

Population dynamics of the periwinkle *Littorina littorea* (Linnaeus, 1758) in the East Frisian Wadden Sea

Diplomarbeit

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Animal Biodiversity and Evolutionary Biology
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Supervisors: Prof. Dr. Gabriele Gerlach, Dr. Thomas Friedl

March 19, 2010

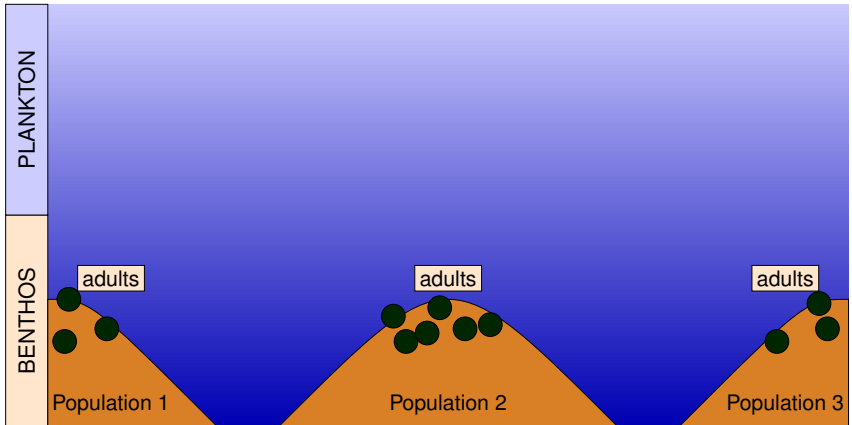
Outline

- 1 Introduction
- 2 Objectives
- 3 Methods
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- 5 Conclusions

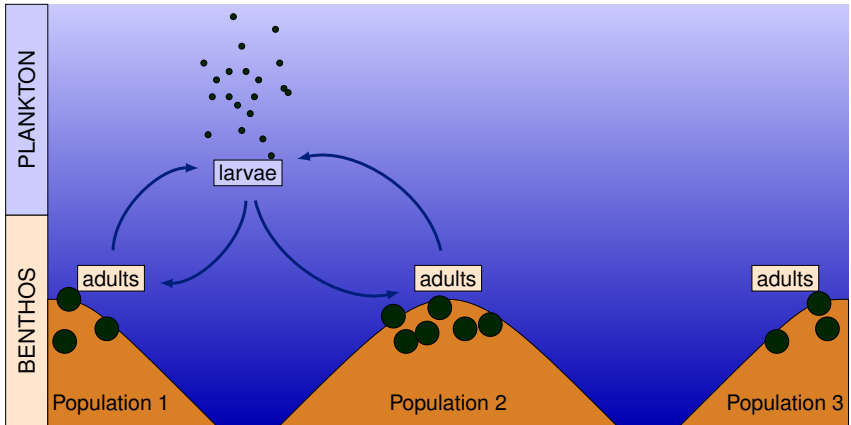
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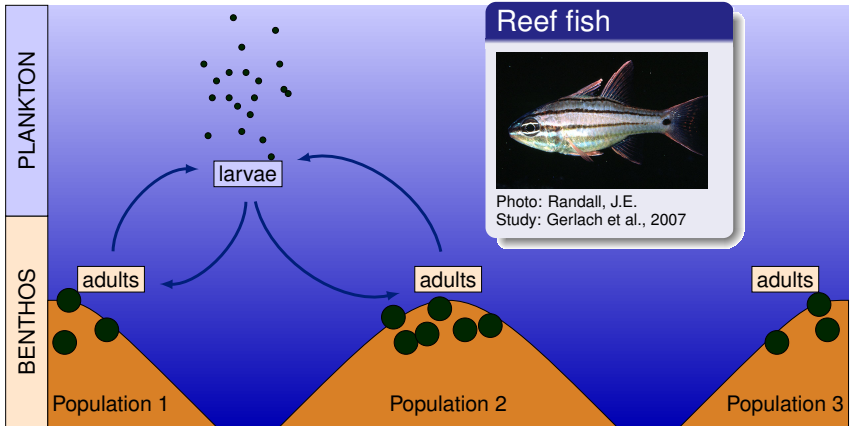
Populations get Connected by Dispersing Larvae



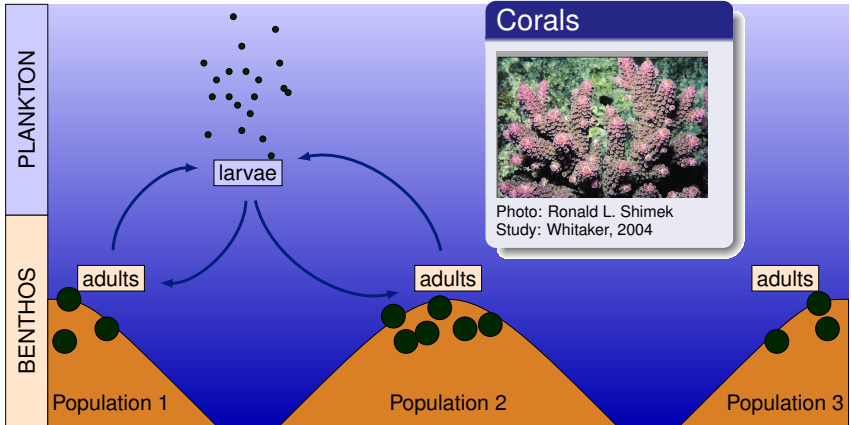
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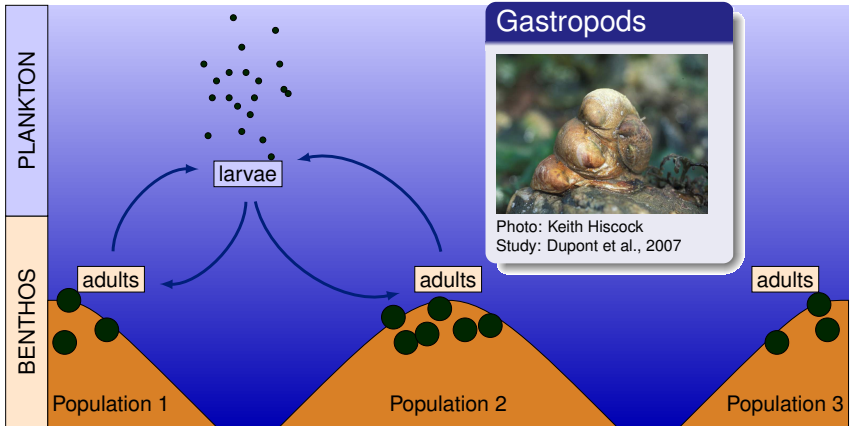
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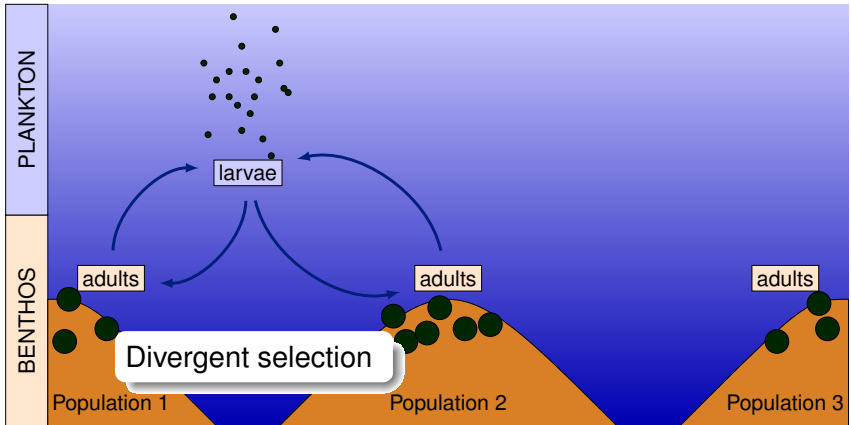
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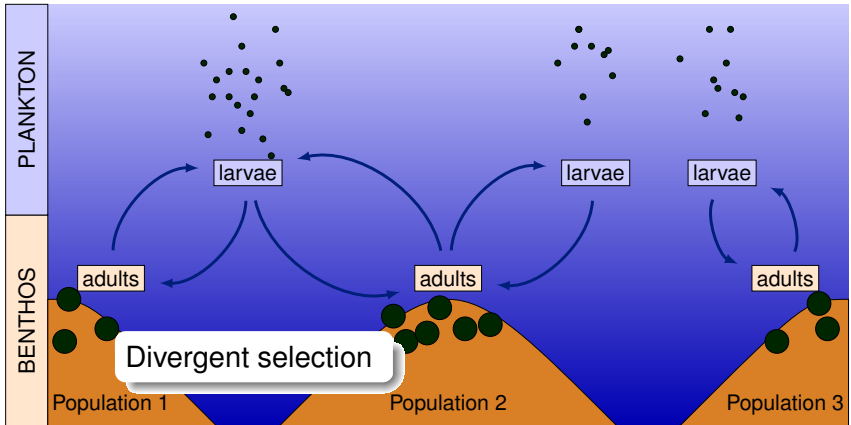
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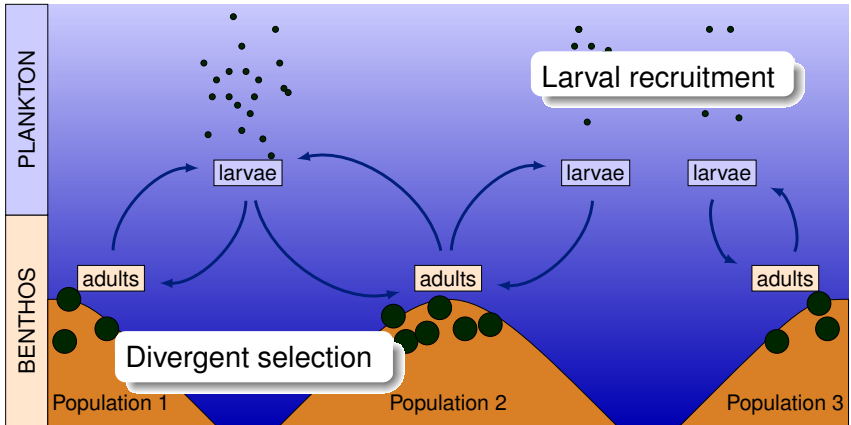
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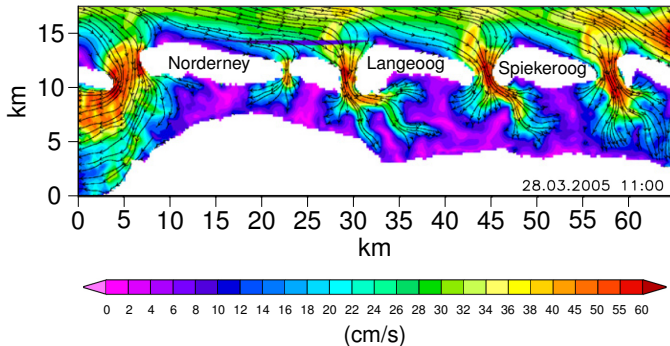
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Populations get Connected by Dispersing Larvae

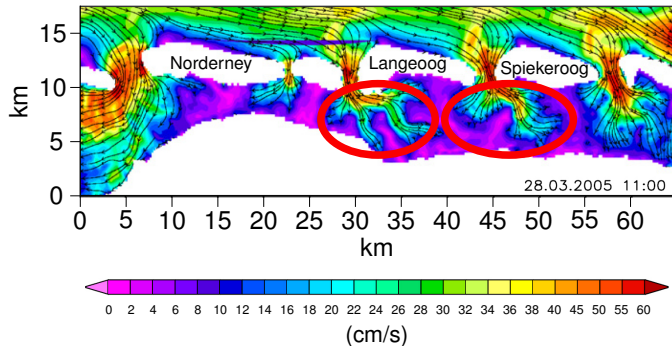


Hydrodynamics of the Wadden Sea



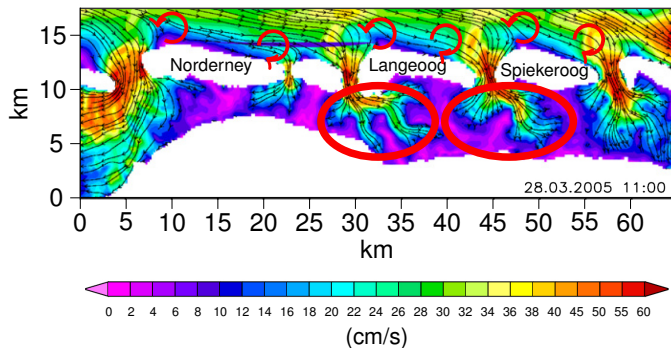
(Staneva et al., 2009)

Hydrodynamics of the Wadden Sea



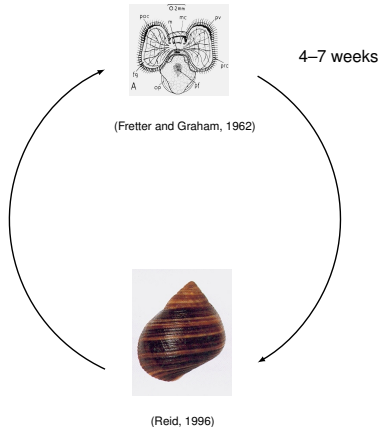
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Hydrodynamics of the Wadden Sea



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The Periwinkle's Life Cycle Includes a Planktotrophic Larva



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Main Objectives of the Study

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- Larval recruitment?
- Population preference?
- Morphological differentiation?
- Genetic differentiation?

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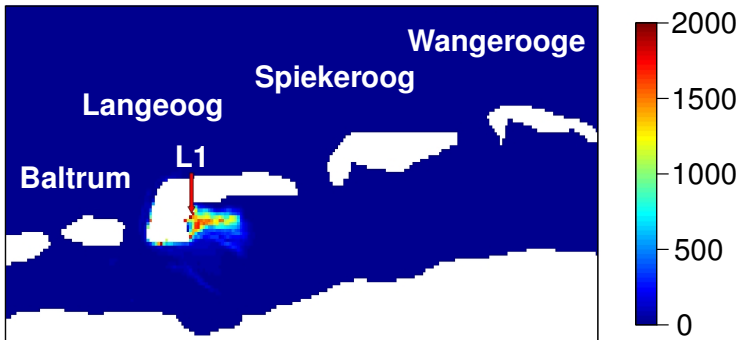
- 1 Introduction
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Outline

3 Methods

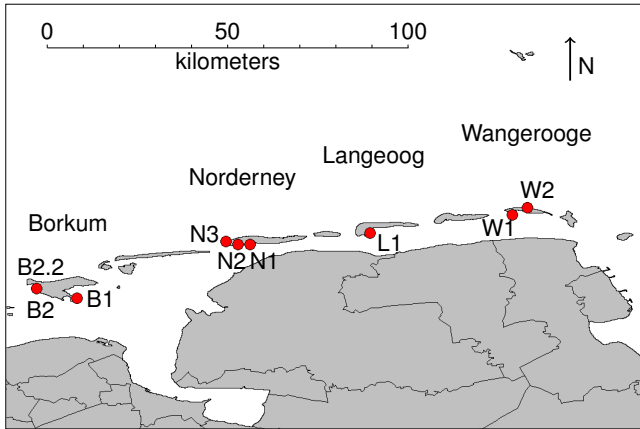
- Larval Recruitment
- Population Preference
- Shell Morphology
- Population Genetics

Larval Dispersal in the Wadden Sea was Simulated

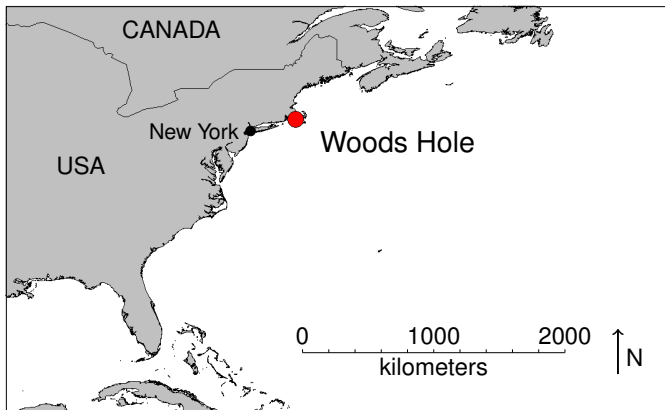


Programmed by: Gräwe, U.

Sampling Sites



Sampling Sites



Outline

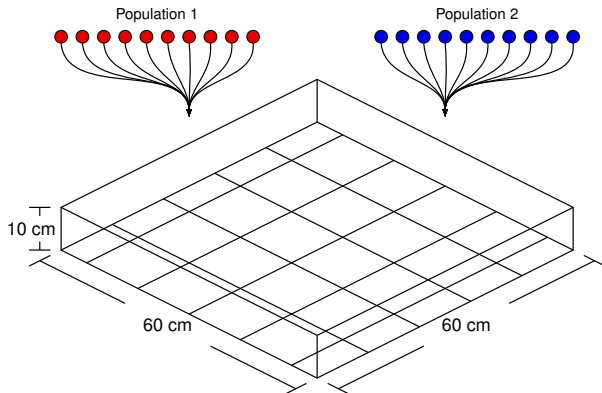
- 3 **Methods**
 - Larval Recruitment
 - Population Preference**
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Conspecifics Aggregate on Hard Bottom Substrate

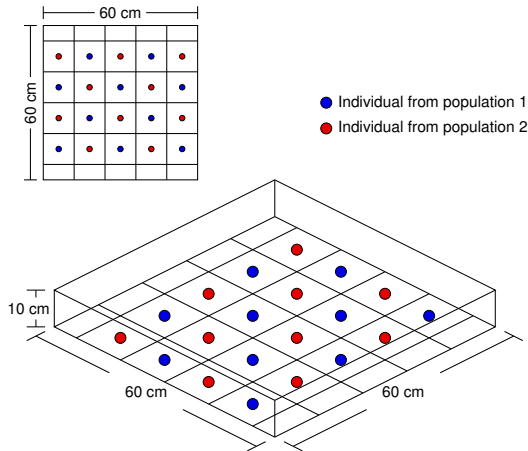


(Geller–Grimm, 2000)

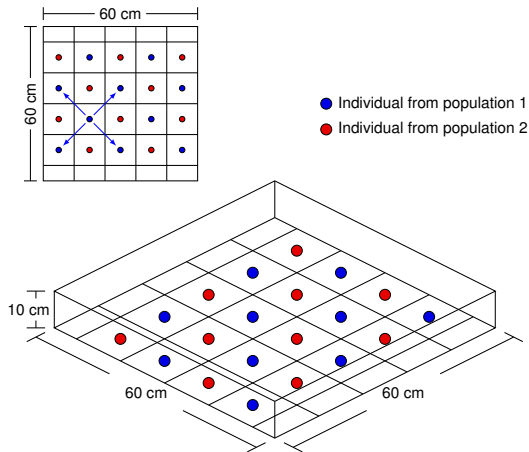
Snails of 2 Populations Aggregated in Basins



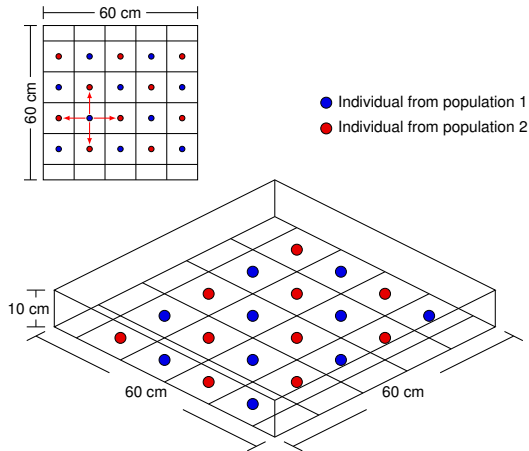
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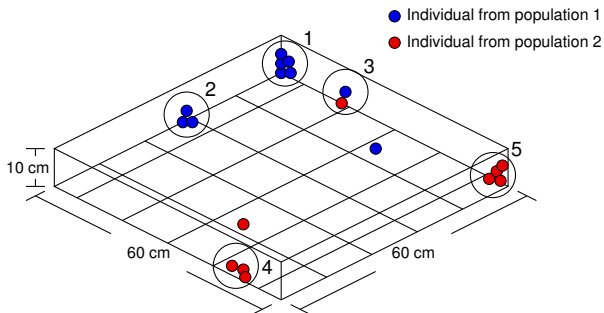


Snails of 2 Populations Aggregated in Basins



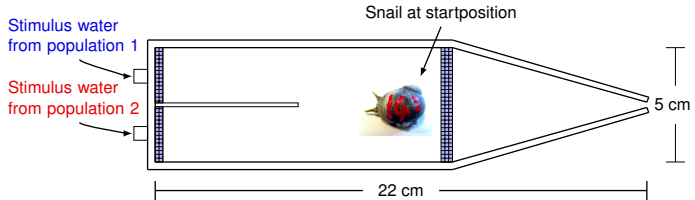
Analysis of Aggregation Experiments

... one hour later

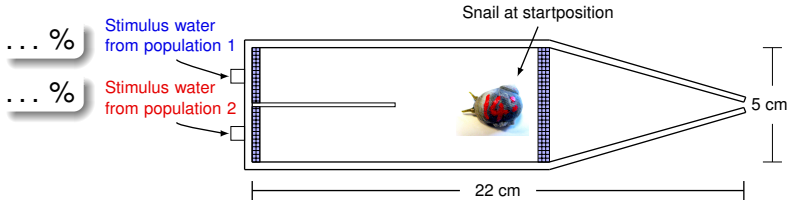


- Population Preference Index PPI -

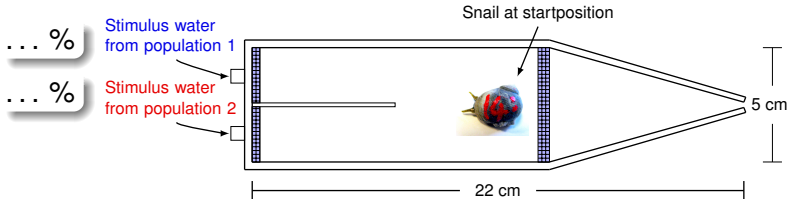
Testing Snails in Olfactory Choice Flumes



Testing Snails in Olfactory Choice Flumes



Testing Snails in Olfactory Choice Flumes

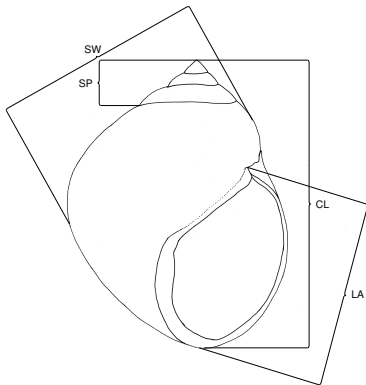


Wilcoxon signed-rank test

Outline

- 3 **Methods**
 - Larval Recruitment
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 - **Shell Morphology**
 - Population Genetics

Measurements of the Shell



Linear discriminant analysis

Outline

- 3 **Methods**
 - Larval Recruitment
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 - Shell Morphology
 - **Population Genetics**

Genetic Differentiation at Microsatellite Markers

- 48–55 individuals/population
- 5 microsatellite loci
- Differentiation index D_{est} (Jost, 2008)

Outline

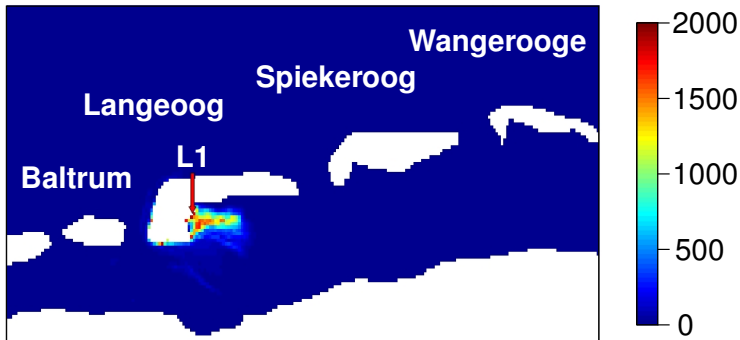
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4 Results

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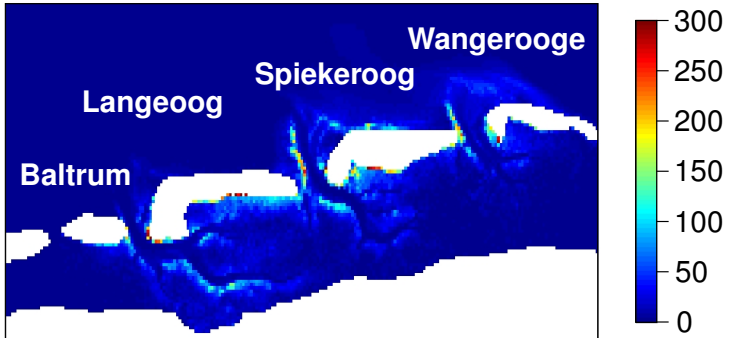
No Local Recruitment by Passive Drift in the EFWS



Programmed by: Gräwe, U.

No Local Recruitment by Passive Drift in the EFWS

... one week later



Programmed by: Gräwe, U.

Outline

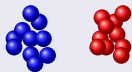
4

Results

- Larval Recruitment
- **Population Preference**
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Snails Prefer Conspecifics of the Own Population

Population-wise aggregation



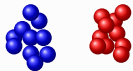
PPI significant ($p \leq 0.1$) in 6 of 17 tests

Attraction to volatile chemicals

No significant preference in any of 18 tests

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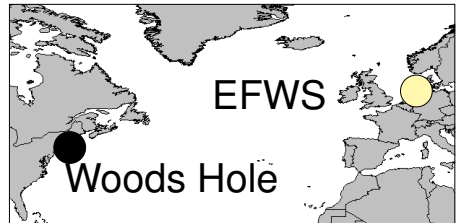
Outline

- 4 **Results**
 - Larval Recruitment
 - Population Preference
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Populations Differ Morphologically

Shell morphology differs between . . .

- Woods Hole – EFWS
- North coasts – South coasts
- North coasts
- South coasts

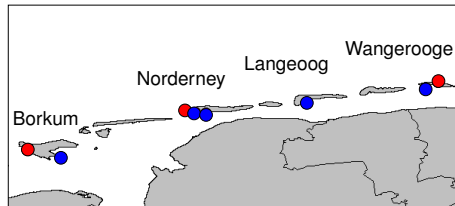


Wilks' Lambda = 0.867, $p < 0.001$ ***

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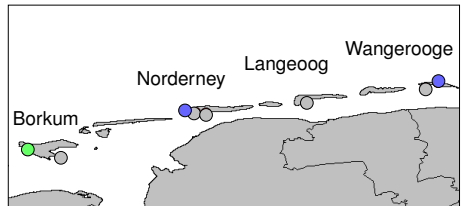


Wilks' Lambda = 0.802, $p < 0.001$ ***

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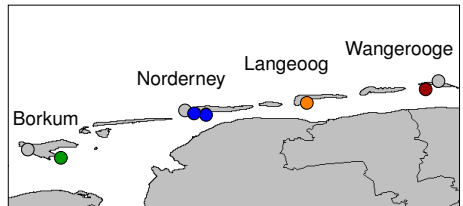


Wilks' Lambda = 0.135, $p < 0.001$ ***

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Wilks' Lambda = 0.731, $p < 0.001$ ***

Outline

4

Results

- Larval Recruitment
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- **Population Genetics**

Genetic Distance ...

... between Woods Hole and East Frisian populations

$$D_{\text{est}} = 0.033\text{--}0.057^{***}$$
$$p \leq 0.05$$

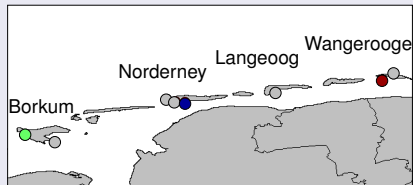


Genetic Distance ...

... between islands

$$D_{\text{est}} = -0.007 - 0.001$$

$$p > 0.05$$



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Do the Results Indicate Reproductive Isolation?

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Unanswered questions

- Larval behavior?
- Intrinsic differences
- Recognition cues?
- Assortative mating?
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- Phenotypic plasticity?

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Overall conclusion

Acknowledgements

Gabriele Gerlach

Thomas Glatzel

Thomas Friedl

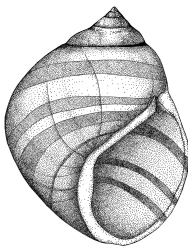
Ulf Gräwe

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Achim Wehrmann

Anke Müller

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Wattenmeerstiftung

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Jana Deppermann

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Marén Bökamp

For Further Reading I



Reid, D.G. (1996)

Systematics and Evolution of Littorina.

The Ray Society, London.



Cowen, R.K. & Sponaugle, S. (2009)

Larval dispersal and marine population connectivity

Annual Review of Marine Science 1:443–466.

For Further Reading II



Staneva, J.; Stanev, E.V.; Wolff, J.-O.; Badewien, T.H.; Reuter, R.; Flemming, B.; Bartholomä, A. & Bolding, K. (2009)

Hydrodynamics and sediment dynamics in the German Bight. A focus on observations and numerical modelling in the East Frisian Wadden Sea.

Continental Shelf Research 29(1):302–319.

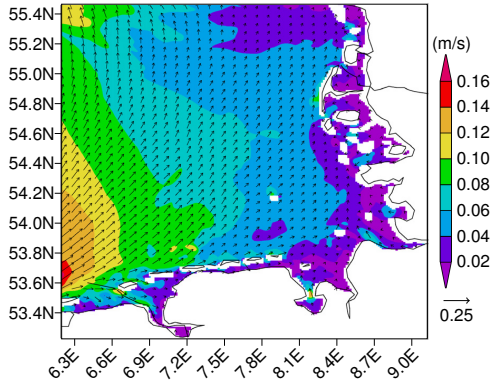


Jost, L. (2008)

Gst and its relatives do not measure differentiation.

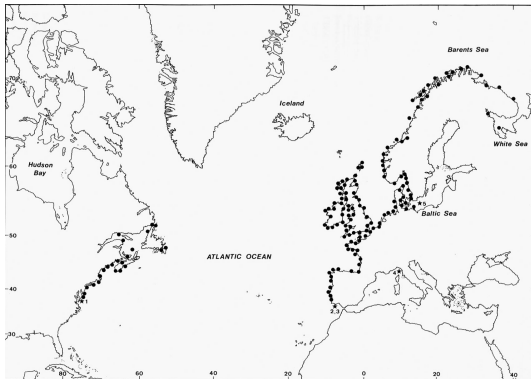
Molecular Ecology 17(18):4015–4026.

Residual Current in the German Bight



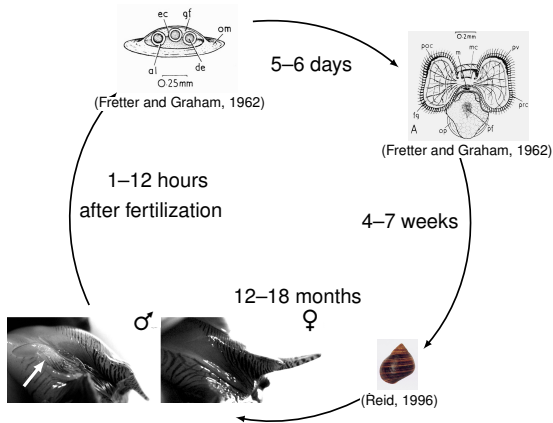
(Staneva et al., 2009)

L. littorea Occurs on Both Sides of the Atlantic



(Reid, 1996)

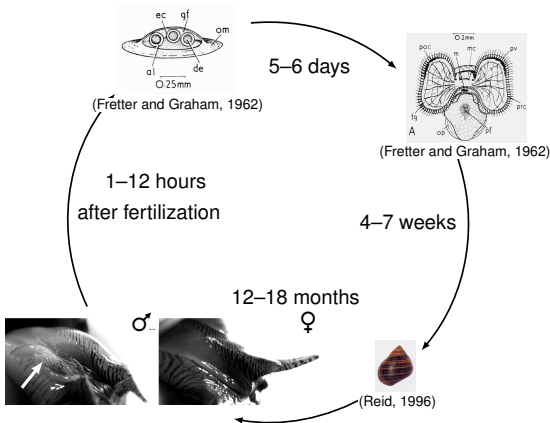
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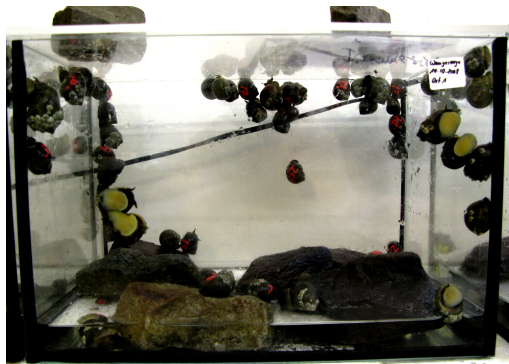
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The Periwinkle's Life Cycle Includes a Planktotrophic Larva



Sampled Snails Were Kept in Aquaria



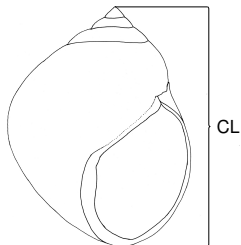
Snails Were Individually Characterized



Shell height

Barnacle fouling

Sex



Snails Were Individually Characterized



Shell height

Barnacle fouling

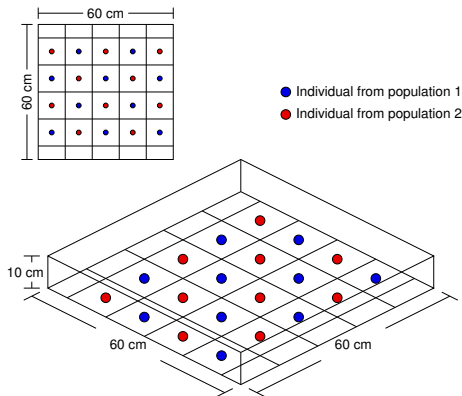
Sex



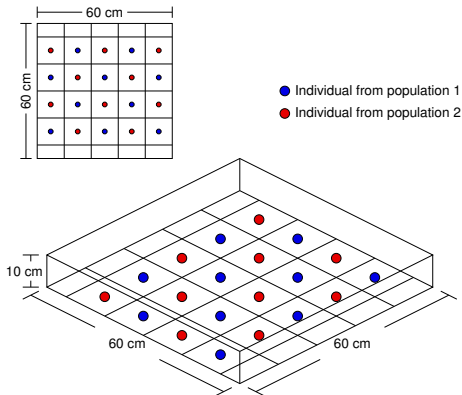
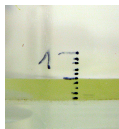
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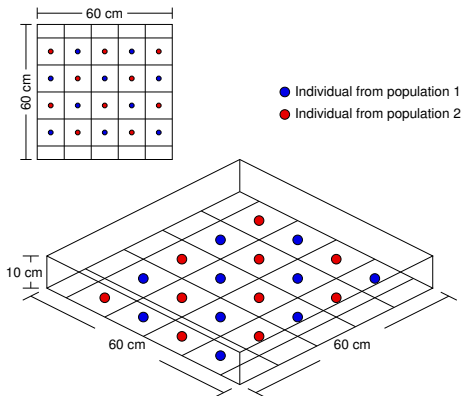
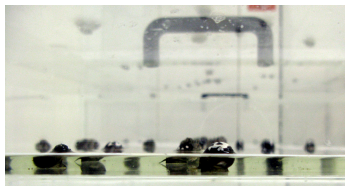
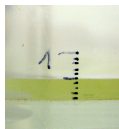
Aggregation Experiments Were Performed in Special Basins



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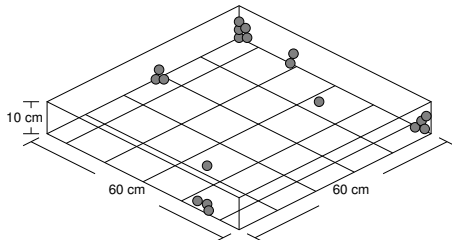


Aggregation Experiments Were Performed in Special Basins



Detailed Analysis of Aggregation experiments

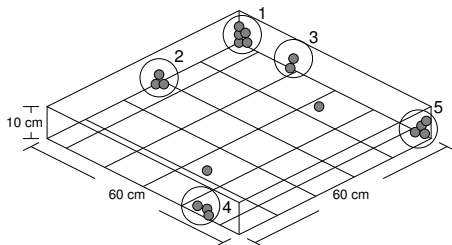
... one hour later



... 15 tests at least



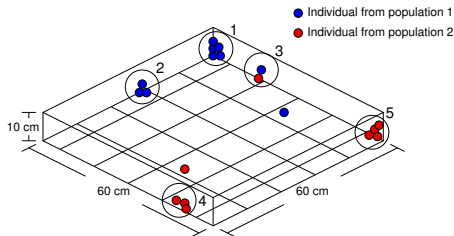
Detailed Analysis of Aggregation experiments



Are certain types of conspecifics preferred?

- Snails of the same population
- Snails of the same sex
- Snails of the same size

Detailed Analysis of Aggregation experiments

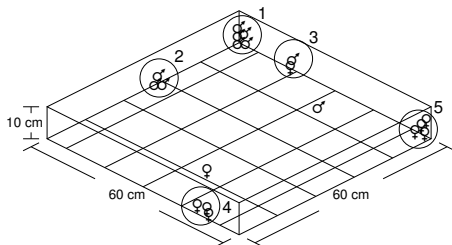


- PPI -

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Detailed Analysis of Aggregation experiments

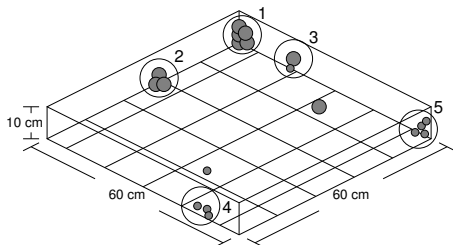


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Detailed Analysis of Aggregation experiments

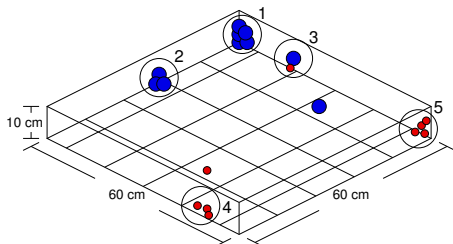


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Detailed Analysis of Aggregation experiments



PPI and Size-PI, both high

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Defining the Population Preference Index

Population mixture



$$\bar{p} =$$

$$var =$$

Real population preference



$$\bar{p} =$$

$$var =$$

Ambiguous



$$\bar{p} =$$

$$var =$$

Defining the Population Preference Index

Population mixture



$$\bar{p} =$$

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Real population preference



$$\bar{p} =$$

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Ambiguous



$$\bar{p} =$$

$$var =$$

Defining the Population Preference Index

Population mixture



$$\bar{p} = 0.5$$

$$var =$$

Real population preference



$$\bar{p} =$$

$$var =$$

Ambiguous



$$\bar{p} =$$

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Defining the Population Preference Index

Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

Real population preference



$$\bar{p} =$$

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Ambiguous



$$\bar{p} =$$

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Defining the Population Preference Index

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Real population preference



$$\bar{p} =$$

$$var =$$

Ambiguous

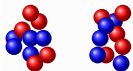


$$\bar{p} =$$

$$var =$$

Defining the Population Preference Index

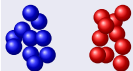
Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

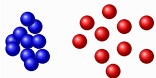
Real population preference



$$\bar{p} = 0.5$$

$$var =$$

Ambiguous

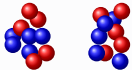


$$\bar{p} =$$

$$var =$$

Defining the Population Preference Index

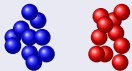
Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

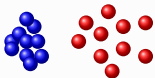
Real population preference



$$\bar{p} = 0.5$$

$$var = 0.263$$

Ambiguous

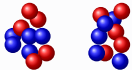


$$\bar{p} =$$

$$var =$$

Defining the Population Preference Index

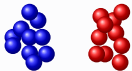
Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

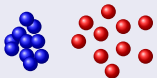
Real population preference



$$\bar{p} = 0.5$$

$$var = 0.263$$

Ambiguous

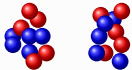


$$\bar{p} =$$

$$var =$$

Defining the Population Preference Index

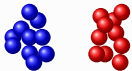
Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

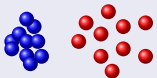
Real population preference



$$\bar{p} = 0.5$$

$$var = 0.263$$

Ambiguous



$$\bar{p} = 1.0$$

$$var =$$

Defining the Population Preference Index

Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

Real population preference



$$\bar{p} = 0.5$$

$$var = 0.263$$

Ambiguous



$$\bar{p} = 1.0$$

$$var = 0.000$$

Defining the Population Preference Index

Population mixture



$$\bar{p} = 0.5$$

$$\text{var} = 0.000$$

Real population preference



$$\bar{p} = 0.5$$

$$\text{var} = 0.263$$

Ambiguous



$$\bar{p} = 1.0$$

$$\text{var} = 0.000$$

Defining the Population Preference Index

Population mixture



$$\bar{p} = 0.5$$

$$PPI = 0.000$$

Real population preference



$$\bar{p} = 0.5$$

$$PPI = 0.263$$

Ambiguous



$$\bar{p} = 1.0$$

$$PPI = 0.000$$

Defining the Population Preference Index in Detail

Population mixture



$$\bar{p} =$$

$$var =$$

Real population preference



$$\bar{p} =$$

$$var =$$

Ambiguous



$$\bar{p} =$$

$$var =$$

Defining the Population Preference Index in Detail

Population mixture



$$\bar{p} = \frac{\frac{5}{10} * 10 + \frac{5}{10} * 10}{20}$$

var =

Real population preference



\bar{p} =

var =

Ambiguous

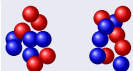


\bar{p} =

var =

Defining the Population Preference Index in Detail

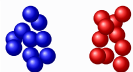
Population mixture



$$\bar{p} = 0.5$$

$$\text{var} = \frac{\left(\frac{5}{10} - 0.5\right)^2 * 10 + \left(\frac{5}{10} - 0.5\right)^2 * 10}{19}$$

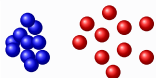
Real population preference



$$\bar{p} =$$

$$\text{var} =$$

Ambiguous



$$\bar{p} =$$

$$\text{var} =$$

Defining the Population Preference Index in Detail

Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

Real population preference



$$\bar{p} =$$

$$var =$$

Ambiguous

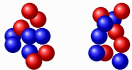


$$\bar{p} =$$

$$var =$$

Defining the Population Preference Index in Detail

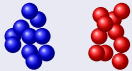
Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

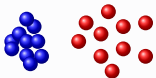
Real population preference



$$\bar{p} = \frac{\frac{10}{10} * 10 + \frac{0}{10} * 10}{20}$$

$$var =$$

Ambiguous

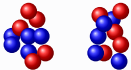


$$\bar{p} =$$

$$var =$$

Defining the Population Preference Index in Detail

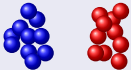
Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

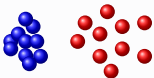
Real population preference



$$\bar{p} = 0.5$$

$$var = \frac{(\frac{10}{10} - 0.5)^2 * 10 + (\frac{0}{10} - 0.5)^2 * 10}{19}$$

Ambiguous

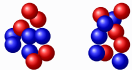


$$\bar{p} =$$

$$var =$$

Defining the Population Preference Index in Detail

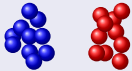
Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

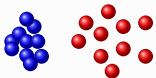
Real population preference



$$\bar{p} = 0.5$$

$$var = 0.263$$

Ambiguous



$$\bar{p} =$$

$$var =$$

Defining the Population Preference Index in Detail

Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

Real population preference



$$\bar{p} = 0.5$$

$$var = 0.263$$

Ambiguous



$$\bar{p} = \frac{\frac{10}{10} * 10}{10}$$

$$var =$$

Defining the Population Preference Index in Detail

Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

Real population preference



$$\bar{p} = 0.5$$

$$var = 0.263$$

Ambiguous



$$\bar{p} = 1.0$$

$$var = \frac{\left(\frac{10}{10} - 1\right)^2 * 10}{9}$$

Defining the Population Preference Index in Detail

Population mixture



$$\bar{p} = 0.5$$

$$var = 0.000$$

Real population preference



$$\bar{p} = 0.5$$

$$var = 0.263$$

Ambiguous



$$\bar{p} = 1.0$$

$$var = 0.000$$

Defining the Population Preference Index in Detail

Population mixture



$$\bar{p} = 0.5$$

$$\text{var} = 0.000$$

Real population preference



$$\bar{p} = 0.5$$

$$\text{var} = 0.263$$

Ambiguous



$$\bar{p} = 1.0$$

$$\text{var} = 0.000$$

Defining the Population Preference Index in Detail

Population mixture



$$\bar{p} = 0.5$$

$$PPI = 0.000$$

Real population preference



$$\bar{p} = 0.5$$

$$PPI = 0.263$$

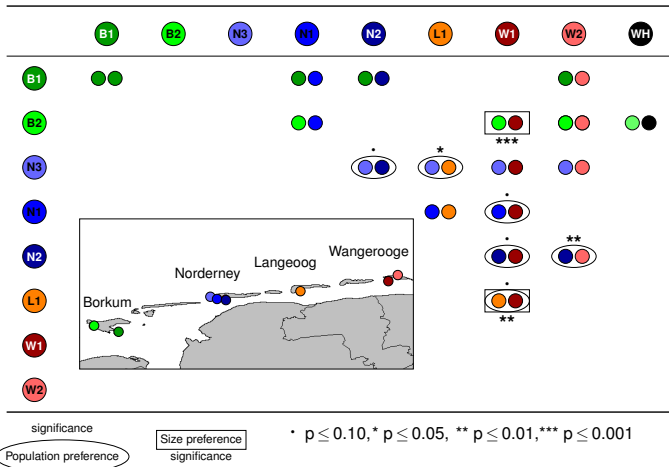
Ambiguous



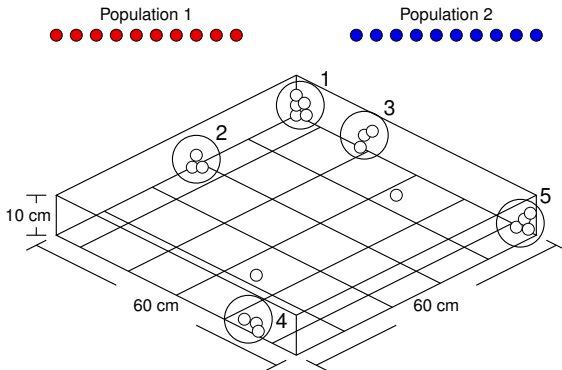
$$\bar{p} = 1.0$$

$$PPI = 0.000$$

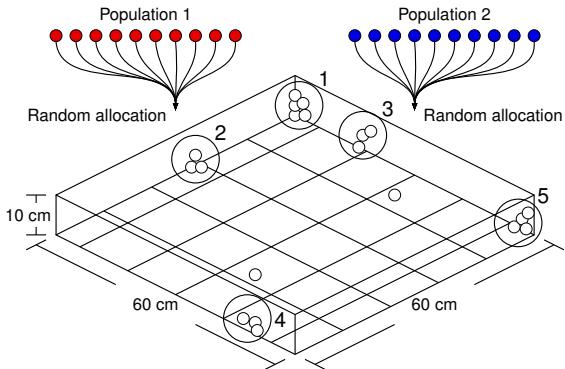
Snails Aggregate Assortatively



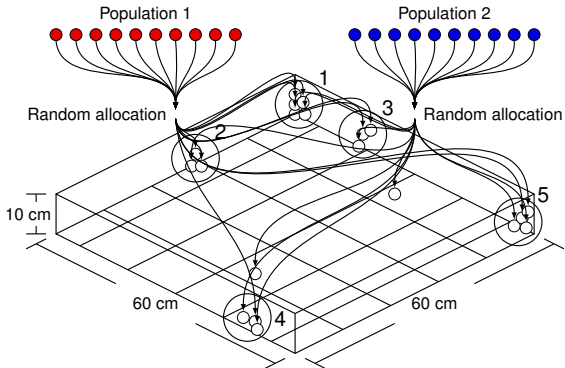
Simplified Monte Carlo Simulation



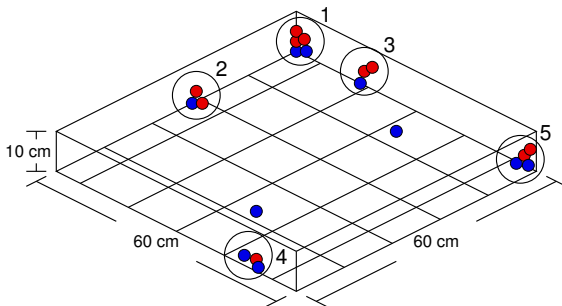
Simplified Monte Carlo Simulation



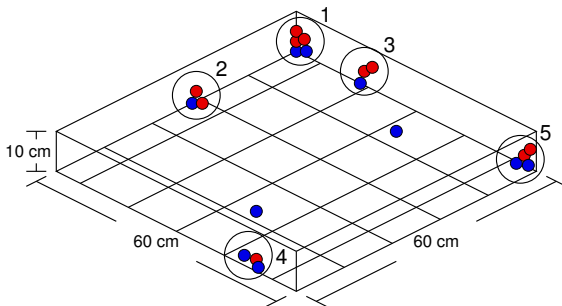
Simplified Monte Carlo Simulation



Simplified Monte Carlo Simulation

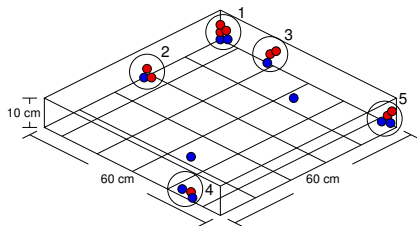


Simplified Monte Carlo Simulation

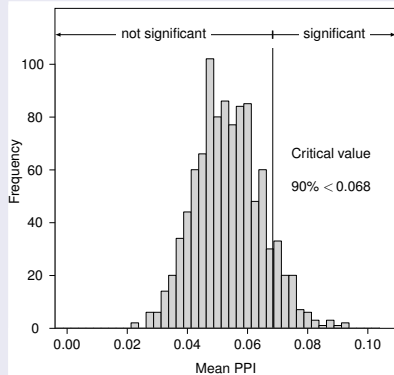


Calculation of PPI

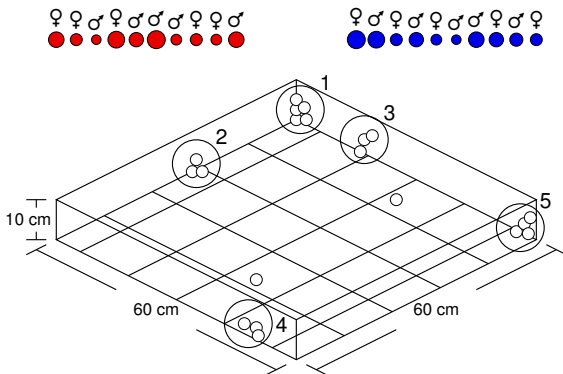
Simplified Monte Carlo Simulation



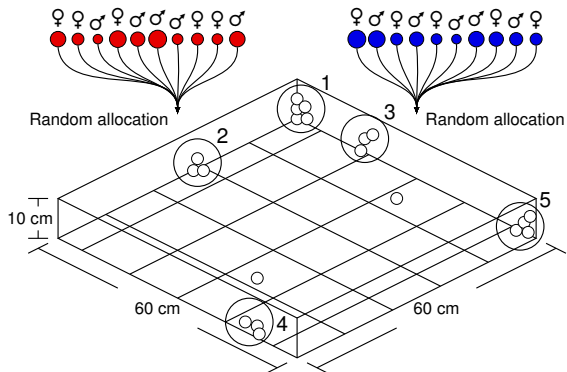
A histogram of PPI values



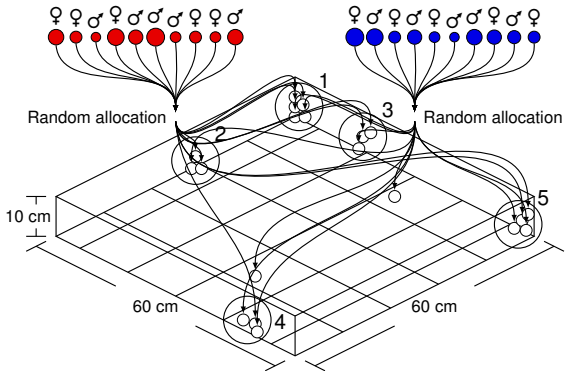
Detailed Monte Carlo Simulation



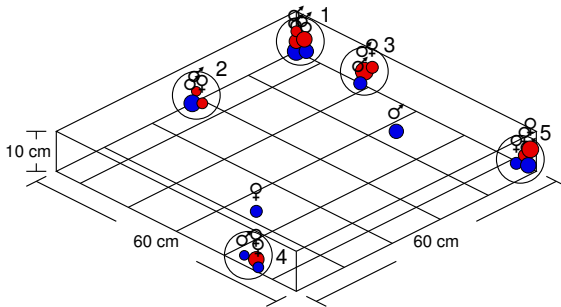
Detailed Monte Carlo Simulation



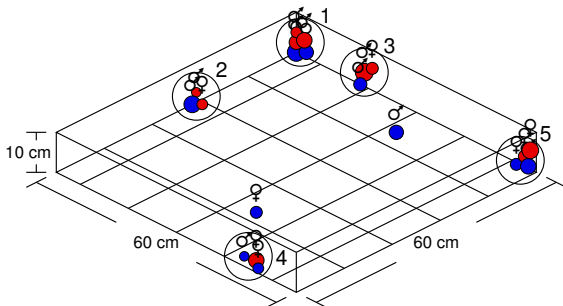
Detailed Monte Carlo Simulation



Detailed Monte Carlo Simulation



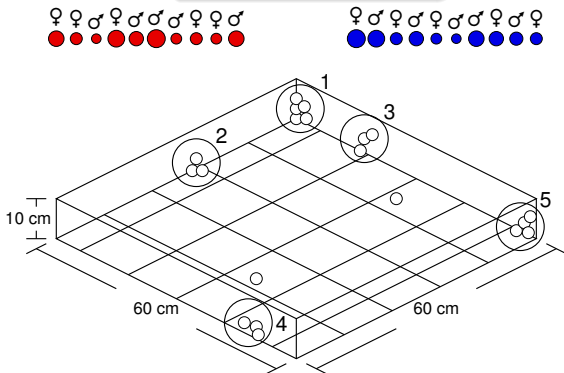
Detailed Monte Carlo Simulation



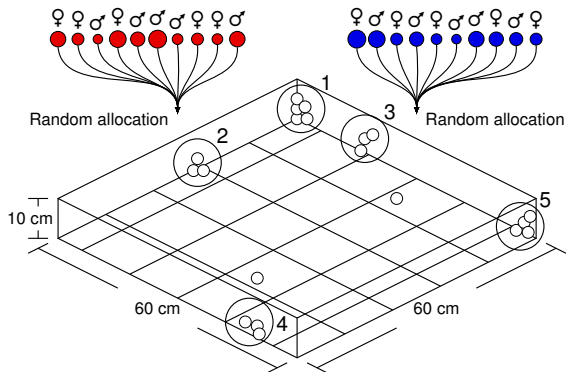
Calculation of PPI, Sex-PI and Size-PI

Detailed Monte Carlo Simulation

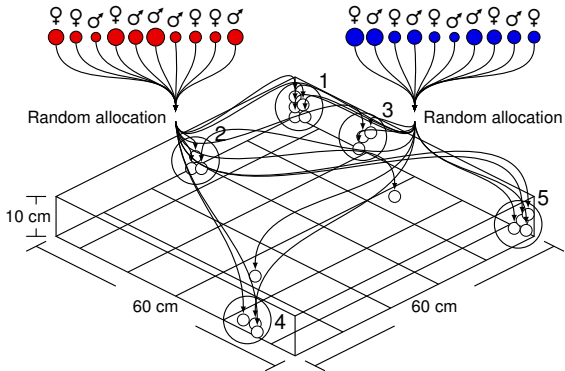
1000-fold repetition



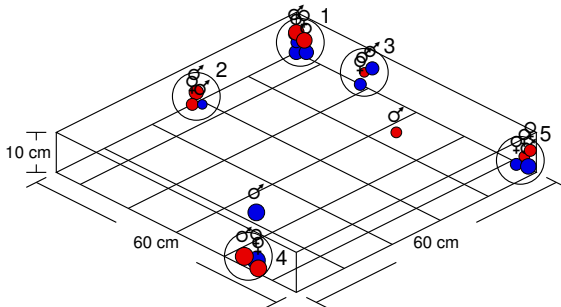
Detailed Monte Carlo Simulation



Detailed Monte Carlo Simulation

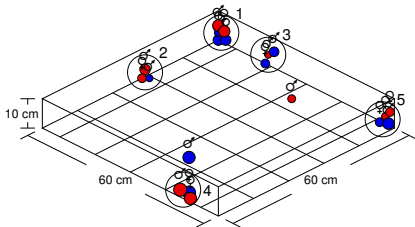


Detailed Monte Carlo Simulation

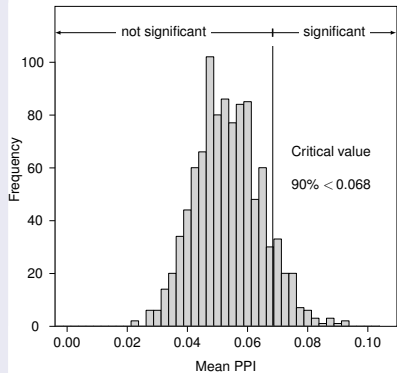


1000-fold calculation of PPI, Sex-PI and Size-PI

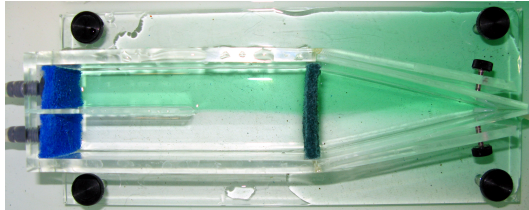
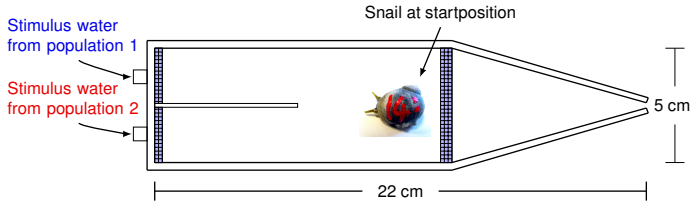
Detailed Monte Carlo Simulation



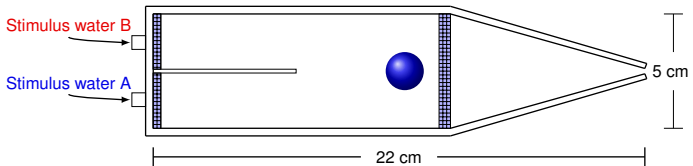
A histogram of PPI values



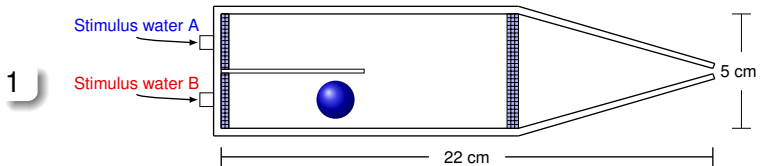
Testing Snails in Olfactory Flumes



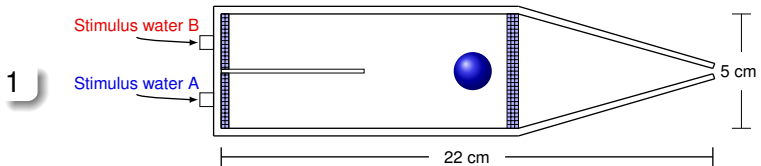
Testing Snails in Olfactory Flumes in Detail



Testing Snails in Olfactory Flumes in Detail



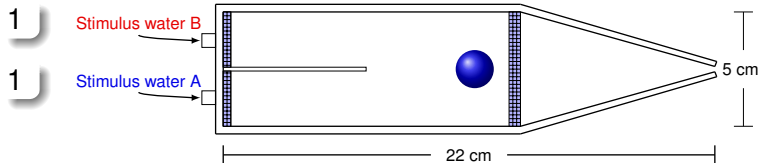
Testing Snails in Olfactory Flumes in Detail



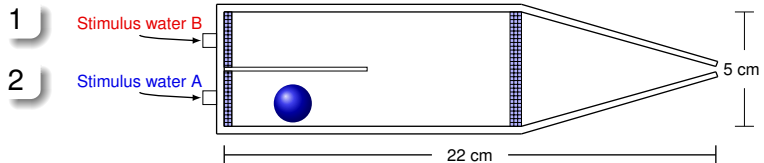
Testing Snails in Olfactory Flumes in Detail



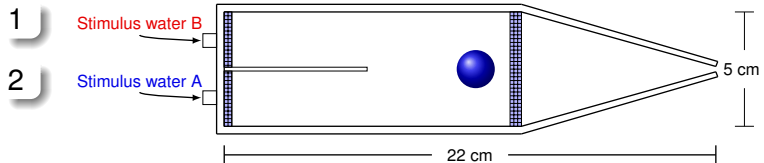
Testing Snails in Olfactory Flumes in Detail



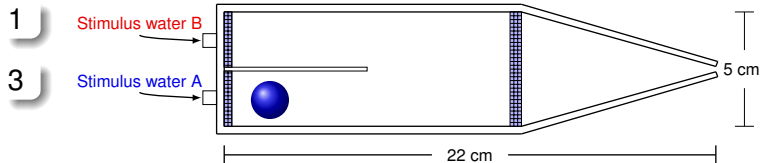
Testing Snails in Olfactory Flumes in Detail



Testing Snails in Olfactory Flumes in Detail



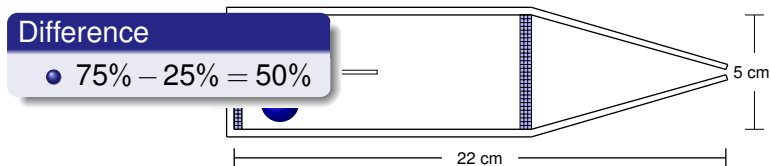
Testing Snails in Olfactory Flumes in Detail



Testing Snails in Olfactory Flumes in Detail



Testing Snails in Olfactory Flumes in Detail



Testing Snails in Olfactory Flumes in Detail

15 Differences

50%

25%

.

.

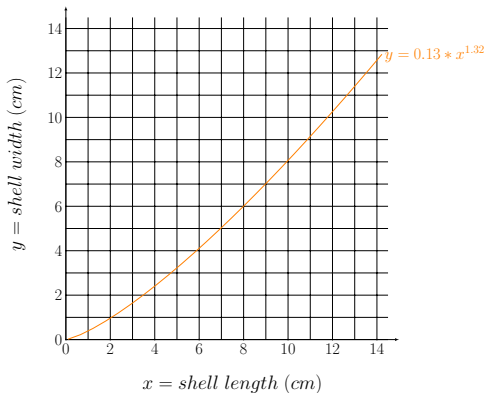
.

0%

Wilcoxon signed-rank
test

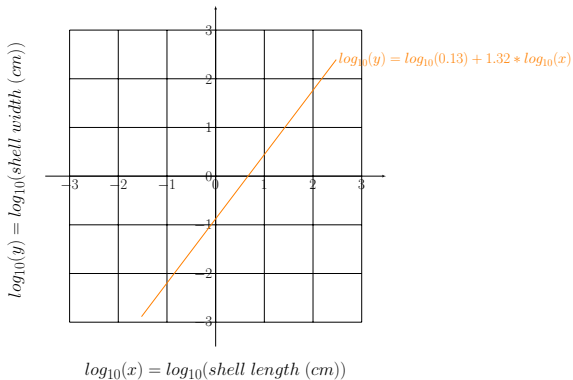
Allometric correction

Arithmetic plot

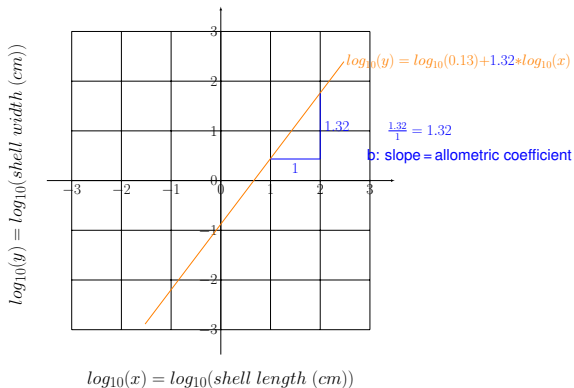


Allometric correction

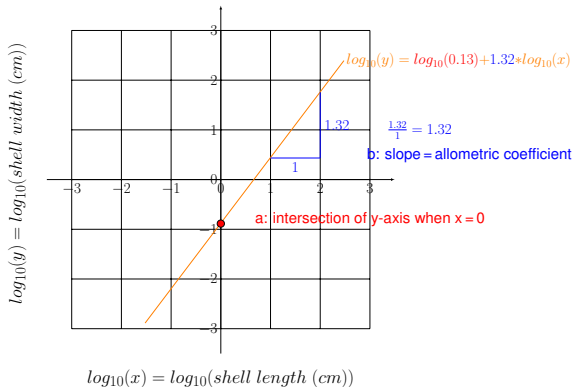
Logarithmic plot



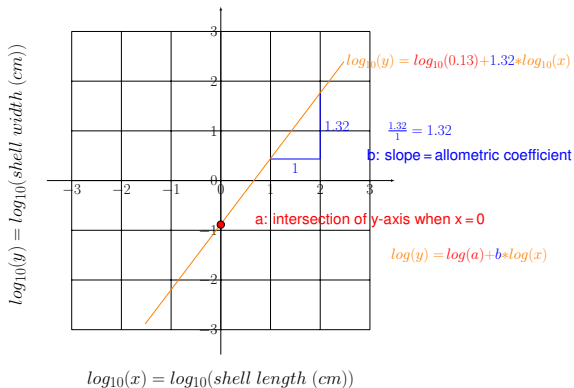
Allometric correction



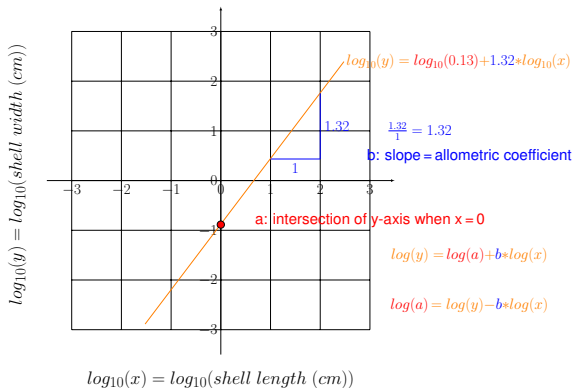
Allometric correction



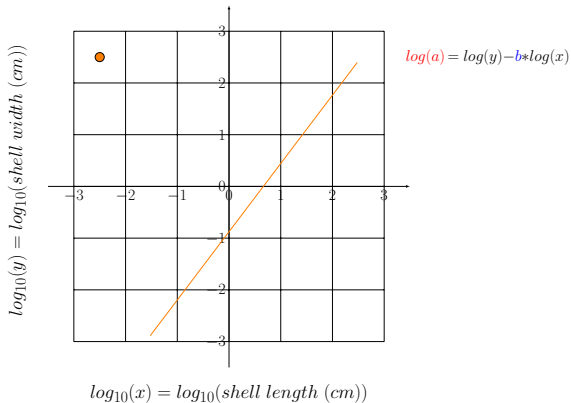
Allometric correction



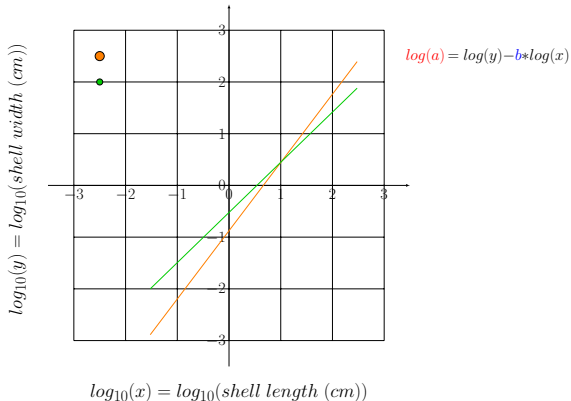
Allometric correction



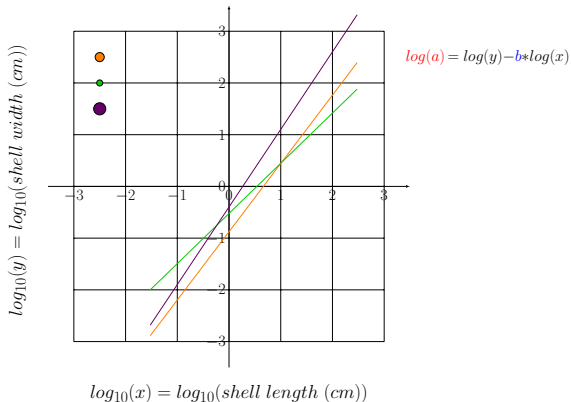
Allometric correction



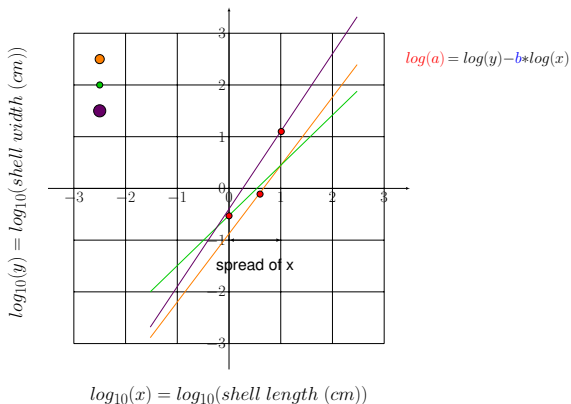
Allometric correction



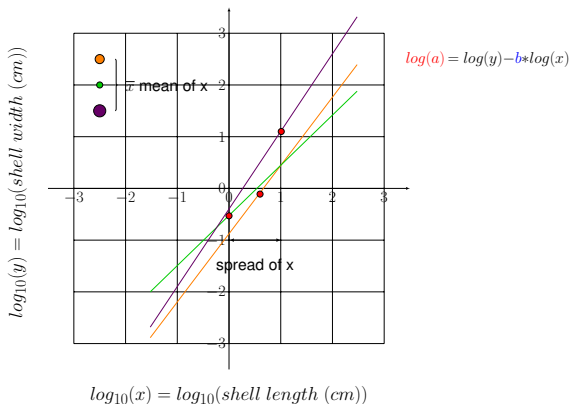
Allometric correction



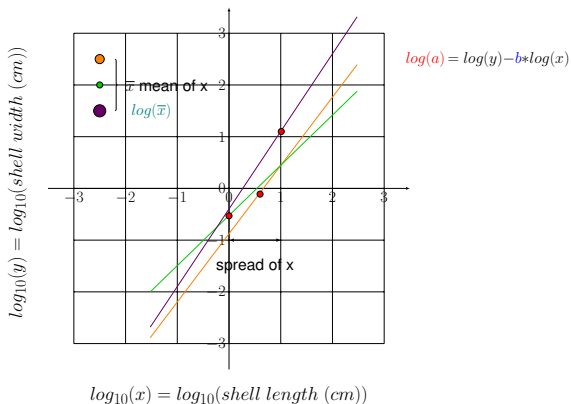
Allometric correction



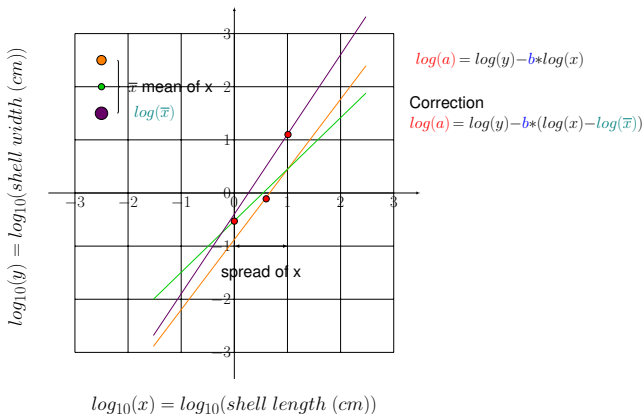
Allometric correction



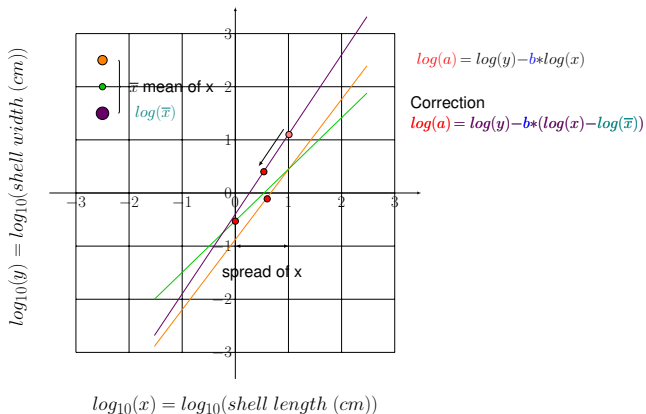
Allometric correction



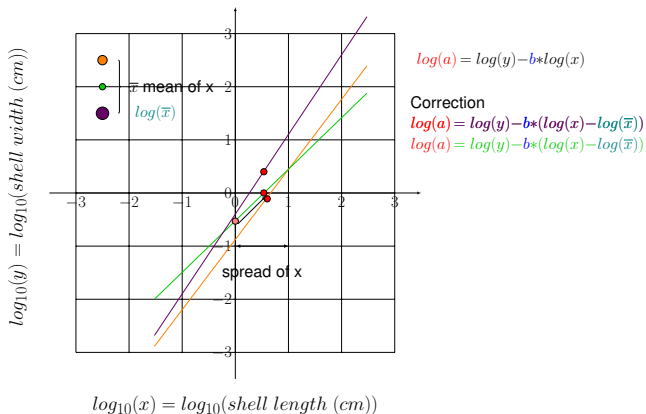
Allometric correction



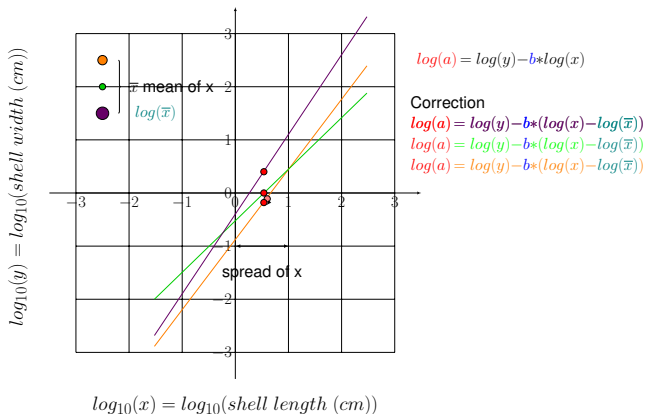
Allometric correction



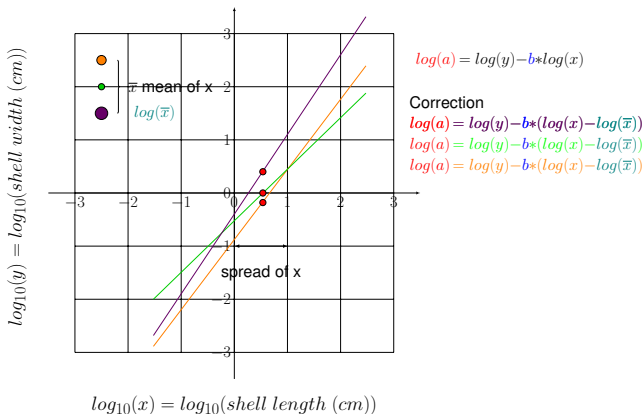
Allometric correction



Allometric correction



Allometric correction



Genetic Differentiation at Microsatellite Markers 1

Pop1



Pop2



Genetic Differentiation at Microsatellite Markers 1

Pop1

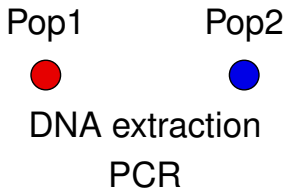


Pop2

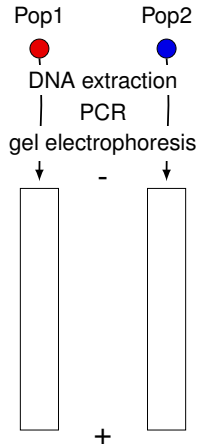


DNA extraction

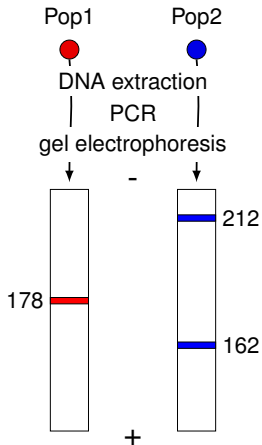
Genetic Differentiation at Microsatellite Markers 1



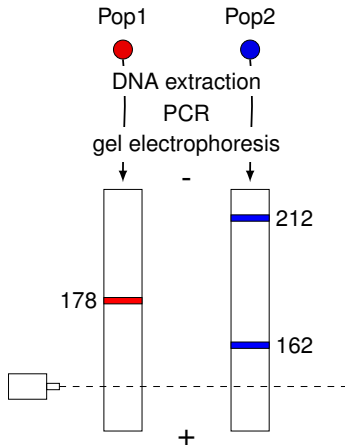
Genetic Differentiation at Microsatellite Markers 1



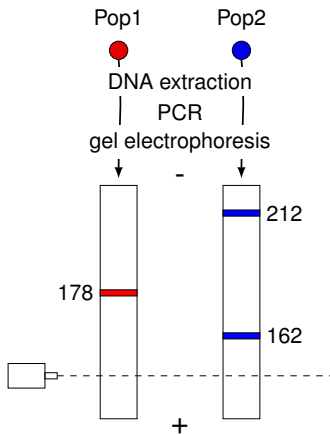
Genetic Differentiation at Microsatellite Markers 1



Genetic Differentiation at Microsatellite Markers 1

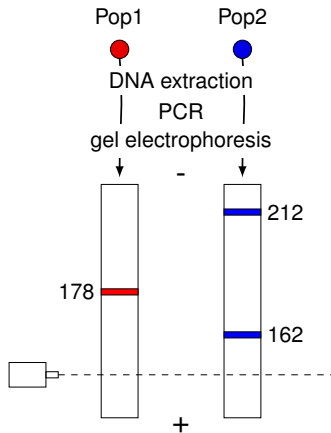


Genetic Differentiation at Microsatellite Markers 1



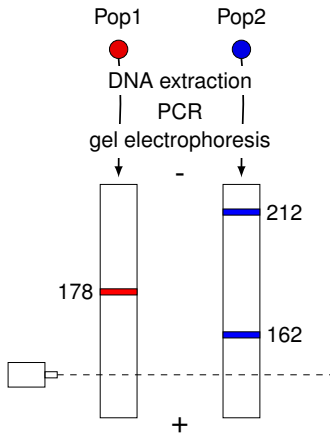
Pop1		Pop2	
allele1	allele2	allele1	allele2
178	178	212	162

Genetic Differentiation at Microsatellite Markers 1



Pop1		Pop2	
allele1	allele2	allele1	allele2
178	178	212	162
178	234	162	162
234	234	212	212
234	178	212	162
...
...
...

Genetic Differentiation at Microsatellite Markers 1



Pop1		Pop2	
allele1	allele2	allele1	allele2
178	178	212	162
178	234	162	162
234	234	212	212
234	178	212	162
...
...
...

Differentiation index D_{est}

Genetic Differentiation at Microsatellite Markers 2

GTA
CAT

Genetic Differentiation at Microsatellite Markers 2

GTAGTAGTAGTAGTAGTA
CATCATCATCATCATCAT

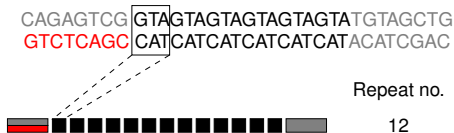
Genetic Differentiation at Microsatellite Markers 2

GTAGTAGTAGTAGTA
CATCATCATCATCAT

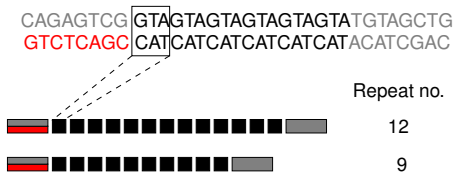
Genetic Differentiation at Microsatellite Markers 2

CAGAGTCG **GTAG** TAGTAGTAGTAGTATGTAGCTG
GTCTCAGC **CAT** CATCATCATCATCATACATCGAC

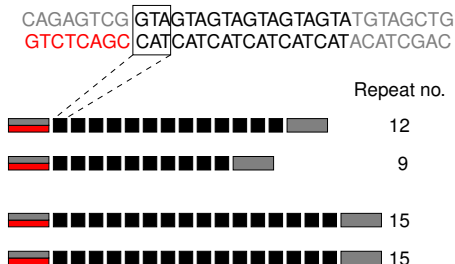
Genetic Differentiation at Microsatellite Markers 2



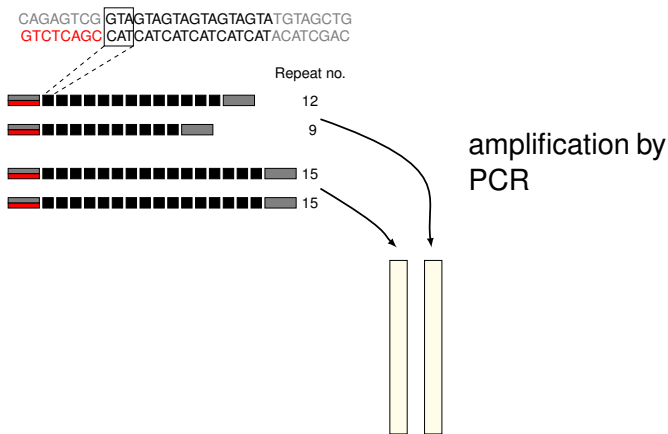
Genetic Differentiation at Microsatellite Markers 2



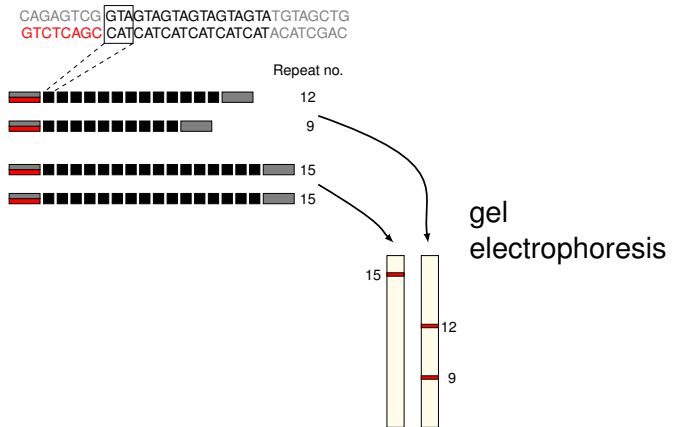
Genetic Differentiation at Microsatellite Markers 2



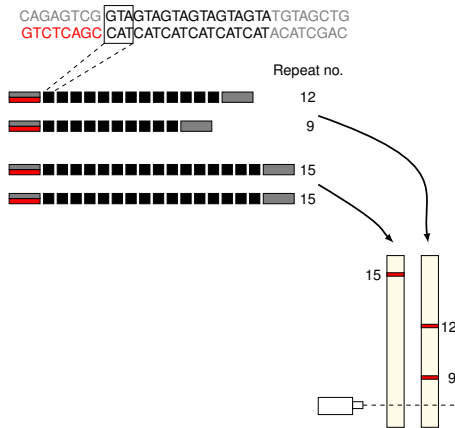
Genetic Differentiation at Microsatellite Markers 2



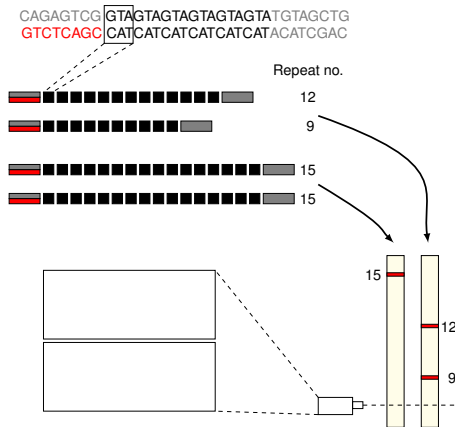
Genetic Differentiation at Microsatellite Markers 2



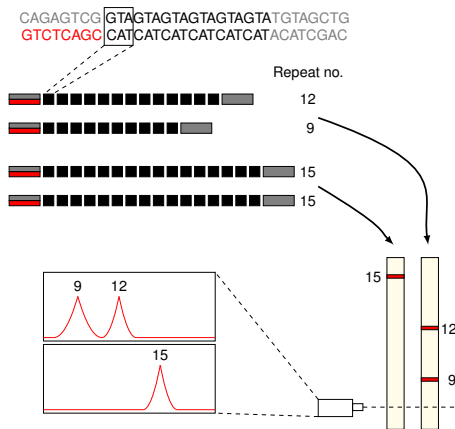
Genetic Differentiation at Microsatellite Markers 2



Genetic Differentiation at Microsatellite Markers 2



Genetic Differentiation at Microsatellite Markers 2



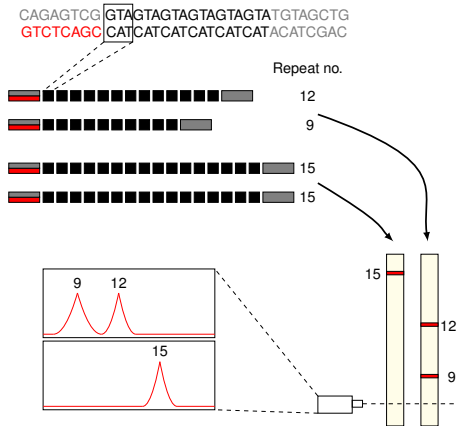
Genetic Differentiation at Microsatellite Markers 2

Pop1

165 165
230 165
230 230
165 230
230 230
165 165
165 165
230 165

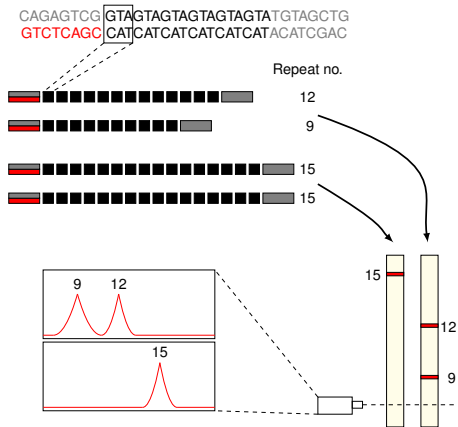
Pop2

170 170
198 170
198 198
170 198
198 198
170 170
170 170
198 170



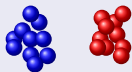
Genetic Differentiation at Microsatellite Markers 2

Pop1	Pop2
165 165	170 170
230 165	198 170
230 230	198 198
165 230	170 198
230 230	198 198
165 165	170 170
165 165	170 170
230 165	198 170

Difference D_{est} 

Snails Prefer Conspecifics of the own Population

Population-wise aggregation



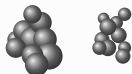
PPI significant ($p \leq 0.1$) in 6 of 17 tests

Sex-bias aggregation



Sex-PI significant ($p \leq 0.1$) in 0 of 17 tests

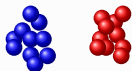
Size-wise aggregation



Size-PI significant ($p \leq 0.1$) in 2 of 17 tests

Snails Prefer Conspecifics of the own Population

Population-wise aggregation



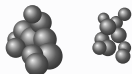
PPI significant ($p \leq 0.1$) in 6 of 17 tests

Sex-bias aggregation



Sex-PI significant ($p \leq 0.1$) in 0 of 17 tests

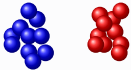
Size-wise aggregation



Size-PI significant ($p \leq 0.1$) in 2 of 17 tests

Snails Prefer Conspecifics of the own Population

Population-wise aggregation



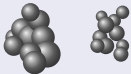
PPI significant ($p \leq 0.1$) in 6 of 17 tests

Sex-bias aggregation



Sex-PI significant ($p \leq 0.1$) in 0 of 17 tests

Size-wise aggregation



Size-PI significant ($p \leq 0.1$) in 2 of 17 tests

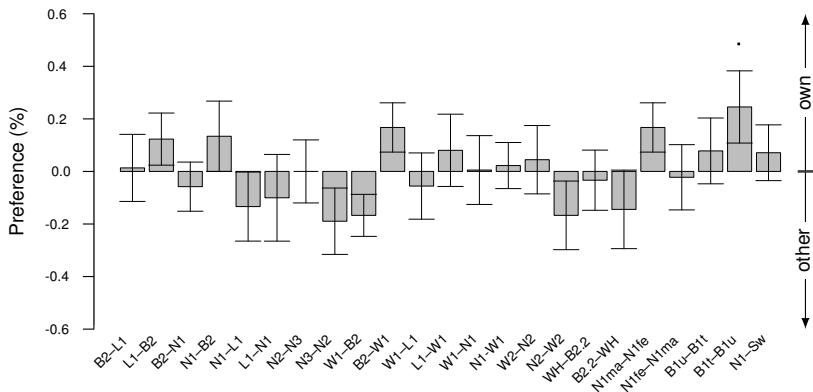
Snails Prefer Conspecifics of the own Population

Populations
differ
intrinsically

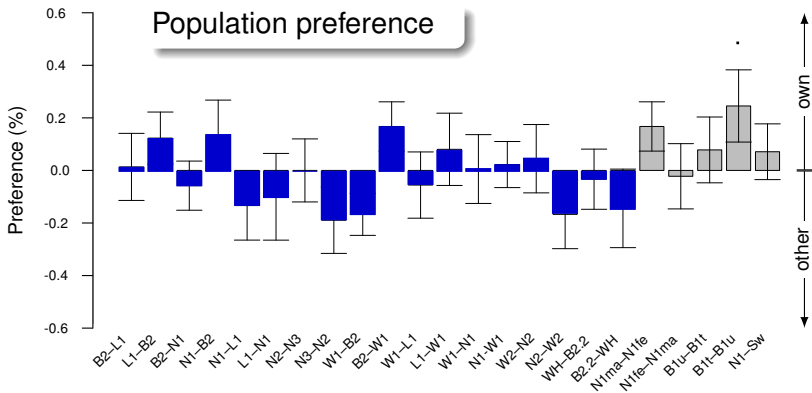
Snails Prefer Conspecifics of the own Population

... aggregation frequency
increases
during the
mating season

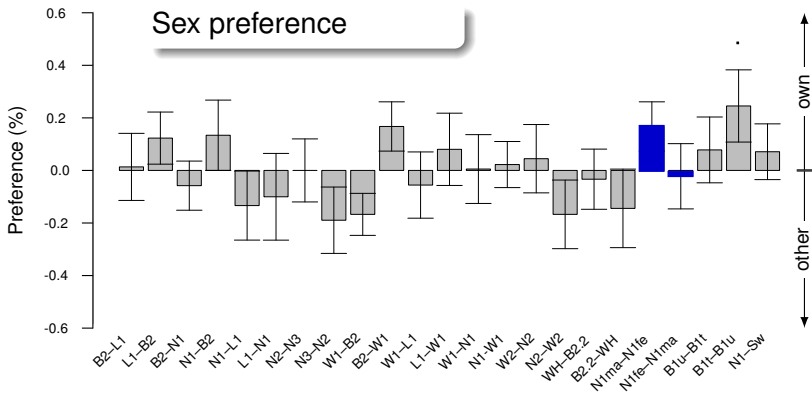
Snails do not Prefer any Volatile Chemicals



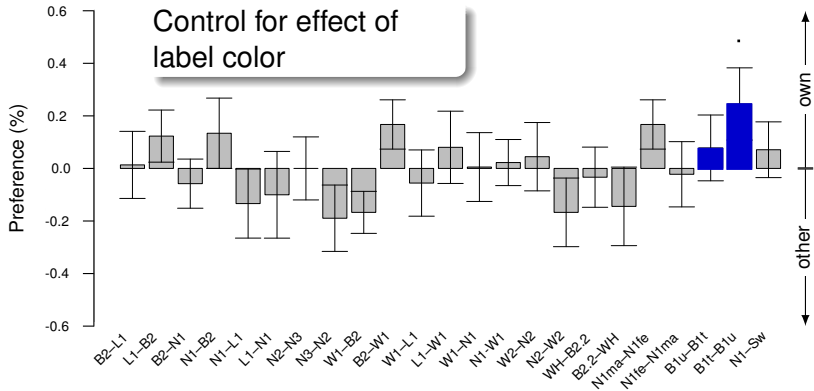
Snails do not Prefer any Volatile Chemicals



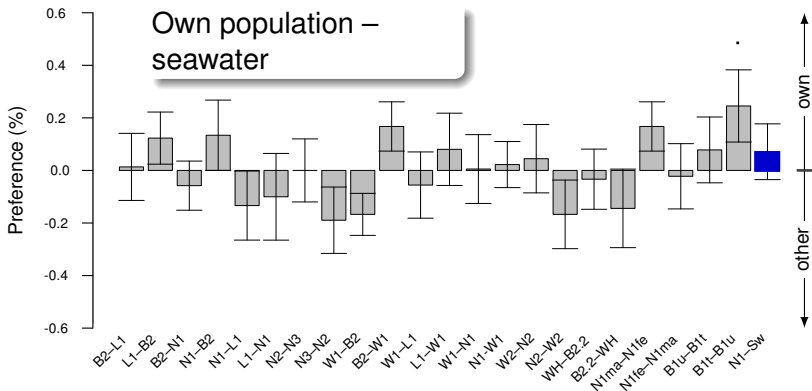
Snails do not Prefer any Volatile Chemicals



Snails do not Prefer any Volatile Chemicals



Snails do not Prefer any Volatile Chemicals

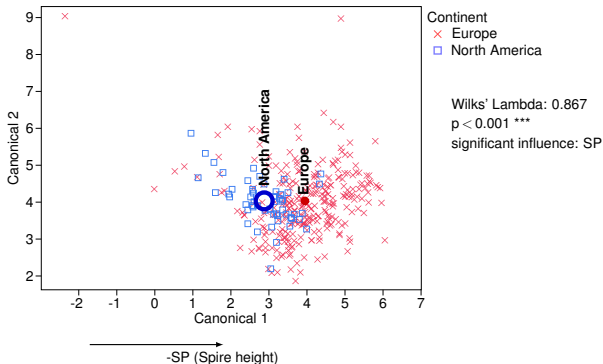


Snails do not Prefer any Volatile Chemicals

Populations
are
not discriminated
by
volatile chemicals

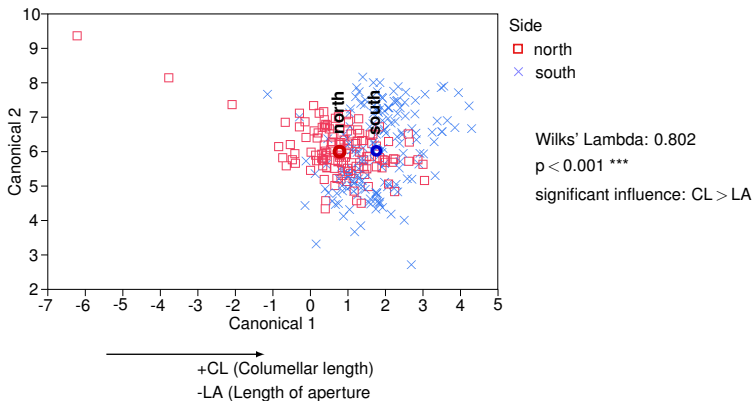
Results of Discriminant analyzes

EFWS – Woods Hole



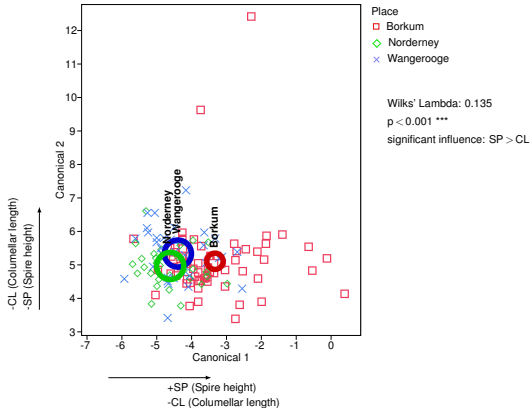
Results of Discriminant analyzes

North coasts – South coasts



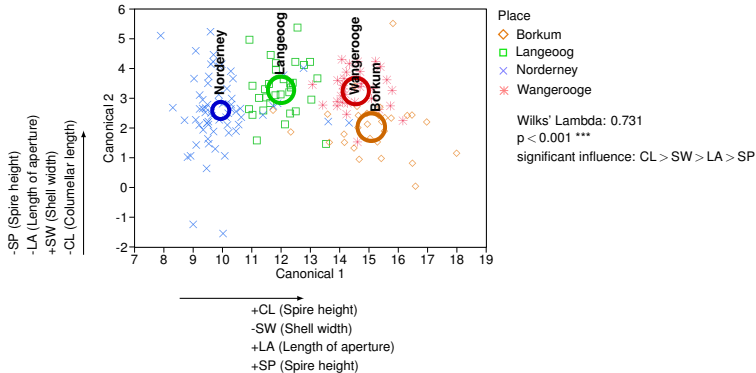
Results of Discriminant analyzes

Within north coasts



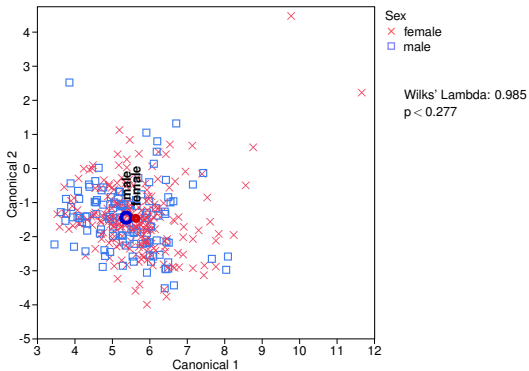
Results of Discriminant analyzes

Within south coasts



Results of Discriminant analyzes

Sexes



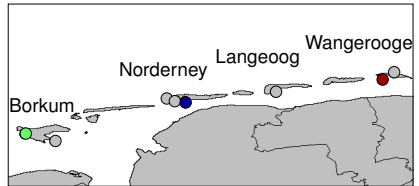
Genetic (D_{est}) and Geographic (km) Distance

	B2●	W1●	N2●	WH●	
B2●	...	0.011	-0.007	0.033	*
W1●	82.5	...	0.006	0.056	**
N2●	38.0	39.9	...	0.057	*
WH●	5662.8	5730.7	5692.3	...	

Genetic (D_{est}) and Geographic (km) Distance

Within the EFWS

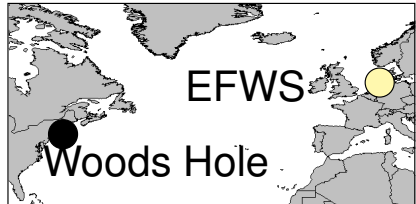
	B2 ●	W1 ●	N2 ●	WH ●	
B2 ●	...	0.011	-0.007	0.033	*
W1 ●	82.5	...	0.006	0.056	**
N2 ●	38.0	39.9	...	0.057	*
WH ●	5662.8	5730.7	5692.3	...	



Genetic (D_{est}) and Geographic (km) Distance

Between the EFWS and Woods Hole

	B2 ●	W1 ●	N2 ●	WH ●	
B2 ●	...	0.011	-0.007	0.033	*
W1 ●	82.5	...	0.006	0.056	**
N2 ●	38.0	39.9	...	0.057	*
WH ●	5662.8	5730.7	5692.3	...	



Genetic (D_{est}) and Geographic (km) Distance

Wadden Sea
Populations
are
not differentiated
at
neutral loci