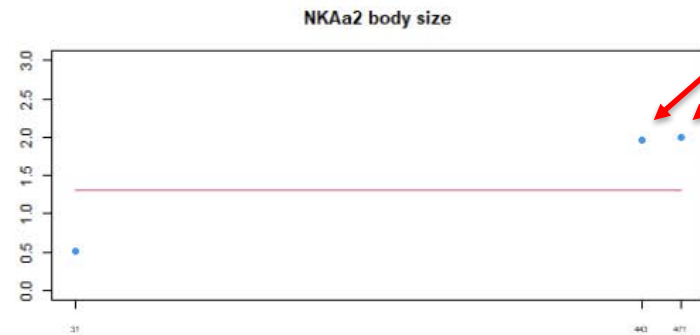
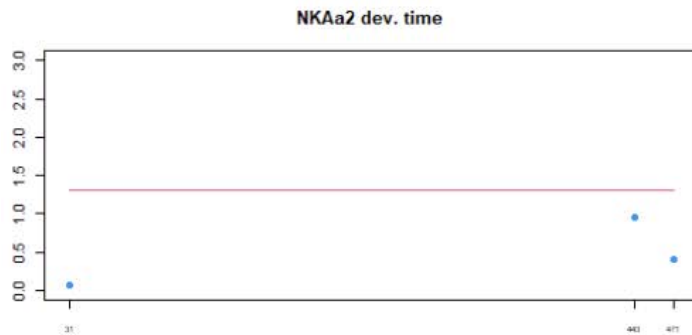
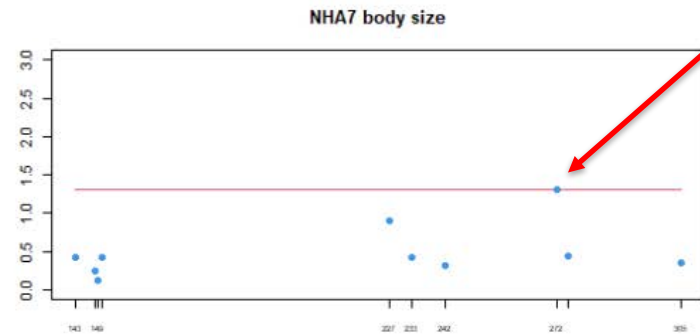
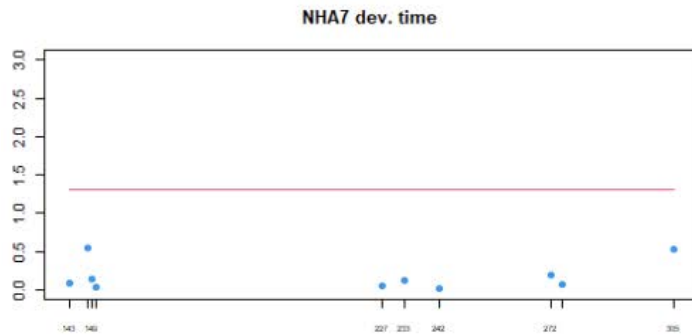
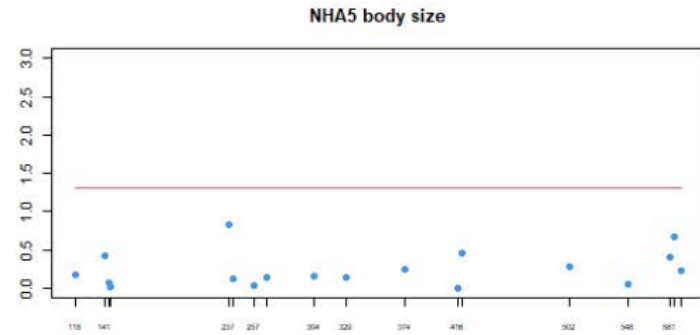
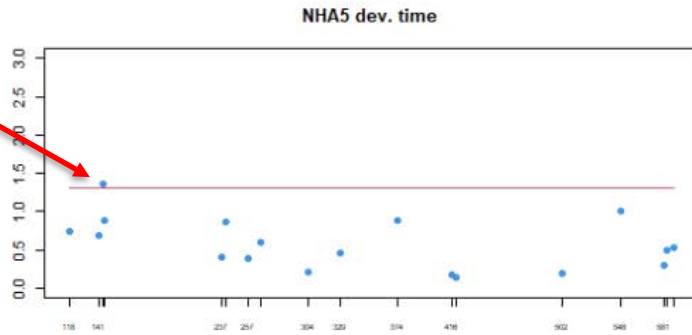


NKAa2



Differential distribution of salt- and freshwater haplotypes in salt- and freshwater treatments

II – Preliminary results block 1



$$Y = \mu + SNP_i + sex + (1|F0)$$

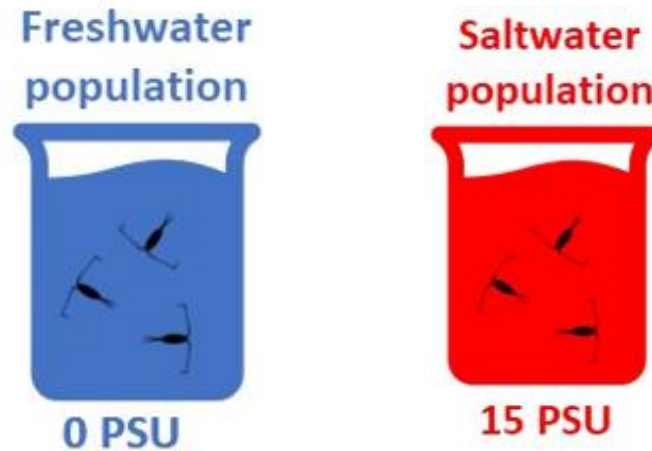
II – Next steps

Genotyping block 2

Finer resolution on genetic association

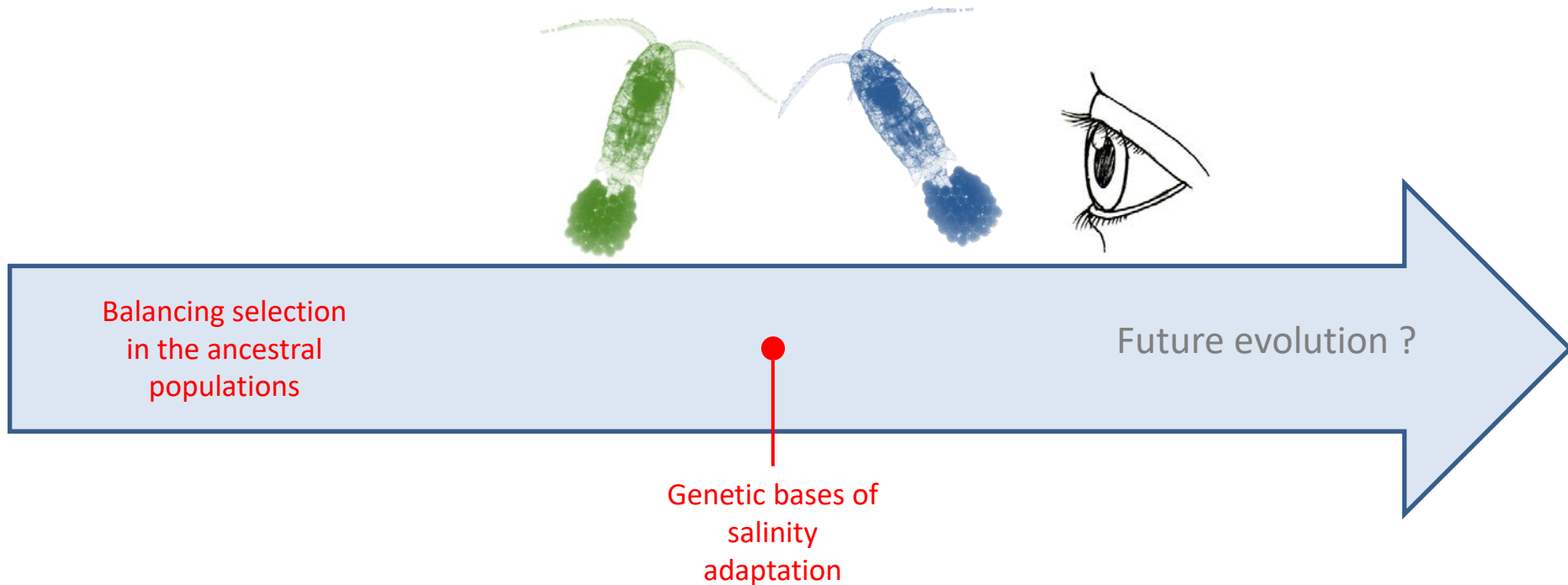
Pool-seq

Shifts in genome-wide allele frequencies between FW and SW



II – Conclusions

Identifying the fitness effects of osmoregulatory genes in freshwater conditions



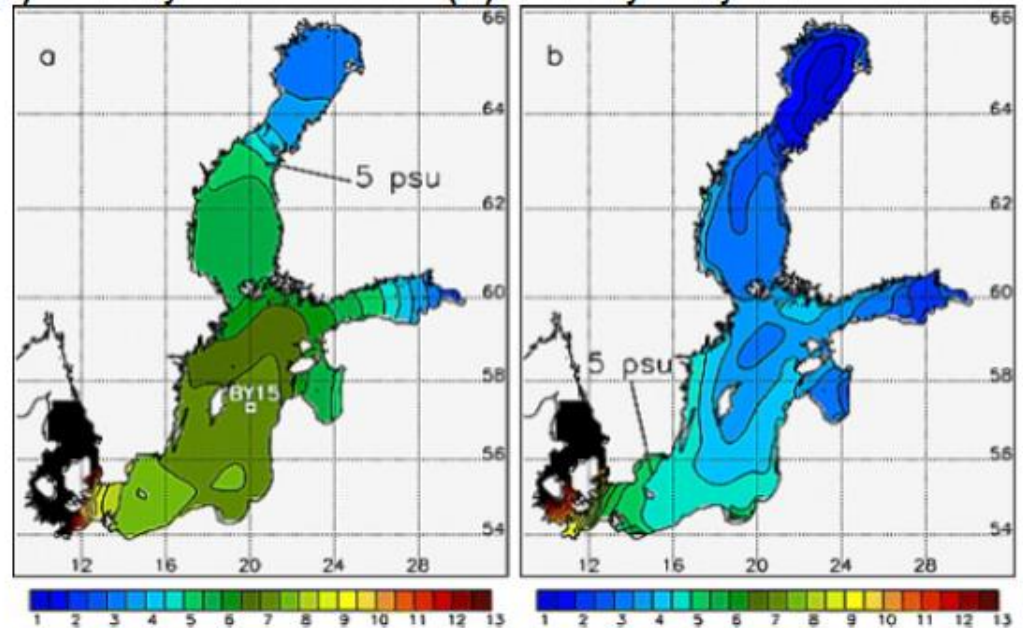
II – Conclusions

Salinity decrease in the Sea

Strong selection pressure on marine populations

Using data from genetic association in predictive models of evolutionary rescue

(a) Salinity before 1996 (b) Salinity Projections 2071-2100



Meier et al. 2006

Take home messages

Evolution is predictable (sometimes)

Take home messages

Evolution is predictable (sometimes)

**Importance of ancestral pop. history,
genetic architecture of traits, genomic
landscape, etc.**

Take home messages

Evolution is predictable (sometimes)

Importance of ancestral pop. history,
genetic architecture of traits, genomic
landscape, etc.

**Important for predicting/modelling
response to future selection pressures**

Thank you

Relaxed risk of predation drives parallel evolution of stickleback behavior

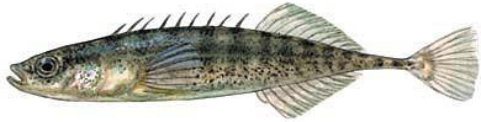
Antoine Fraimout,^{1,2,3} Elisa Päiviö,¹ and Juha Merilä^{1,2}

Age-dependent genetic architecture across ontogeny of body size in sticklebacks

Antoine Fraimout¹, Zitong Li^{1,2}, Mikko J. Sillanpää³ and Juha Merilä^{1,4}

Contact: fraimout.antoine@gmail.com

Thank you



Elisa Päiviö
Juha Merilä
Niina Nurmi
Miinastiina Issakainen
Niko Björkell
Nicolas Navarro
Benjamin Weigel
Pierre Nouhaud



Benny Kleinerman
Teresa Popp
Corentin Baumlin
Estelle Dupré
Dorian Decamus
Delphine Bonnet
Catherine Lorin-Nebel
Carol Lee



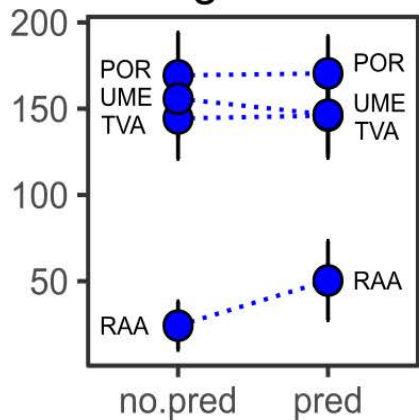
SUOMEN AKATEMIA
FINLANDS AKADEMI
ACADEMY OF FINLAND



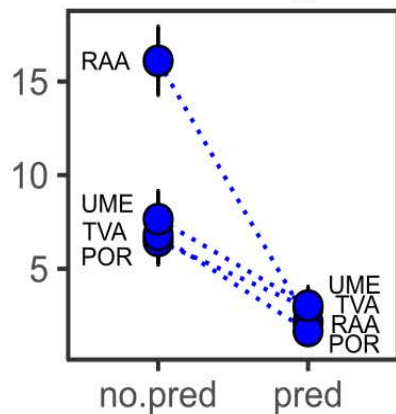
UNIVERSITY OF HELSINKI



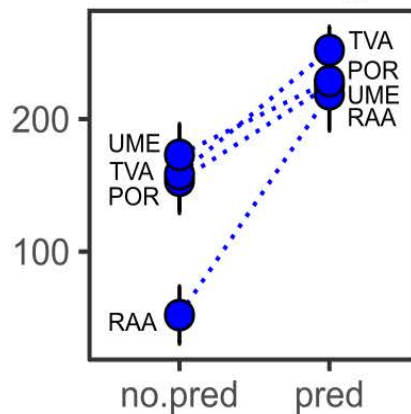
Emergence time



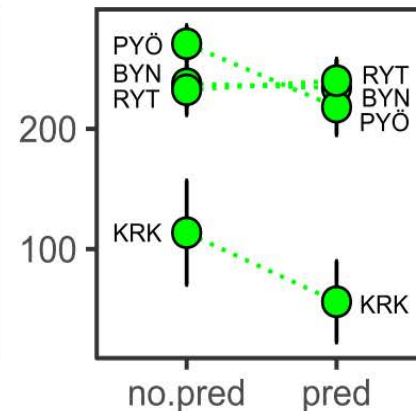
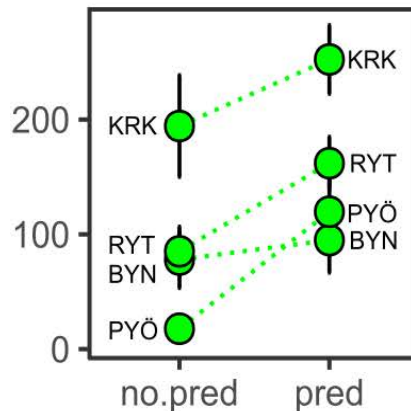
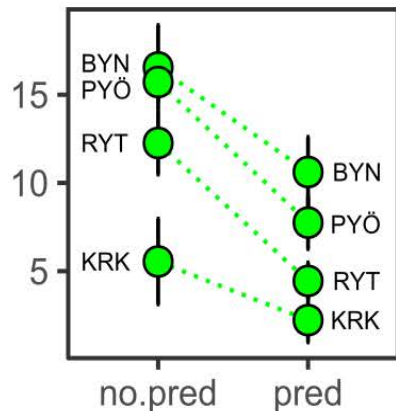
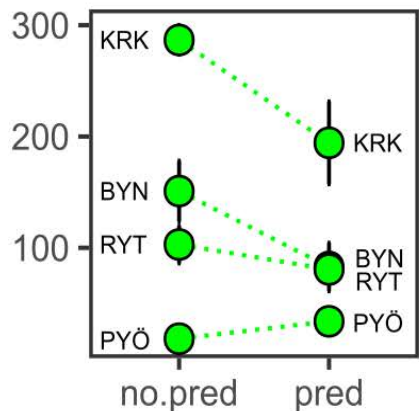
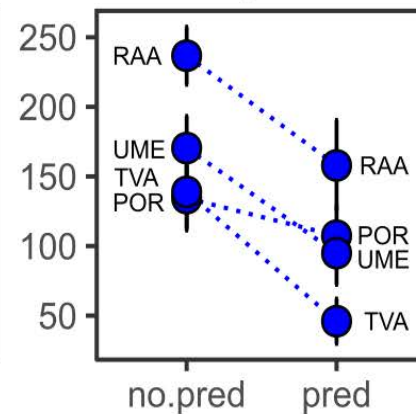
Feeding



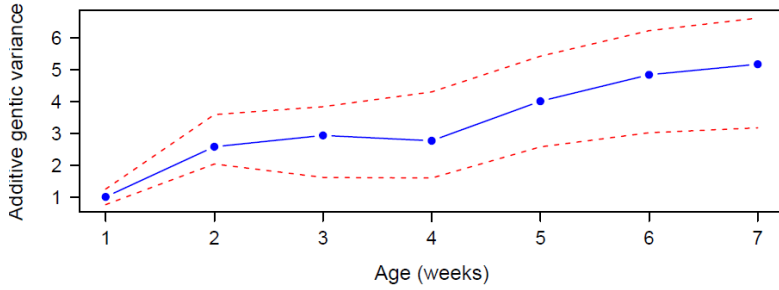
Risk-taking



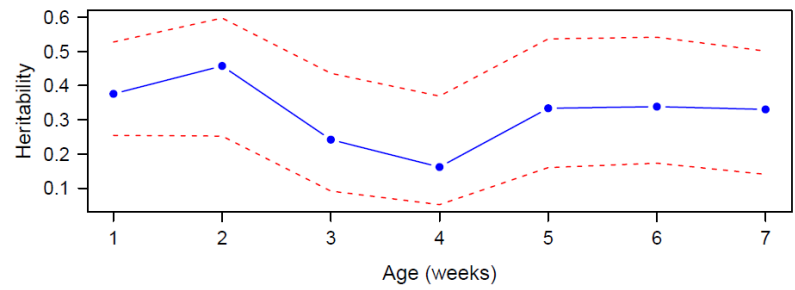
Open



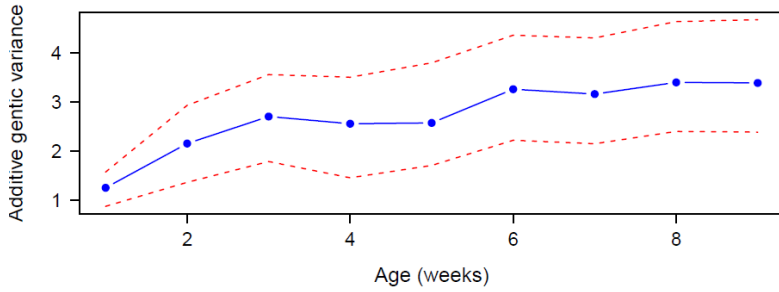
HEL x RYT | V_a



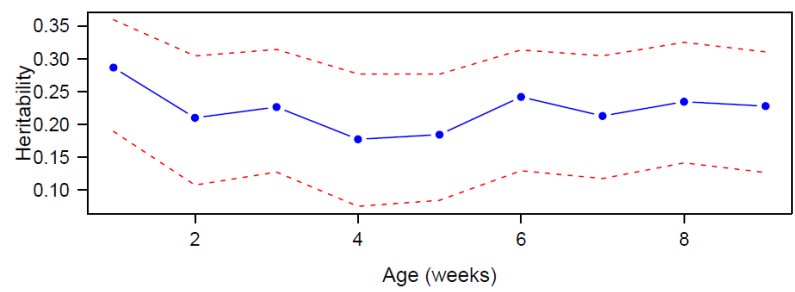
HEL x RYT | h^2



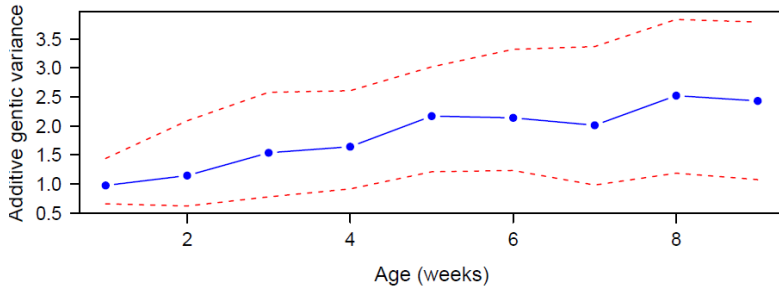
HEL x PYÖ | V_a



HEL x PYÖ | h^2



HEL x BYN | V_a



HEL x BYN | h^2

