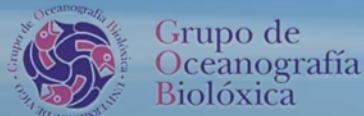


# Control of the structure of marine picoplankton communities by turbulence and nutrient supply dynamics



Grupo de  
Oceanografía  
Biolóxica

PhD candidate: Jose Luis Otero Ferrer

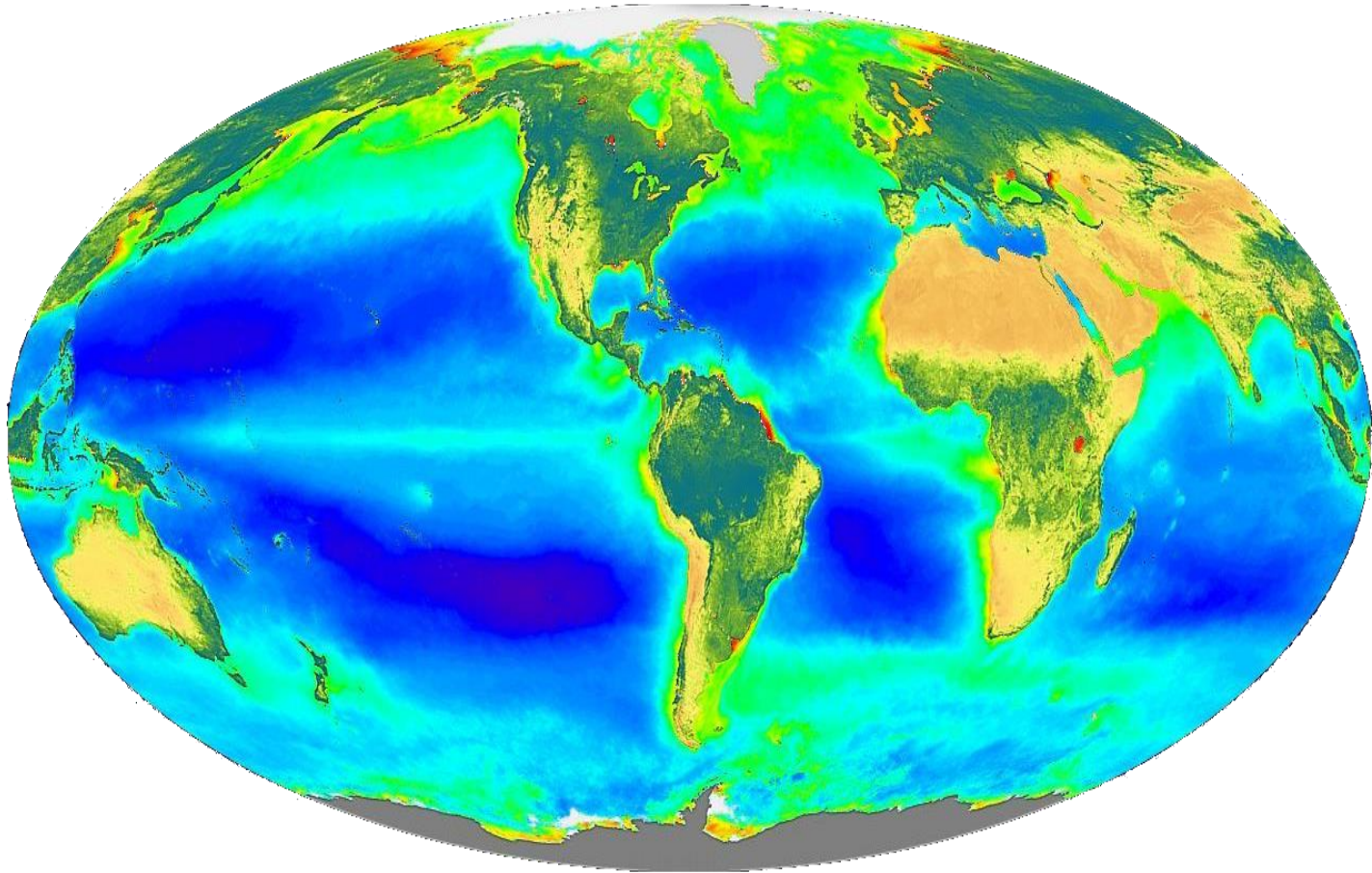


Supervisors:  
Beatriz Mouríño  
Pedro Cermeño

# Introduction

# The importance of phytoplankton

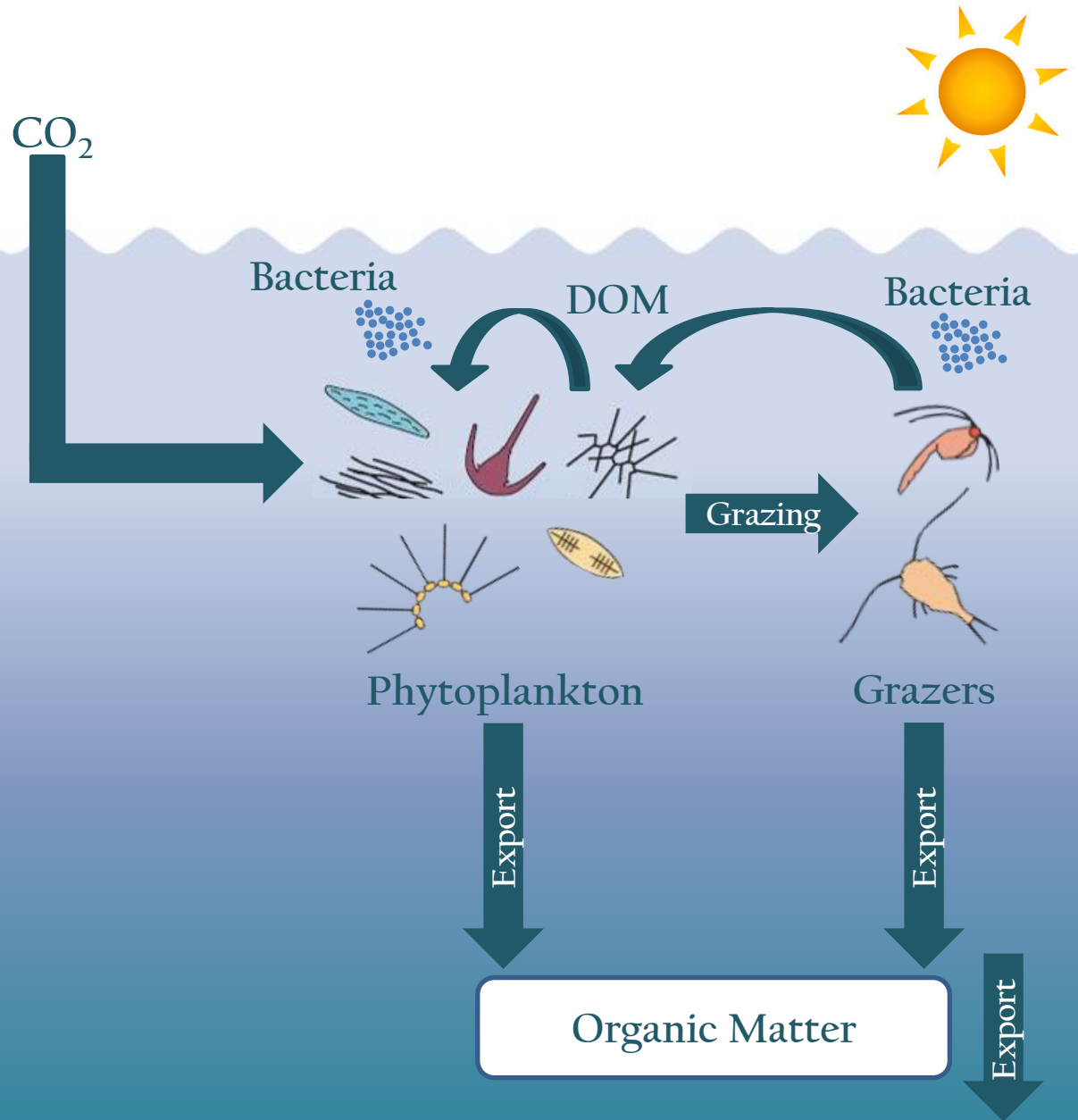
INTRODUCTION



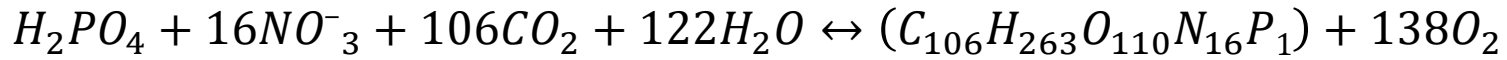
MODIS Science Team

# Phytoplankton and the biological carbon pump

INTRODUCTION

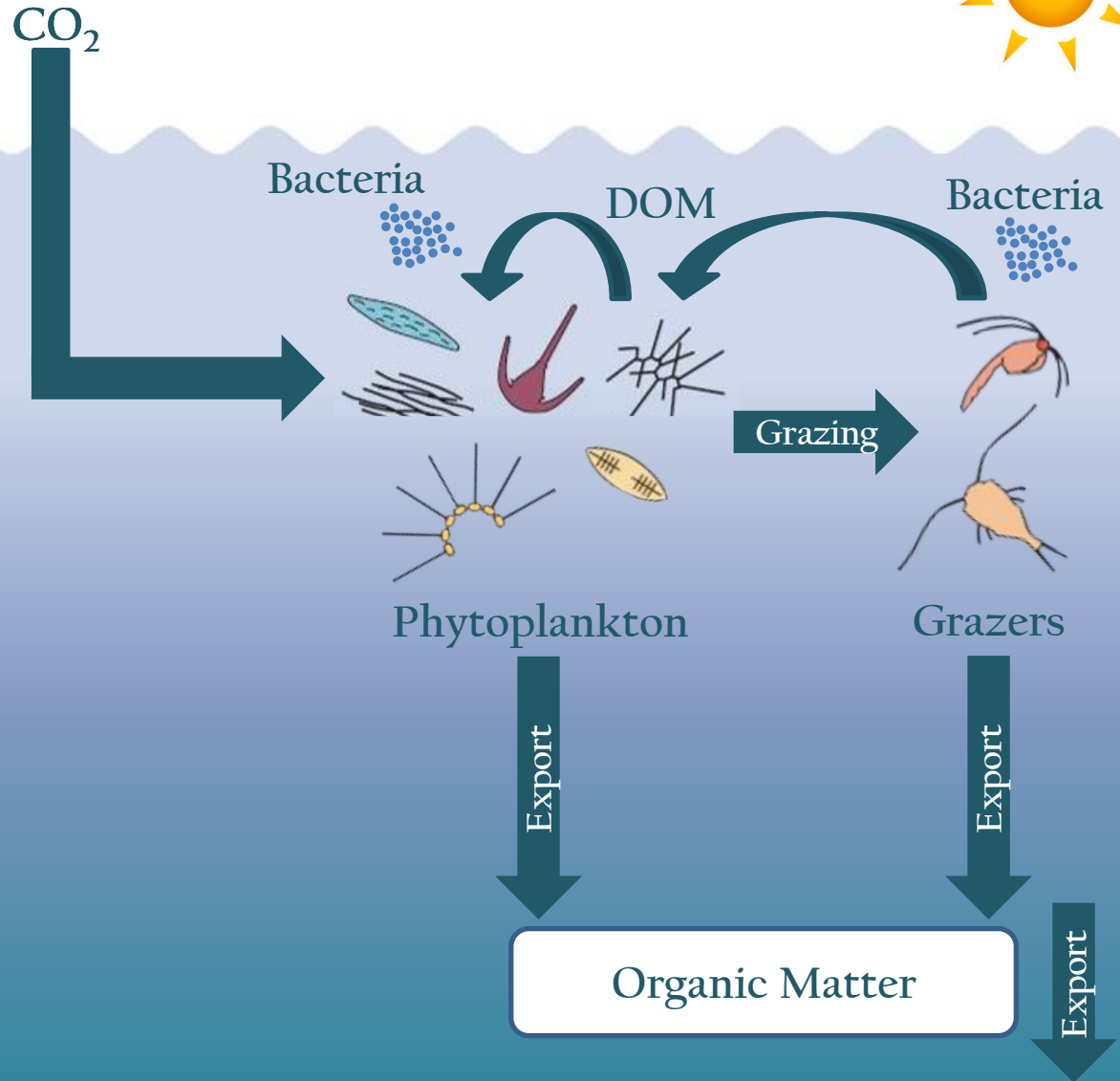


# Phytoplankton and the biological carbon pump

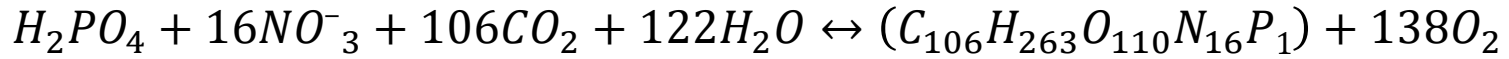


INTRODUCTION

**Redfield Ratios**  
C:N = 6.6  
N:P = 16



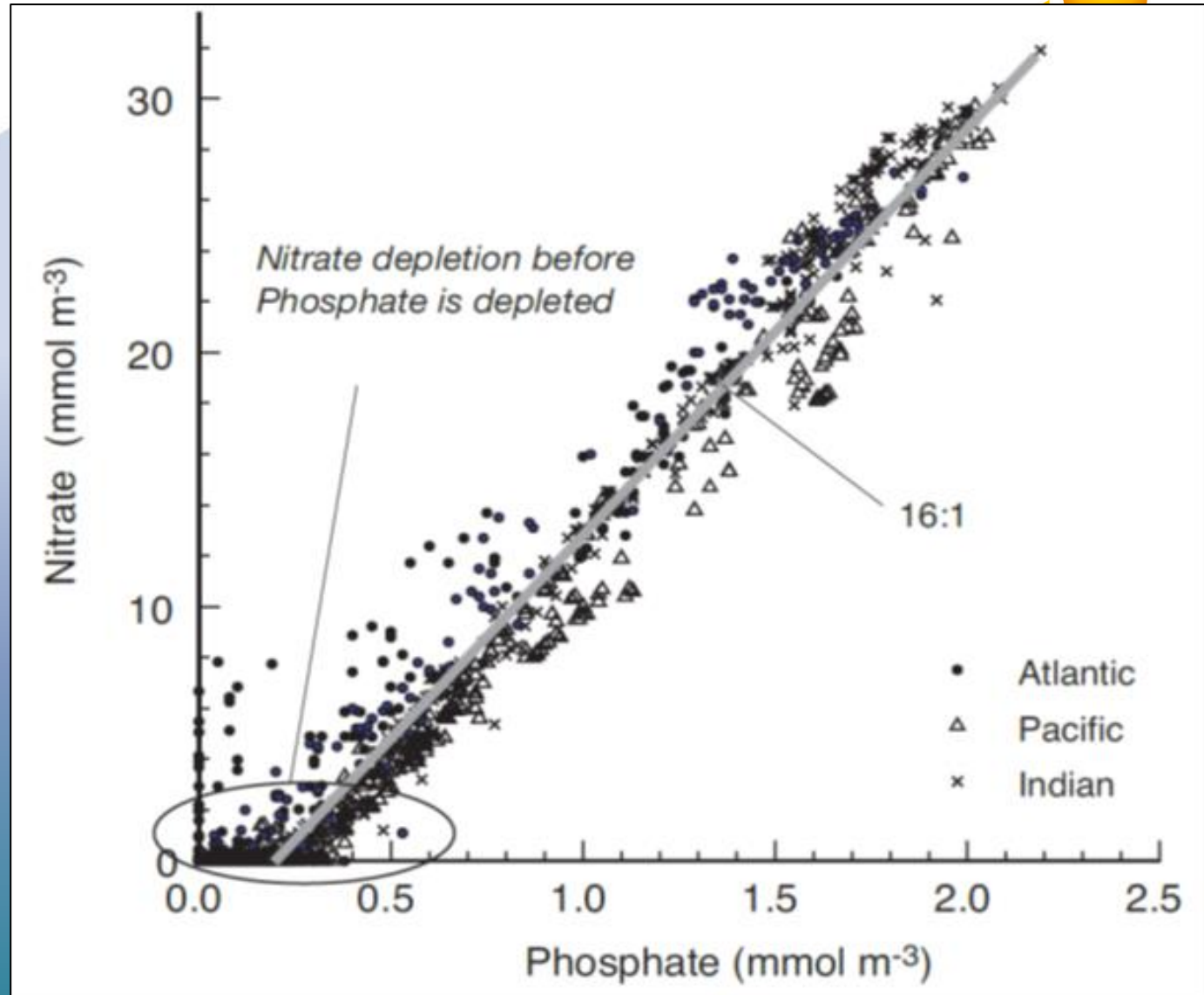
# Phytoplankton and the biological carbon pump



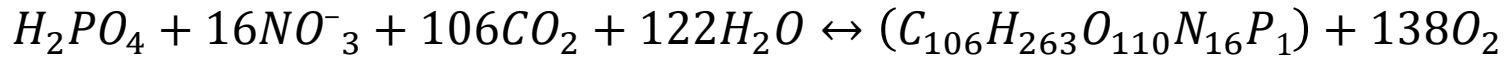
## Redfield Ratios

C:N = 6.6

N:P = 16

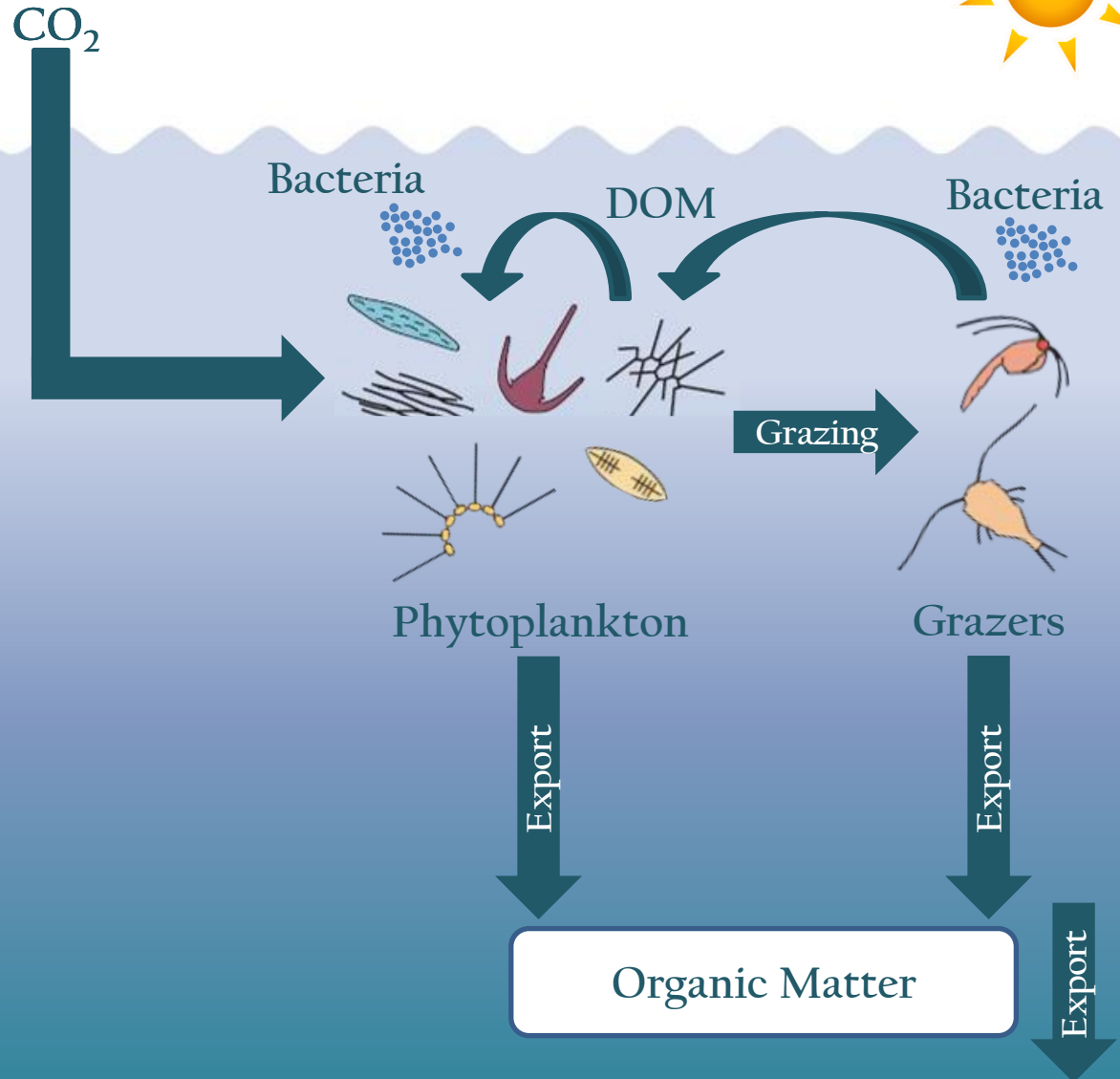


# Phytoplankton and the biological carbon pump



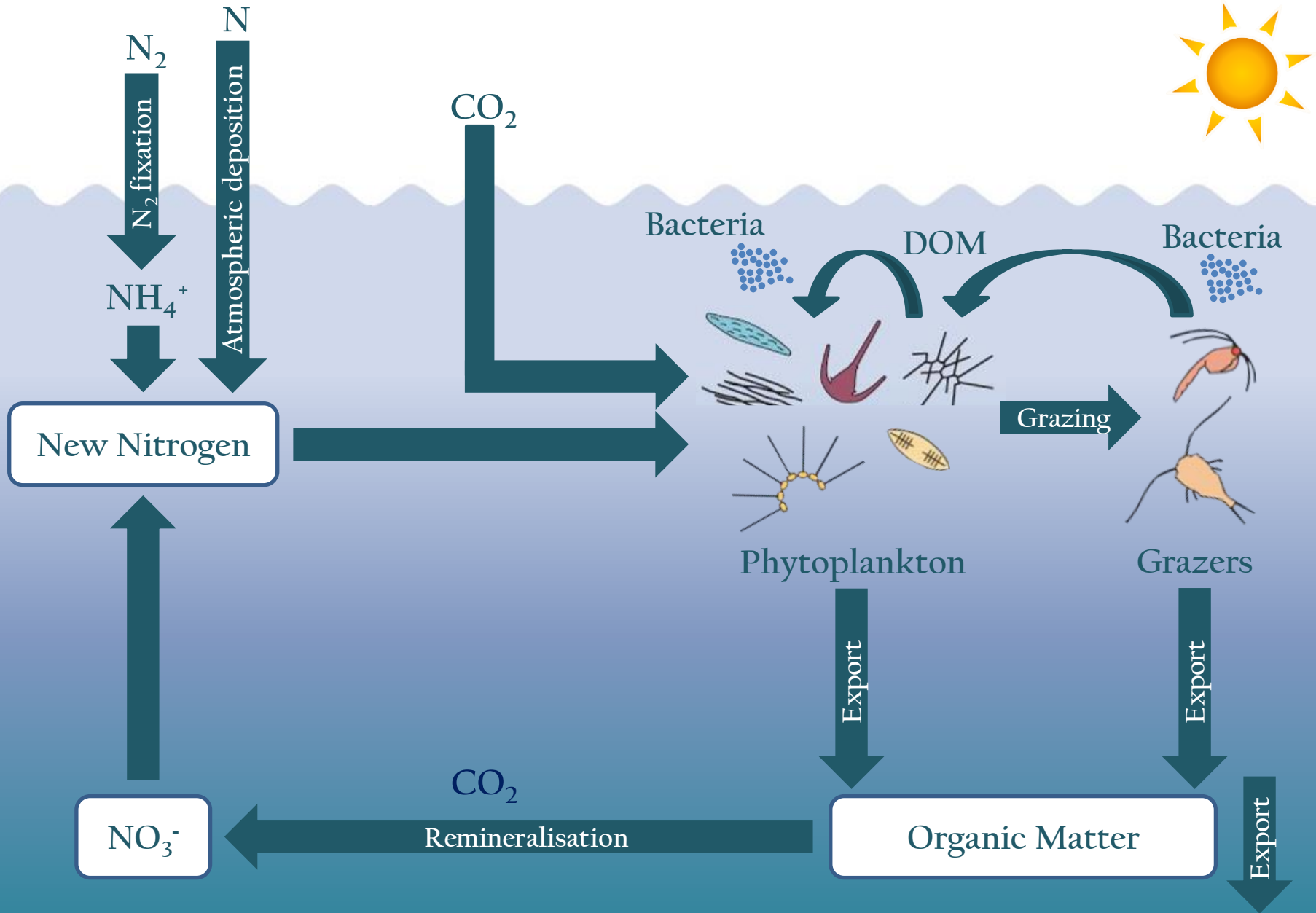
INTRODUCTION

**Redfield Ratios**  
C:N = 6.6  
N:P = 16



# Relevance of nitrogen and supply mechanisms

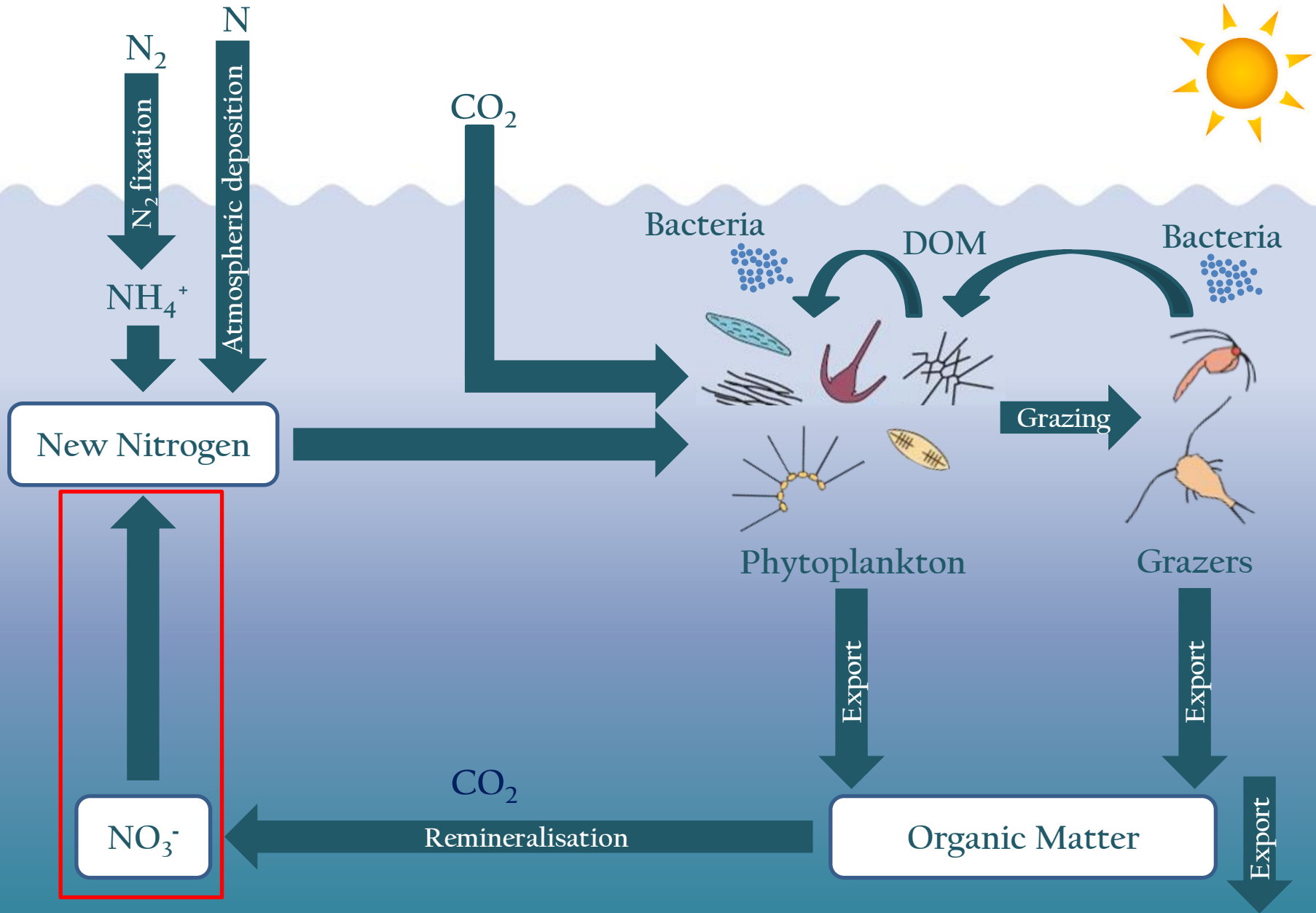
INTRODUCTION



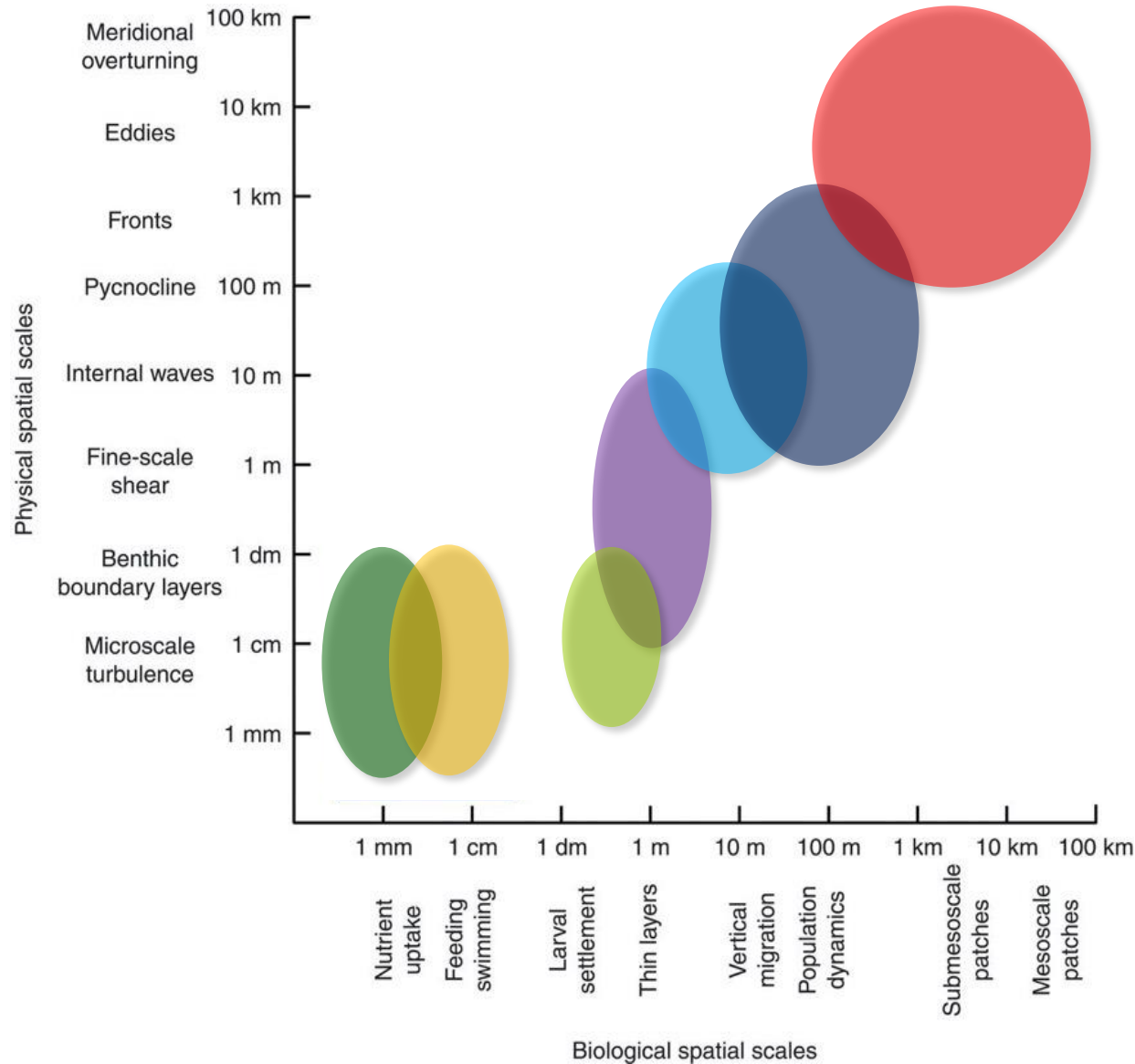


# Relevance of nitrogen and supply mechanisms

INTRODUCTION



# Turbulence effects over biological data



# How is turbulence measured?



- Microstructure shear sensor
- CTD

# Microstructure turbulence profiler (MSS)



❑ Microstructure shear sensor



Disipation rate of turbulent kinetic energy ( $\epsilon$ ).

❑ CTD



Brunt–Väisälä frequency ( $N$ ).

# Microstructure turbulence profiler (MSS)

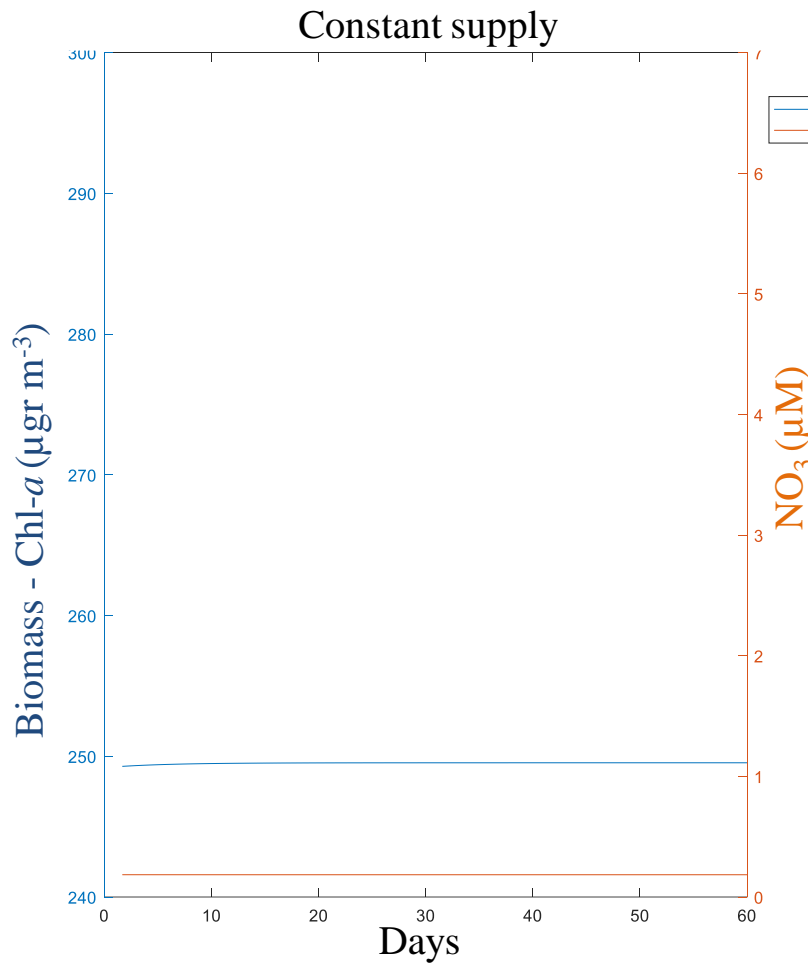


- ❑ Microstructure shear sensor → Disipation rate of turbulent kinetic energy ( $\epsilon$ ).
- ❑ CTD → Brunt–Väisälä frequency ( $N$ ).

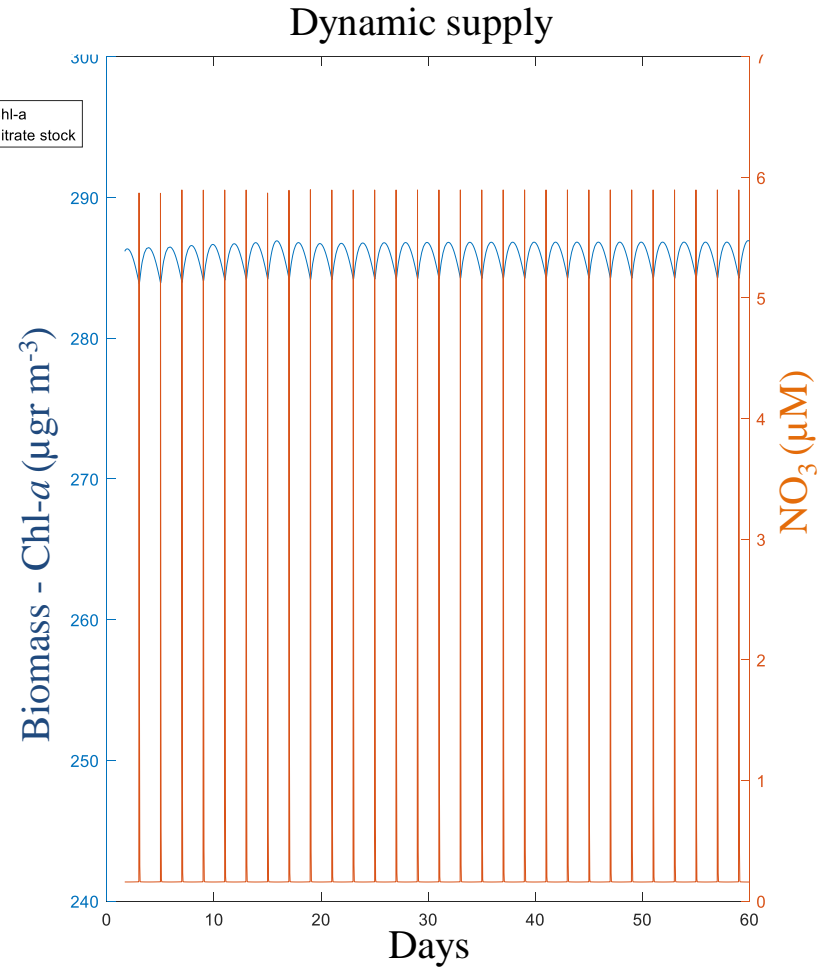
Vertical diffusivity ( $K_z$ ):

$$K_z = 0.2 \frac{\epsilon}{N^2}$$

# Nutrient stock and nutrient flux

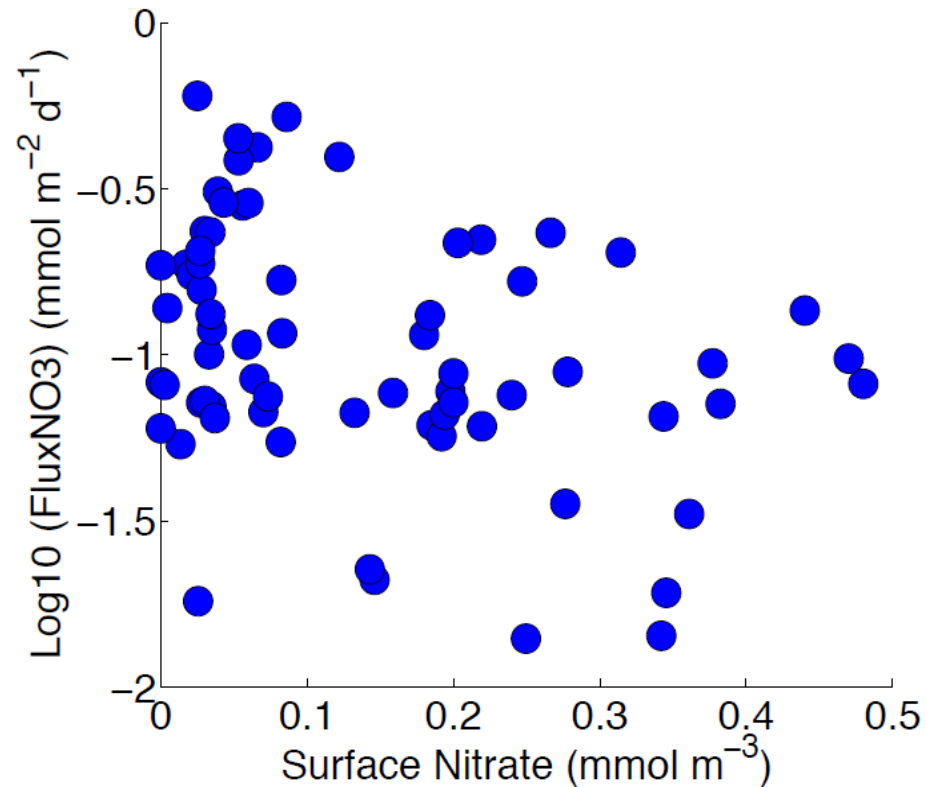


$$\frac{dNO_3}{dt} = \text{Supply} - \text{Uptake} = 0$$



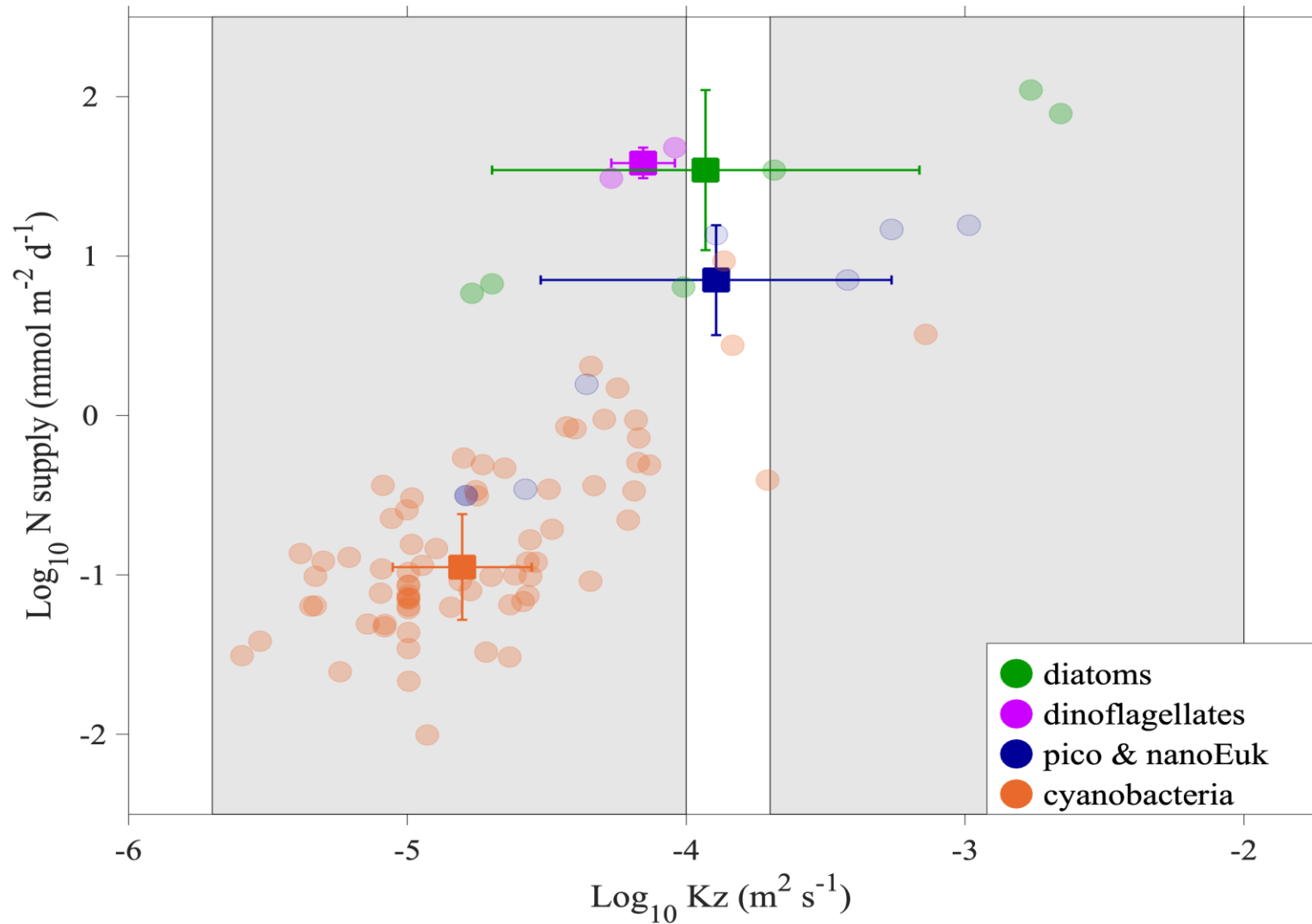
$$\frac{dNO_3}{dt} = \text{Supply} - \text{Uptake} \neq 0$$

# Nutrient stock and nutrient flux in Atlantic Ocean



The variability in nutrient stock **can be disconnected** from changes in nutrient supply (Mouriño-Carballido *et al.* 2011)

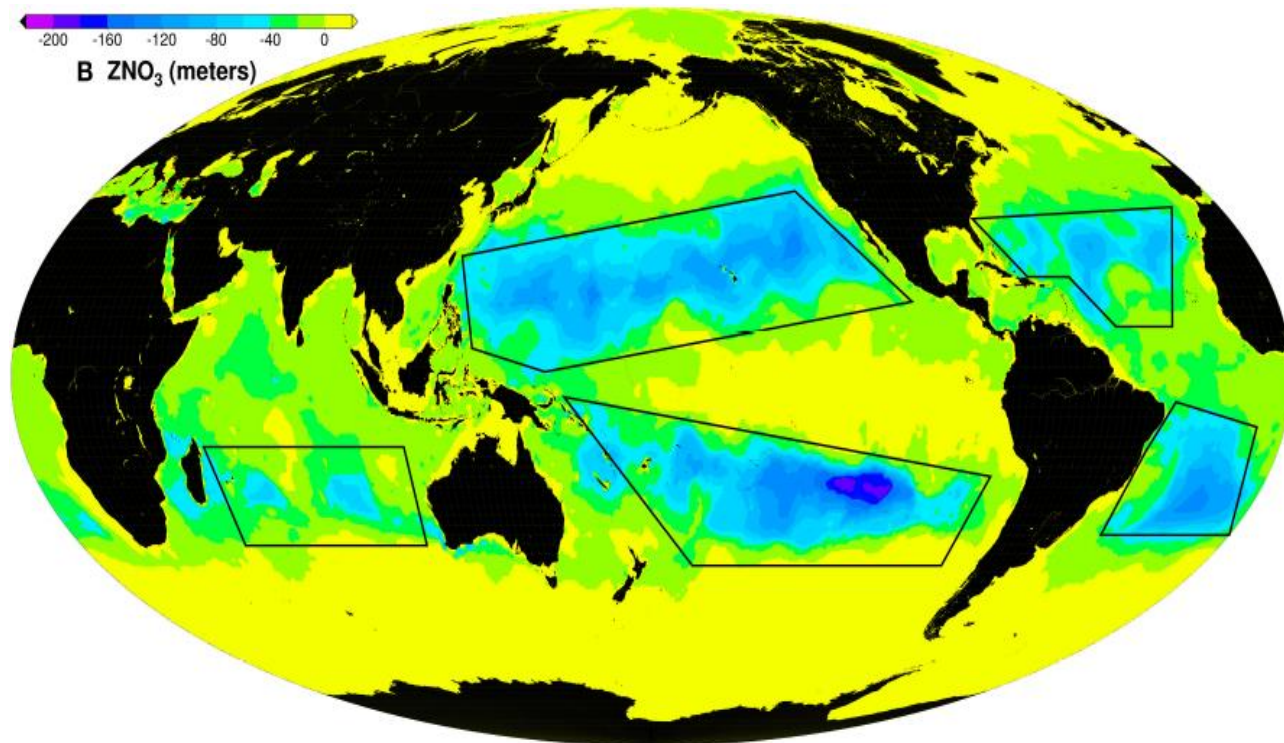
# Competition dynamics



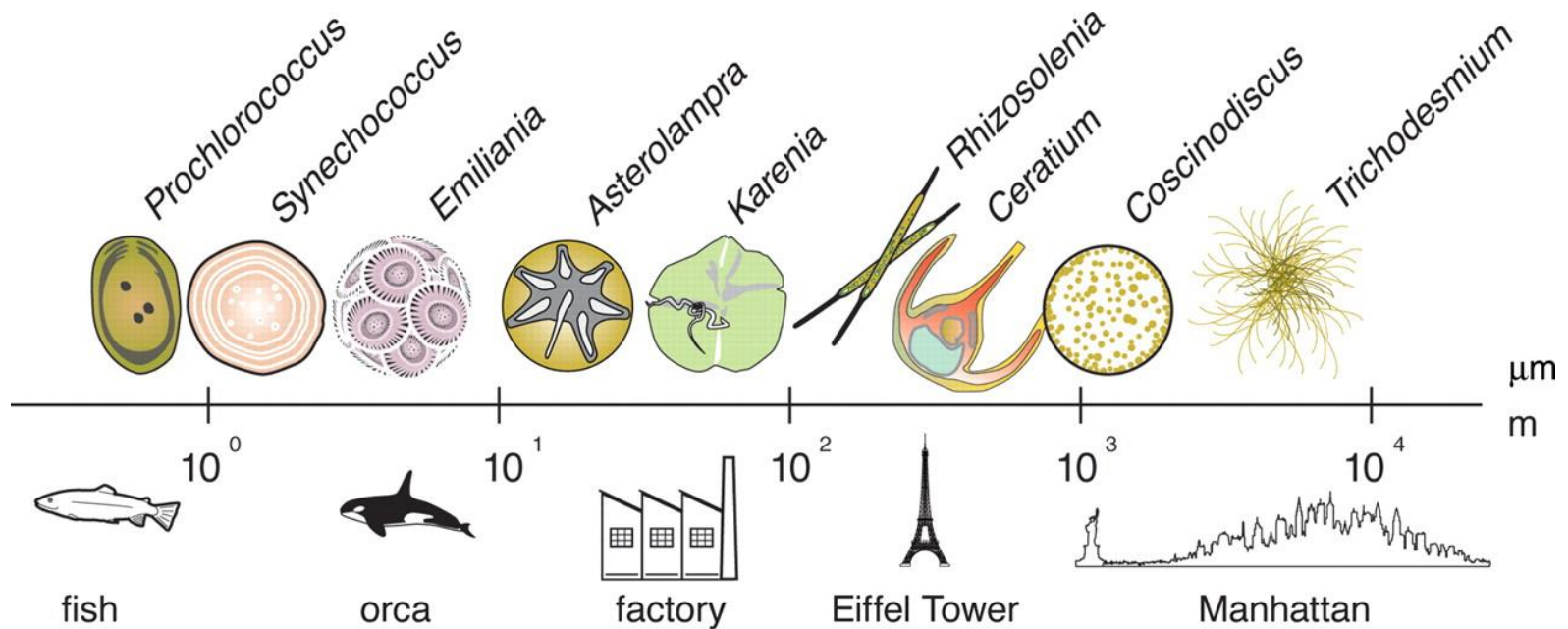


# Why picoplankton?

- The most abundant organisms in the ocean
- Picophytoplankton often dominate primary production in gyres
- Expected future expansion of gyres area in a future ocean scenario



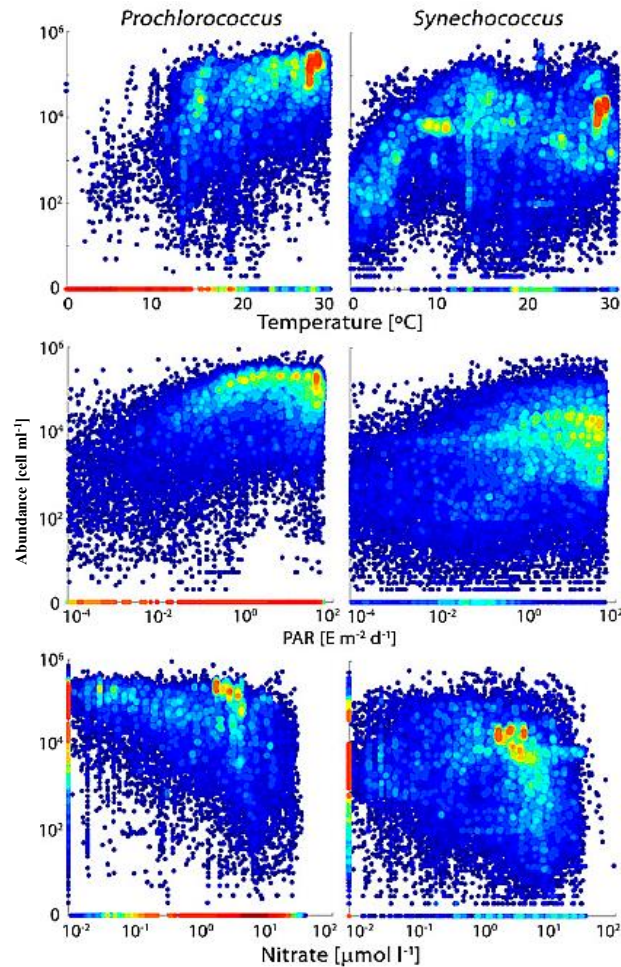
# Which groups do picoplankton include ?



Finkel, 2010

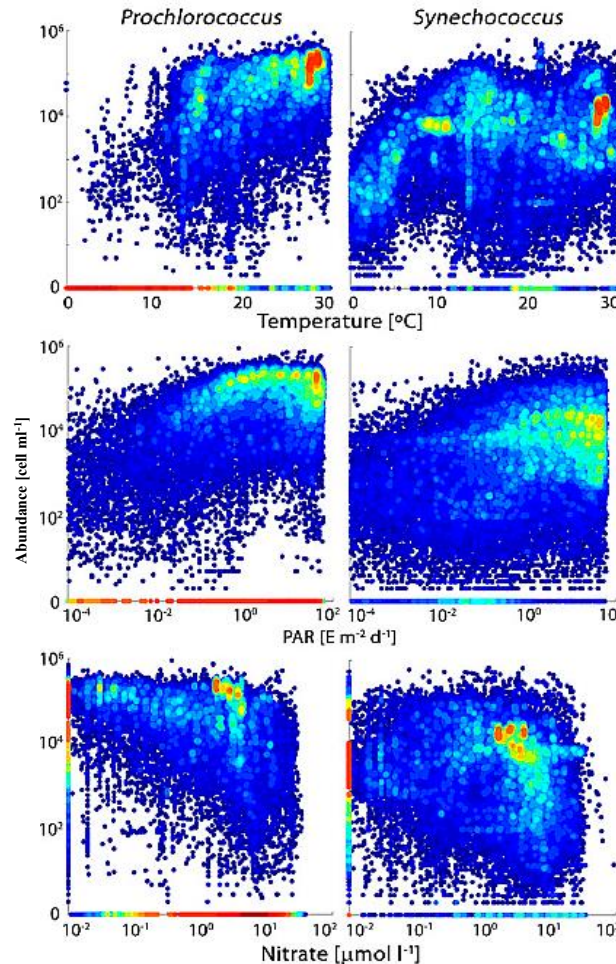
<u>Bacterioplankton</u>	<u>Cyanobacteria</u>	<u>Picoeukaryotes</u>
LNA	<i>Prochlorococcus</i>	
HNA	<i>Synechococcus</i>	

# Environmental control factors in the distribution of picophytoplankton



# Environmental control factors in the distribution of picophytoplankton

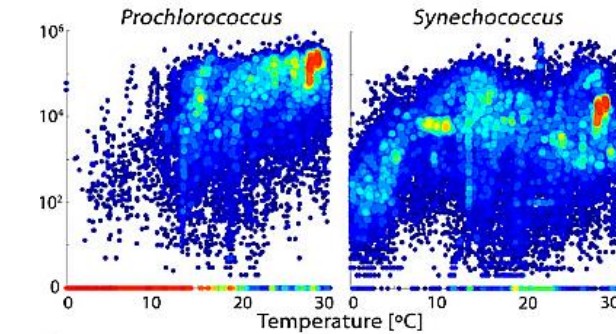
Temperature



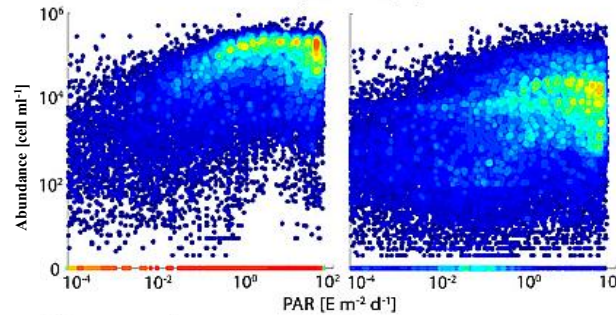
Light

# Environmental control factors in the distribution of picophytoplankton

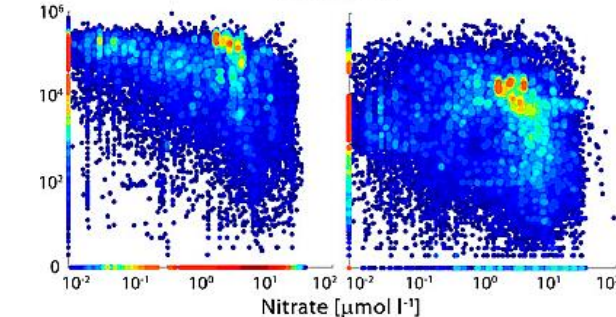
Temperature



Light

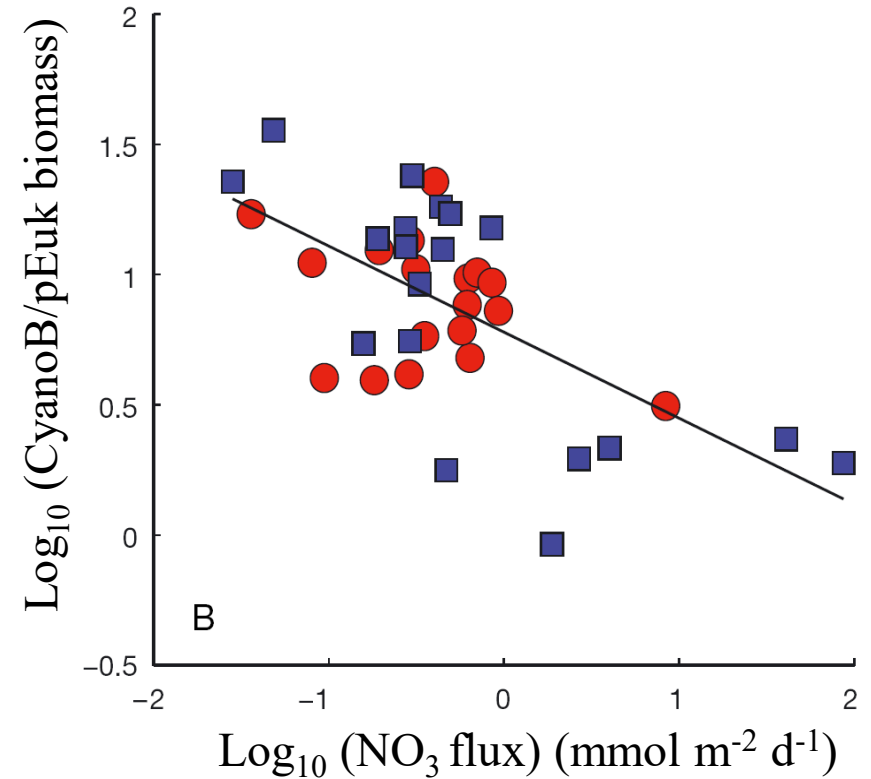
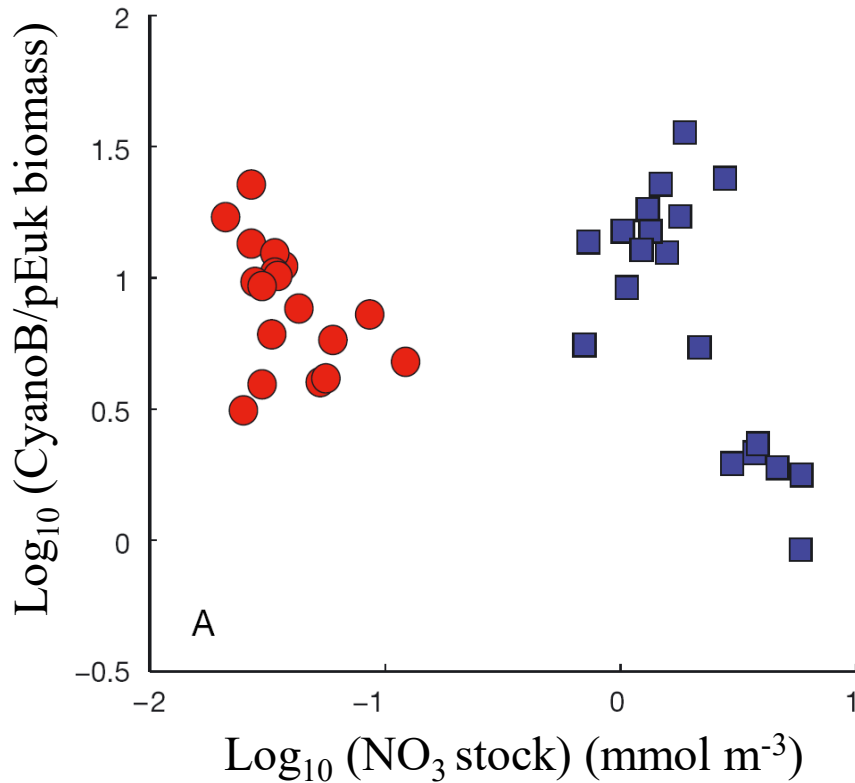


Nutrients



**Temperature & Light** are the main control factors of the regional distributions of both *Prochlorococcus* and *Synechococcus* (Flombaum *et al.*, 2013).

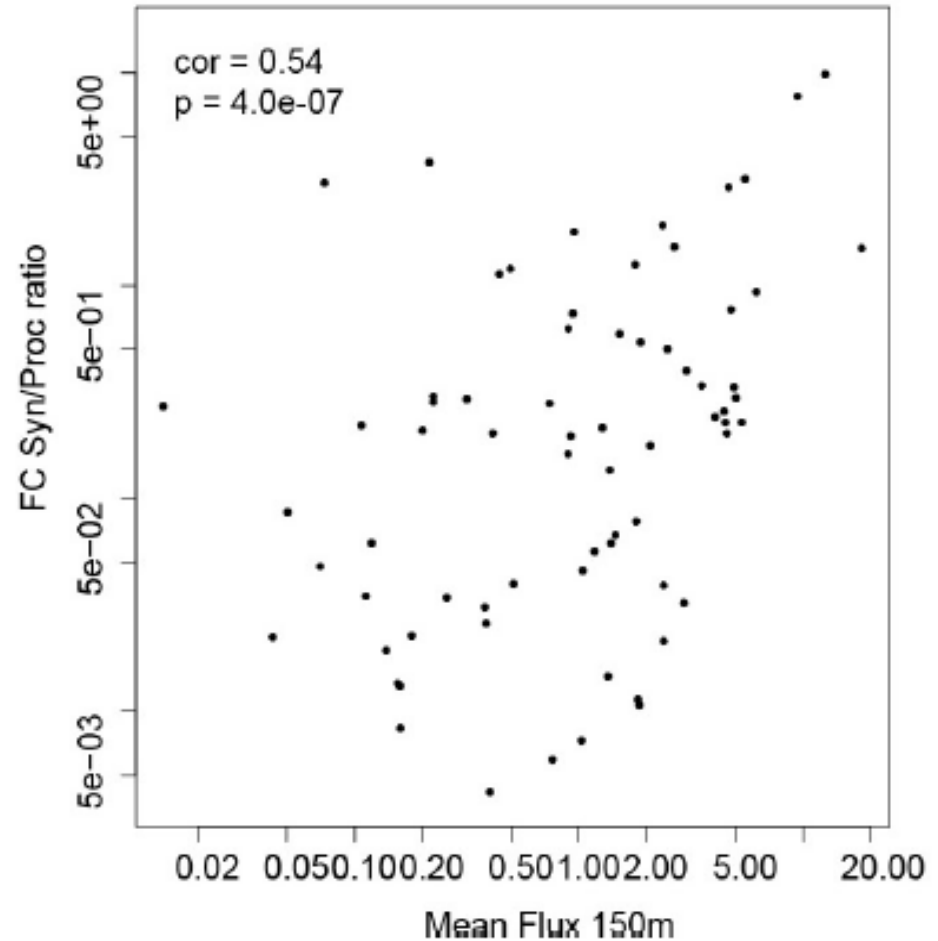
# Environmental control factors in the distribution and activity of picoplankton

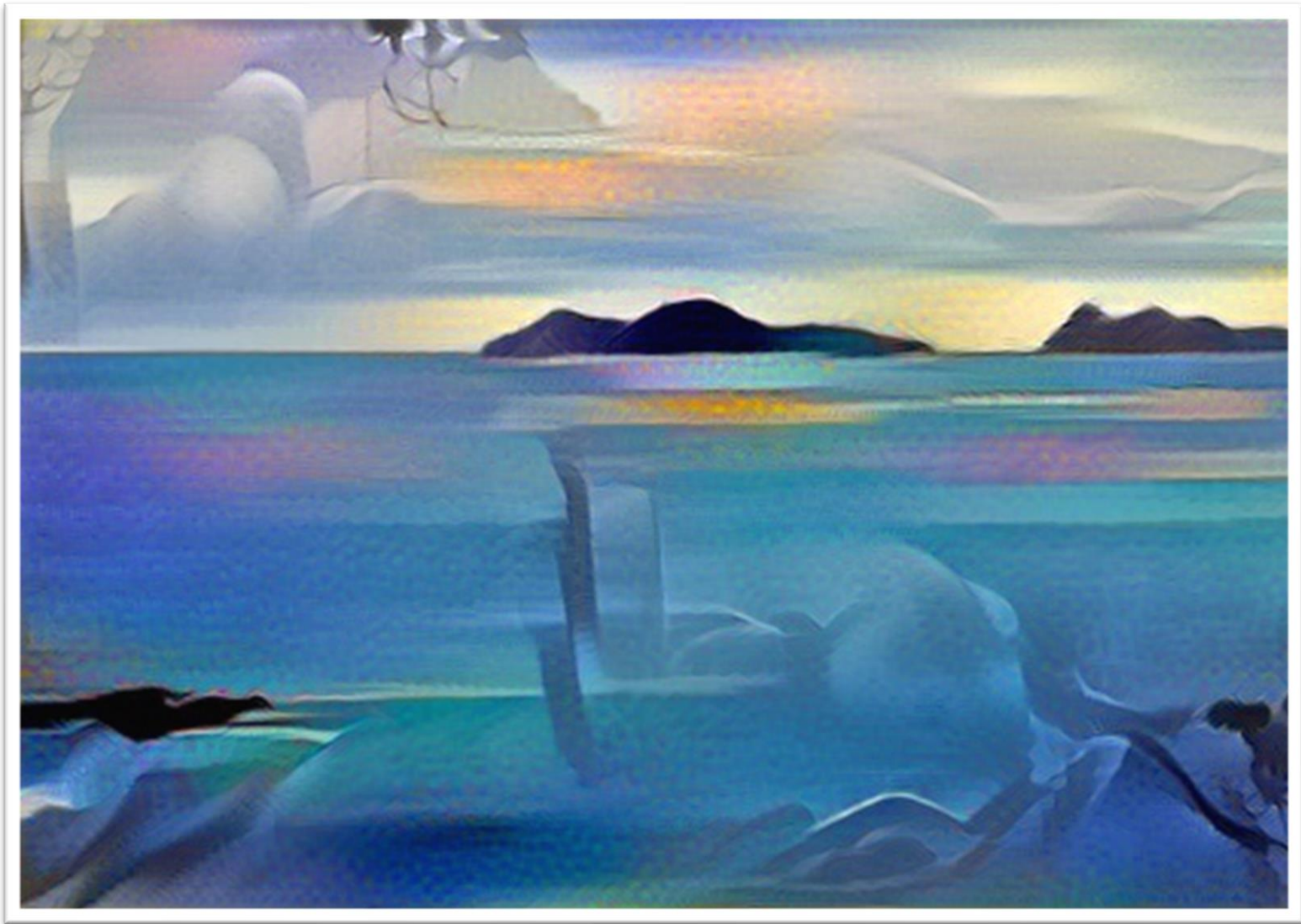


*Reproduced from Mouriño-Carballido et al. (2016)*

# Biogeochemical implications of picoplankton

- Aggregation (Richardson & Jackson, 2007):
  - Available for copepods (fast-sinking fecal pellets).
  - Increase sinking velocity
- Southern ocean (Lomas & Moran, 2011):
  - Pico and nanoplankton export  $33 \pm 27\%$  of the total carbon





**Hypothesis and objectives**



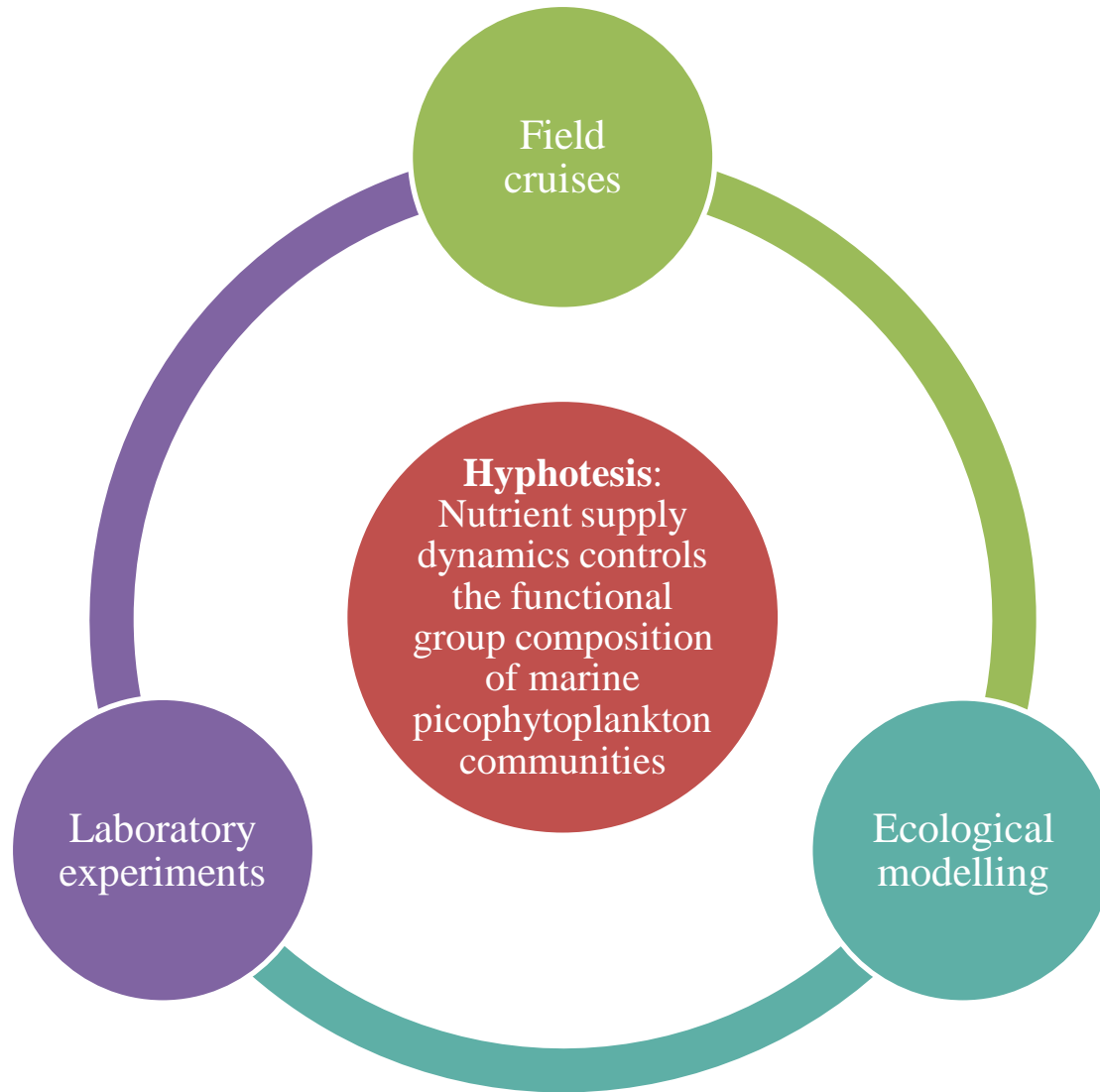
# Hypothesis

**Nutrient** supply **dynamics** (constant versus variable supply) **controls** the structure of marine **picoplankton** communities.

# Objectives

1. To **quantify** the role of **temperature**, **light**, and **nitrate fluxes** as factors controlling the distribution of autotrophic and heterotrophic picoplankton subgroups.
2. To **describe** the **ecological niches** of the various components of the **picoplankton community**.
3. To explore the **effect** of **nitrate supply dynamics** on the competitive dynamics of two model marine picophytoplankton species, namely, the cyanobacterium *Synechococcus* sp. and the picoeukaryote *Micromonas pusilla*.
4. To build a prediction model and obtain the first **climatology** of **nitrate diffusion** into the **euphotic zone**.
5. To **predict** the change in the structure of **picophytoplankton communities** (the cyanobacteria to picoeukaryotes ratio) in a **future ocean scenario**.

# Research approach



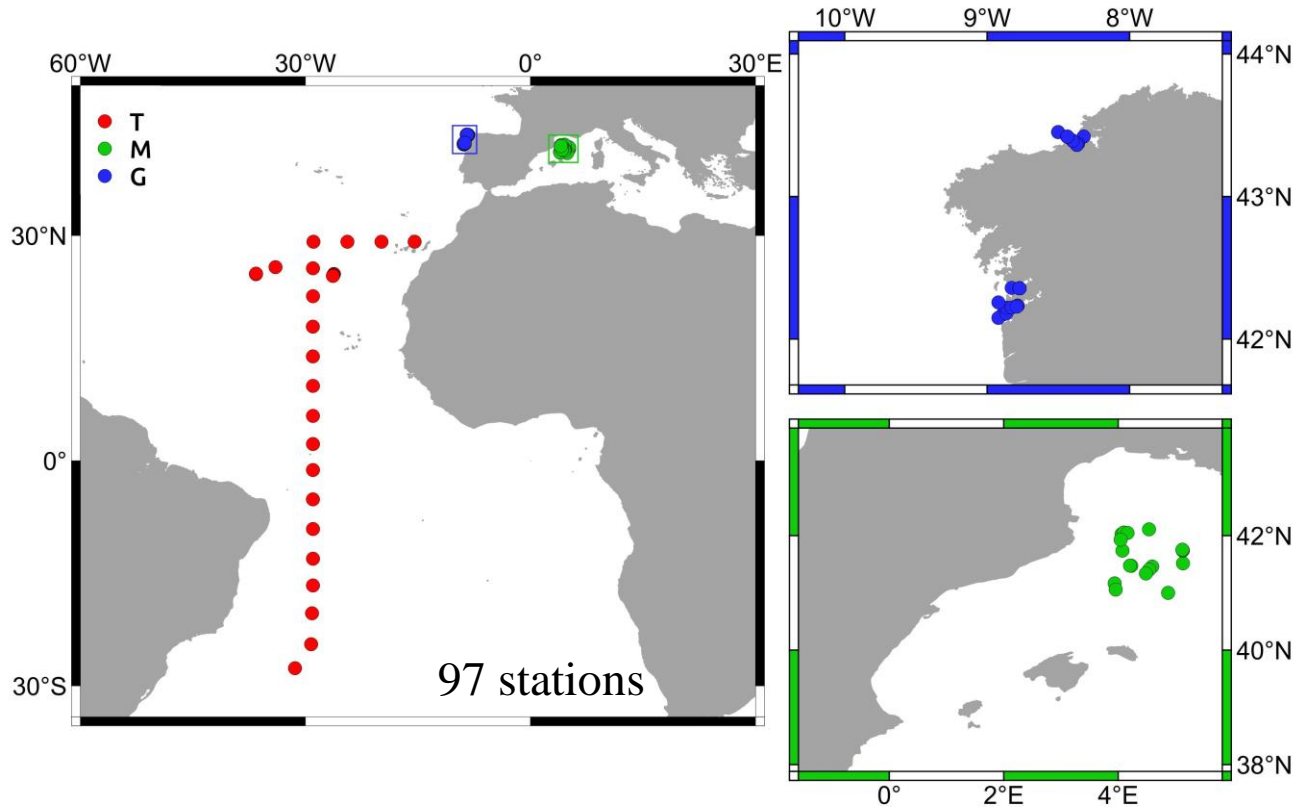


## **Chapter II: Factors controlling picoplankton community structure**

# Objectives

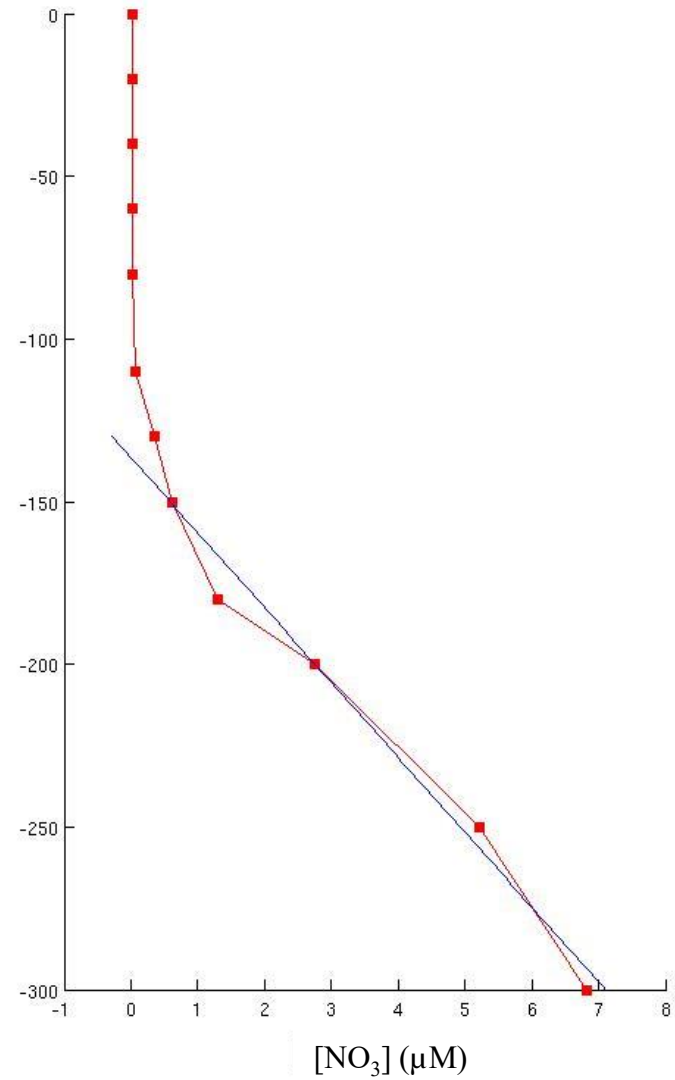
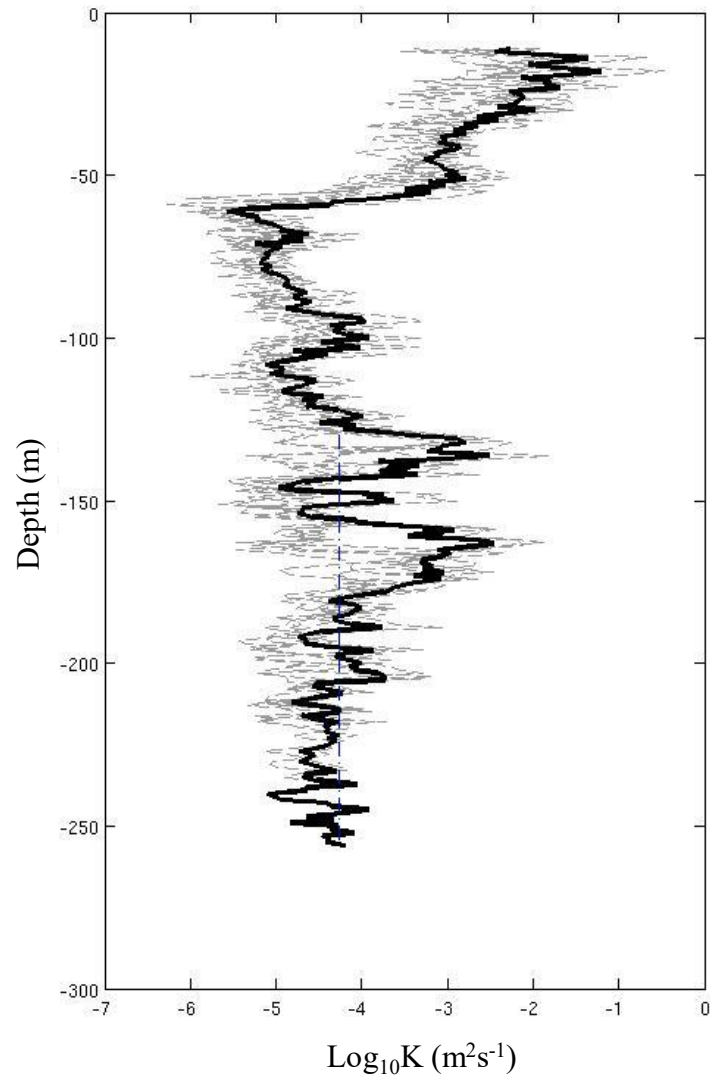
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# Dataset of biological & physical data (2006-2015)

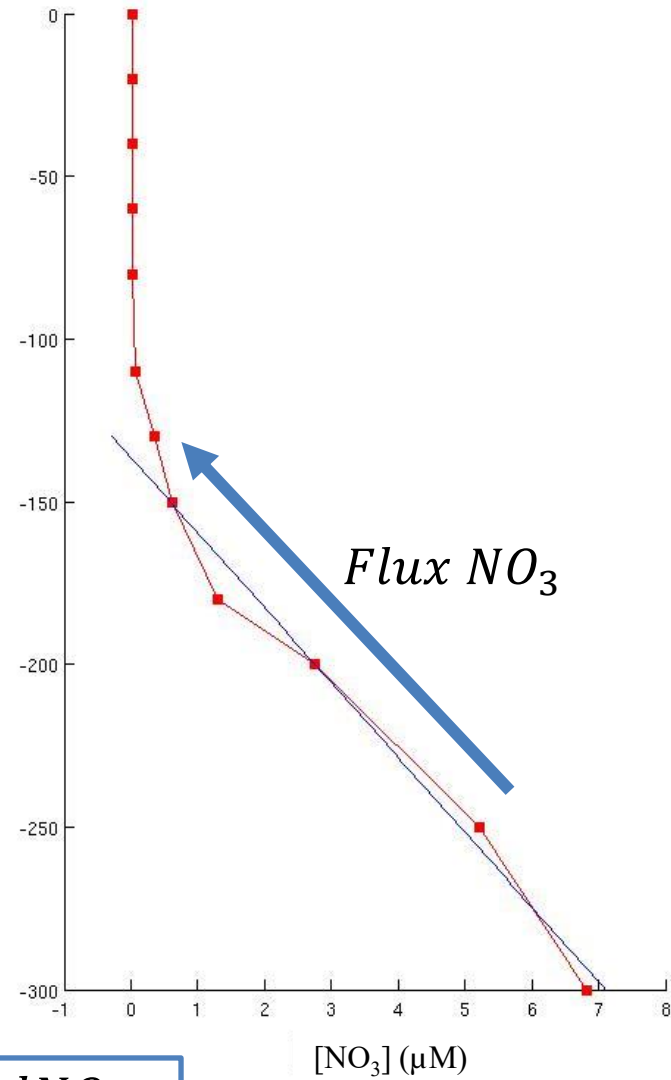
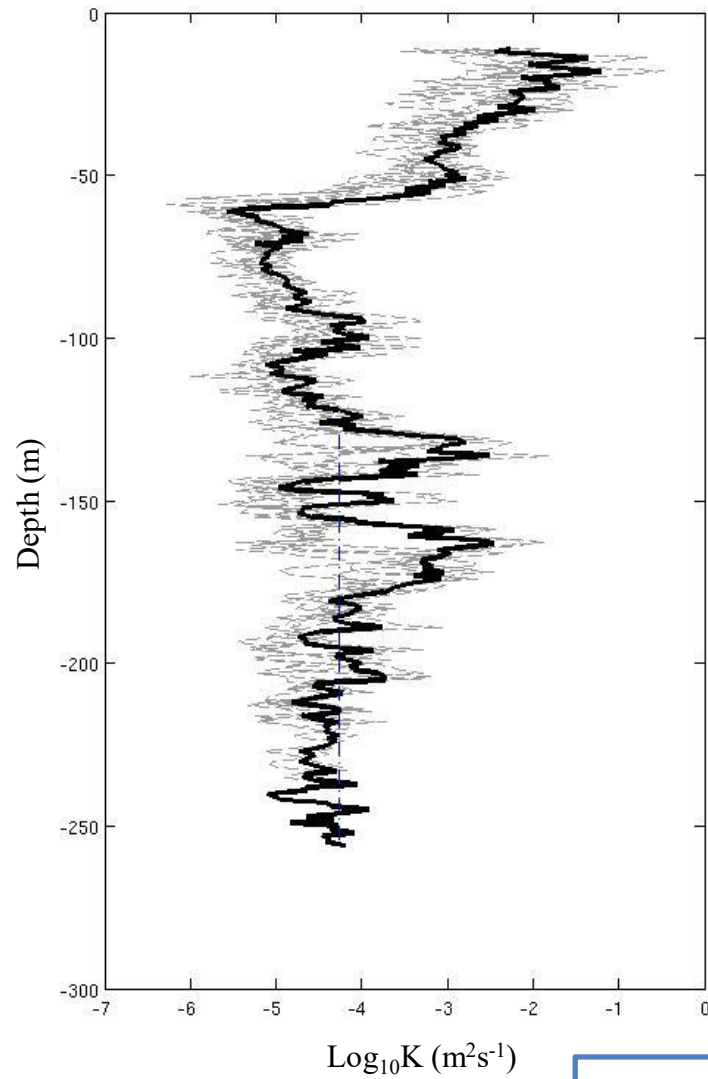


- Vertical dissipation rate (Kz)
- Nutrients
- PAR (Satellite)
- Picoplankton biomass (Cytometry)

# Nitrate diffusive flux



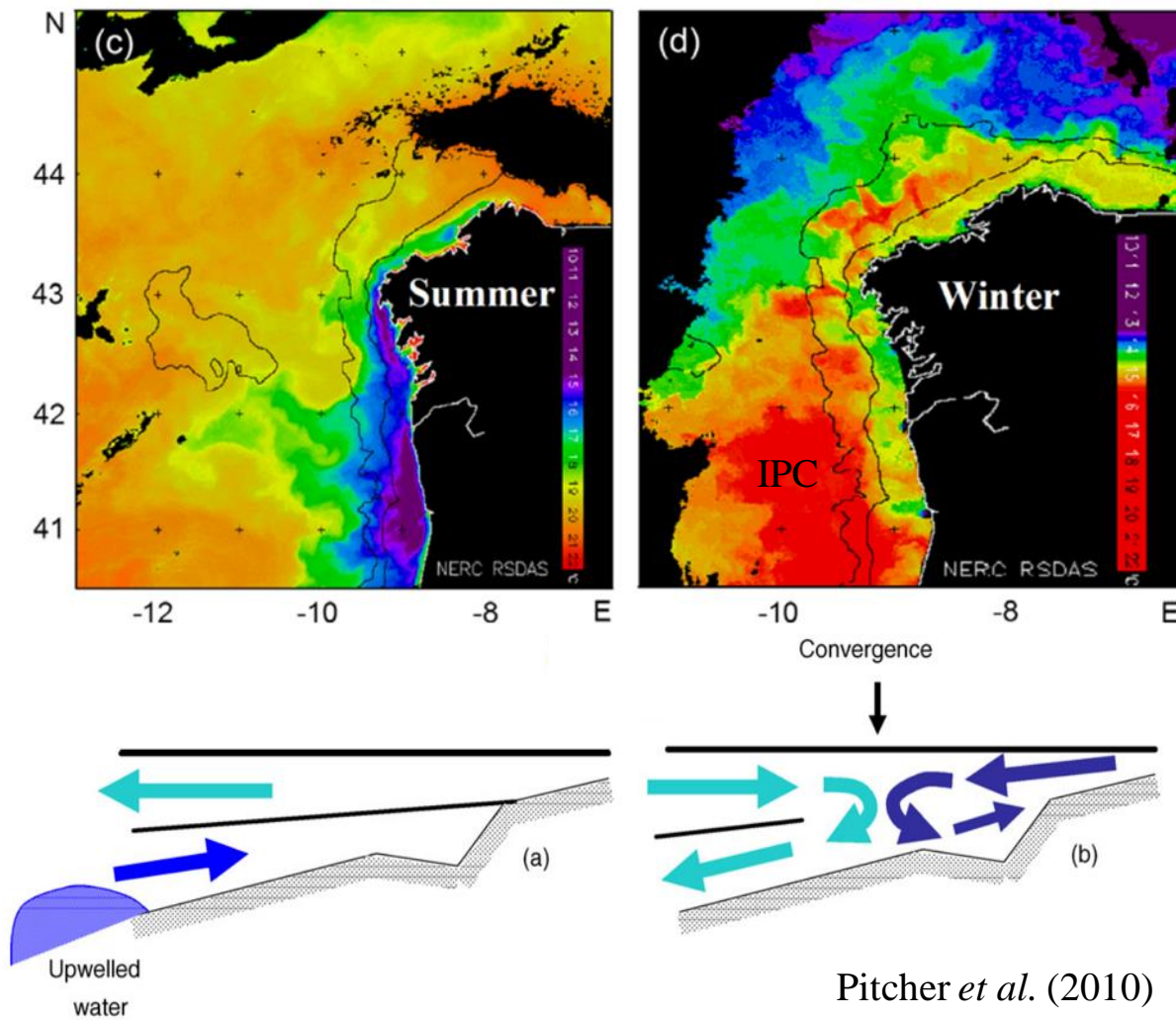
# Nitrate diffusive flux



$$F = -K_z \frac{d\text{NO}_3^-}{dz}$$

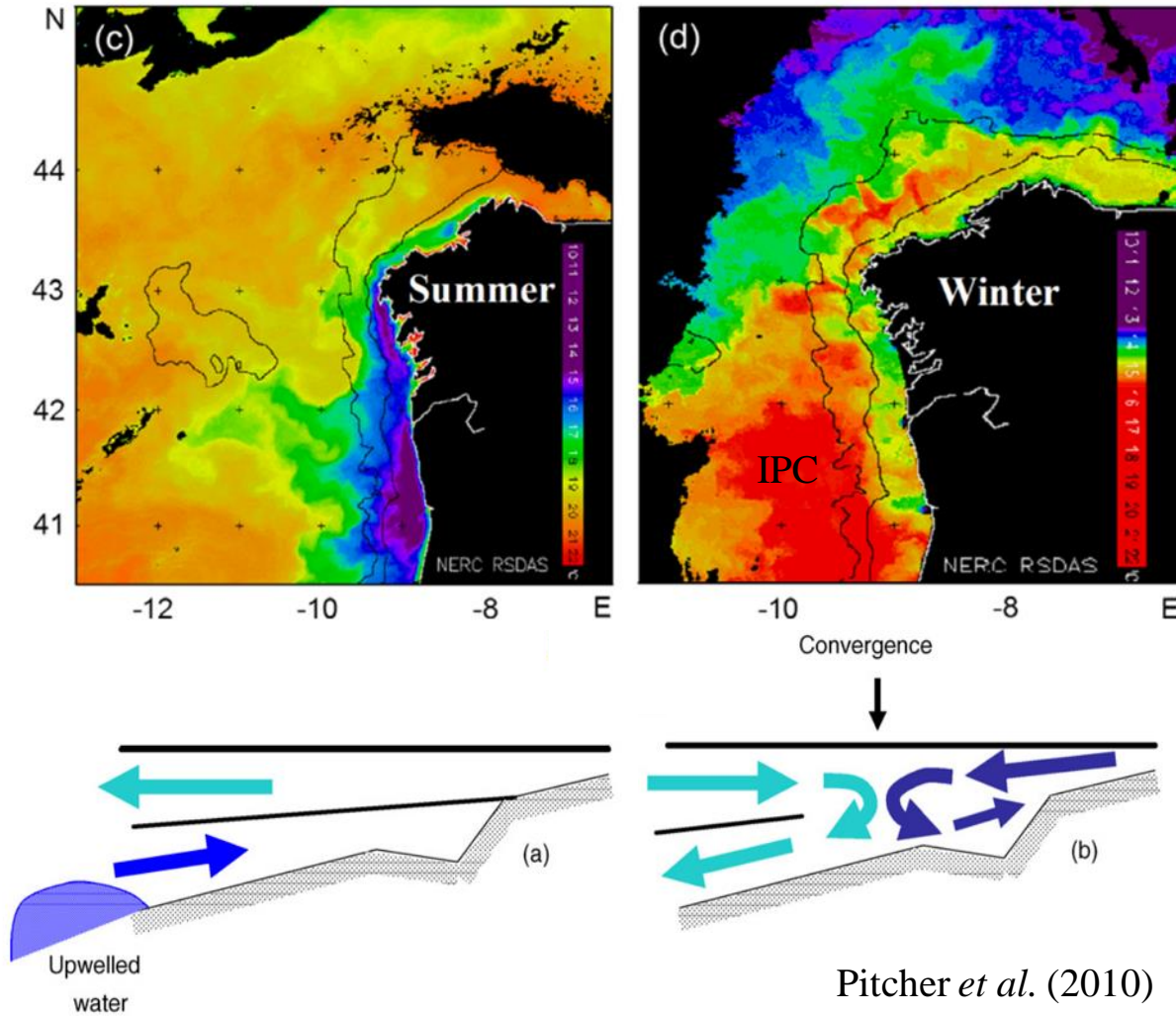


# Nitrate advective flux



Pitcher *et al.* (2010)  
Crespo *et al.* (2006)

# Nitrate advective flux



- Area ( $\text{m}^2$ )
- Coast (km)
- Averaged depth
- Upwelling index
- Depth Nitrate concentration

Pitcher *et al.* (2010)  
 Crespo *et al.* (2006)

# **Analysis**

# Analysis

## Generalized Additive Models (GAM)

$$y_j = I + s(SST) + s(PAR) + s(\log(NO_3Flux)) + Error$$

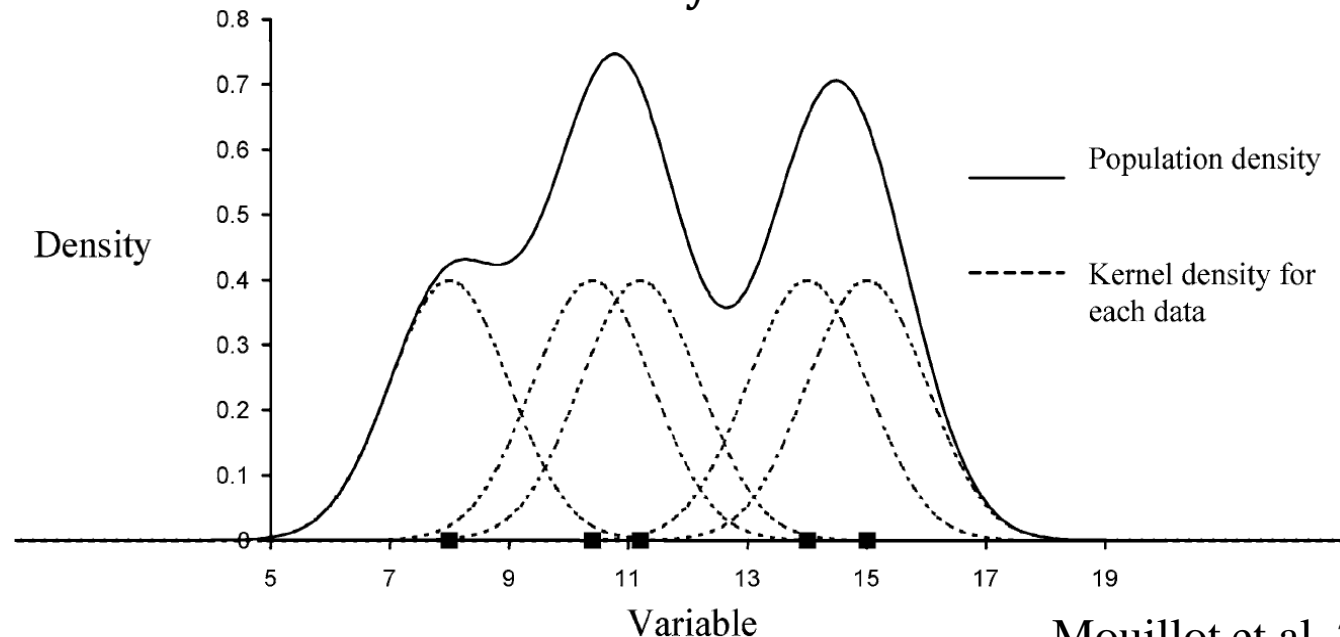
# Analysis

## Generalized Additive Models (GAM)

$$y_j = I + s(SST) + s(PAR) + s(\log(NO_3Flux)) + Error$$

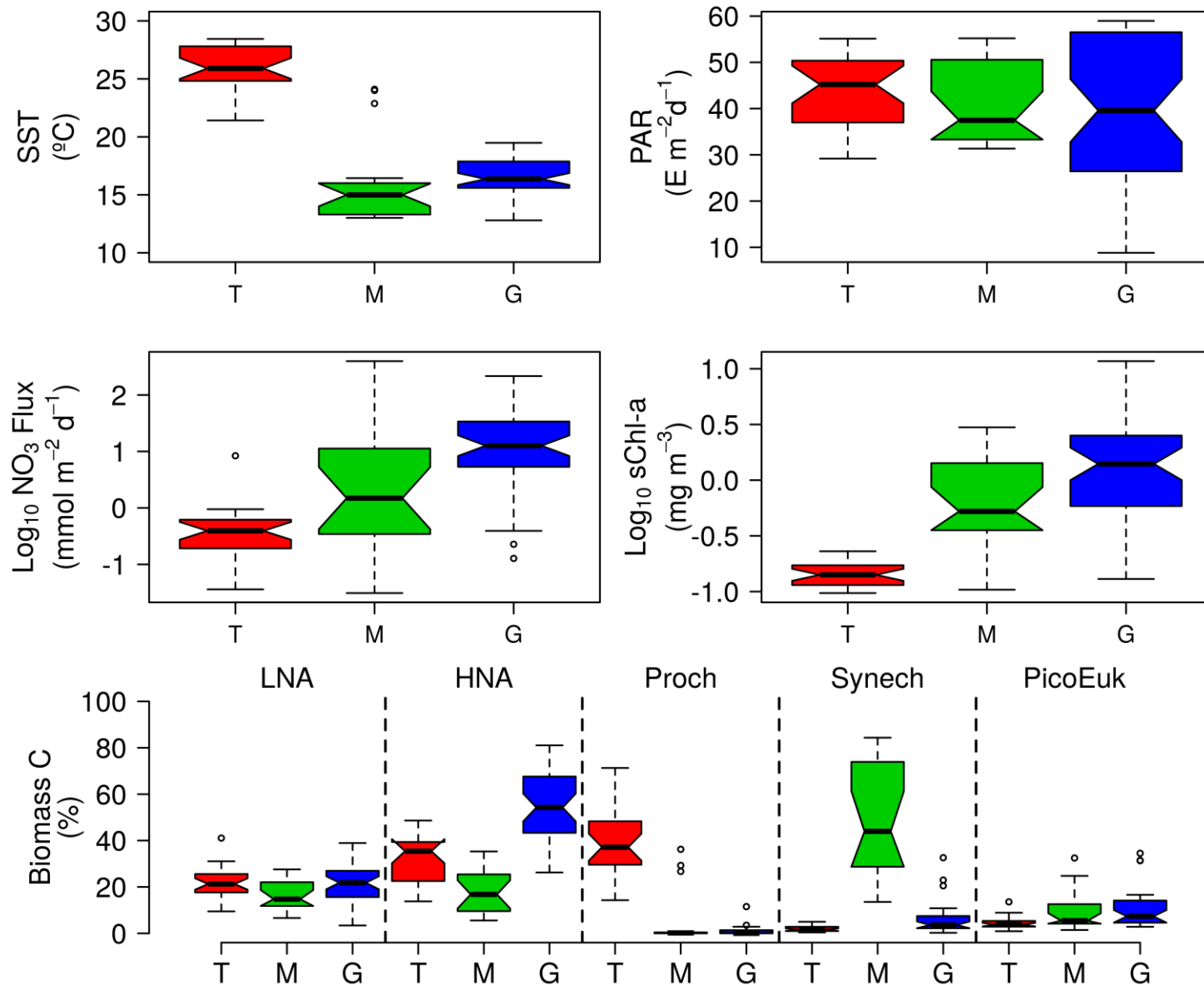
## Kernel density & Niche overlap

$$NO_{K_{i,j,t}} = 1 - 1/2 \int |f_{it}(x) - f_{jt}(x)| dx$$

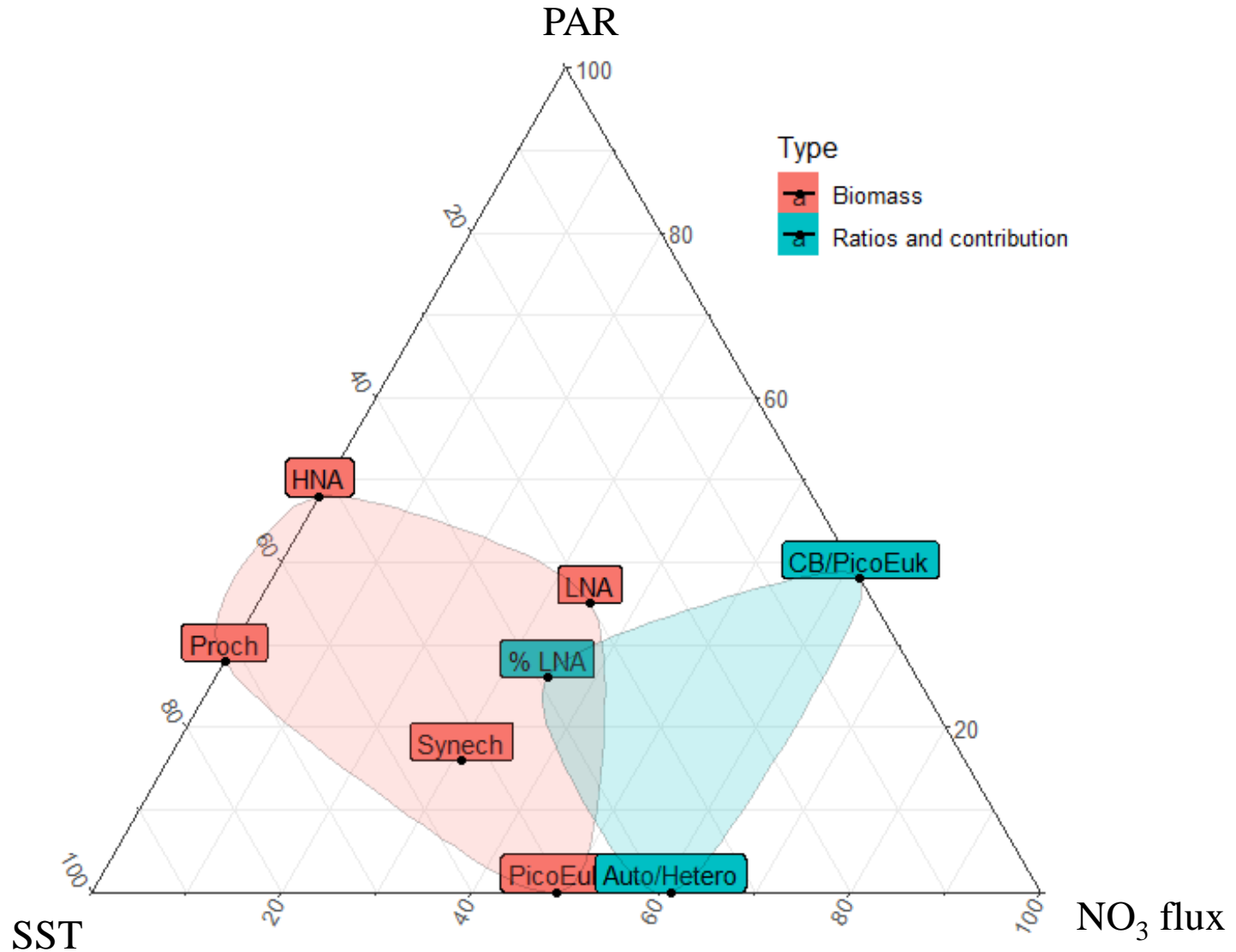


Mouillot et al. 2005

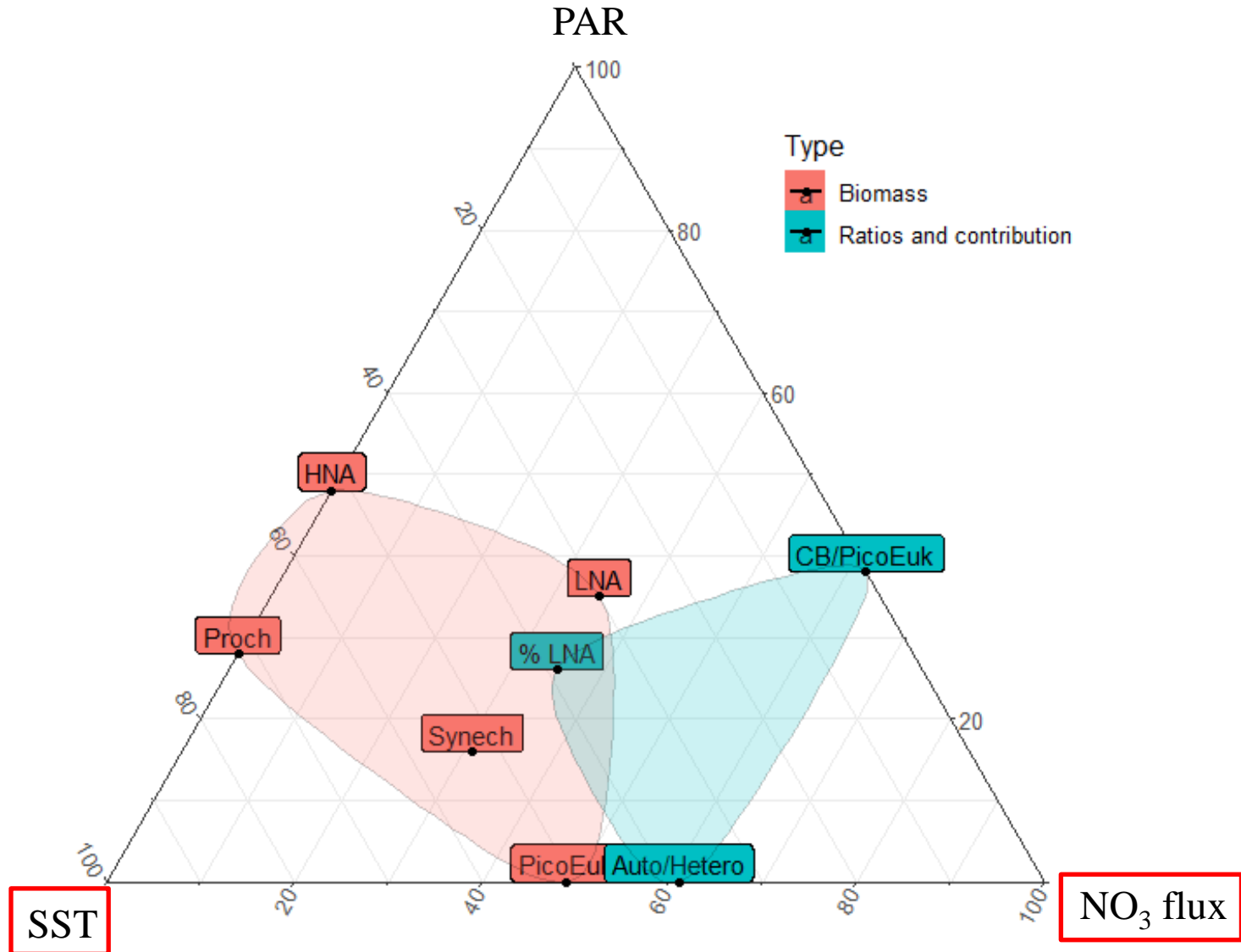
# Variability in $\text{NO}_3$ flux, control factors and biomass



# Relevance of control factors in biomass groups (GAM)

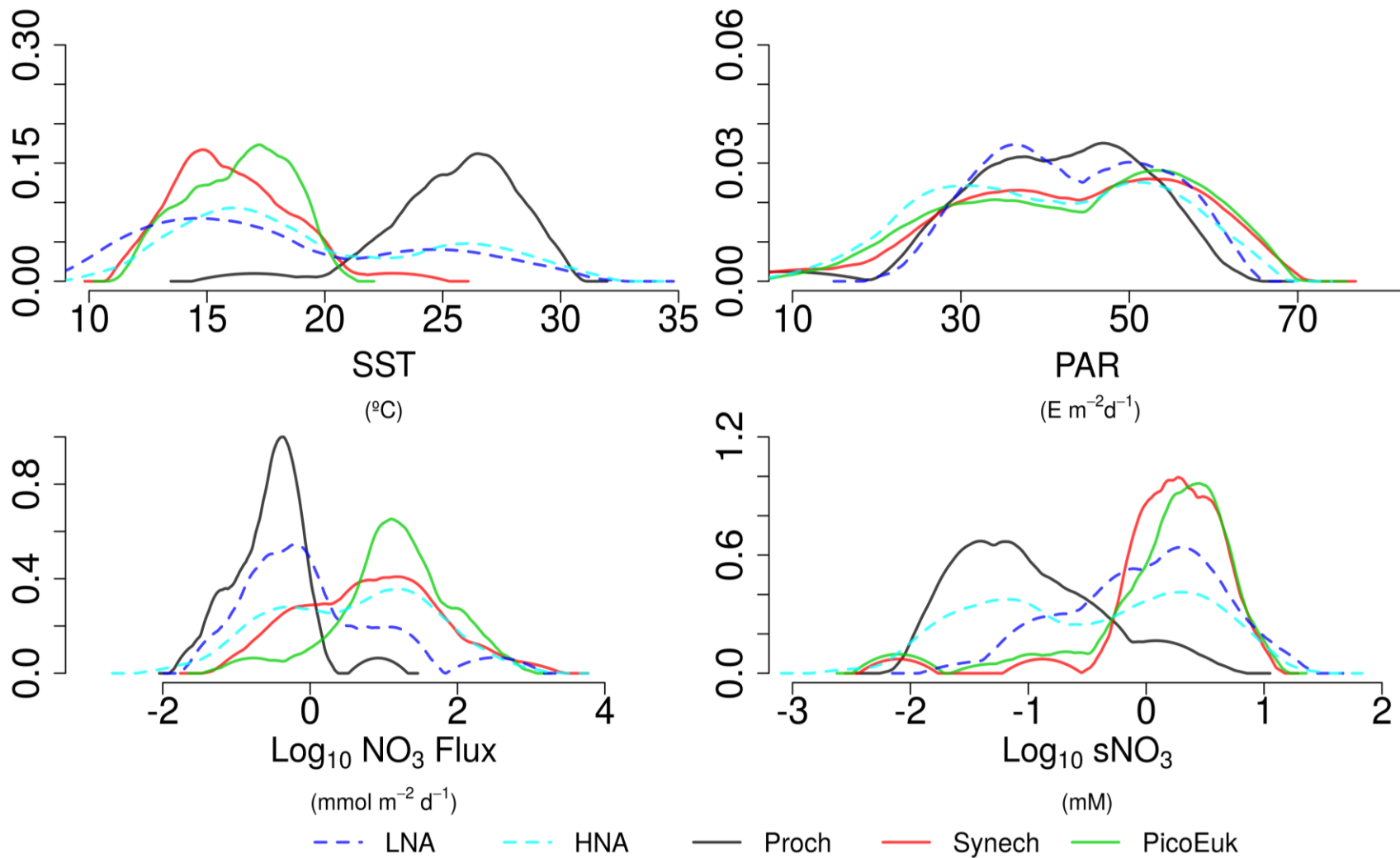


# Relevance of control factors in biomass groups (GAM)

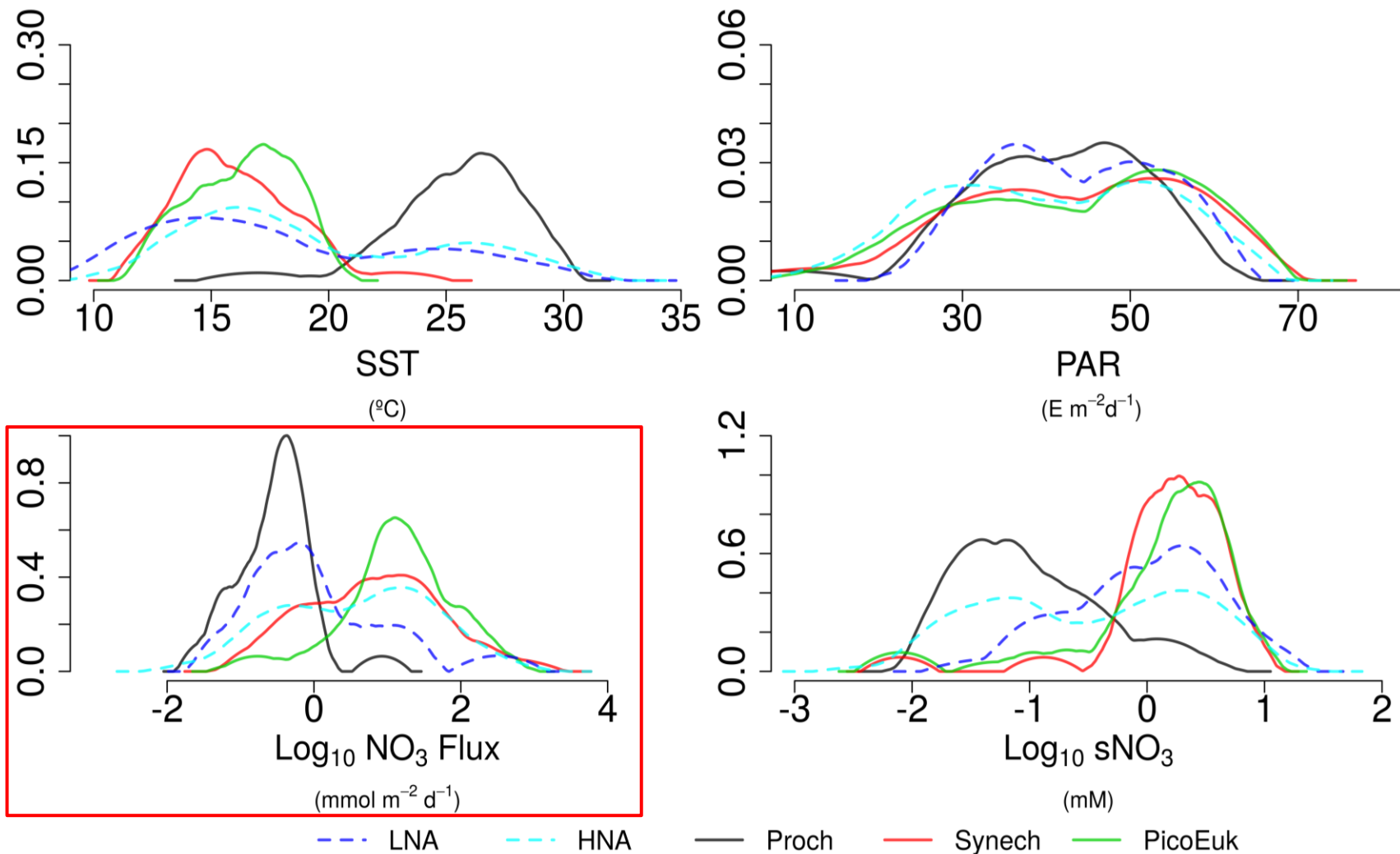




# Niche partitioning



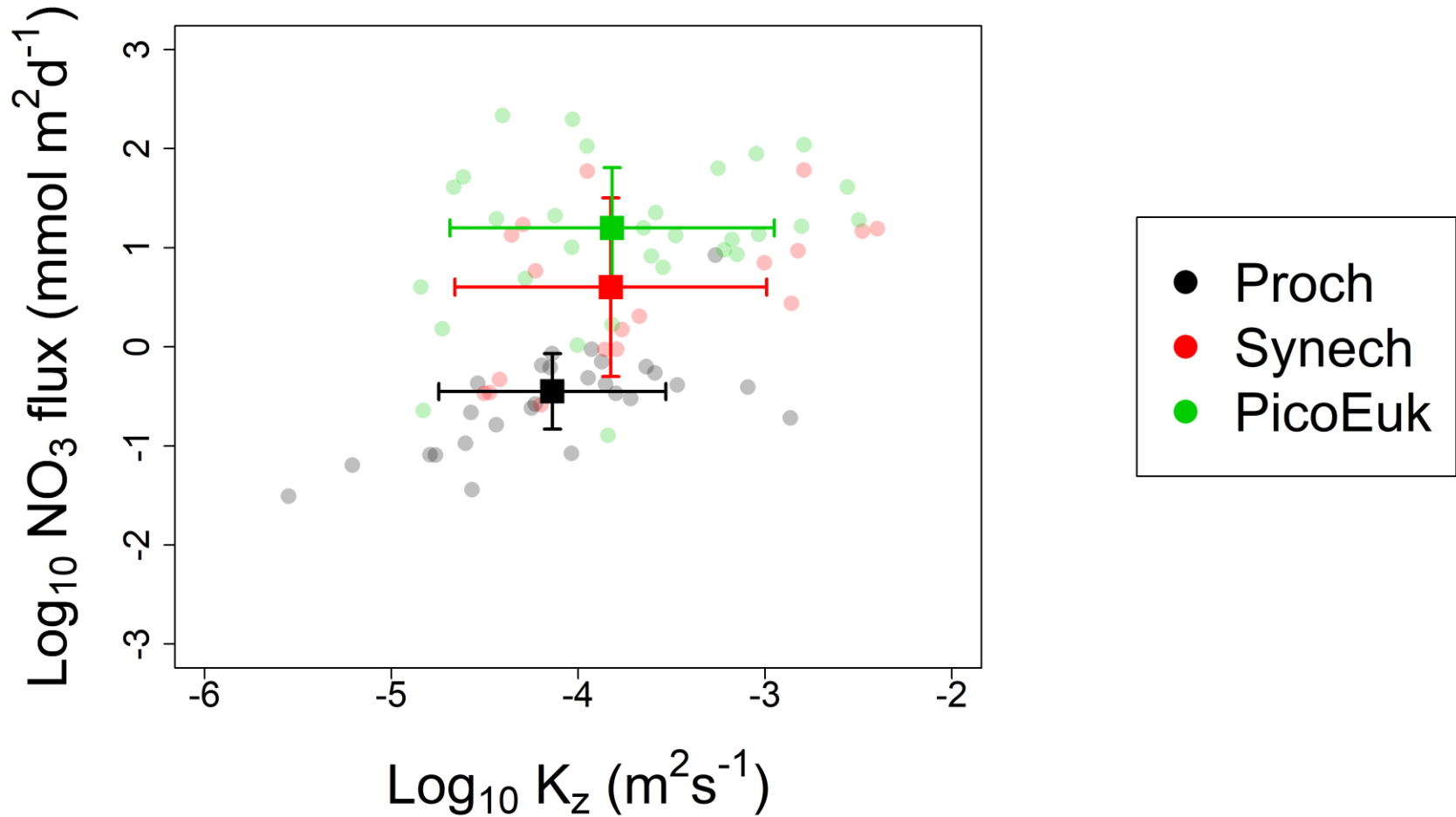
# Niche partitioning





**Chapter III:** *Micromonas pusilla* and *Synechococcus* competition under constant and dynamic conditions

# Dominance of picoplankton groups vs mixing and $\text{NO}_3$

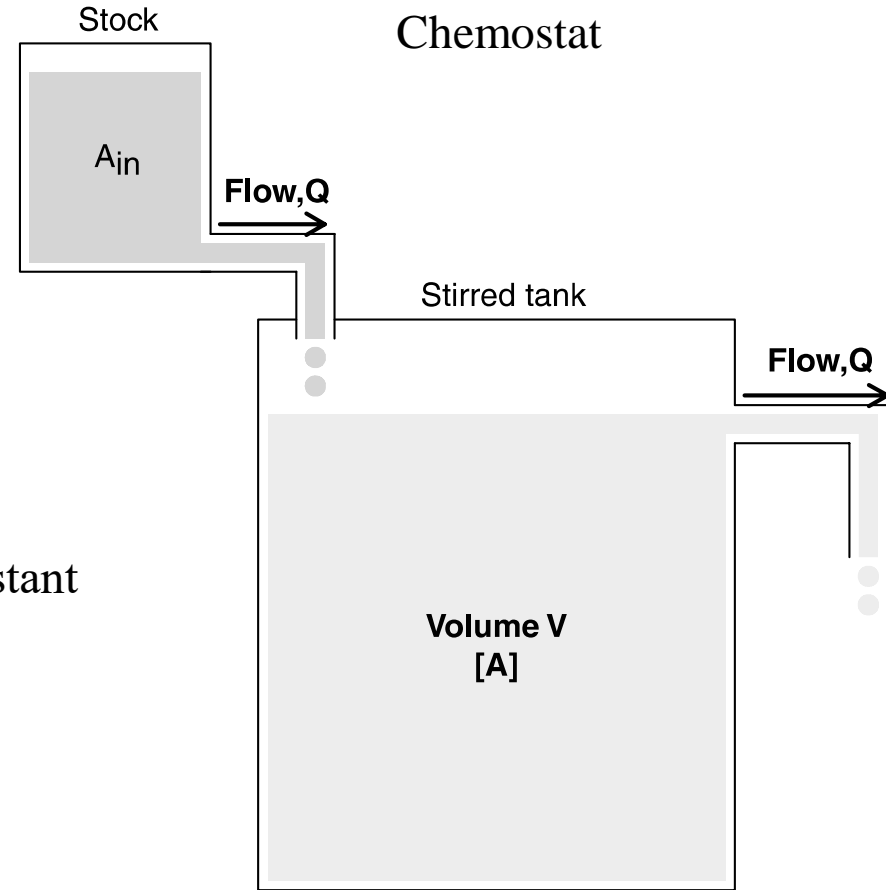
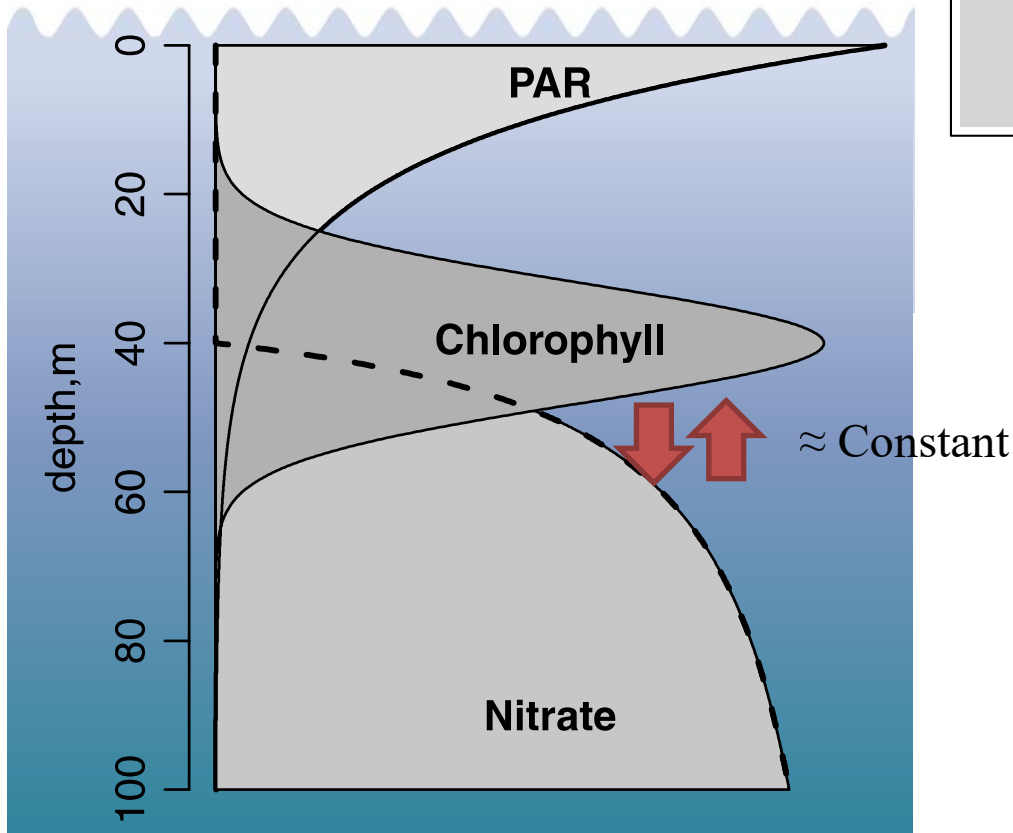


# Objectives

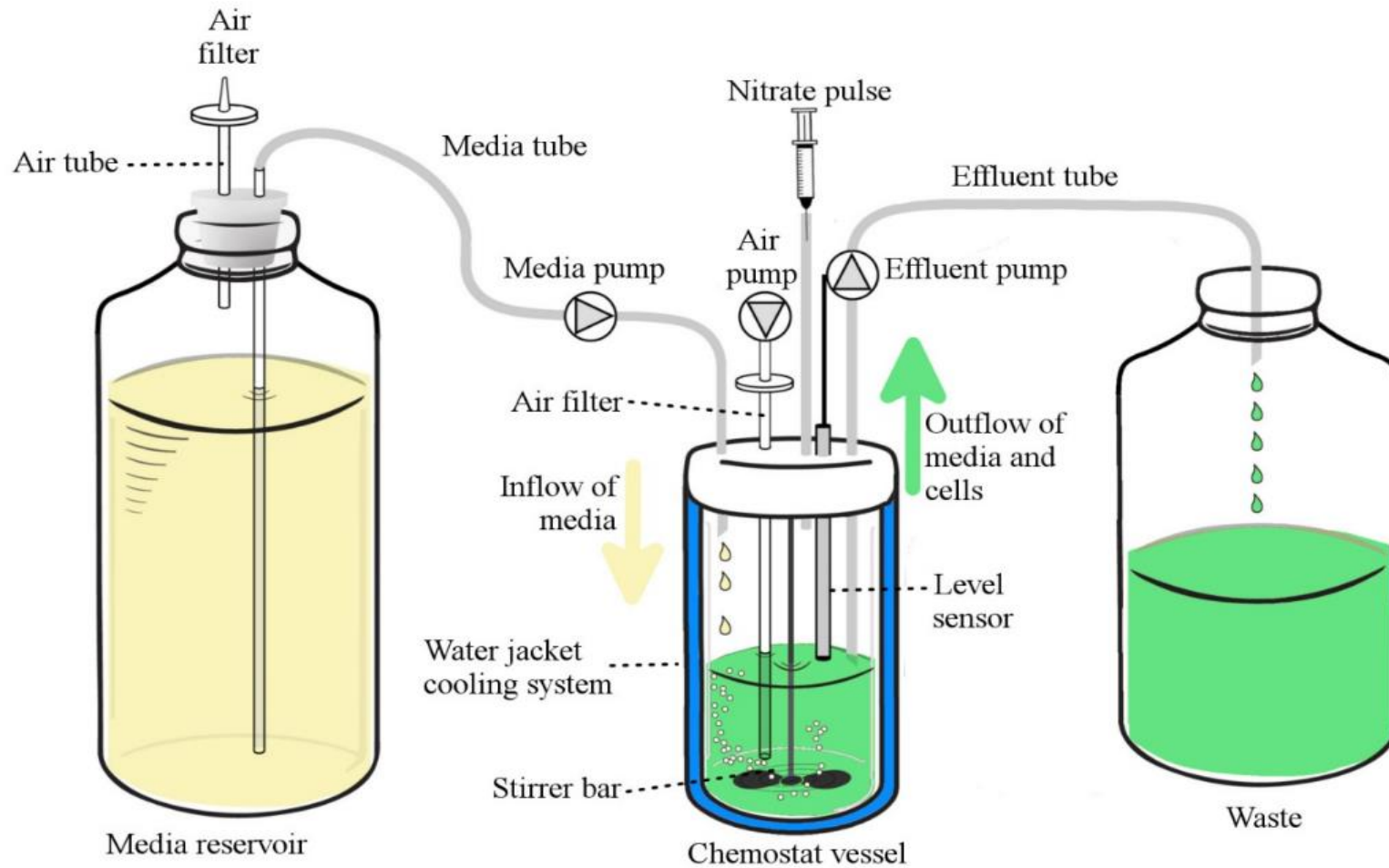
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# Steady state and chemostats

Open waters



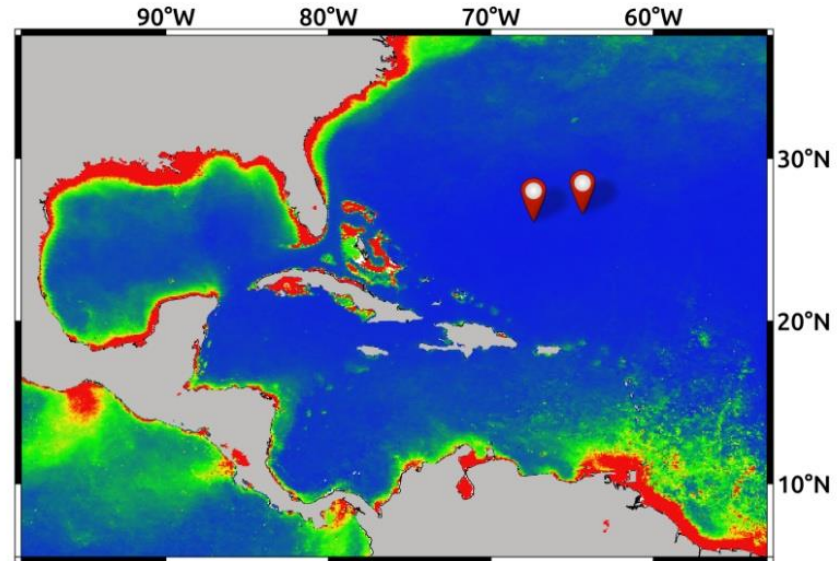
# Competition experiments



Population monitoring was carried using Flow Cytometry

# Experimental design

- Groups
  - *Synechococcus* (RCC-2366)
  - *Micromonas pusilla* (RCC-450)

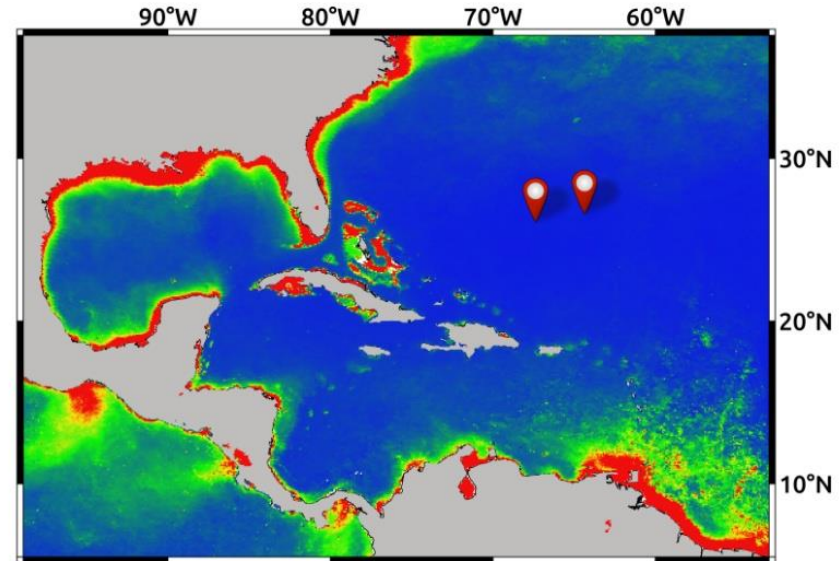


Yearly average surface chlorophyll-*a*



# Experimental design

- Groups
  - Synechococcus* (RCC-2366)
  - Micromonas pusilla* (RCC-450)
- Fully-acclimated populations
  - Modified PCRS-11 medium (N:P, 5-1)
  - Light: 100  $\mu\text{E}$
  - Temperature: 21°C
  - Steady-state (Dilution rate: 0.2  $\text{d}^{-1}$ )
- Perturbation (5  $\mu\text{M NO}_3$ )
  - 0.5 pulses  $\text{d}^{-1}$
  - 1 pulses  $\text{d}^{-1}$  \*
  - 2 pulses  $\text{d}^{-1}$
  - 3 pulses  $\text{d}^{-1}$



Yearly average surface chlorophyll-*a*



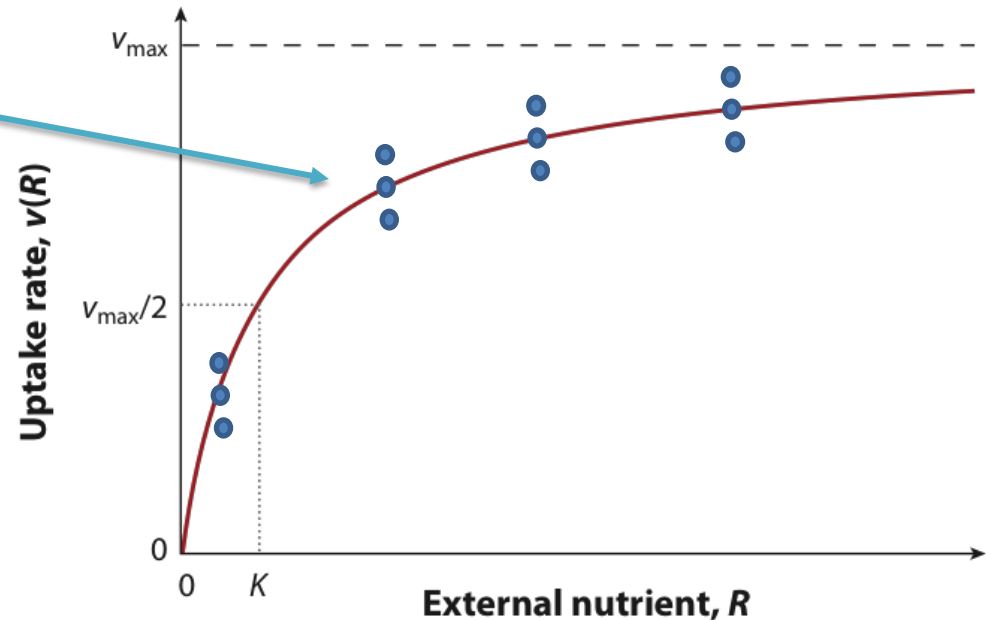
Sartorius Biostat Plus

# Uptake experiments

- ❑ Similar light and temperature conditions
- ❑ Short  $\text{NO}_3$  incubations (Bulk concentration)
- ❑  $[\text{NO}_3]$ : 0.5, 1, 1.5, 2.5, 5, 10, 25  $\mu\text{M}$ .
- ❑ Gentle filtration ( $\varnothing$  0.45  $\mu\text{m}$ )



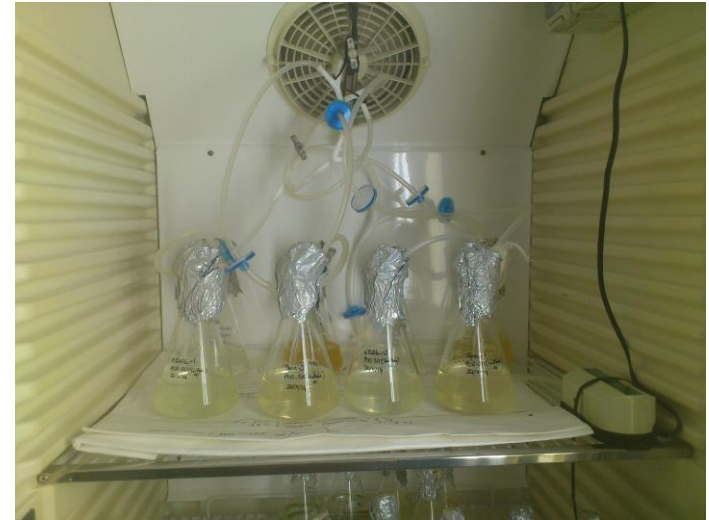
$d\text{NO}_3/dt$



# Uptake experiments

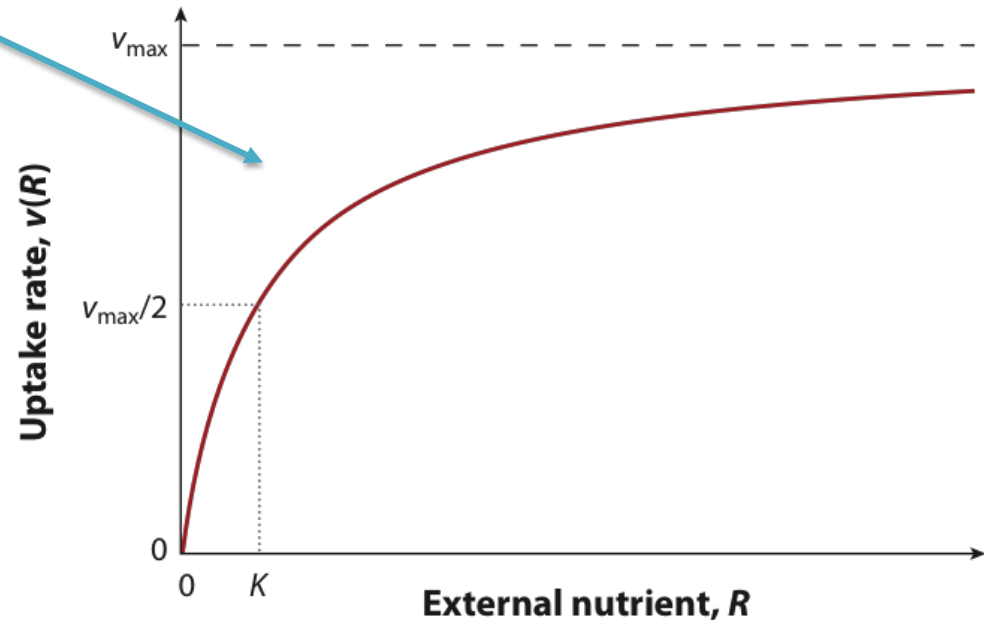
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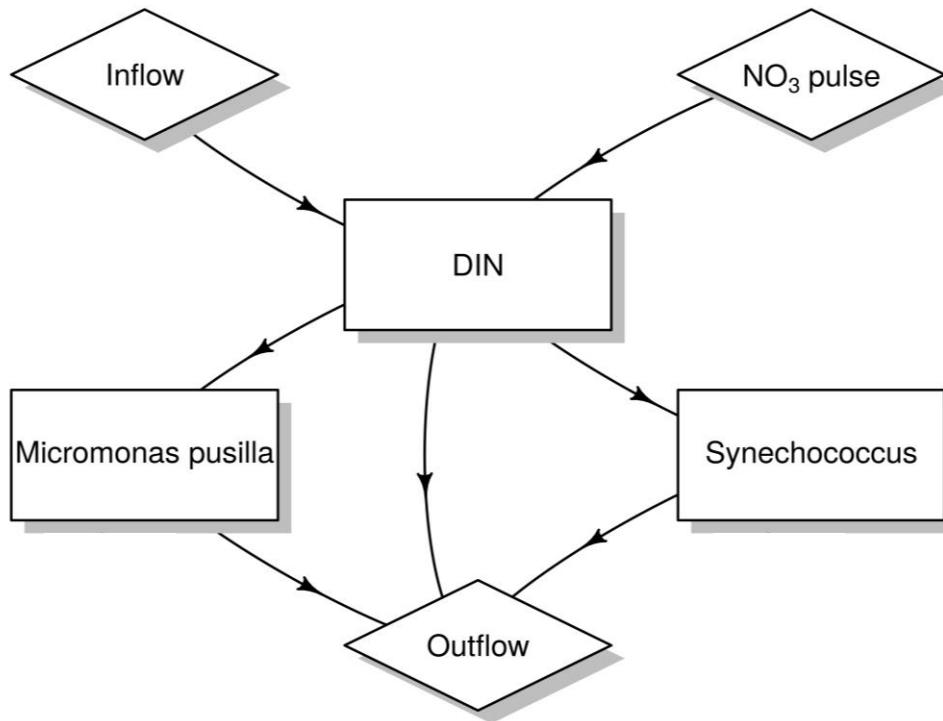
$$d\text{NO}_3 / dt$$


Under steady state conditions

$$R^* = \frac{D}{(\mu_{max} - D)} * K$$

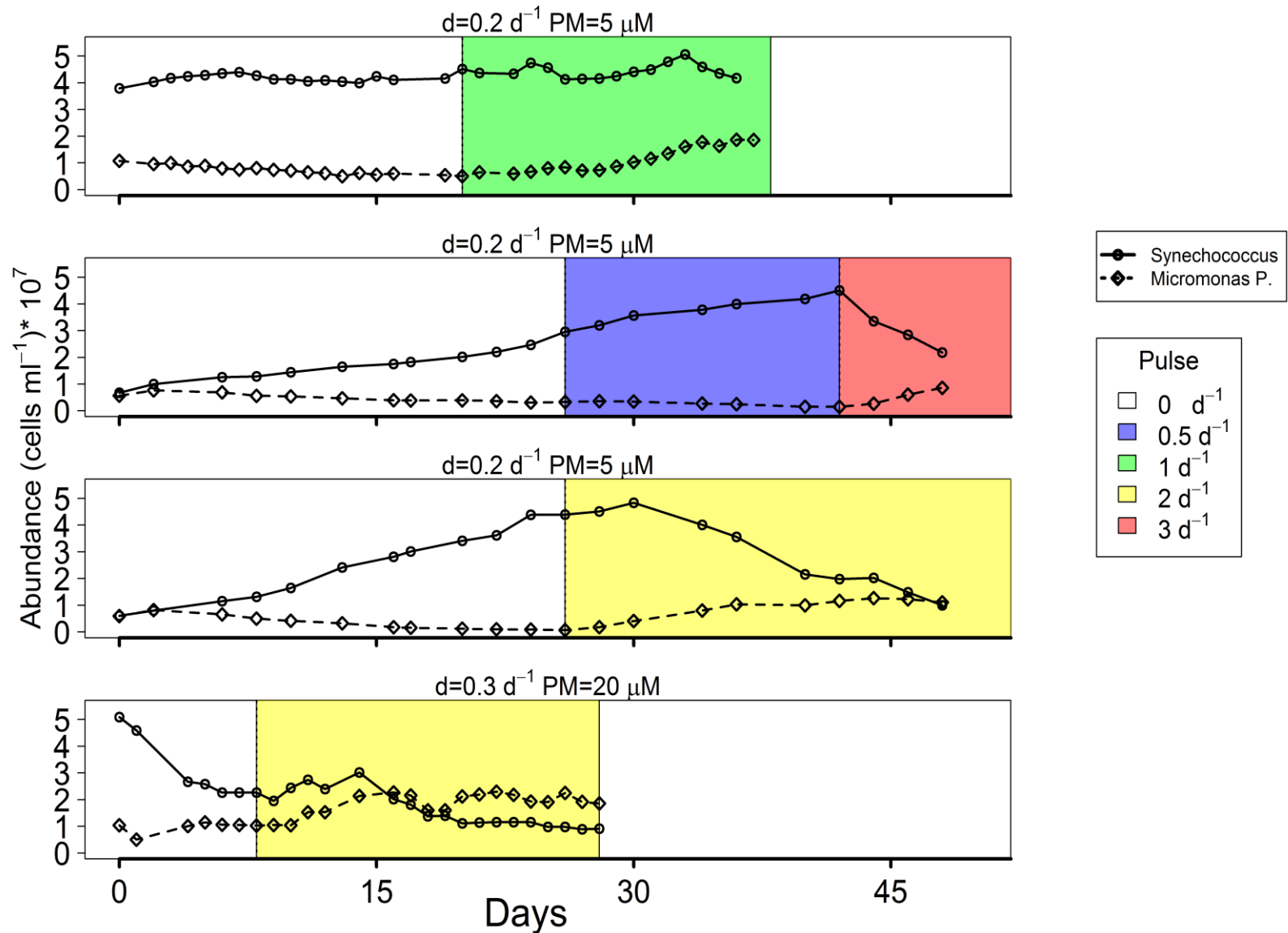


# Ecological modelling and calibration

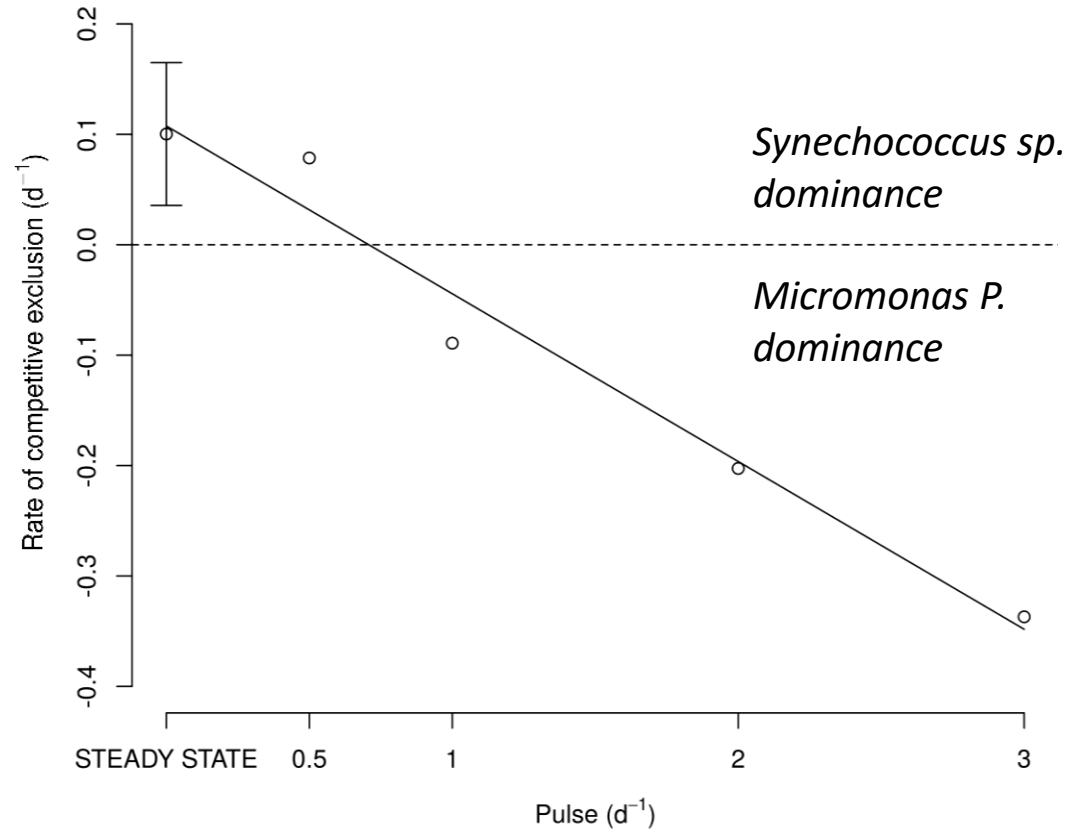
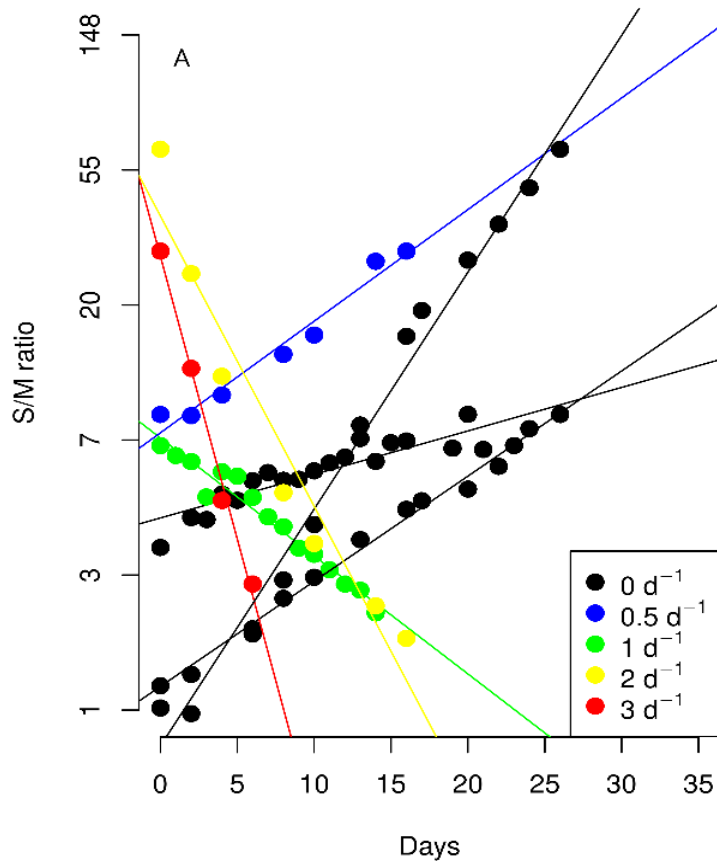


- ❑ Droop model
- ❑ Delayed Rejection Adaptive Metropolis Algorithm (DRAM):
  - ❑ Uptake and batch experiments parameters used as initial parameters.
  - ❑ Use one experiment to calibrate and use the other 3 to test.

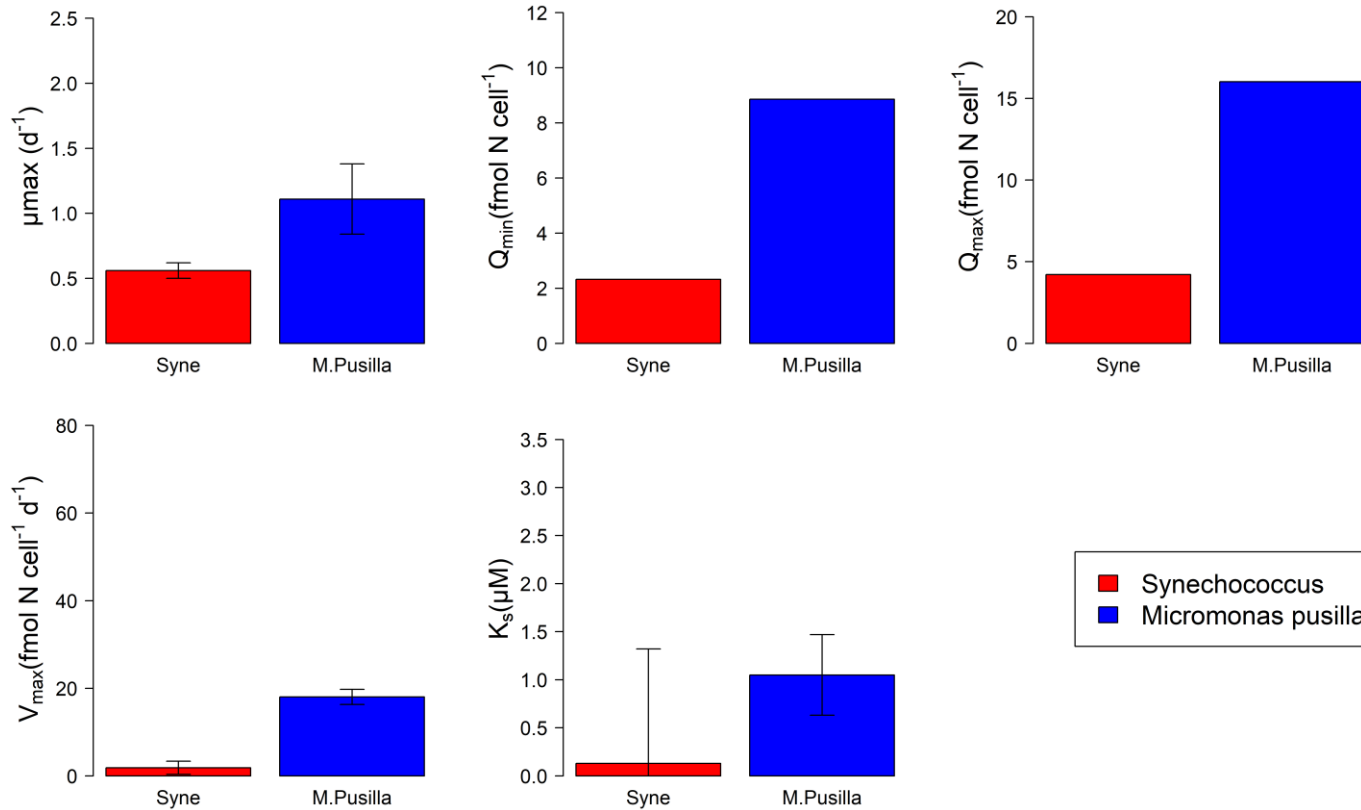
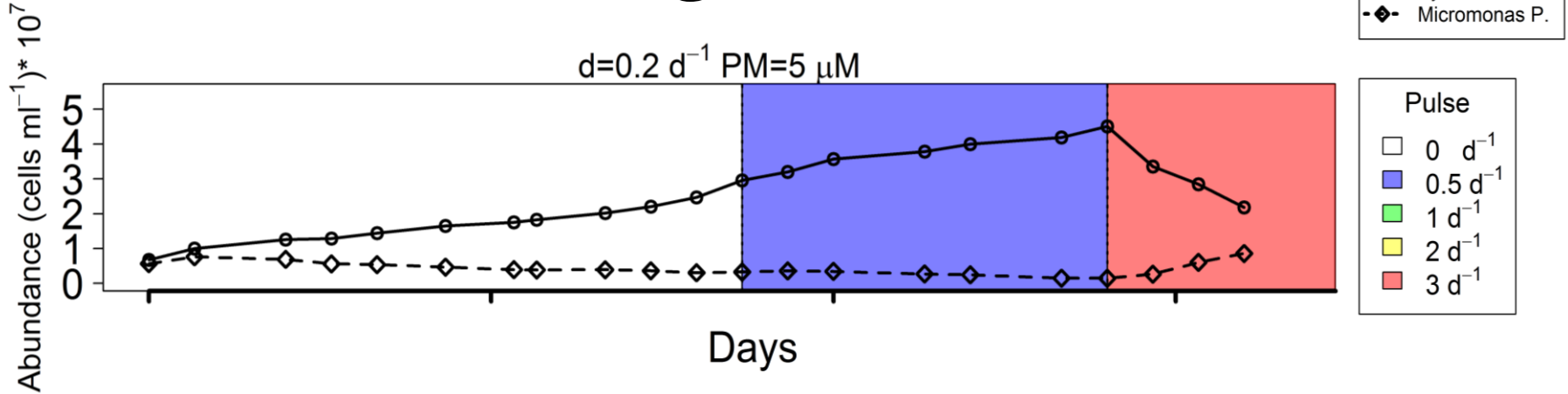
# Competition experiments – Time series



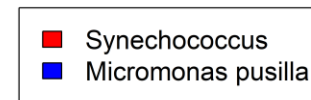
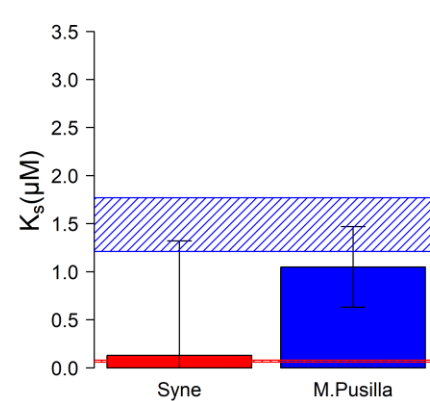
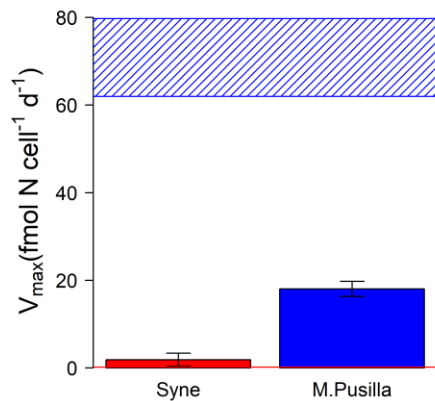
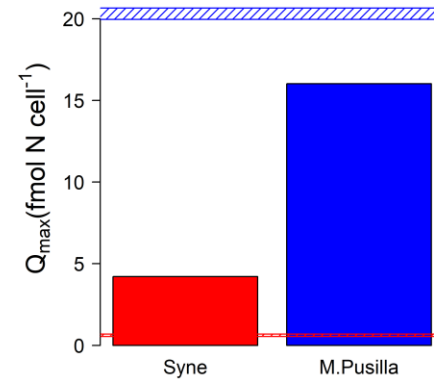
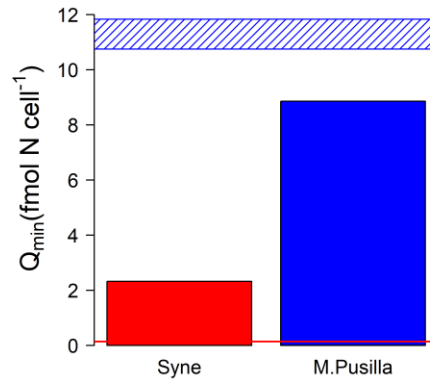
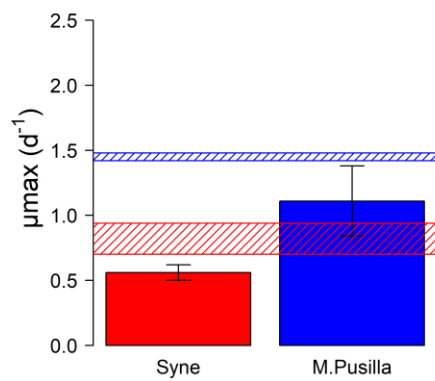
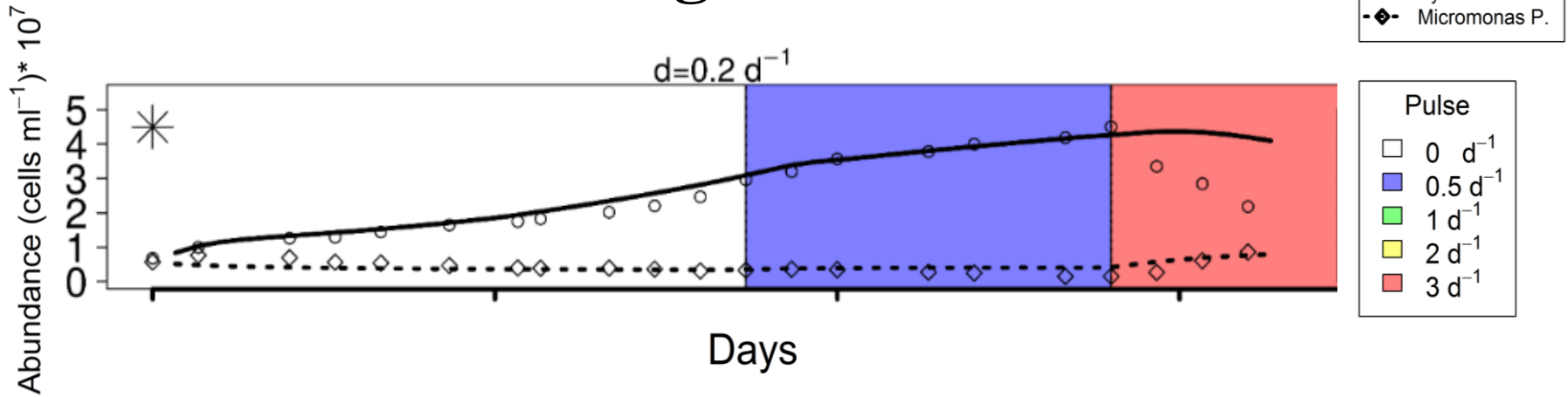
# Competitive exclusion rate



# Modelling - Calibration

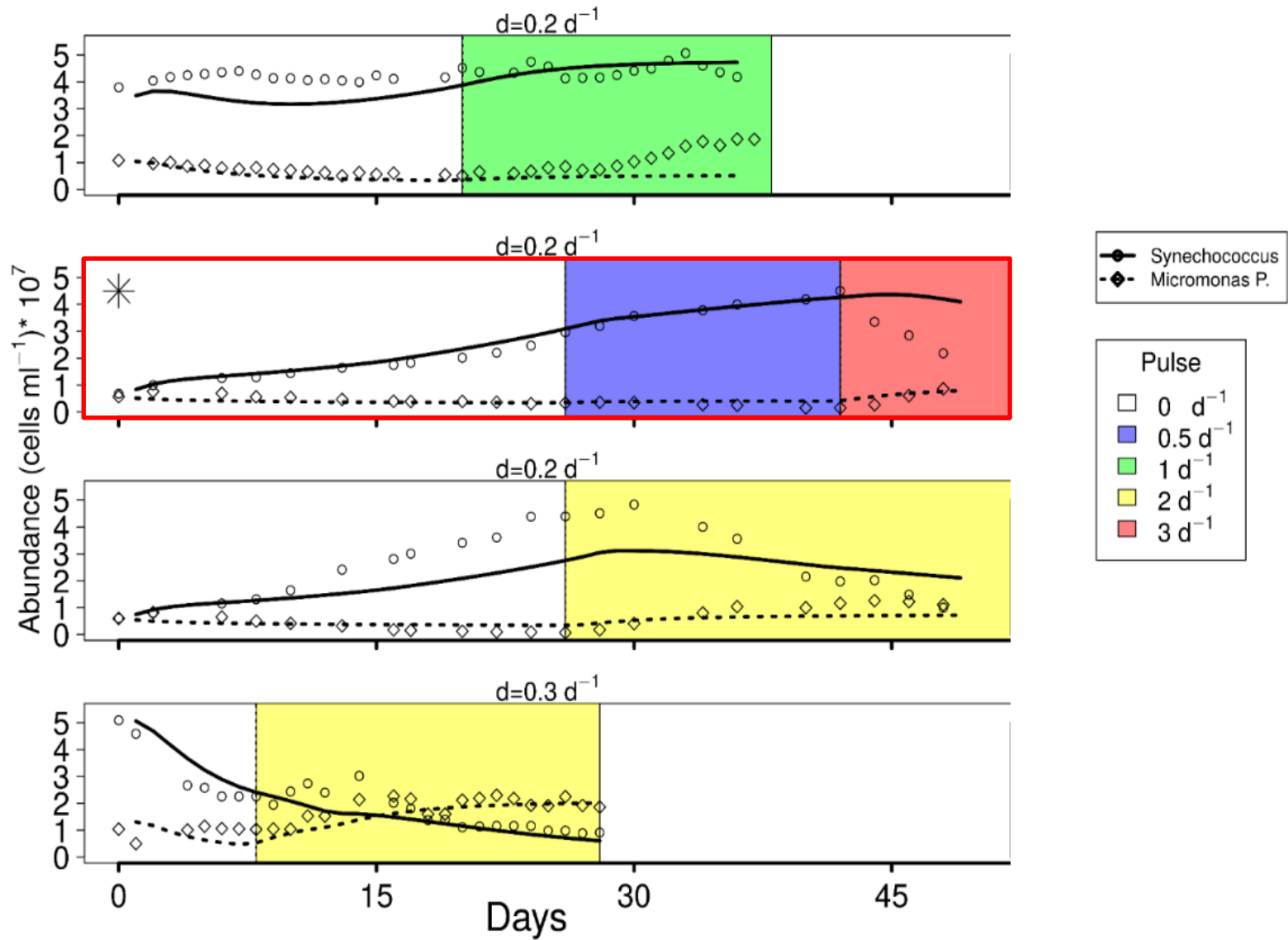


# Modelling - Calibration

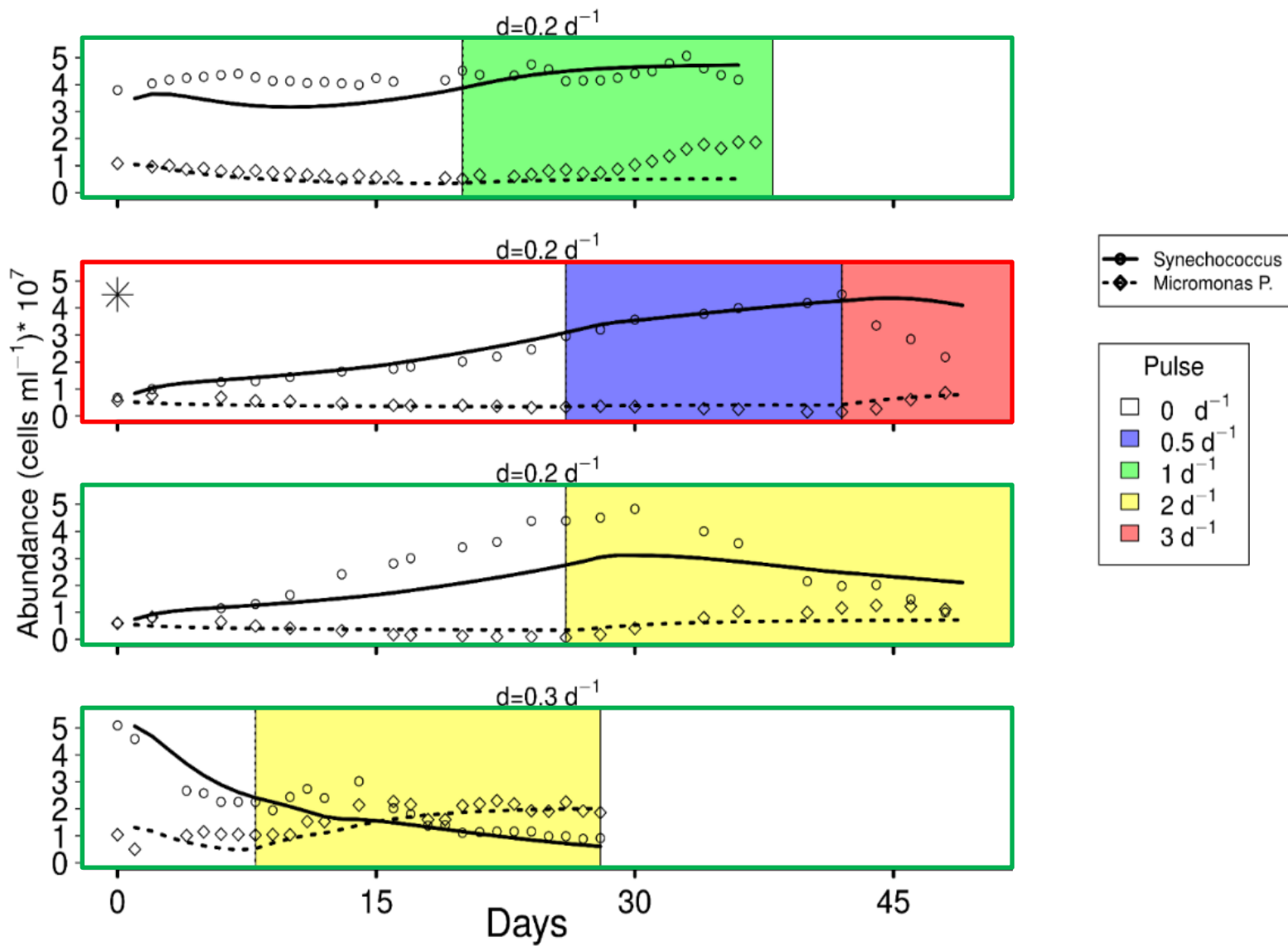




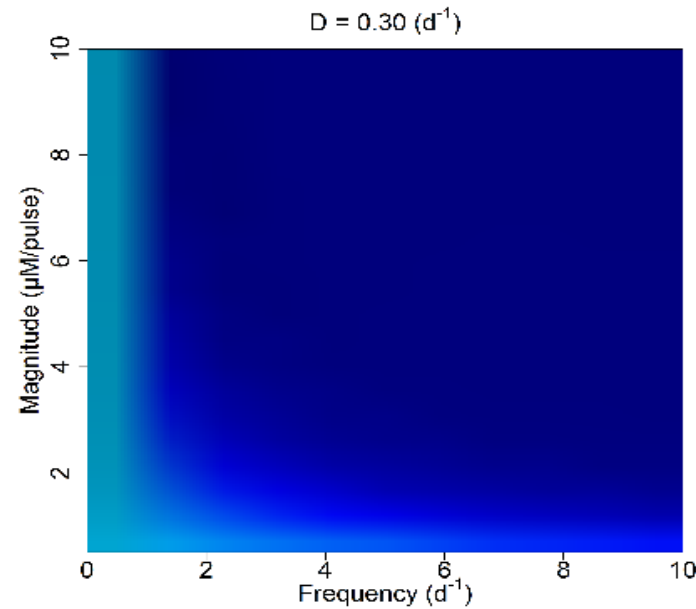
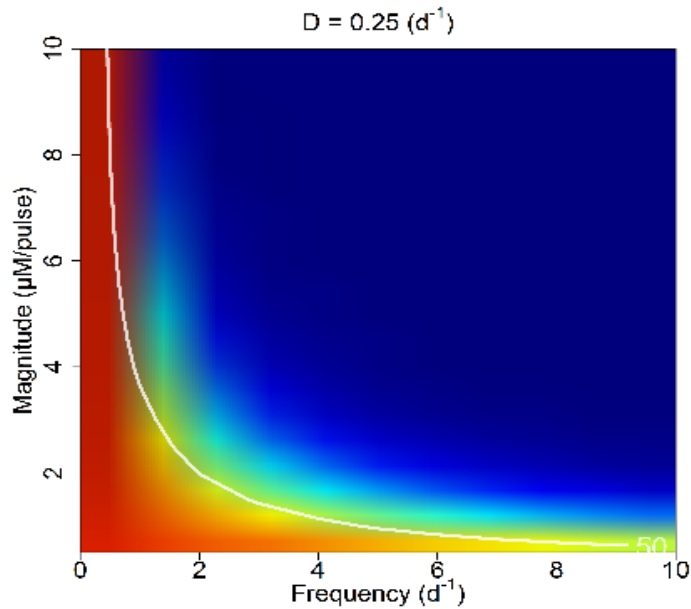
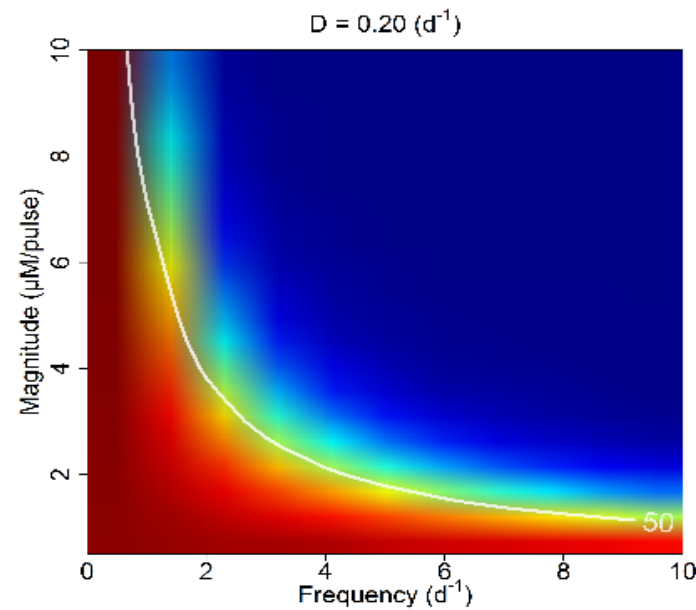
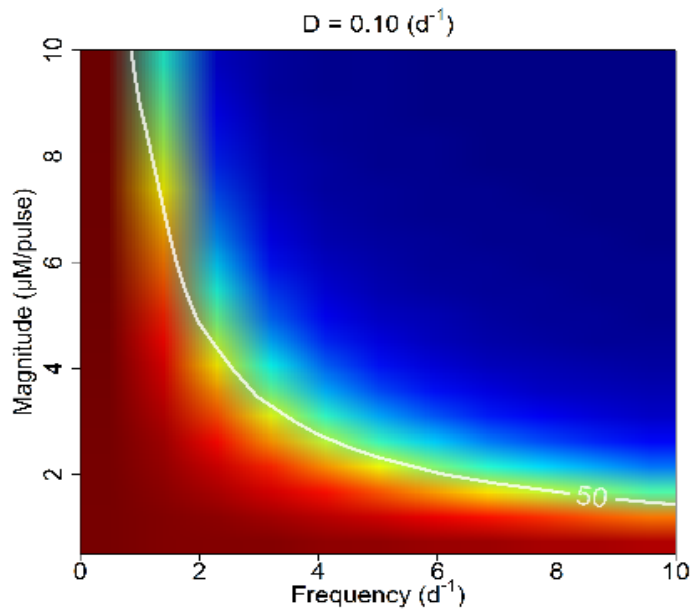
# Modelling - Calibration



# Modelling - Calibration



# Competition experiments - Modelling



*Synechococcus*

%

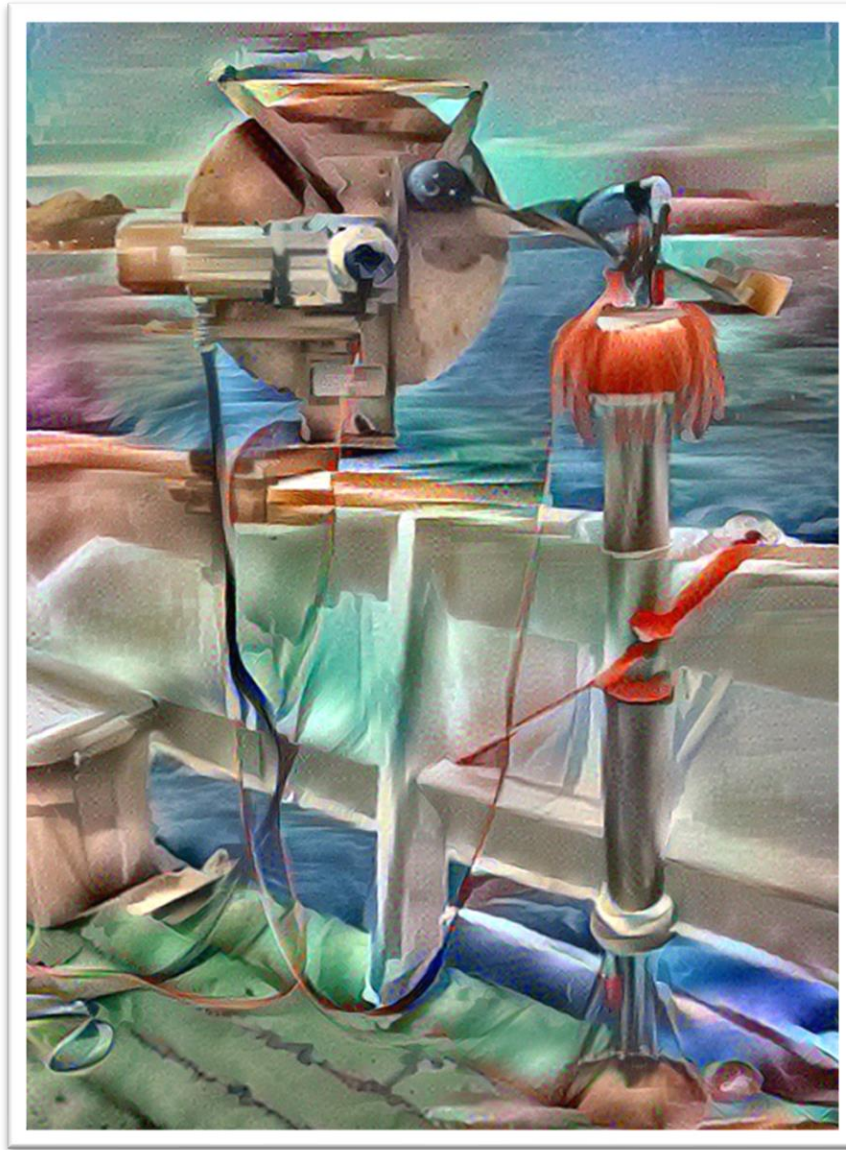
80

60

40

20

*Micromonas P.*

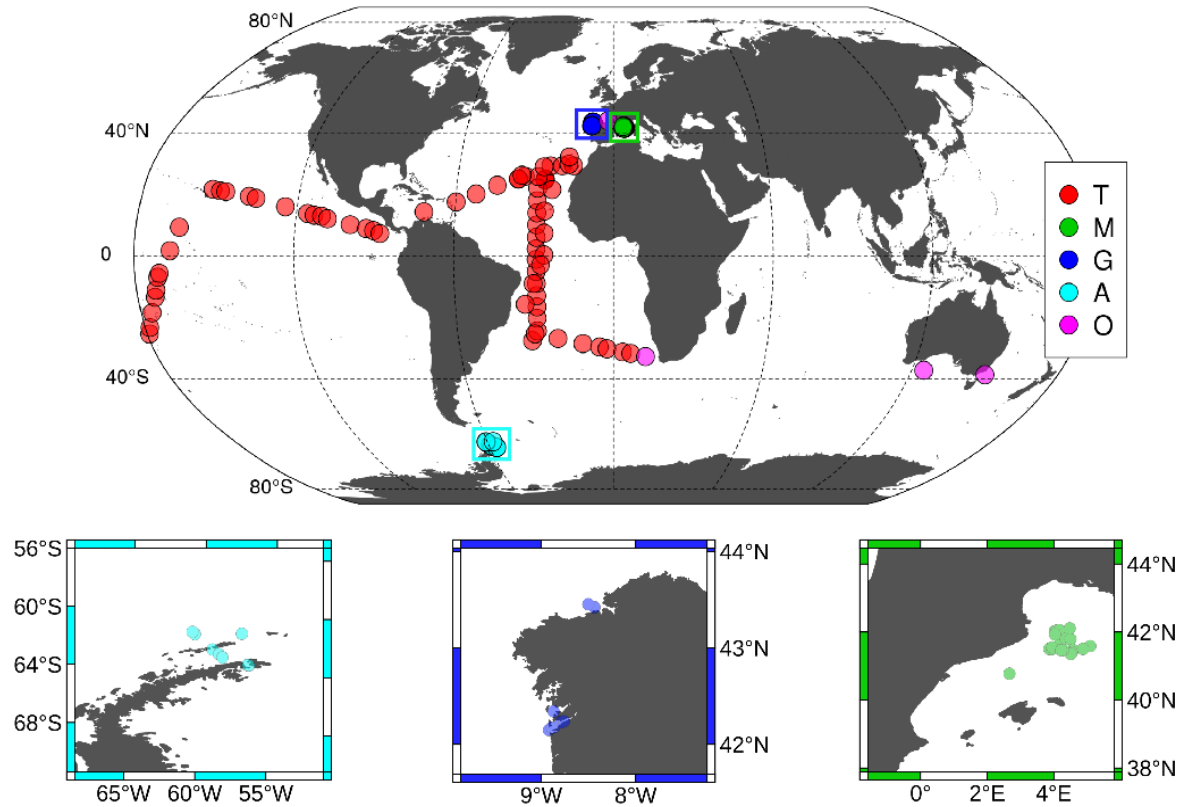


## **Chapter IV: Climatology of the vertical nutrient supply and future cyanobacteria to picoeukaryotes ratio**

# Objectives

1. To **quantify** the role of **temperature**, **light**, and **nitrate fluxes** as factors controlling the distribution of autotrophic and heterotrophic picoplankton subgroups.
2. To **describe** the **ecological niches** of the various components of the **picoplankton community**.
3. To explore the **effect of nitrate supply dynamics** on the competitive dynamics of two model marine picophytoplankton species, namely, the cyanobacterium *Synechococcus* sp. and the picoeukaryote *Micromonas pusilla*.
4. To build a prediction model and obtain the first **climatology** of **nitrate diffusion** into the **euphotic zone**.
5. To **predict** the change in the structure of **picophytoplankton communities** (the cyanobacteria to picoeukaryotes ratio) in a **future ocean scenario**.

# Dataset of microstructure turbulence (2006-2015)



**16 cruises; 181 stations**

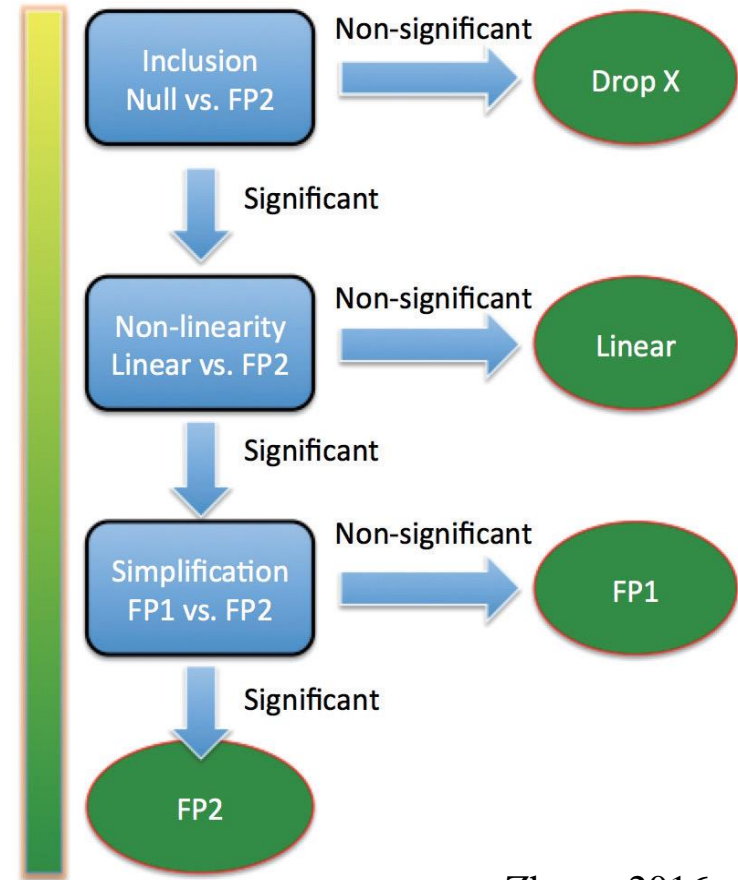
- 181 Microturbulence (MST, 0-300 m)
- Nitrate concentration (0-200 m):
  - 172 Observations
  - 6 WOA09 database
  - 3 Nitrate-density relationship

# Multivariable fractional polynomial method (MFP)

## Independent variables

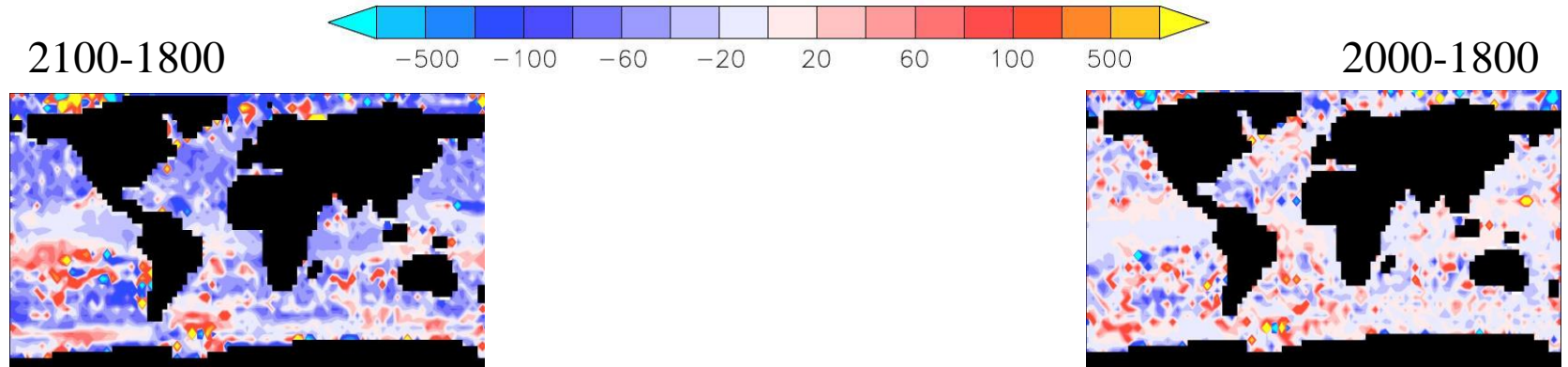
Stratification	Nitrate	Chlorophyll- <i>a</i>
SST	sNO <sub>3</sub>	DCM
SSS	nitraD	maxChl- <i>a</i>
MLD	grNO <sub>3</sub>	sChl- <i>a</i>
maxN <sup>2</sup>		
dmaxN <sup>2</sup>		
avrN <sup>2</sup>		

## MFP algorithm



Zhang, 2016

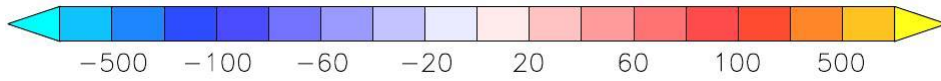
# Future scenario (2100)



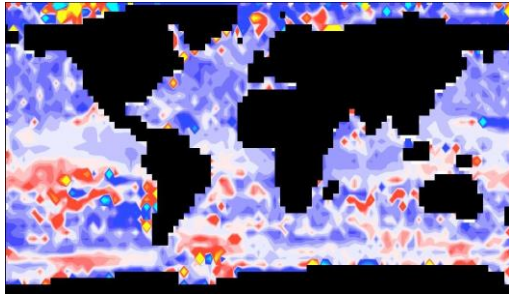
Lewandowska *et al.*, 2014



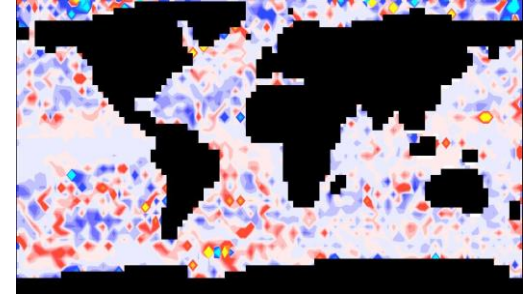
# Future scenario (2100)



2100-1800

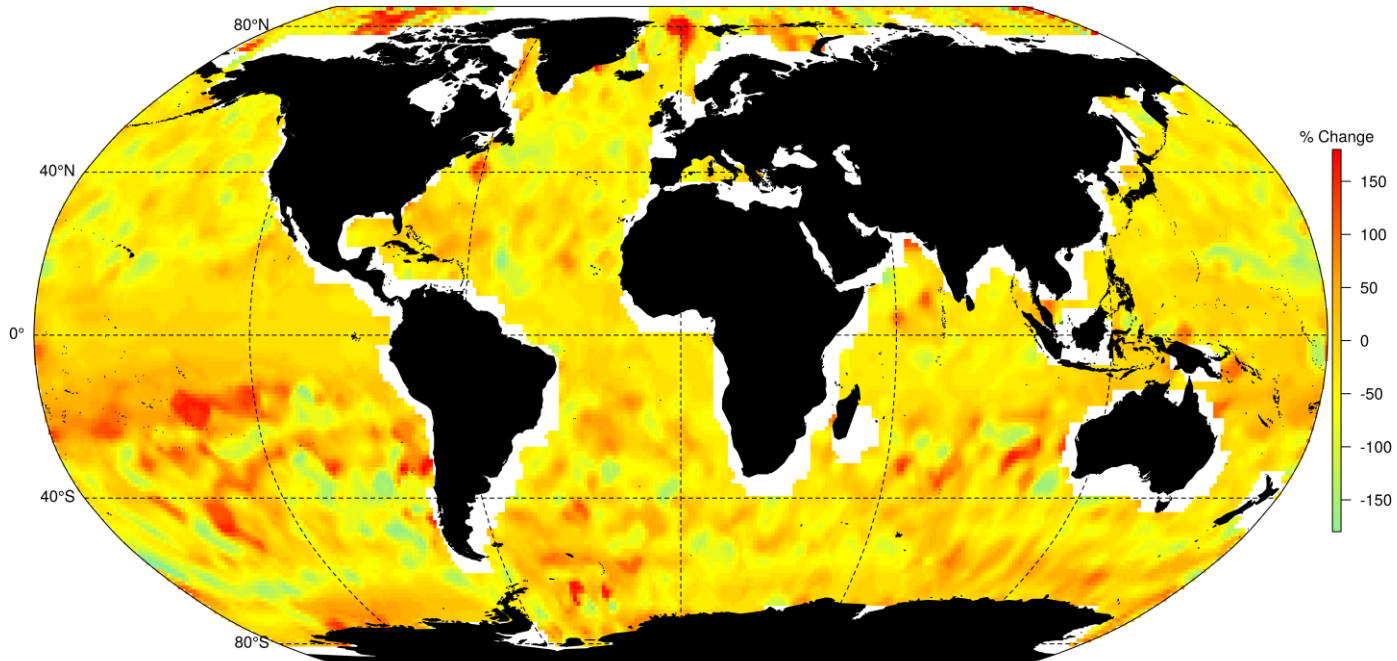


2000-1800

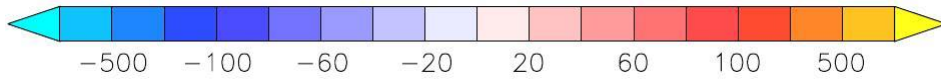


Lewandowska *et al.*, 2014

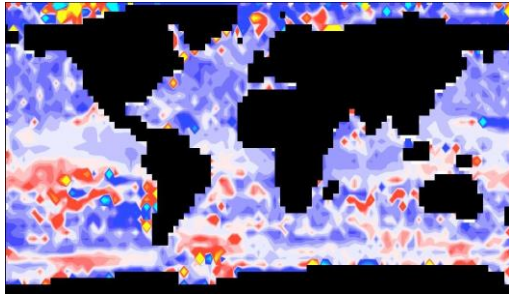
2100-2000



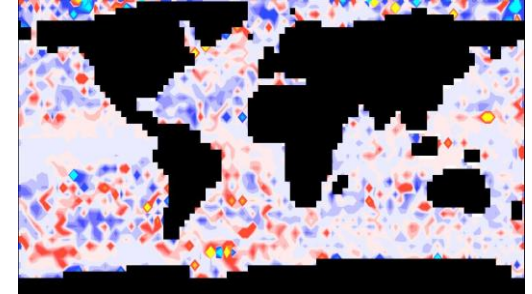
# Future scenario (2100)



2100-1800

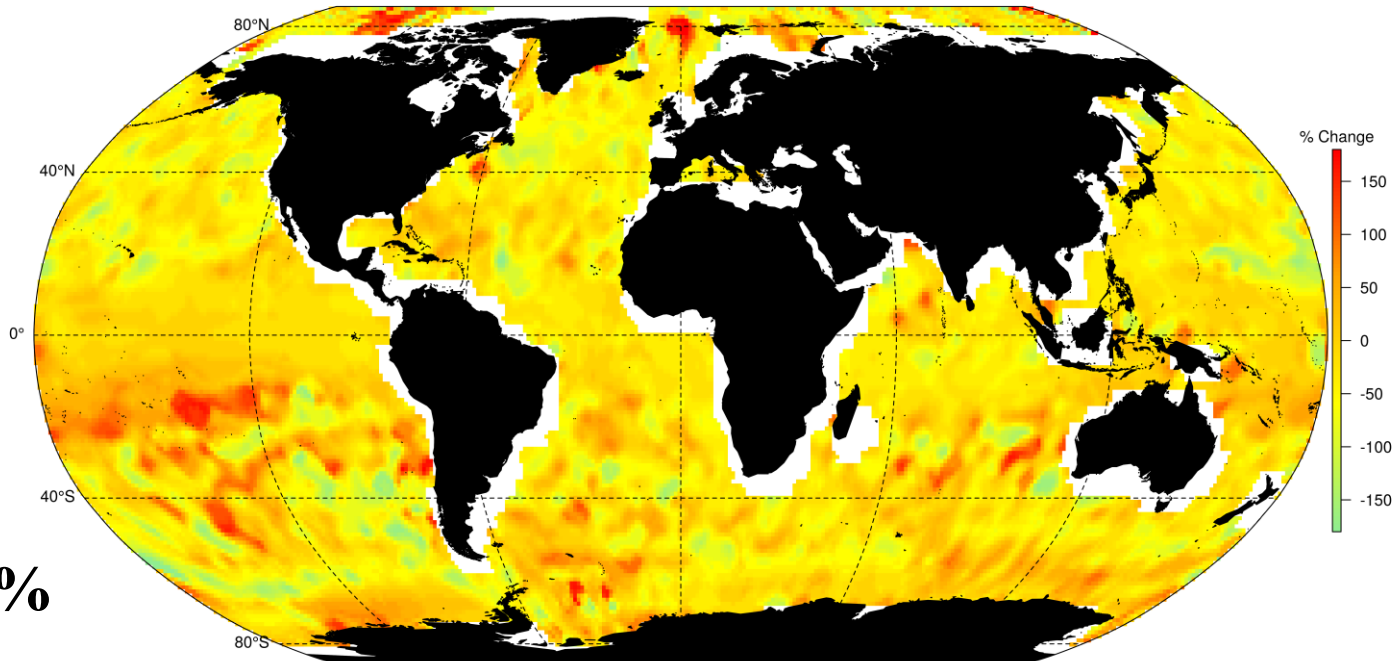


2000-1800



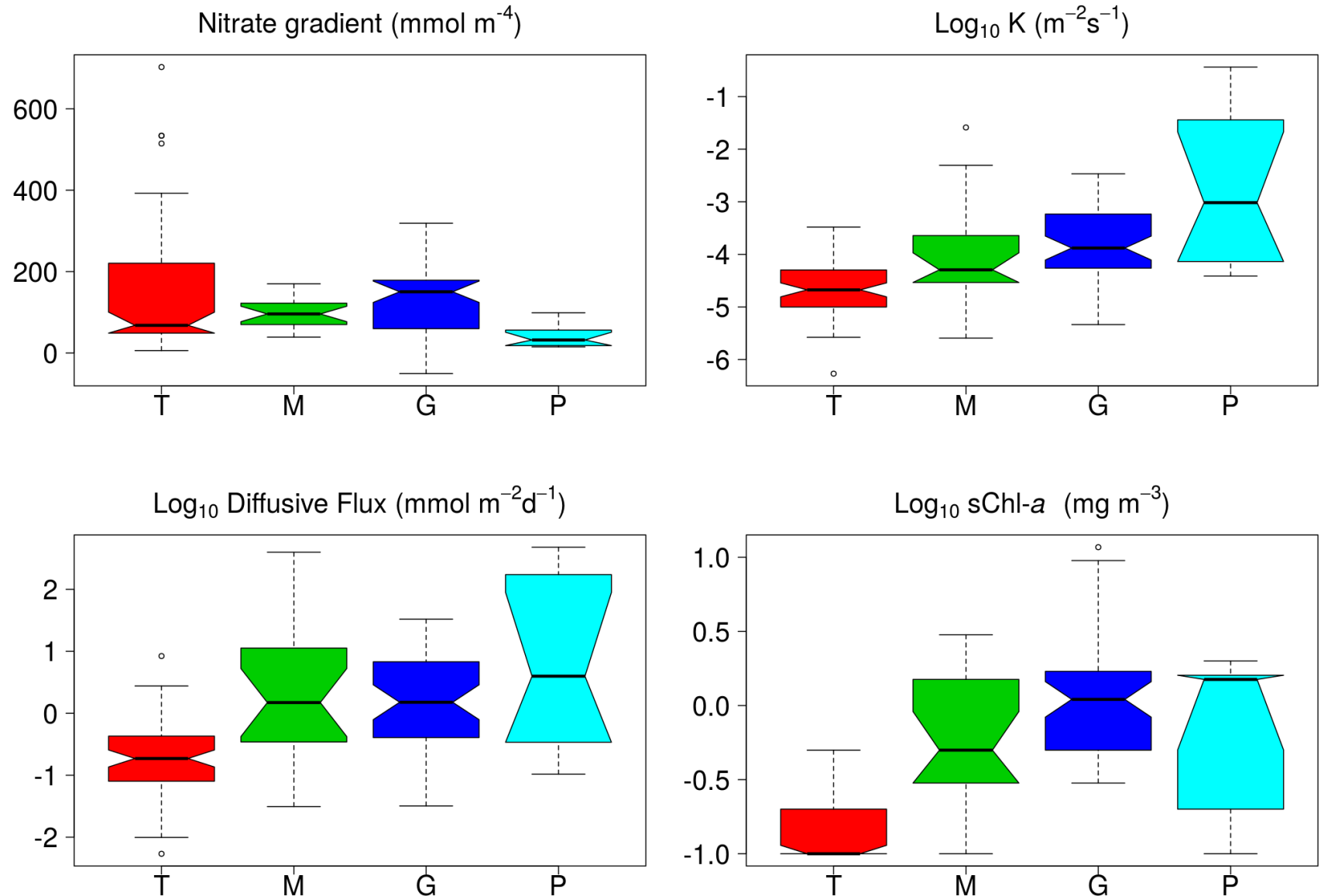
Lewandowska *et al.*, 2014

2100-2000



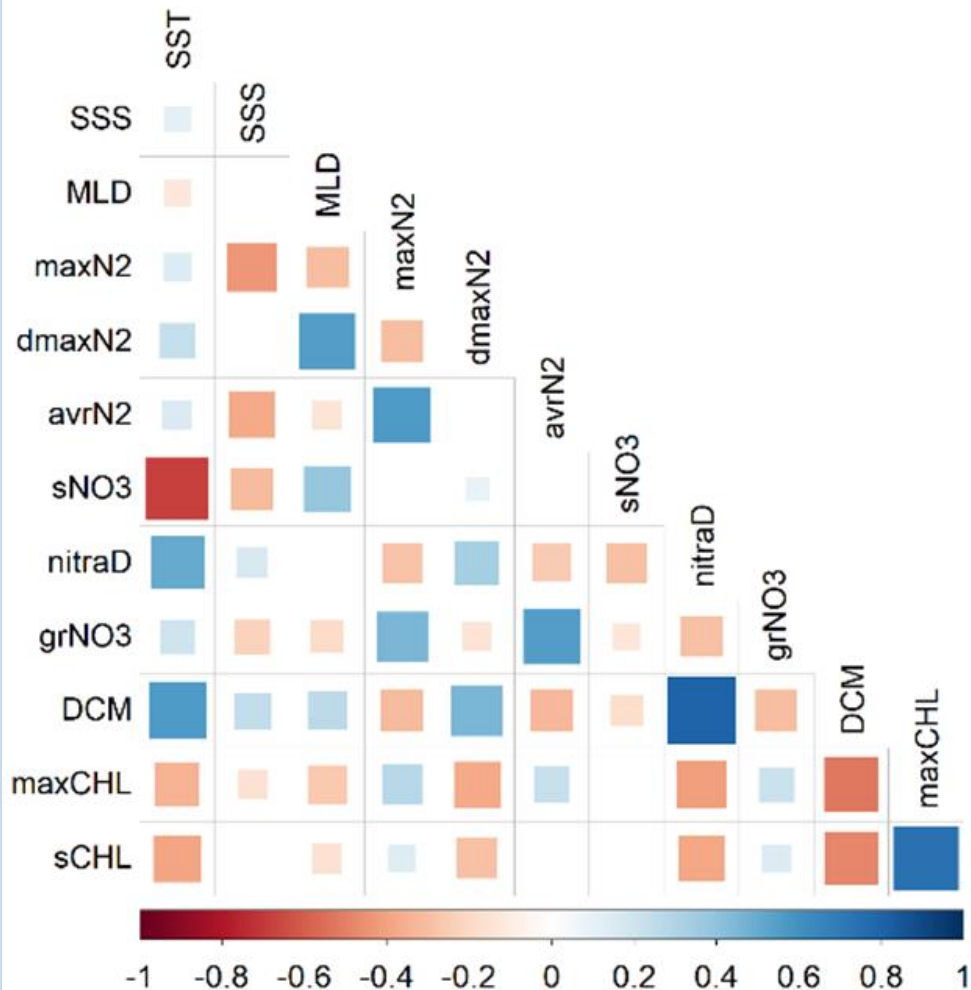
20%

# Variability in $\text{NO}_3$ gradient, $K$ , $\text{NO}_3$ flux and $\text{sChl-}a$



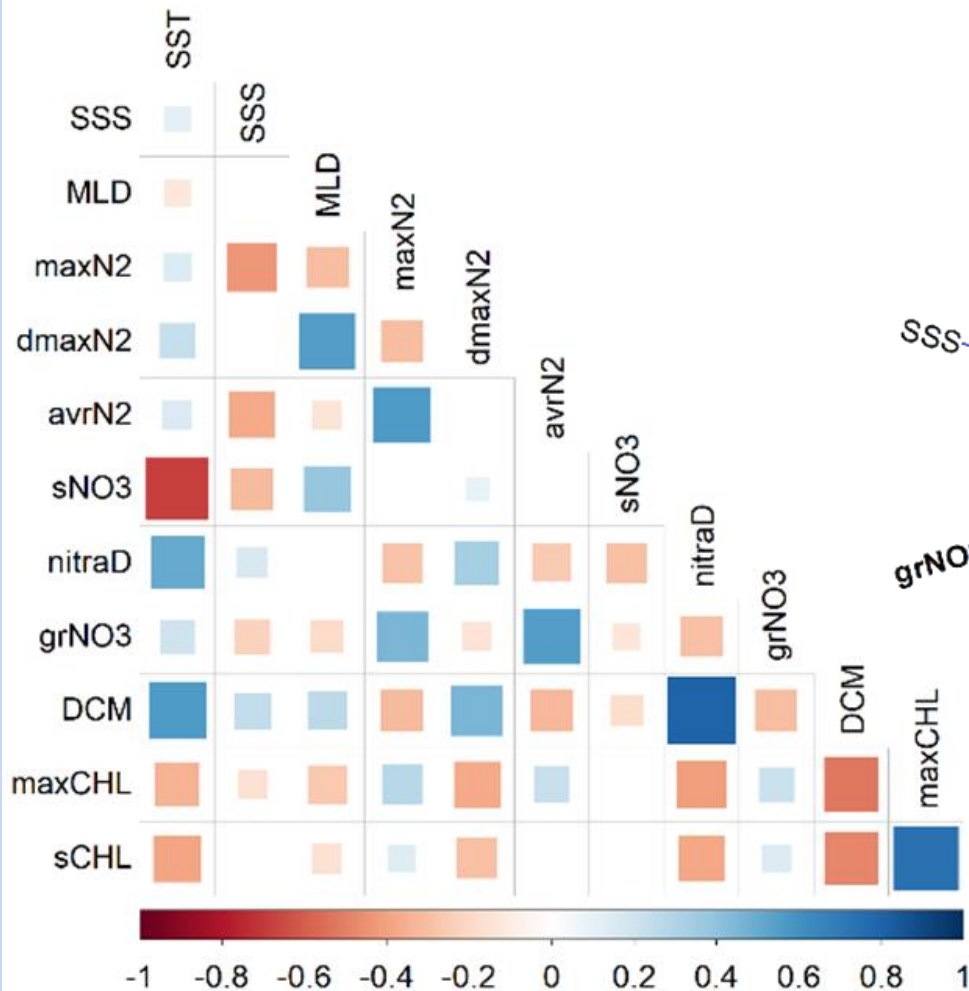
# Collinearity in the dataset

Correlation matrix

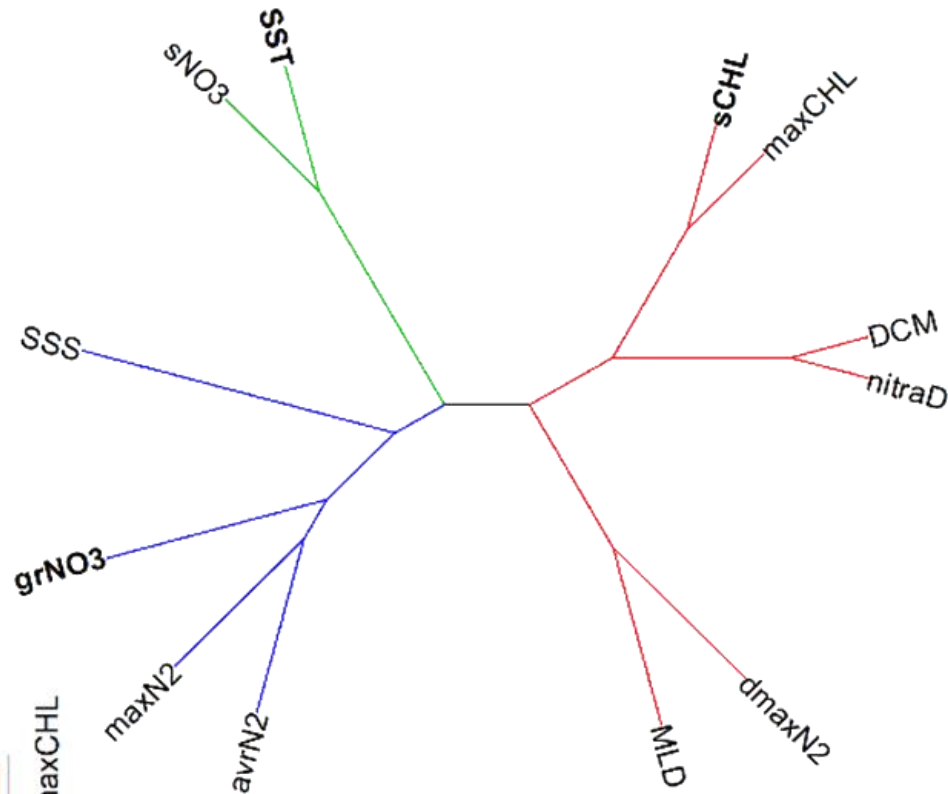


# Collinearity in the dataset

Correlation matrix

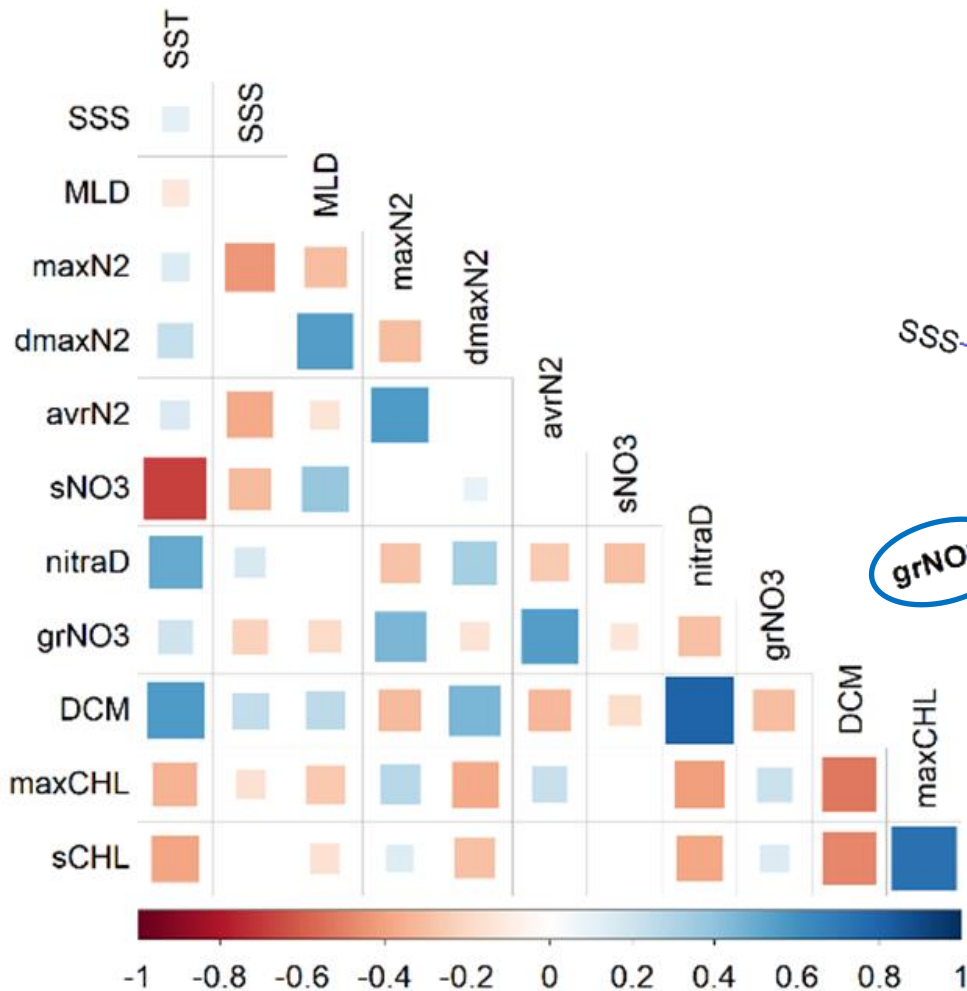


Cluster

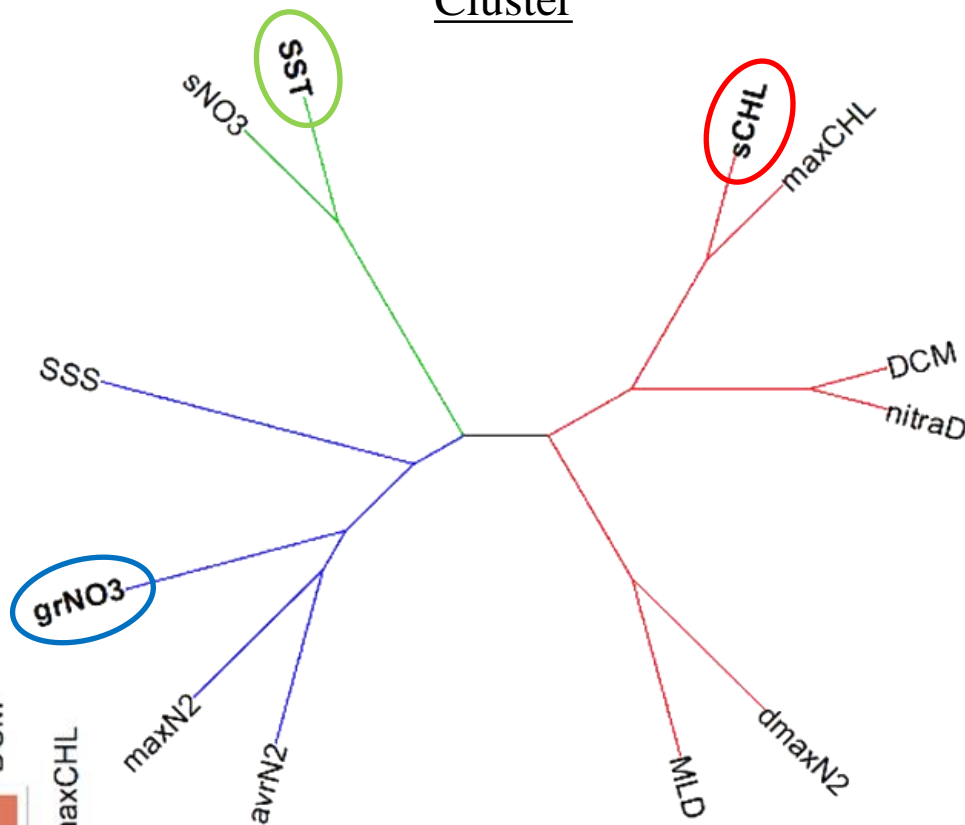


# Collinearity in the dataset

Correlation matrix



Cluster



# Multivariable fractional polynomial method (MFP)

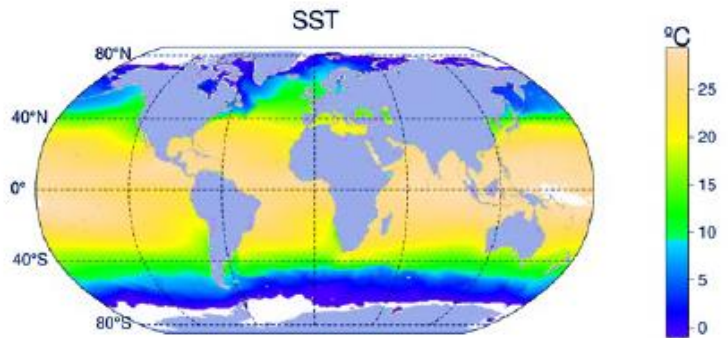
	R <sup>2</sup> -adj	AIC
<b>Tropical and subtropical</b>		
$FNO_3 = f(\text{grNO}_3, \text{SSS}, \text{sNO}_3, \text{avrN}_2)$	0.75	143
$FNO_3 = f(\text{grNO}_3, \text{SST})$	0.41	189
<b>NW Mediterranean</b>		
$FNO_3 = f(\text{avrN}_2)$	0.68	72
$FNO_3 = f(\text{SST}, \text{sChla})$	0.64	77
<b>NW Galician upwelling</b>		
$FNO_3 = f(\text{grNO}_3, \text{maxChla})$	0.64	77
$FNO_3 = f(\text{grNO}_3)$	0.51	110
<b>Antartic</b>		
$FNO_3 = f(\text{SST})$	0.75	38
<b>Global</b>		
$FNO_3 = f(\text{SST}, \text{grNO}_3, \text{sChla}, \text{DCM})$	0.55	545
$FNO_3 = f(\text{SST}, \text{grNO}_3, \text{sChla})$	0.52	553

# Multivariable fractional polynomial method (MFP)

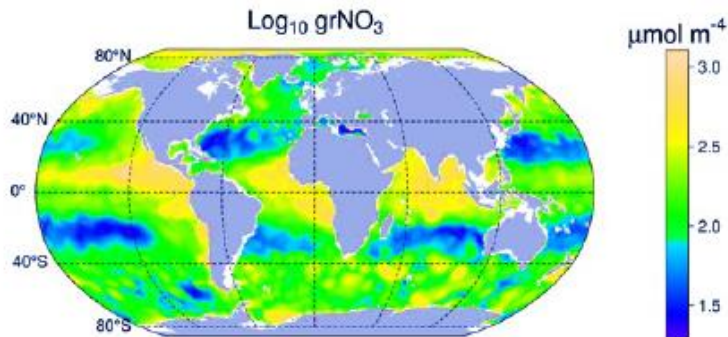
	R <sup>2</sup> -adj	AIC
<b>Tropical and subtropical</b>		
$FNO_3 = f(\text{grNO}_3, \text{SSS}, \text{sNO}_3, \text{avrN}_2)$	0.75	143
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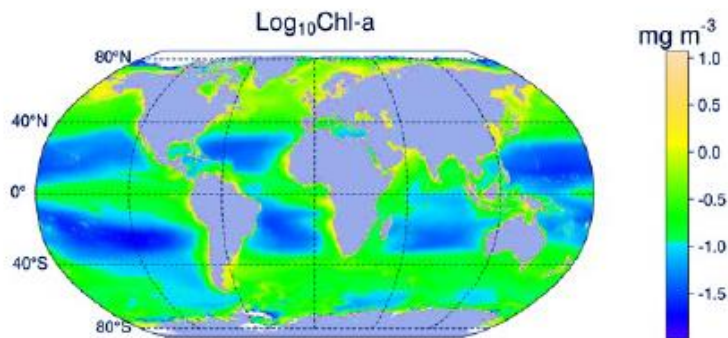
# Prediction of $\text{NO}_3$ turbulent diffusion



SST from WOA13

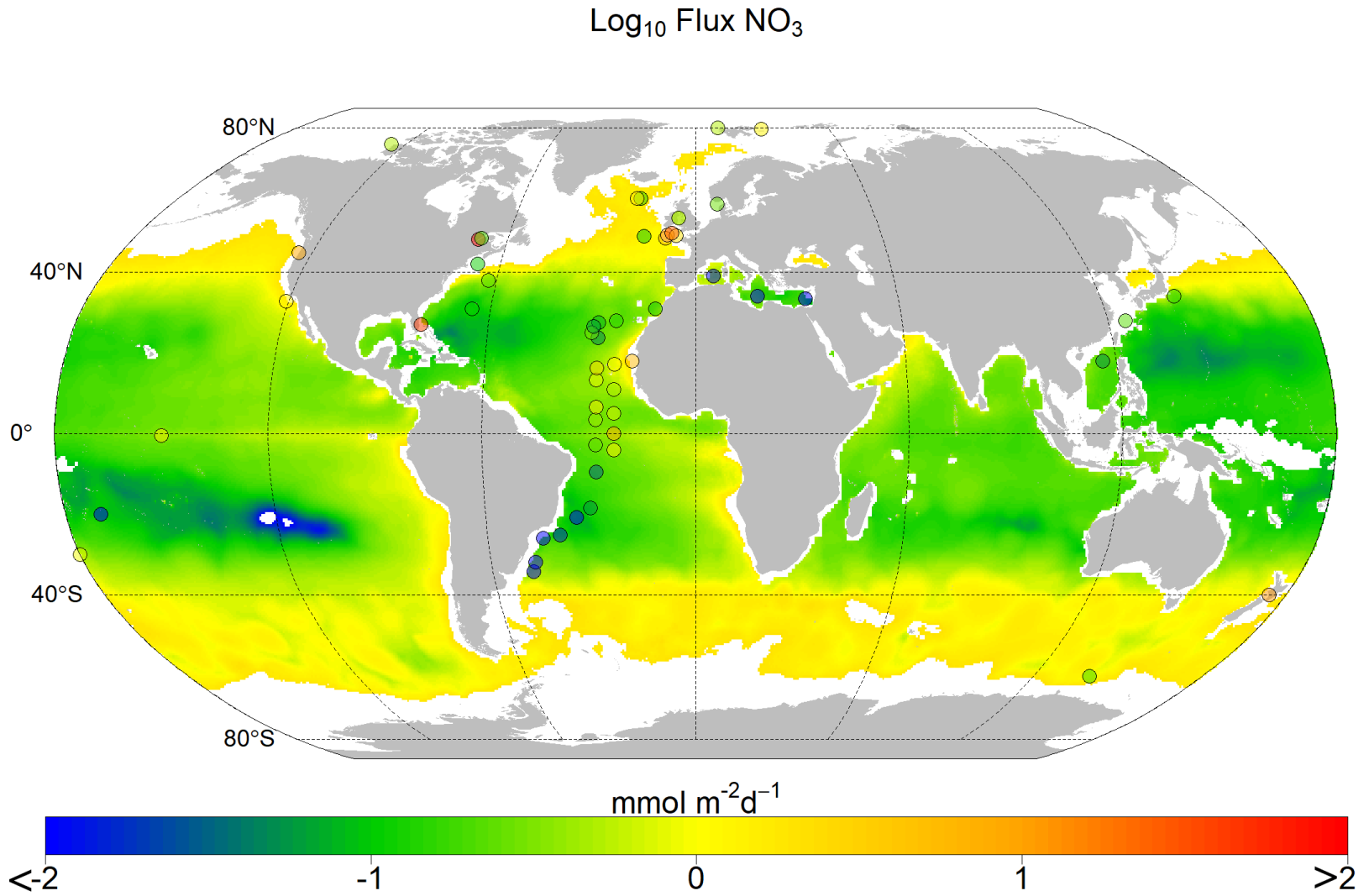


$\text{grNO}_3$  from WOA13



$s\text{Chl-a}$  from Globecolour (1998-2017)

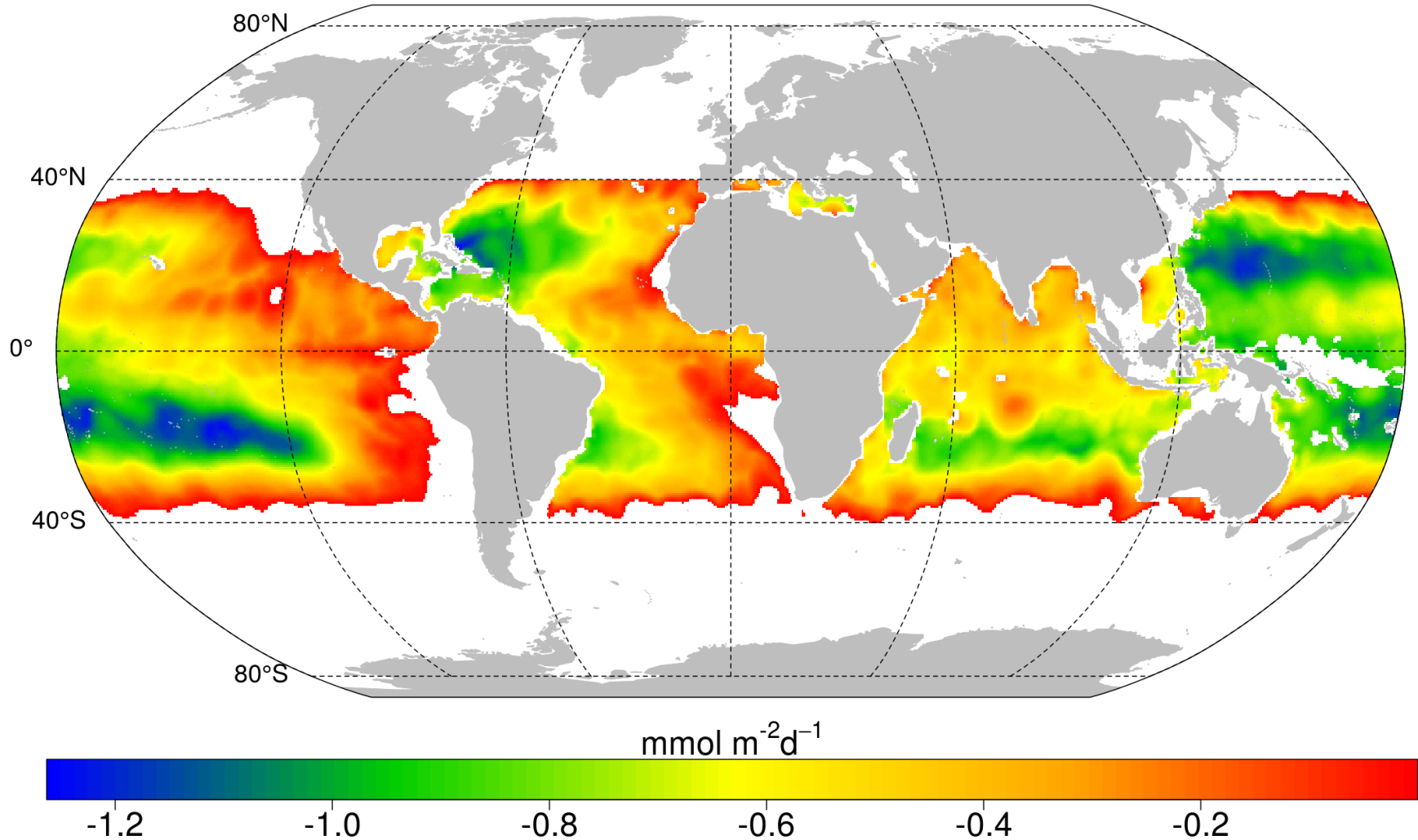
# Prediction of $\text{NO}_3$ turbulent diffusion + observations



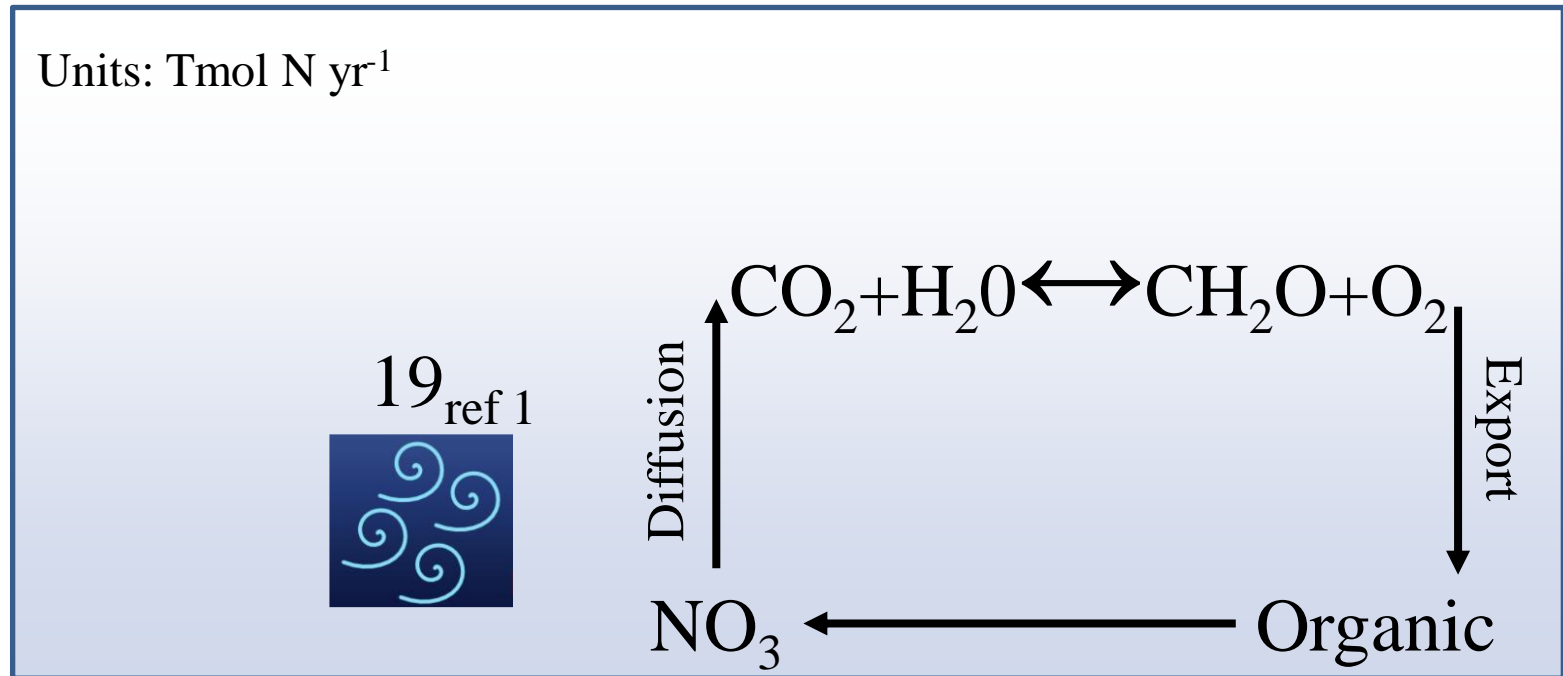
# Prediction of $\text{NO}_3$ diffusion for $40^\circ\text{N} - 40^\circ\text{S}$

$\text{Log}_{10}$  Flux  $\text{NO}_3$

$\text{NO}_3$  Flux  $< 1 \text{ mmol m}^{-2} \text{ d}^{-1}$   
 $\text{sChl-}a < 1 \text{ mg m}^{-3}$

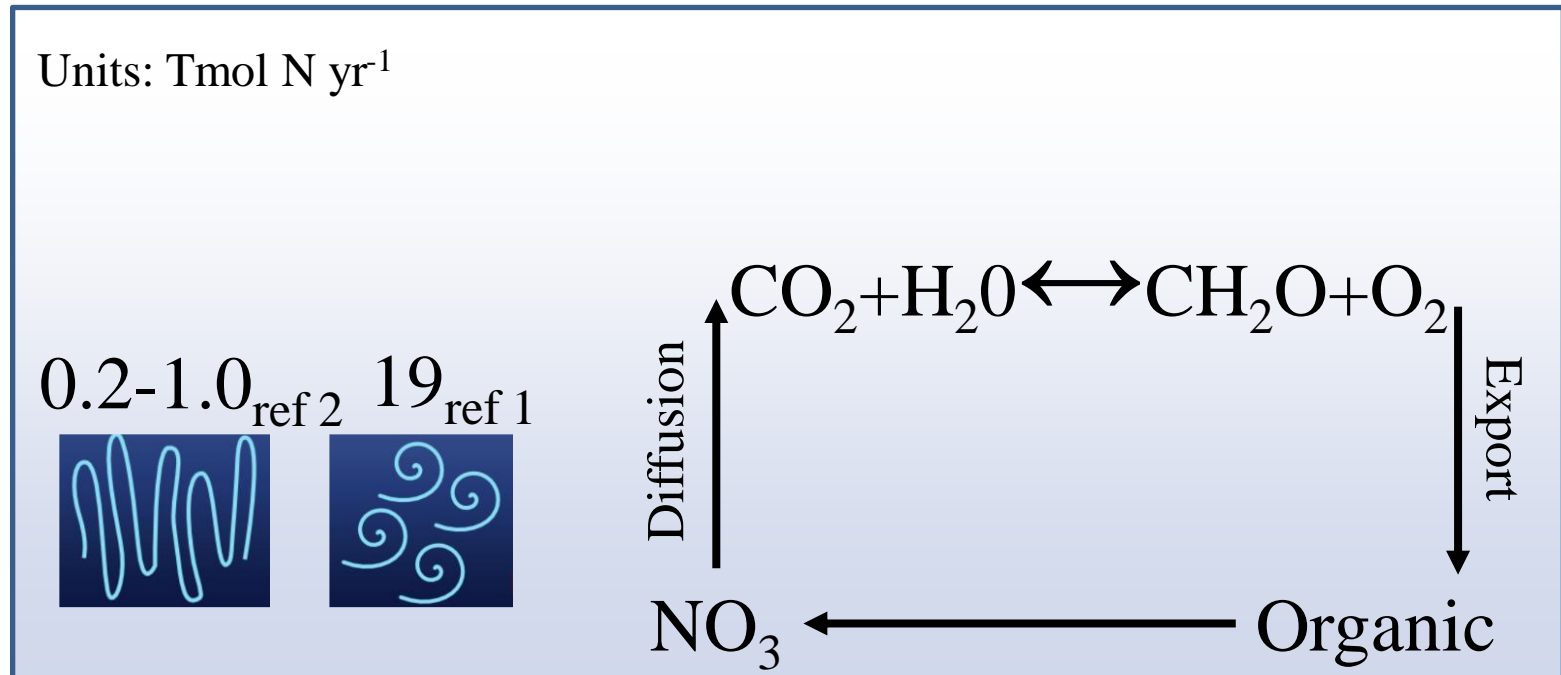


# Relevance of diffusive nitrogen fluxes in tropical and subtropical areas



<sup>1</sup>This study

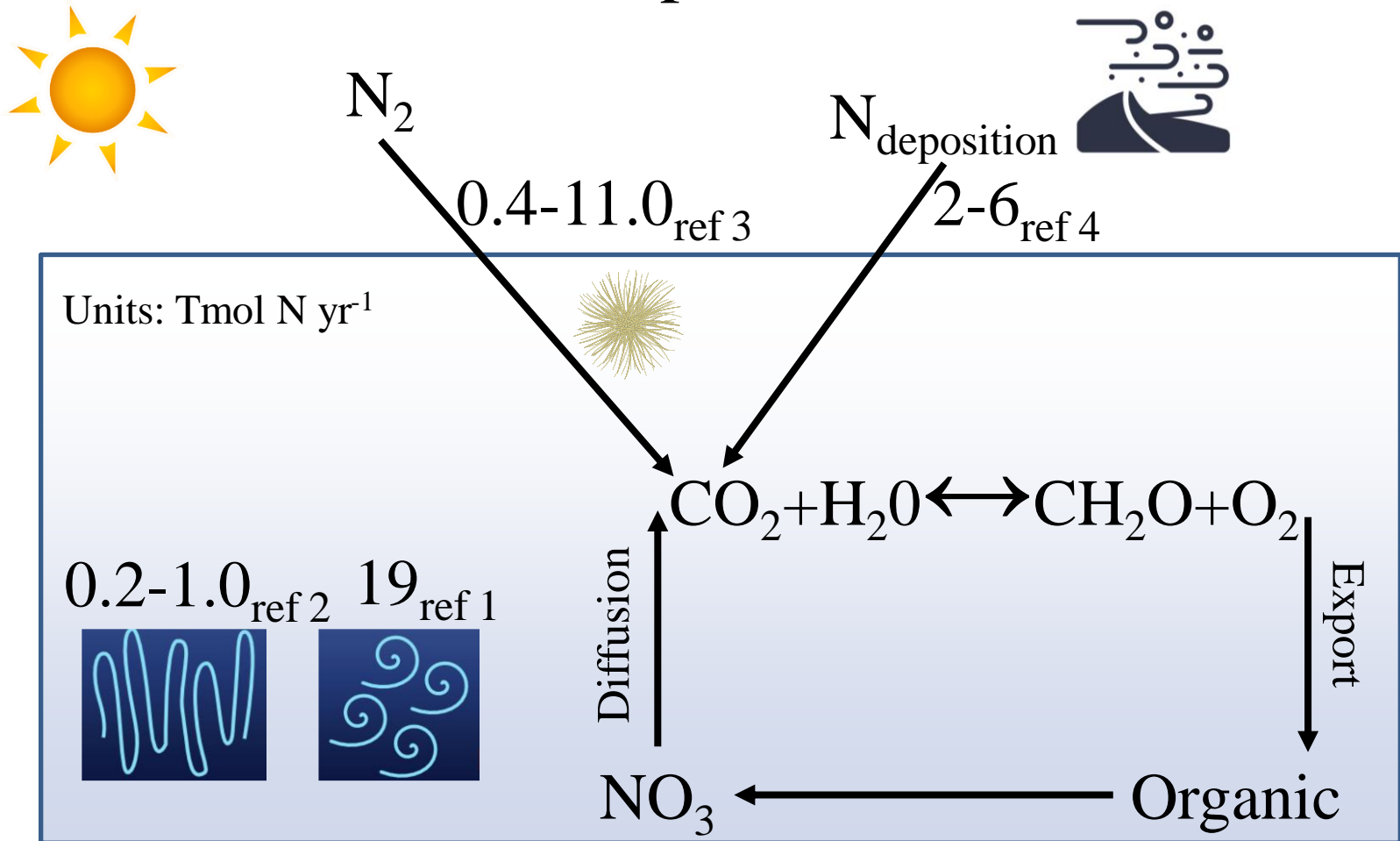
# Relevance of diffusive nitrogen fluxes in tropical and subtropical areas



<sup>1</sup>This study

<sup>2</sup>Fernández-Castro et al. (2015)

# Relevance of diffusive nitrogen fluxes in tropical and subtropical areas



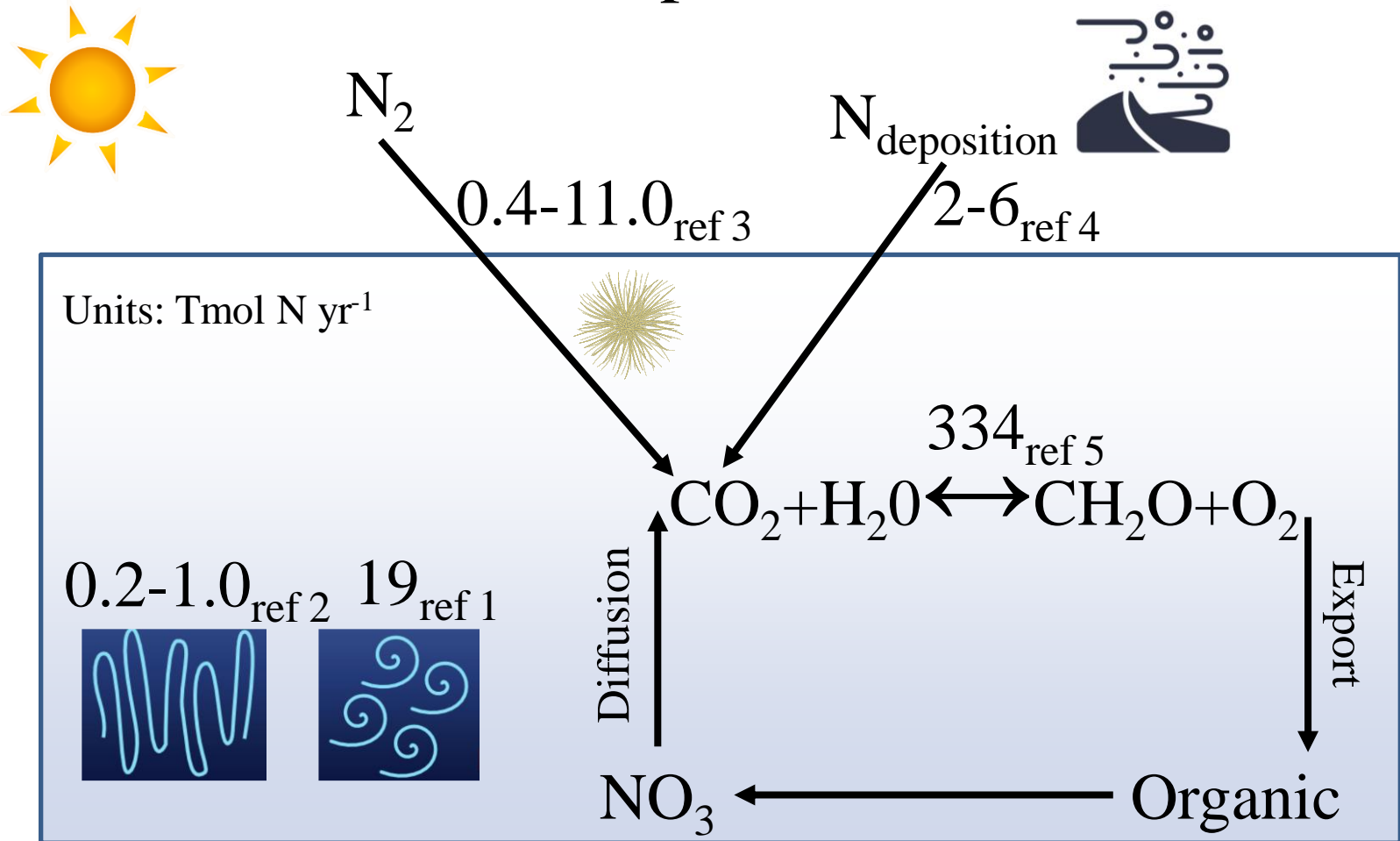
<sup>1</sup>This study

<sup>2</sup>Fernández-Castro et al. (2015)

<sup>3</sup>Carpenter & Capone (2008)

<sup>4</sup>Okin *et al.* (2011)

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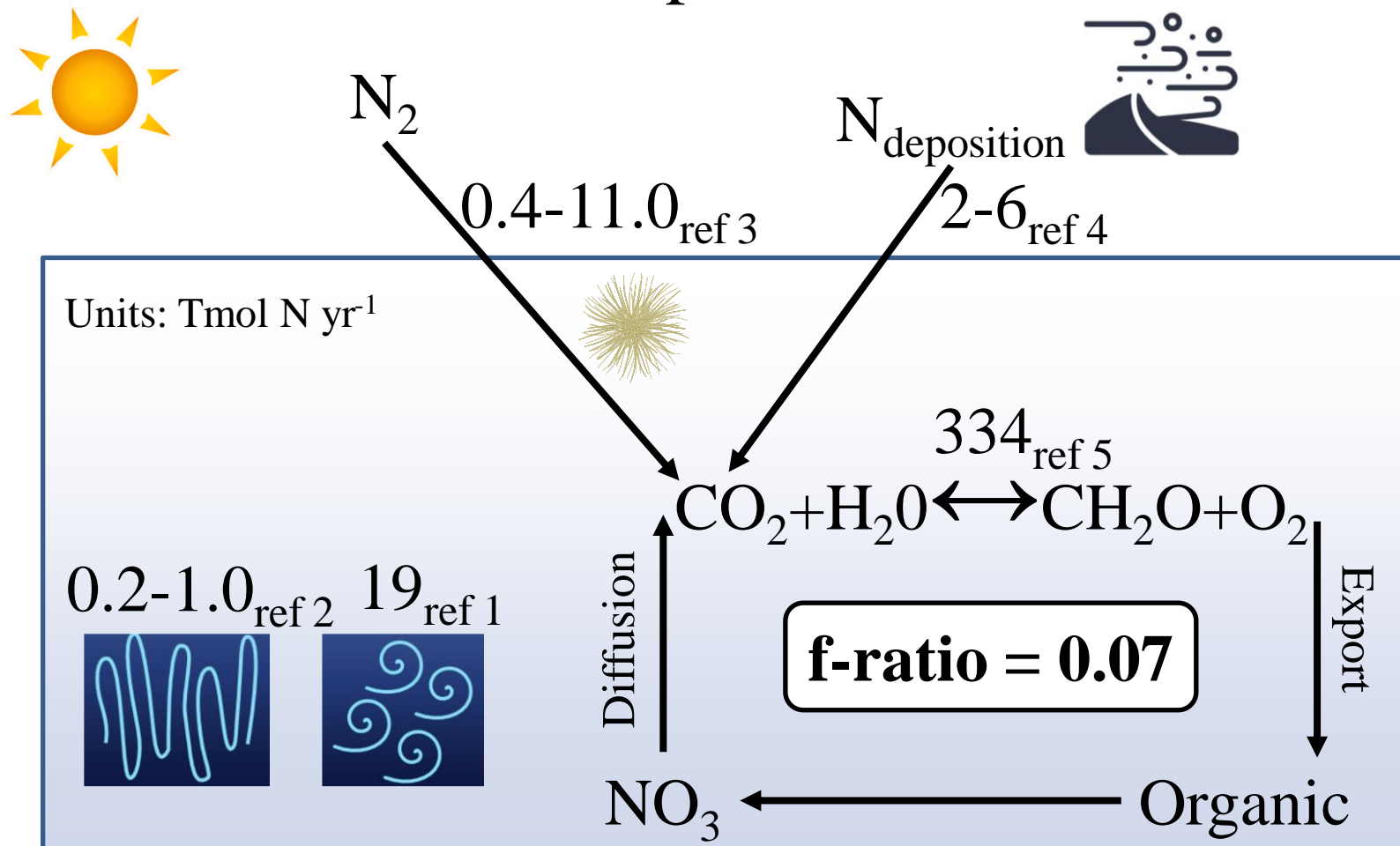
<sup>5</sup>NPP(Uitz et al, 2008)

20% ratio phyto respiration to GP (Geider, 1992)

23% DOC production (Teira et al, 2001)

Variable stoichiometry (Galbraith & Martiny, 2015)

# Relevance of diffusive nitrogen fluxes in tropical and subtropical areas



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<sup>5</sup>NPP(Uitz et al, 2008)

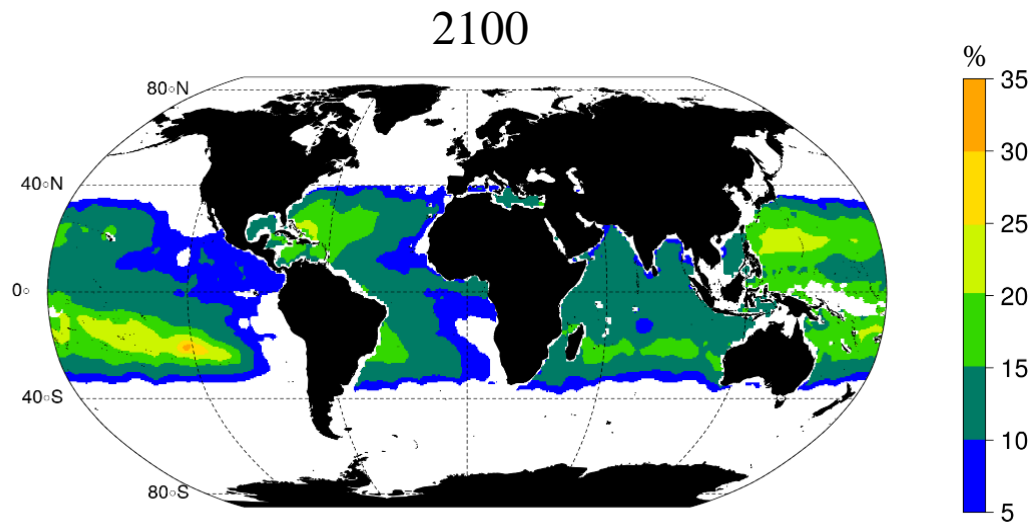
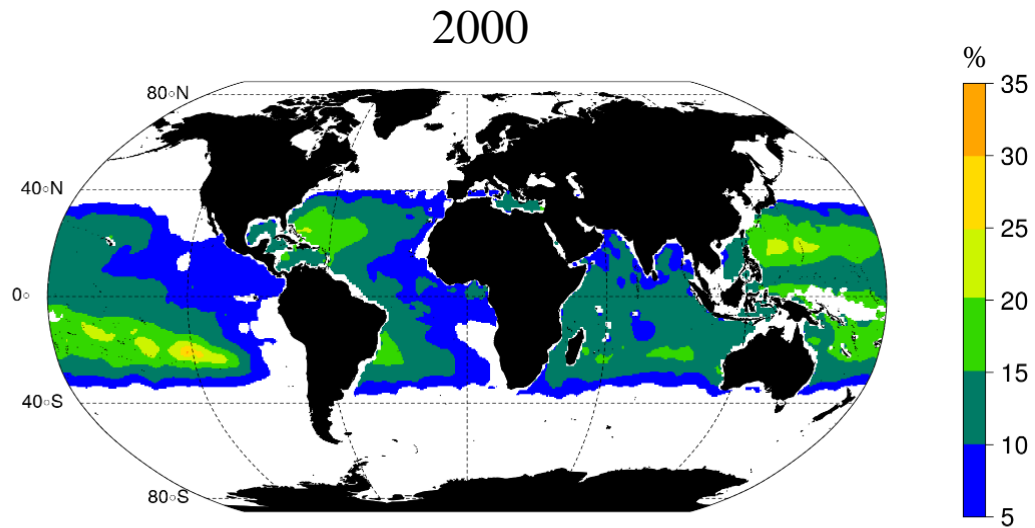
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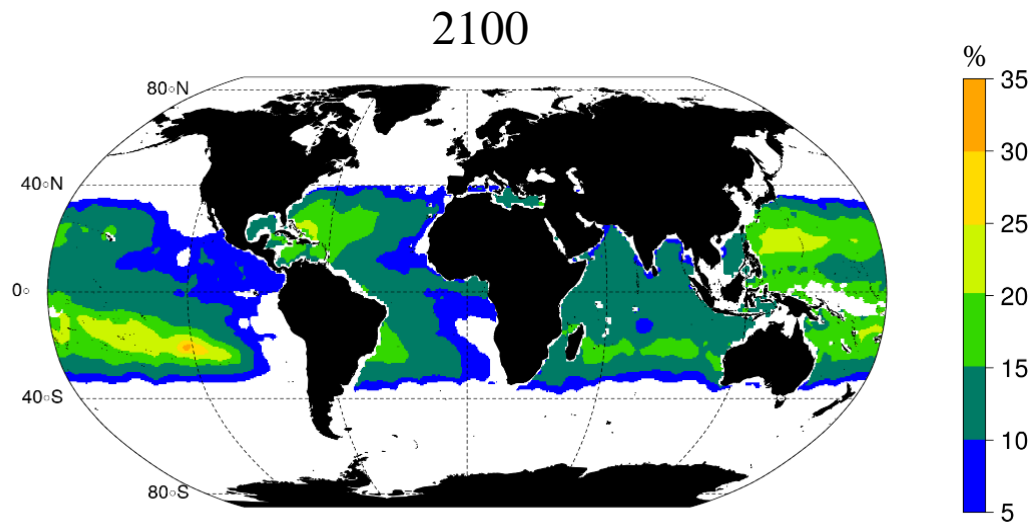
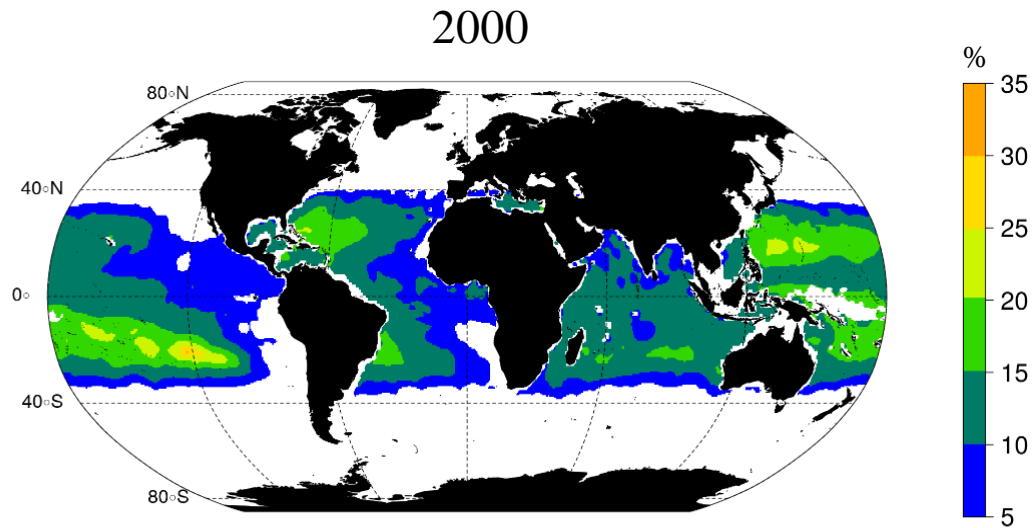
Variable stoichiometry (Galbraith & Martiny, 2015)




# Present and future of cyanoB/pEuk ratio



# Present and future of cyanoB/pEuk ratio



 **8%**



**Conclusions**

## OBJECTIVE I

To **quantify** the role of **temperature**, **light**, and **nitrate fluxes** as factors controlling the distribution of autotrophic and heterotrophic picoplankton subgroups.

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To **quantify** the role of **temperature**, **light**, and **nitrate fluxes** as factors controlling the distribution of autotrophic and heterotrophic picoplankton subgroups.



### CONCLUSION I

**Temperature** and **nitrate supply** were **more relevant than light** in predicting the biomass of most picoplankton subgroups, except for *Prochlorococcus* and low-nucleic-acid (LNA) prokaryotes, for which irradiance also played a significant role.

## OBJECTIVE II

To **describe** the **ecological niches** of the various components of the **picoplankton community**.

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To **describe** the **ecological niches** of the various components of the **picoplankton community**.



## CONCLUSION II y III

*Prochlorococcus* and **LNA prokaryotes** were more abundant in warmer waters where the **nitrate fluxes** were **low**, *Synechococcus* and high-nucleic-acid (**HNA**) **bacteria** prevailed in cooler environments characterized by **intermediate or high** levels of **nitrate supply**, and finally the niche of **picoeukaryotes** was defined by **low temperatures** and **high nitrate supply**.

**Nitrate supply** was the **only factor** that allowed the **distinction among the ecological niches** of all autotrophic and heterotrophic picoplankton subgroups.

### OBJECTIVE III

To explore the **effect** of **nitrate supply dynamics** on the competitive dynamics of two model marine picophytoplankton species, namely, the cyanobacterium *Synechococcus* sp. and the picoeukaryote *Micromonas pusilla*.



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To explore the **effect of nitrate supply dynamics** on the competitive dynamics of two model marine picophytoplankton species, namely, the cyanobacterium *Synechococcus* sp. and the picoeukaryote *Micromonas pusilla*.



### CONCLUSION IV, V y VI

**Nitrate supply dynamics controlled the outcome of competition** between the cyanobacterium *Synechococcus* and the picoeukaryote *M. pusilla*.

Under continuous nitrate limitation conditions (**steady-state**), *M. pusilla* was **outcompeted by *Synechococcus* sp.**, the **result** of the competition was **reversed** in nutrient supply dynamics scenarios.

The **rate of competitive exclusion of *Synechococcus*** was a **linear function of the frequency of nitrate pulses**, demonstrating that there is a window of opportunity for the coexistence of both species.

#### OBJECTIVE IV

To build a prediction model and obtain the first **climatology** of **nitrate diffusion** into the **euphotic zone**.

**OBJECTIVE IV**

To build a prediction model and obtain the first **climatology** of **nitrate diffusion** into the **euphotic zone**.

**CONCLUSION VII y VIII**

A model including **three predictors** (surface temperature, nitrate vertical gradient, and surface chlorophyll-*a*) **explained 57%** of the **variance** in the nitrate diffusive flux.

**Average nitrate diffusion** for oligotrophic regions between 40°N-40°S ( $\sim 20 \text{ Tmol N y}^{-1}$ ) was **comparable** to the **sum** of global estimates of **nitrogen fixation**, **fluvial fluxes** and **atmospheric deposition**.

**OBJECTIVE V**

To **predict** the change in the structure of **picophytoplankton communities** (the cyanobacteria to picoeukaryotes ratio) in a **future** global change **scenario**.

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To **predict** the change in the structure of **picophytoplankton communities** (the cyanobacteria to picoeukaryotes ratio) in a **future** global change **scenario**.

**CONCLUSION IX**

The predicted **decrease of nitrate supply** in tropical and subtropical areas as the result of global change (~20%), would produce an **increase** in the **cyanobacteria to picoeukaryotes biomass ratio** of **8%**.

Universidade de Vigo



Grupo de  
Oceanografía  
Biológica

THANK YOU  
FOR YOUR ATTENTION

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PHD PROGRAM IN MARINE SCIENCE, TECHNOLOGY AND MANAGEMENT



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MINISTERIO  
DE CIENCIA  
E INNOVACIÓN