

Climate change impact on the seaweed *Fucus serratus*, a key foundational species on North Atlantic rocky shores

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University of Nordland

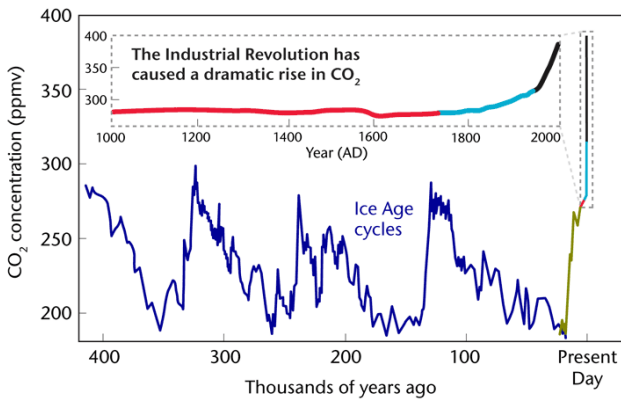
PhD Thesis, 01.06.2010–12.08.2013



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CO₂ increase since the industrial revolution

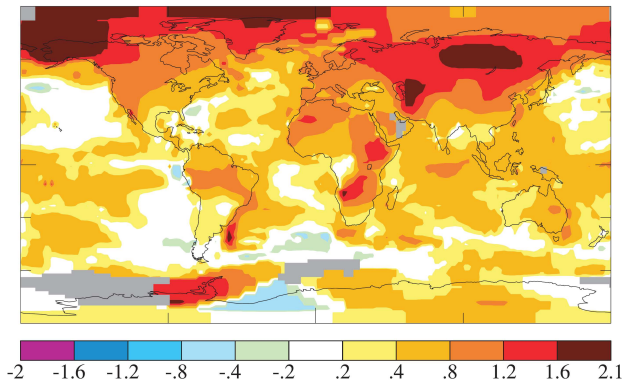
Variations in CO₂ concentrations from ice core records



Recent climate change

2001–2005 mean surface temperature anomaly
(Base Period = 1951–1981)

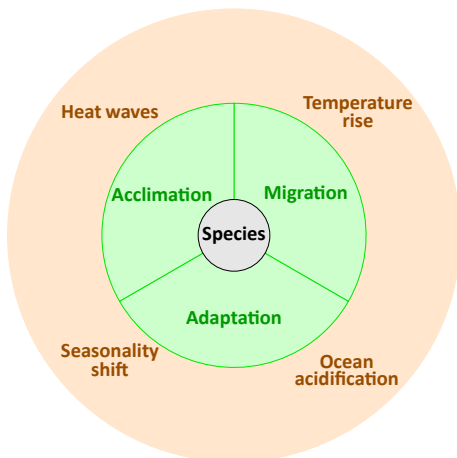
Global mean = 0.54



[Hansen et al., 2006; PNAS]



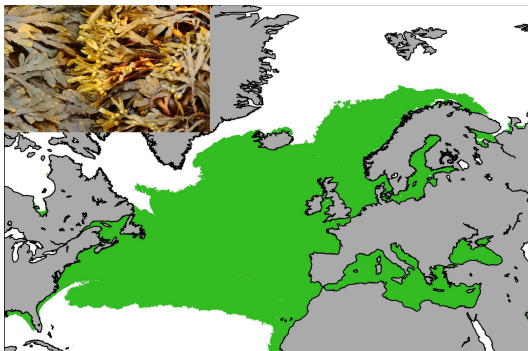
Climate change responses



High sensitivity of intertidal species



Seaweeds are key species in temperate North Atlantic regions



Between the 10°C summer and the 20°C winter isotherm





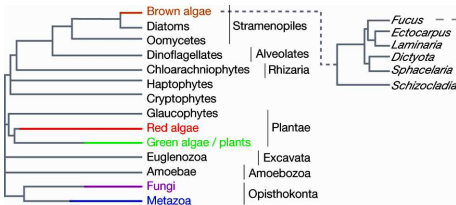
© Hoarau, G., 2010



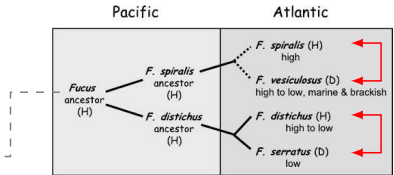
The focal species *Fucus serratus*



Fucus in the tree of life



[Cock et al., 2010; Nature]



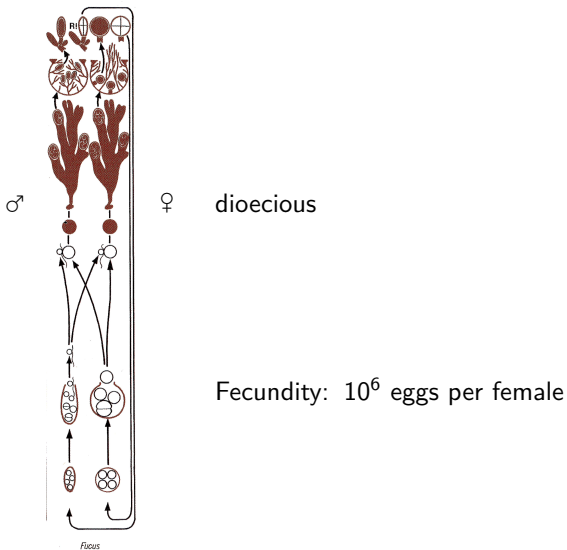
[Coyer et al., 2006; Mol. Phylogenet. Evol.]

Hybridization



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Life cycle and dispersal of *Fucus serratus*

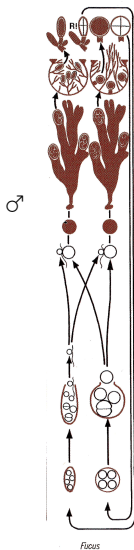


[Braune, 2008; Meeresalgen]



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Life cycle and dispersal of *Fucus serratus*



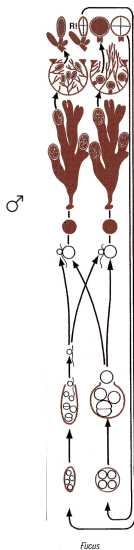
♀ dioecious

zygote dispersal: <10m

Fecundity: 10^6 eggs per female



Life cycle and dispersal of *Fucus serratus*

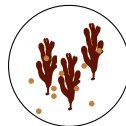


♀

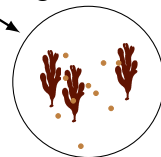
dioecious

zygote dispersal: <10m

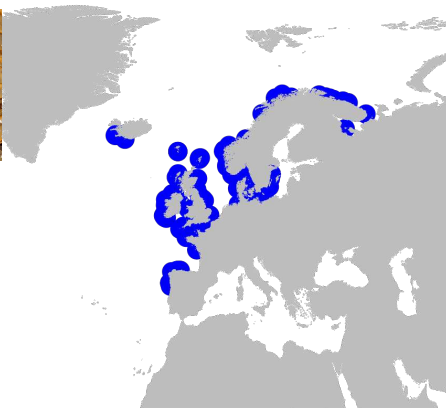
panmictic unit: 0.5–2km

Fecundity: 10^6 eggs per female

low genetic exchange



Distribution of *F. serratus* in the North Atlantic

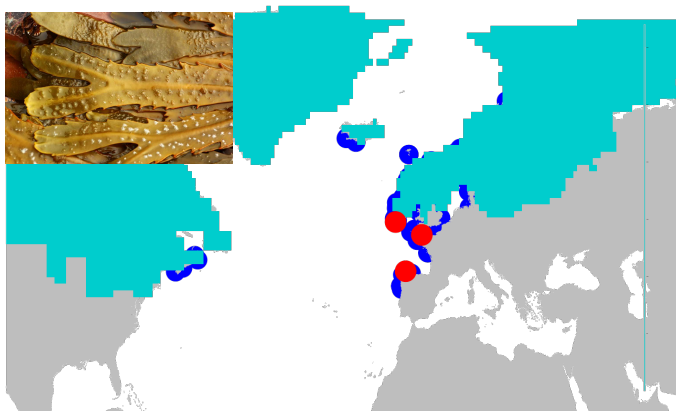


● Occurrence records



Distribution of *F. serratus* in the North Atlantic

Last Glacial Maximum 18-20,000 years ago



● Occurrence records

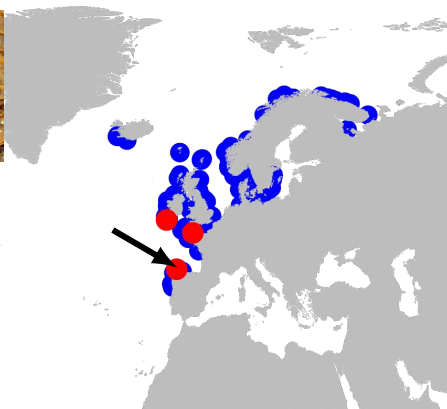
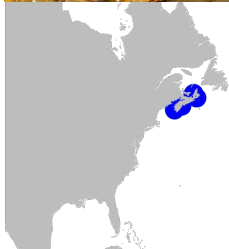
● Glacial Refugia

[Hoarau et al., 2007; Mol. Ecol.]



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Distribution of *F. serratus* in the North Atlantic



● Occurrence records

● Glacial Refugia

[Hoarau et al., 2007; Mol. Ecol.]



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Recent changes in southern edge populations of *F. serratus*



1999



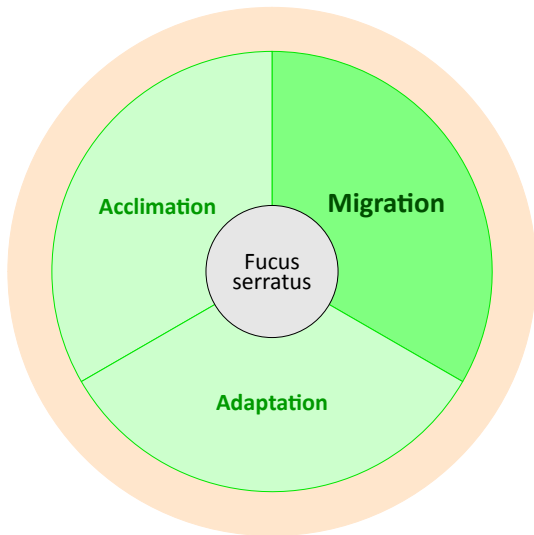
2010

- 90% abundance decline
- Reduced reproductive capacity

[Viejo et al., 2011; *Ecography*]



Objectives



Paper I - Distributional shift

Ecology and Evolution

Open Access

Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal

Alexander Jueterbock¹, Lennert Tyberghein^{2,3}, Heroen Verbruggen⁴, James A. Coyer⁵, Jeanine L. Olsen⁶ & Galice Hoarau¹



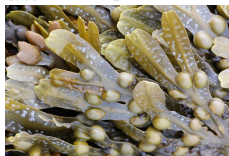
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Specific aims

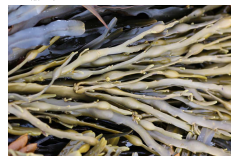
Predominant seaweeds in the North-Atlantic



Fucus serratus



Fucus vesiculosus



Ascophyllum nodosum

- Shores with biggest ecological change?
- Shift as an assemblage?

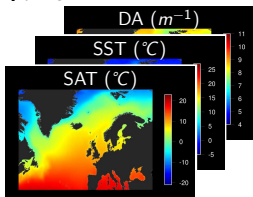


Ecological Niche Modelling

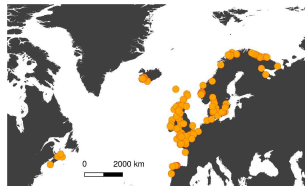
Present-day conditions

Bio-ORACLE database

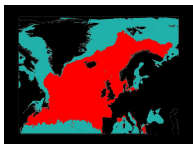
[Tyberghein et al., 2011; Global Ecol. Biogeogr.]



Georeferenced Occurrences



Ecological Niche Model (Maxent [Phillips et al., 2006; Ecol. Model.]



2000

2100 ?

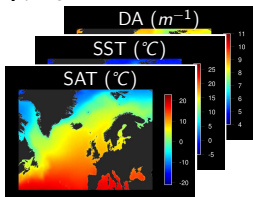
2200 ?

Ecological Niche Modelling

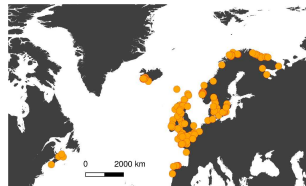
Present-day conditions

Bio-ORACLE database

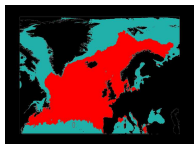
[Tyberghein et al., 2011; Global Ecol. Biogeogr.]



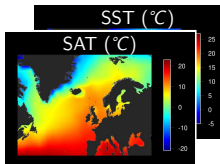
Georeferenced Occurrences



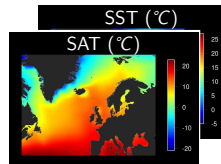
Ecological Niche Model (Maxent [Phillips et al., 2006; Ecol. Model.]



2000



2100 ?



2200 ?

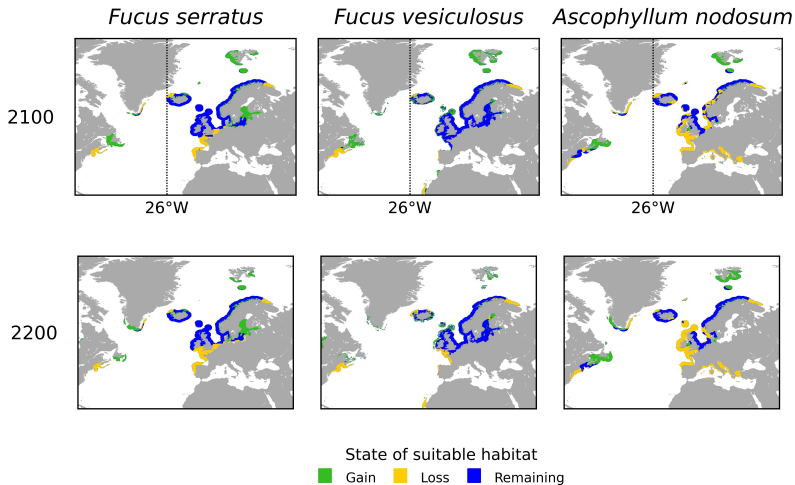
CO₂ emission scenario changes



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Predicted Niche Shifts

Based on the intermediate IPCC scenario A1B



Conclusions

Distribution

- Shores with biggest ecological change?
 - Disappearance from shores south of **Brittany** and from **Nova Scotia**
 - Suitable habitat in the **southern Arctic**
- Shift as an assemblage?



Conclusions

Distribution

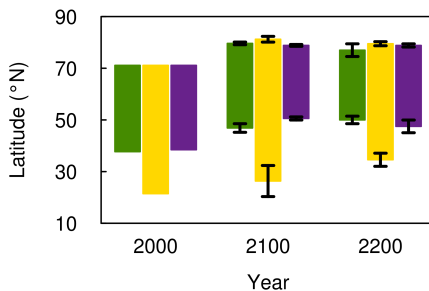
- Shores with biggest ecological change?
 - **Disappearance** from shores south of **Brittany** and from **Nova Scotia**
 - Suitable habitat in the **southern Arctic**
- Shift as an assemblage?



Predominant seaweeds shift northward as an assemblage

East-Atlantic

(b)



■ *F. serratus*

■ *F. vesiculosus*

■ *A. nodosum*



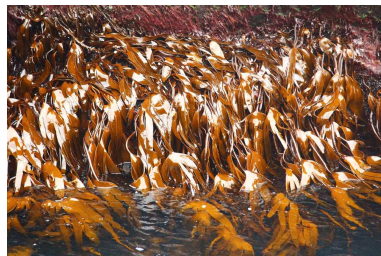
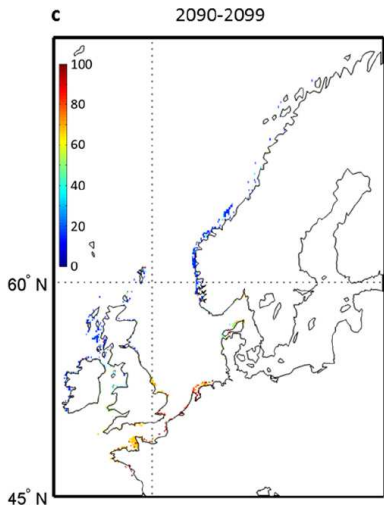
Conclusions

Distribution

- Shores with biggest ecological change?
 - **Disappearance** from shores south of **Brittany** and from **Nova Scotia**
 - Suitable habitat in the **southern Arctic**
- Shift as an assemblage?
 - **Yes**



Climate change impact also on subtidal kelp



Percentage of models forecasting a disappearance of *Laminaria digitata*

[Raybaud et al., 2013; PLOS ONE]



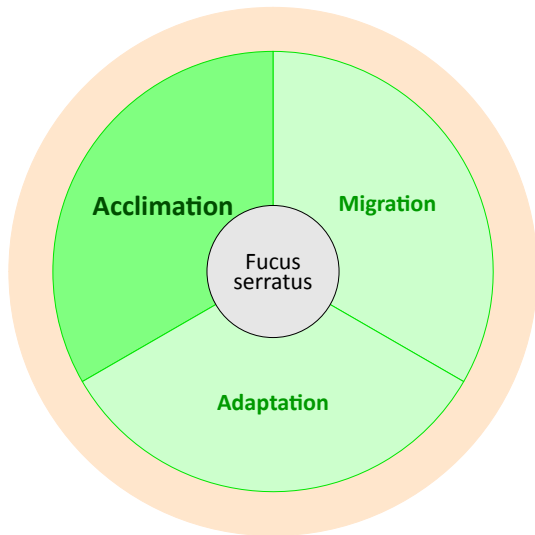
Conclusions

Distribution

- Shores with biggest ecological change?
 - **Disappearance** from shores south of **Brittany** and from **Nova Scotia**
 - Suitable habitat in the **southern Arctic**
- Shift as an assemblage?
 - **Yes**
- **Mitigation by plasticity and adaptation?**



Objectives



Paper II - Phenotypic plasticity

Thermal stress resistance of the brown alga *Fucus serratus* along the North-Atlantic coast: acclimatization potential to climate change

Alexander Jueterbock, Spyros Kollias, Irina Smolina,
Jorge M.O. Fernandes, James A. Coyer, Jeanine L. Olsen, Galice Hoarau

Marine Genomics. Submitted



Specific aims

Plasticity

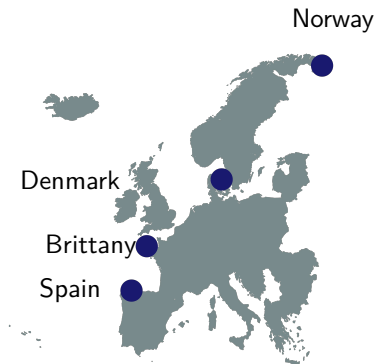
Plasticity along the entire E-Atlantic range of distribution

Local adaptation Population-specific stress response?

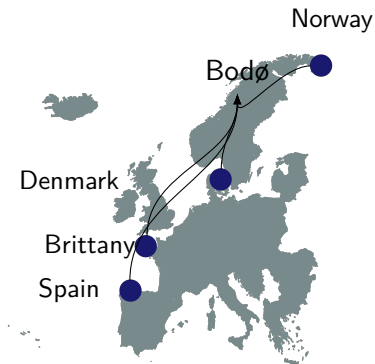
Extinction risk Where will temperatures exceed the species' thermal tolerance?



Common-garden heat stress experiments

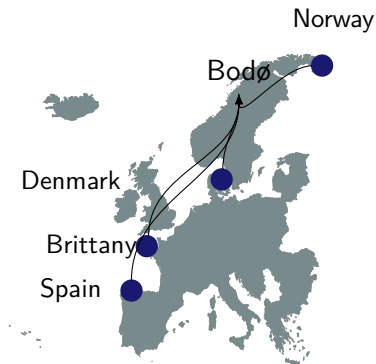
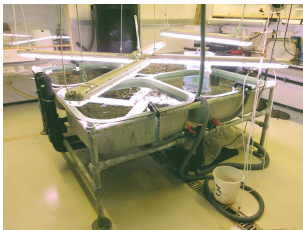


Common-garden heat stress experiments

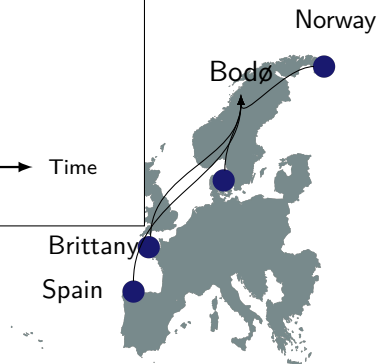
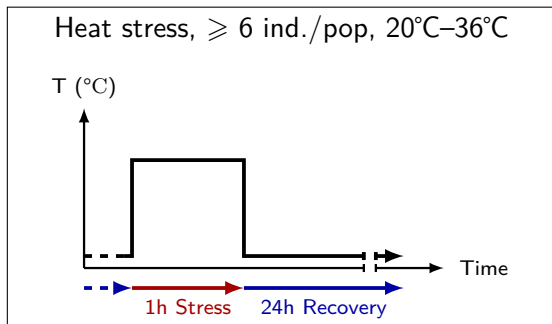


Common-garden heat stress experiments

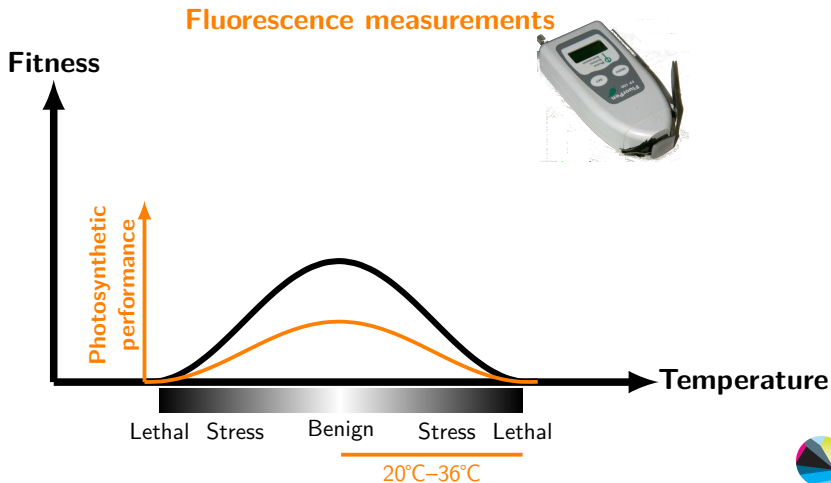
Acclimation at 9°C



Common-garden heat stress experiments

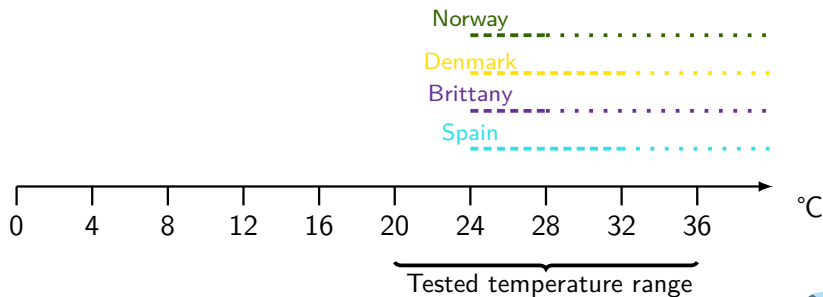


Measuring the physiological stress response



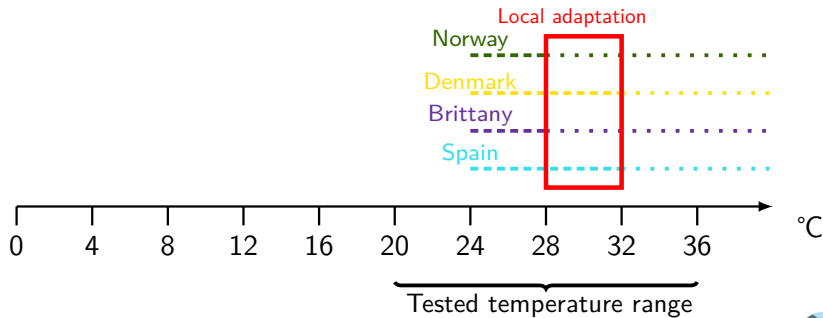
Photosynthetic response

- stress with recovery
- ... stress without recovery

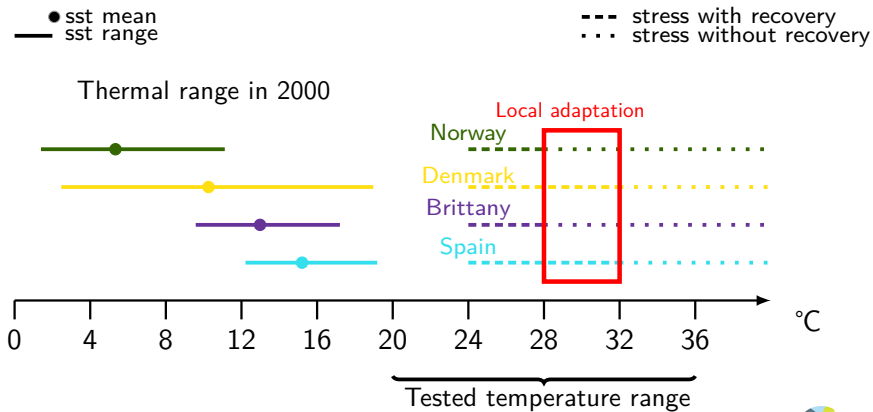


Photosynthetic response

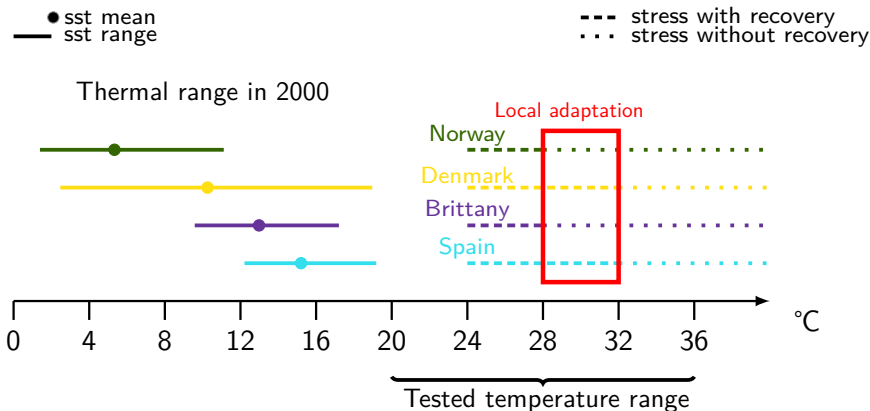
- stress with recovery
- ... stress without recovery



Photosynthetic response



Photosynthetic response

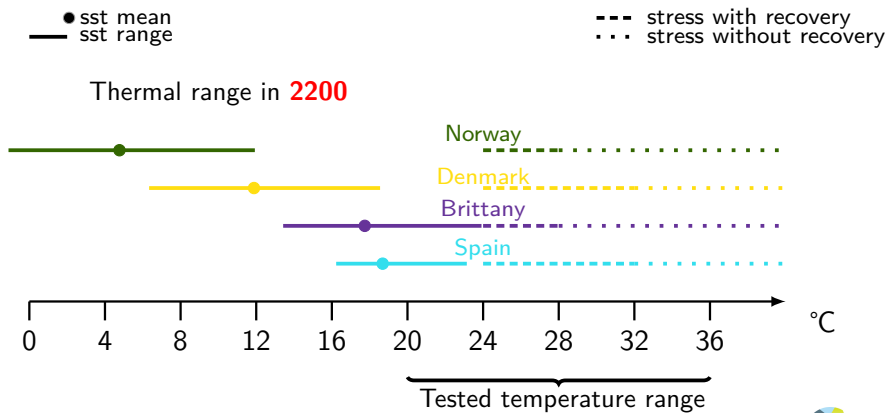


highest upper temperature

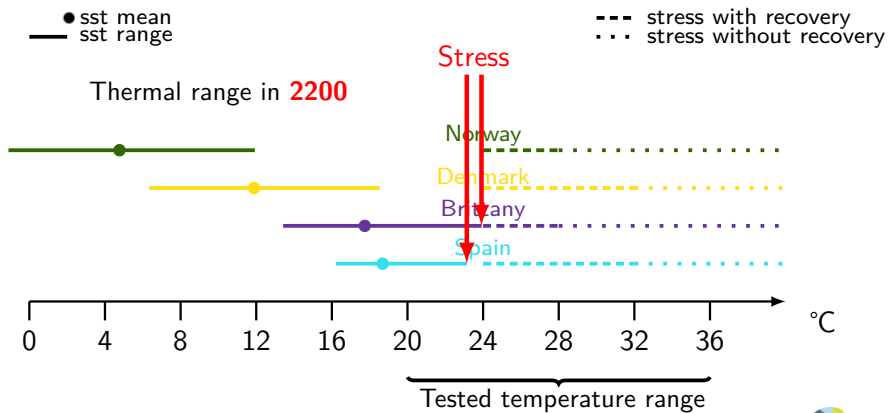
highest tolerance limit



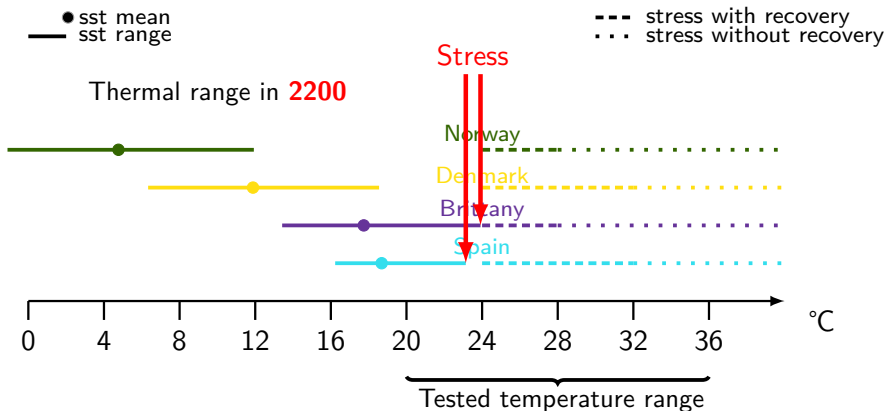
Photosynthetic response



Photosynthetic response



Photosynthetic response



Stress limit reached at the southern range



Conclusions

Plasticity

Plasticity along the entire E-Atlantic range of distribution

Local adaptation Population-specific stress response?

Extinction risk Where will temperatures exceed the species' thermal tolerance?



Conclusions

Plasticity

Plasticity along the entire E-Atlantic range of distribution

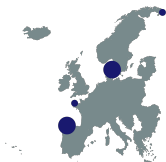
Local adaptation Population-specific stress response?

- Highest resilience in **Denmark and Spain**

Extinction risk Where will temperatures exceed the species' thermal tolerance?

Photosynthetic performance

Resilience



Conclusions

Plasticity

Plasticity along the entire E-Atlantic range of distribution

Local adaptation Population-specific stress response?

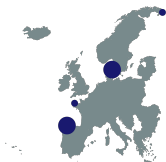
- Highest resilience in **Denmark and Spain**

Extinction risk Where will temperatures exceed the species' thermal tolerance?

- In **Brittany and Spain**

Photosynthetic performance

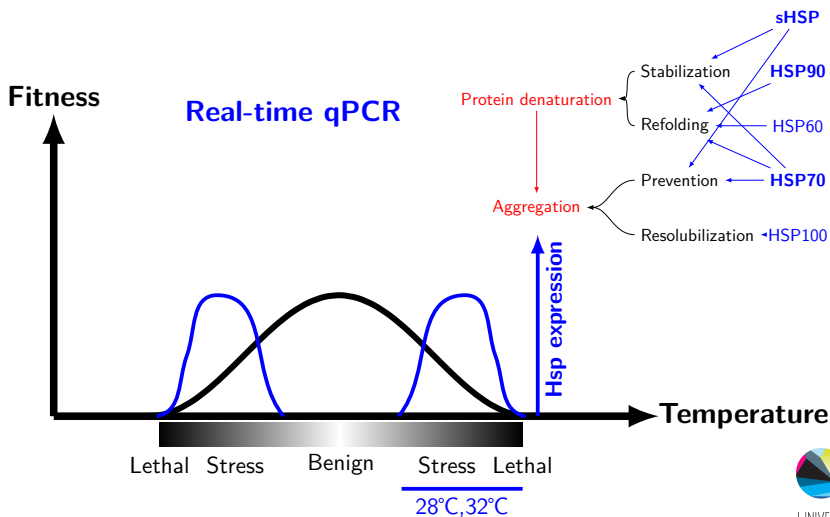
Resilience



Performance
in 2200

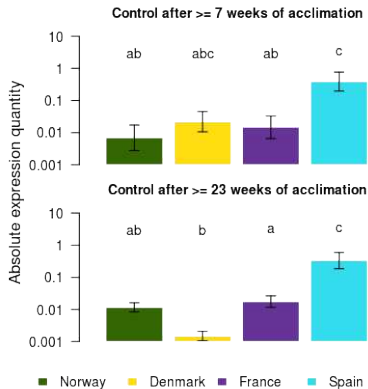


Measuring the physiological stress response

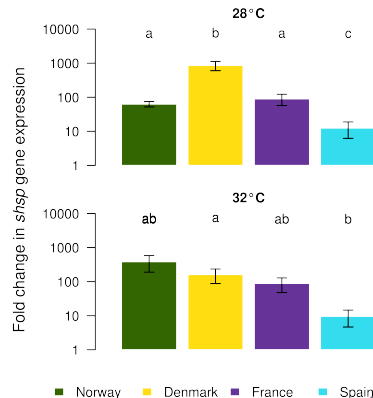


shsp gene expression

Before heat shock exposure

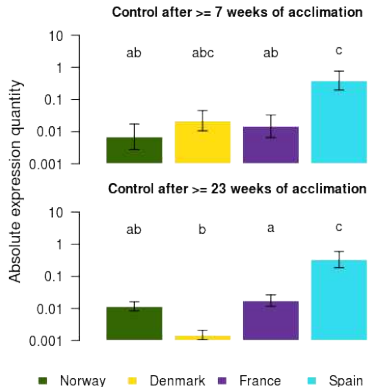


After 24h recovery

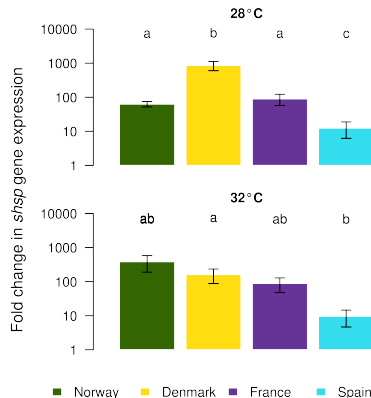


shsp gene expression

Before heat shock exposure



After 24h recovery

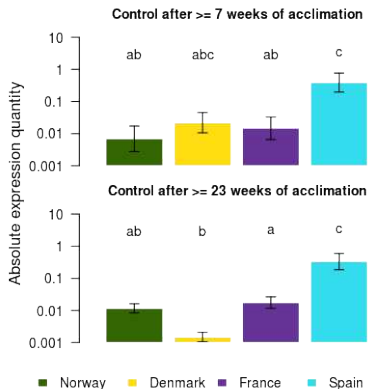


High constitutive expression

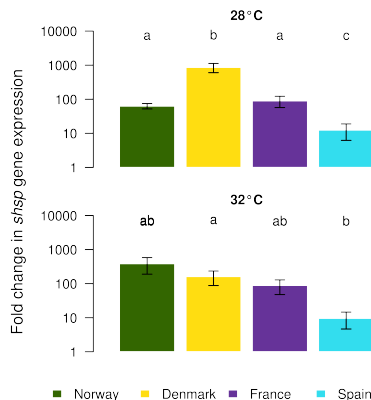


shsp gene expression

Before heat shock exposure



After 24h recovery



High constitutive expression

Reduced responsiveness



Conclusions

Plasticity

Plasticity along the entire E-Atlantic range of distribution

Local adaptation Population-specific stress response?

- Highest resilience in **Denmark and Spain**

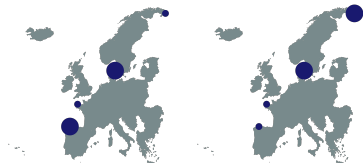
Extinction risk Where will temperatures exceed the species' thermal tolerance?

- In **Brittany and Spain**

Photosynthetic performance

Resilience

Stress in 2200



Conclusions

Plasticity

Plasticity along the entire E-Atlantic range of distribution

Local adaptation Population-specific stress response?

- Highest resilience in **Denmark and Spain**

Extinction risk Where will temperatures exceed the species' thermal tolerance?

- In **Brittany and Spain**

Photosynthetic performance

Resilience



Stress in 2200



hsp expression

Constitutive expression



Conclusions

Plasticity

Plasticity along the entire E-Atlantic range of distribution

Local adaptation Population-specific stress response?

- Highest resilience in **Denmark and Spain**
- **Spain** of reduced responsiveness

Extinction risk Where will temperatures exceed the species' thermal tolerance?

- In **Brittany and Spain**
- **lowest responsiveness in Spain**

Photosynthetic performance

Resilience



Stress in 2200

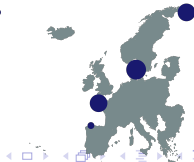


hsp expression

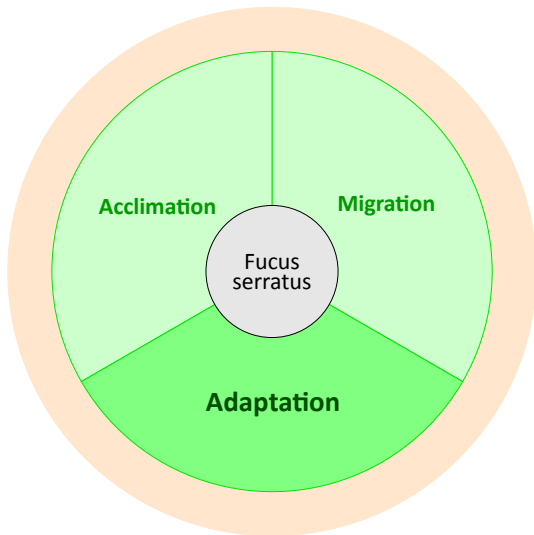
Constitutive expression



Heat shock response



Objectives



Paper III - Genetic changes

A decade of climate change on North Atlantic rocky shores - can the seaweed *Fucus serratus* adapt to rising temperatures?

Alexander Jueterbock, Spyros Kollias, James A. Coyer, Jeanine L. Olsen, Galice Hoarau

Manuscript



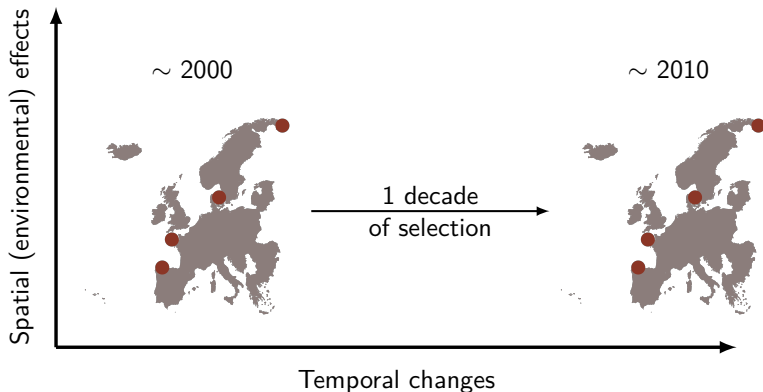
Specific aims

Genetic changes

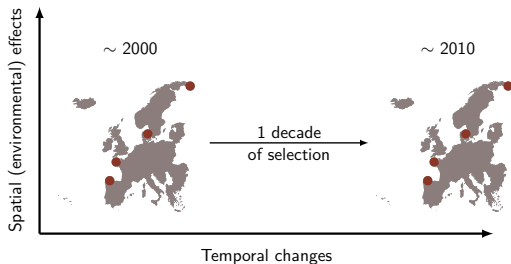
- Assess the **effective population size** N_e of *F. serratus* along its distributional range
- Identify **genetic changes** of *F. serratus* in the NE-Atlantic over the past 10 years



Sampling scheme (50–75 ind./pop)



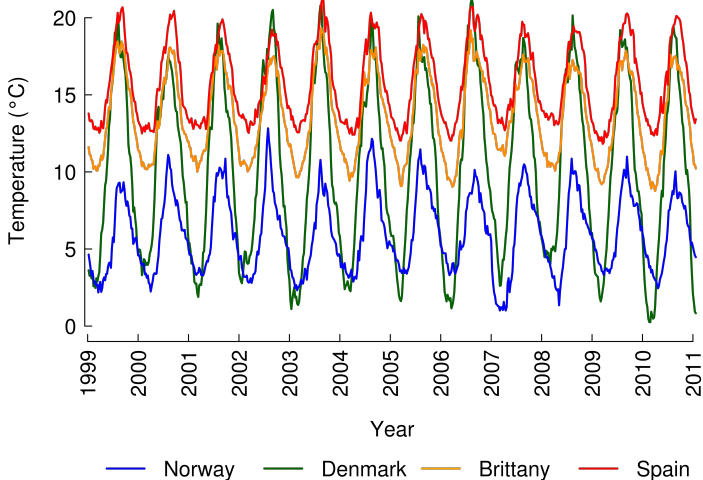
Methods and analysis



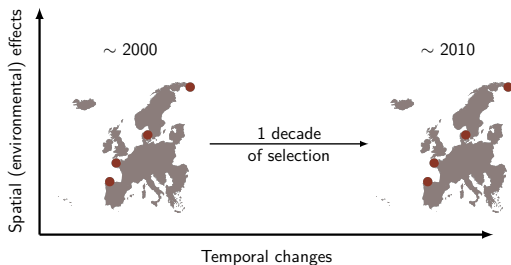
- **Temperature characterization**
- Genotyping
 - 31 microsatellite markers (20 EST-linked)
- Analysis
 - effective population size (N_e)
 - Allelic richness (α)
 - Temperature associated outlier loci



Temperature conditions



Methods and analysis

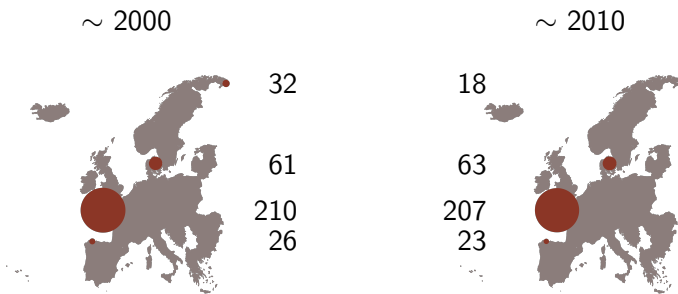


- Temperature characterization
- Genotyping
 - 31 microsatellite markers (20 EST-linked)
- analysis
 - **effective population size (N_e)**
 - Allelic richness (α)
 - Temperature associated outlier loci



Effective population size N_e

Reflecting adaptive capacity



Estimates excluding outlier loci



Conclusions

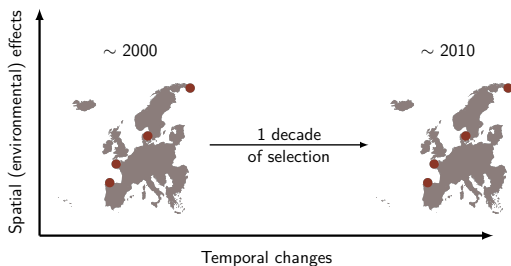
Genetic changes

- Assess the **effective population size** N_e of *F. serratus* along its distributional range
 - **Specifically low at the range limits**
 - **Highest in Brittany**
- Identify **genetic changes** of *F. serratus* in the NE-Atlantic over the past 10 years

N_e in 2010



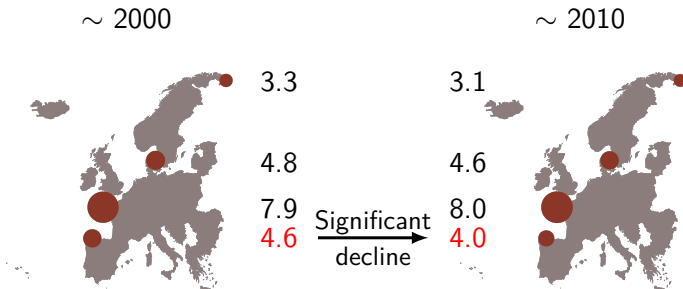
Methods



- Temperature characterization
- Genotyping
 - 31 microsatellite markers (20 EST-linked)
- analysis
 - effective population size (N_e)
 - **Allelic richness** (α)
 - Temperature associated outlier loci



Changes in allelic richness



Conclusions

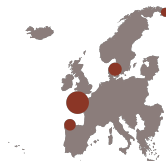
Genetic changes

- Assess the **effective population size** N_e of *F. serratus* along its distributional range
 - Specifically low at the range limits
 - Highest in Brittany
- Identify **genetic changes** of *F. serratus* in the NE-Atlantic over the past 10 years
 - α : **significant decline in Spain**

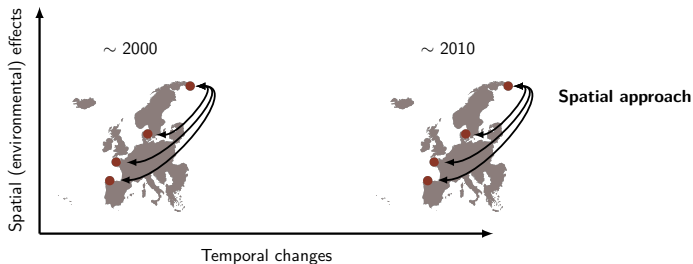
N_e in 2010



α in 2010



Methods and analysis



- Temperature characterization
- Genotyping
 - 31 microsatellite markers (20 EST-linked)
- analysis
 - effective population size (N_e)
 - Allelic richness (α)
 - **Temperature associated outlier loci**



Spatial outlier loci

~ 2000



1: E6, L58

2: F36, F49, L58

3: F19, L58

~ 2010



1: F19, L58

2: E9, F22, F49, L58

3: E9, F19, F60, L58



Spatial outlier loci

~ 2000



~ 2010



Outliers in both years

1: E6, L58

2: F36, F49, L58

3: F19, L58

1: F19, L58

2: E9, F22, F49, L58

3: E9, F19, F60, L58



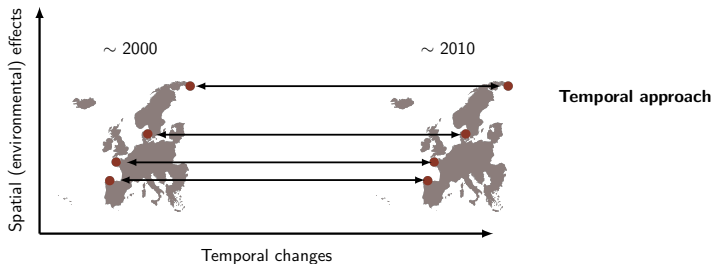
Local adaptation - or?

Examples fo alternative reasons for spatial outliers

- Genetic incompatibilities [Bierne et al., 2011; Mol. Ecol.]
- Isolation-by-distance pattern increases false positive rate [Fourcade et al. 2013; Mol. Ecol., Bierne et al., 2013; Mol. Ecol.]



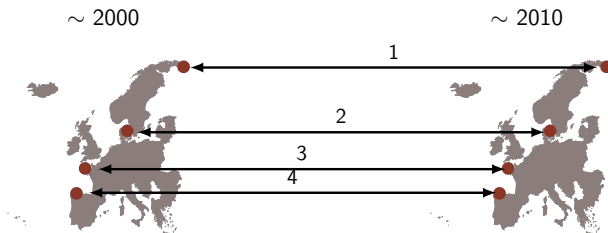
Methods and analysis



- Temperature characterization
- Genotyping
 - 31 microsatellite markers (20 EST-linked)
- analysis
 - effective population size (N_e)
 - Allelic richness (α)
 - **Temperature associated outlier loci**



Temporal outlier loci



1:

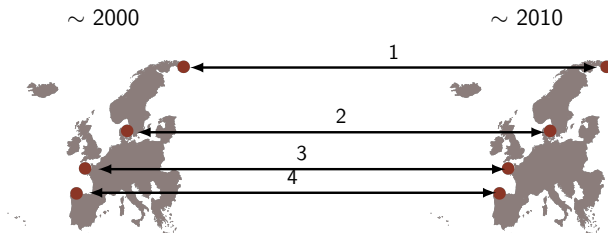
2: F19, F36

3: B113, B128, E6, E9, F12, F72, L58

4: F19, F65, F69, F72



Temporal outlier loci



Highest proportion of outliers: strongest selection

1:

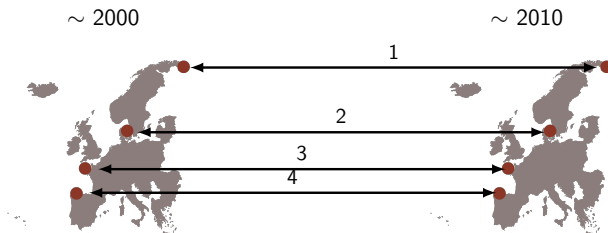
2: F19, F36

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4: F19, F65, F69, F72



Temporal outlier loci



Highest proportion of outliers: strongest selection

Congruent outlier: broad-scale selection

1:

2: F19, F36

3: B113, B128, E6, E9, F12, F72, L58

4: F19, F65, F69, F72



Spatio-temporal outlier loci

Spatial outliers

~ 2000



- 1: E6, L58
- 2: F36, F49, L58
- 3: F19, L58

~ 2010

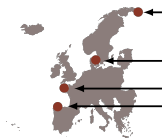


- 1: F19, L58
- 2: E9, F22, F49, L58
- 3: E9, F19, F60, L58

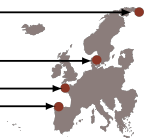
Outliers in both years

Temporal outliers

~ 2000



~ 2010



- 1:
- 2: F19, F36
- 3: B113, B128, E6, E9, F12, F72, L58
- 4: F19, F65, F69, F72

Highest proportion of outliers: strongest selection

Congruent outlier: broad-scale selection



Spatio-temporal outlier loci

Spatial outliers

~ 2000



- 1: E6, L58
- 2: F36, F49, L58
- 3: F19, L58

~ 2010



- 1: F19, L58
- 2: E9, F22, F49, L58
- 3: E9, F19, F60, L58

Outliers in both years

Temporal outliers

~ 2000



~ 2010



Highest proportion of outliers: strongest selection
 Congruent outlier: broad-scale selection

F19 - response to climate change?

- 1:
- 2: F19, F36
- 3: B113, B128, E6, E9, F12, F72, L58
- 4: F19, F65, F69, F72



Conclusions

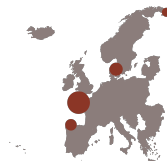
Genetic changes

- Assess the **effective population size** N_e of *F. serratus* along its distributional range
 - Specifically low at the range limits
 - Highest in Brittany
- Identify **genetic changes** of *F. serratus* in the NE-Atlantic over the past 10 years
 - α : significant decline in Spain
 - **Strongest selective pressure in Brittany and Spain**
 - **Locus F19: Adaptive value under climate change?**

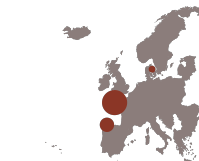
N_e in 2010



α in 2010



Temporal outliers



Overall conclusions

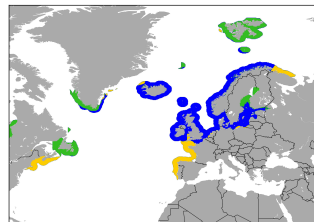
■ Predicted shift

- Biggest changes: Arctic and warm-temperate regions

■ Importance of populations

- Norway: Colonization of the Arctic?
- Denmark: Center of distribution
- Brittany: Center of adaptability
- Spain: Insufficient plasticity and adaptability

F. serratus, 2200, SRES A1B scenario



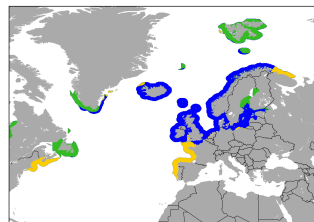
State of suitable habitat
■ Gain ■ Loss ■ Remaining



Overall conclusions

- Predicted shift
 - Biggest changes: Arctic and warm-temperate regions
- Importance of populations
 - Norway: Colonization of the Arctic?
 - Denmark: Center of distribution
 - Brittany: Center of adaptability
 - Spain: Insufficient plasticity and adaptability

F. serratus, 2200, SRES A1B scenario



State of suitable habitat
■ Gain ■ Loss ■ Remaining



Overall conclusions

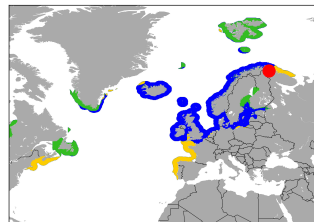
■ Predicted shift

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State of suitable habitat
■ Gain ■ Loss ■ Remaining



Overall conclusions

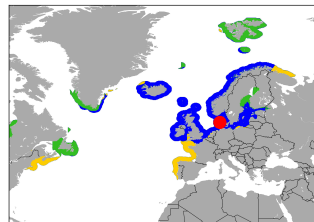
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State of suitable habitat
■ Gain ■ Loss ■ Remaining



Overall conclusions

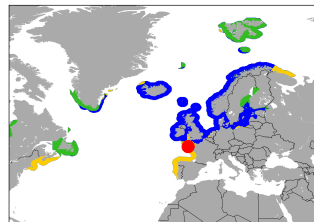
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Overall conclusions

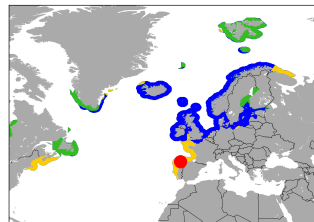
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State of suitable habitat
■ Gain ■ Loss ■ Remaining



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9 Brown algae

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11 Paper II

12 Paper III



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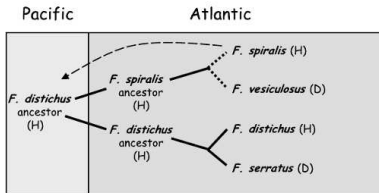
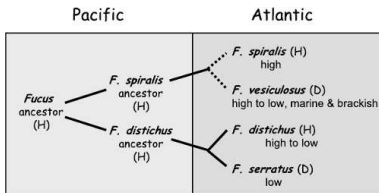


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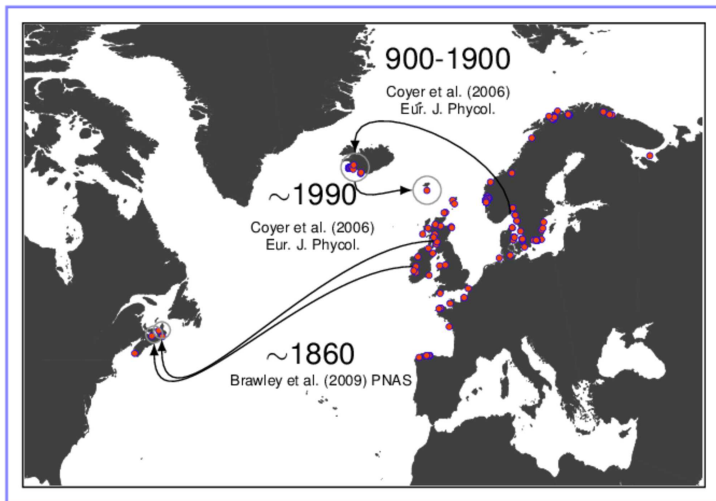
mtDNA based Phylogeny



[Coyer et al., 2006; Mol. Phylogenet. Evol.]



Human introduction



Life cycles of algae



[Braune, 2008; Meeresalgen]



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Choices in Ecological Niche Modeling

Background sites

Occurrence sites

Environmental
conditions

Restriction

Sampling bias correction

Identifying
variable clusters

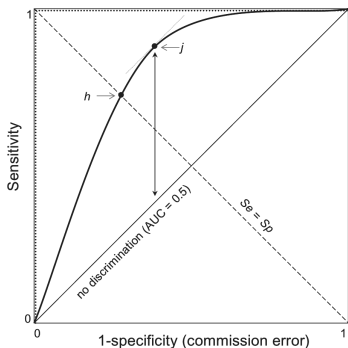
Evaluating
variable importance

Model

Model evaluation
Threshold application



The AUC value



[Jimenez-Valverde, 2012; Global Ecol. Biogeogr.]

Sensitivity: Present, predicted as present

1-Specificity: Absence, predicted as present



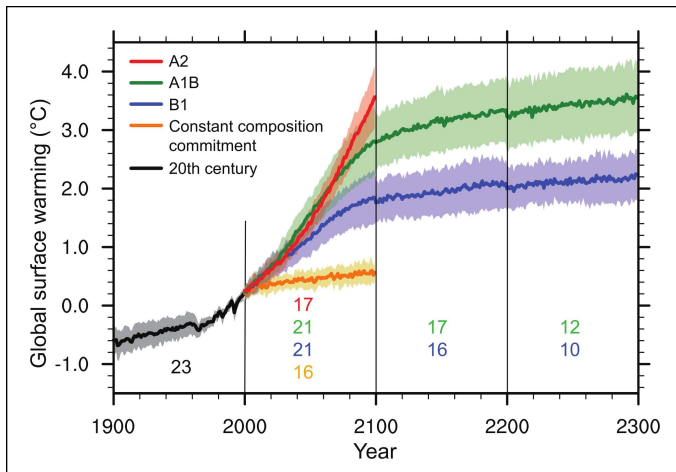
Importance of temperature for algal distribution

Variable	Derivative	Unit	Contribution (%)		
			<i>Fucus serratus</i>	<i>Fucus vesiculosus</i>	<i>Ascophyllum nodosum</i>
SST	Minimum	°C	66	46.4	82.3
SST	Maximum	°C	24.7	42.8	
SST	Mean	°C	9.3		
SAT	Minimum	°C			7.3
Salinity	Mean	PSS			10.4
DA	Minimum	m ⁻¹		10.8	

[Jueterbock et al., 2013; Ecol. Evol.]



SRES CO₂ emission scenarios



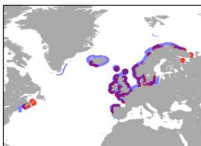
[Meehl et al., 2007; Climate Change 2007]



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Present-day habitat suitability and occurrence sites

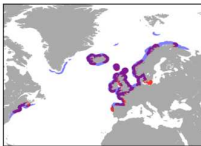
Fucus serratus



Fucus vesiculosus



Ascophyllum nodosum



State of occurrence

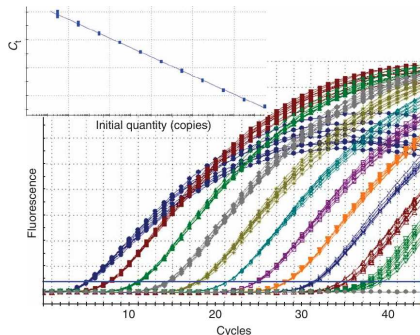
● Recorded ■ Predicted ■ Recorded+Predicted

[Jueterbock et al., 2013; Ecol. Evol.]



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Quantification of gene products



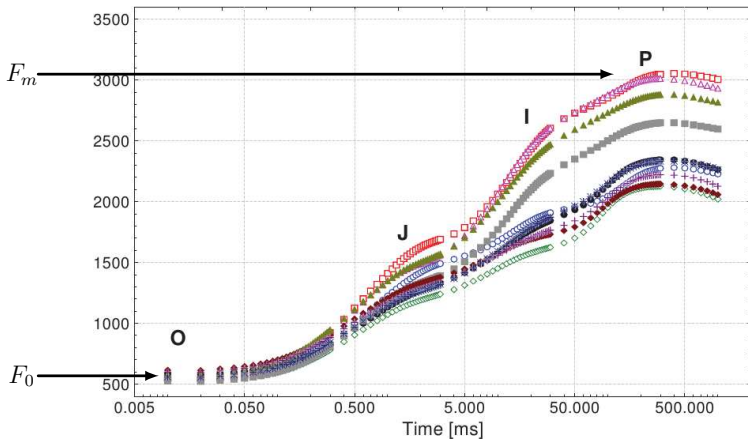
[Nolan et al., 2006; Nature Protocols]

$$\text{Efficiency} = 10^{-1/\text{slope}}$$

$$\text{quantity} = 10^{\frac{Ct-b}{\text{slope}}}$$



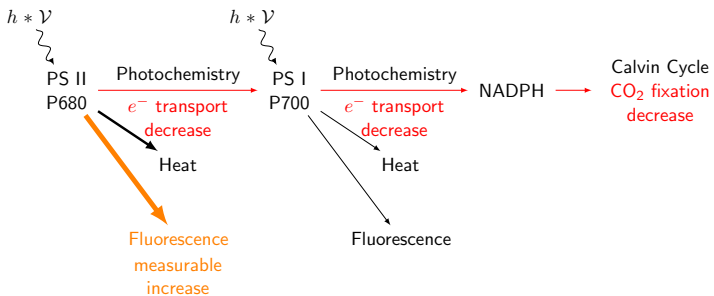
OJIP curve



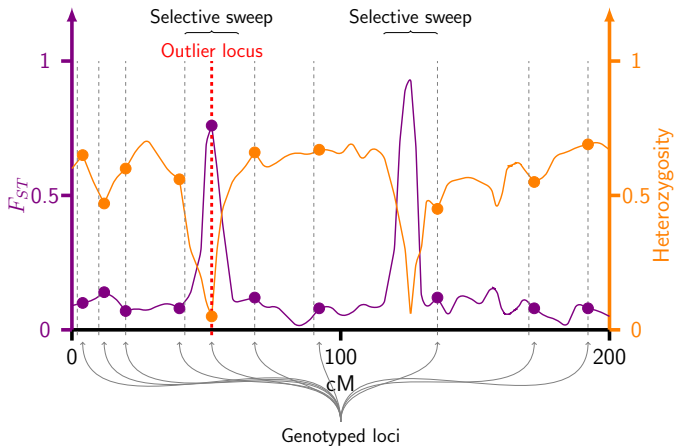
[Bussotti et al., 2010; Scand. J. Forest Res.]



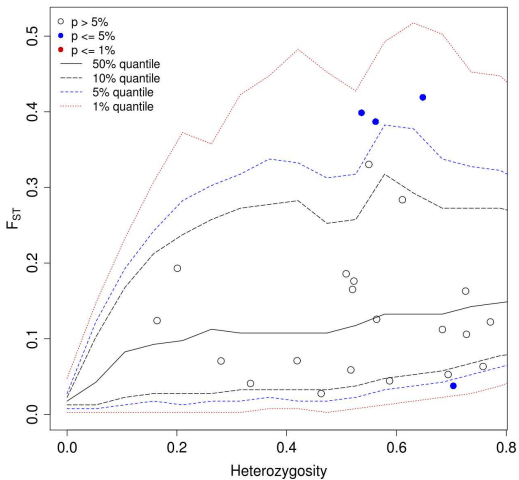
Heat stress effect on photosynthesis



Genome scan for outlier loci



Arlequin - test for outlier loci

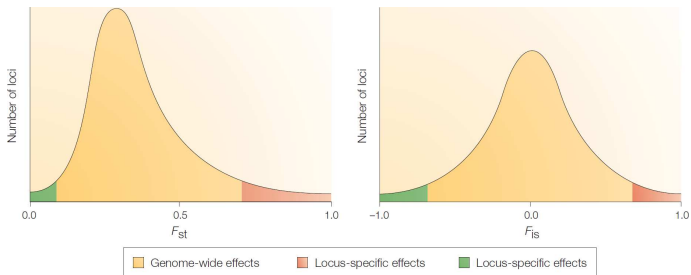


[Excoffier & Lischer, 2010; Mol. Ecol. Res.]



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Identification of outlier loci



[?]



Potential reasons for low N_e values

- Unequal sex ratios
- Variance in family size (individual gametic contribution)
- Fluctuations of population size (potential reason for the low N_e in Spain)
- Reduced gene flow between populations
- Inbreeding



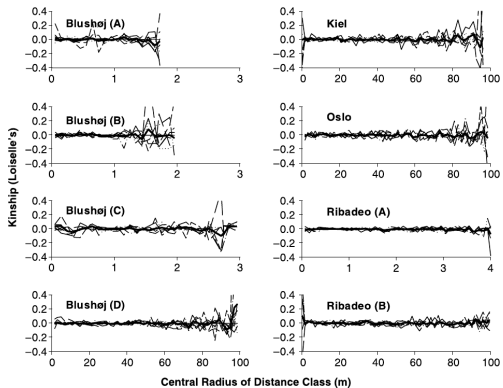
N_e indicates

- The rate of genetic change due to genetic drift is proportional to $\frac{1}{2N_e}$
- The effectiveness of selection over genetic drift (drift dominates if selection $< \frac{1}{2N_e}$)
- Nucleotide diversity $4Nu$ with u being the mutation rate
- In a closed population, N_e can indicate MLH. Gene flow uncouples N_e from genetic stochasticity



Significant F_{IS} values can not be explained by a small-scale family structure

Genetic correlations among individuals



[Coyer et al., 2003; Mol. Ecol.]



Local adaptation - or?

Alternative reasons for spatial outliers

- Geographic distribution that creates correlations in population structure [Fourcade et al. 2013; Mol. Ecol., Bierne et al., 2013; Mol. Ecol.]

Rivers



Oceanic ridges



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Coastlines



Local adaptation - or?

Alternative reasons for spatial outliers

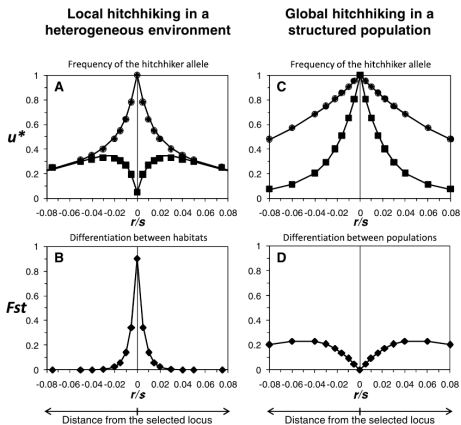
- Background selection against deleterious mutations
[Charlesworth et al., 1997; Genet. Res.]



Local adaptation - or?

Alternative reasons for spatial outliers

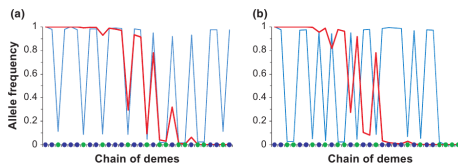
- Species-wide selective sweeps [Bierne, 2010; Evolution]



Local adaptation - or?

Alternative reasons for spatial outliers

- Coupling of endogenous with exogenous gene flow barriers
[Bierne et al., 2011; Mol. Ecol.]



red: endogenous, blue: exogenous alleles



Local adaptation - or?

Alternative reasons for spatial outliers

- Stochastic effects at the wave edge of an expanding population [Excoffier et al., 2009; Annu. Rev. Ecol. Evol. Syst.]

