Body size, light intensity and inorganic nutrient supply determine plankton stoichiometry in mixotrophic plankton food webs

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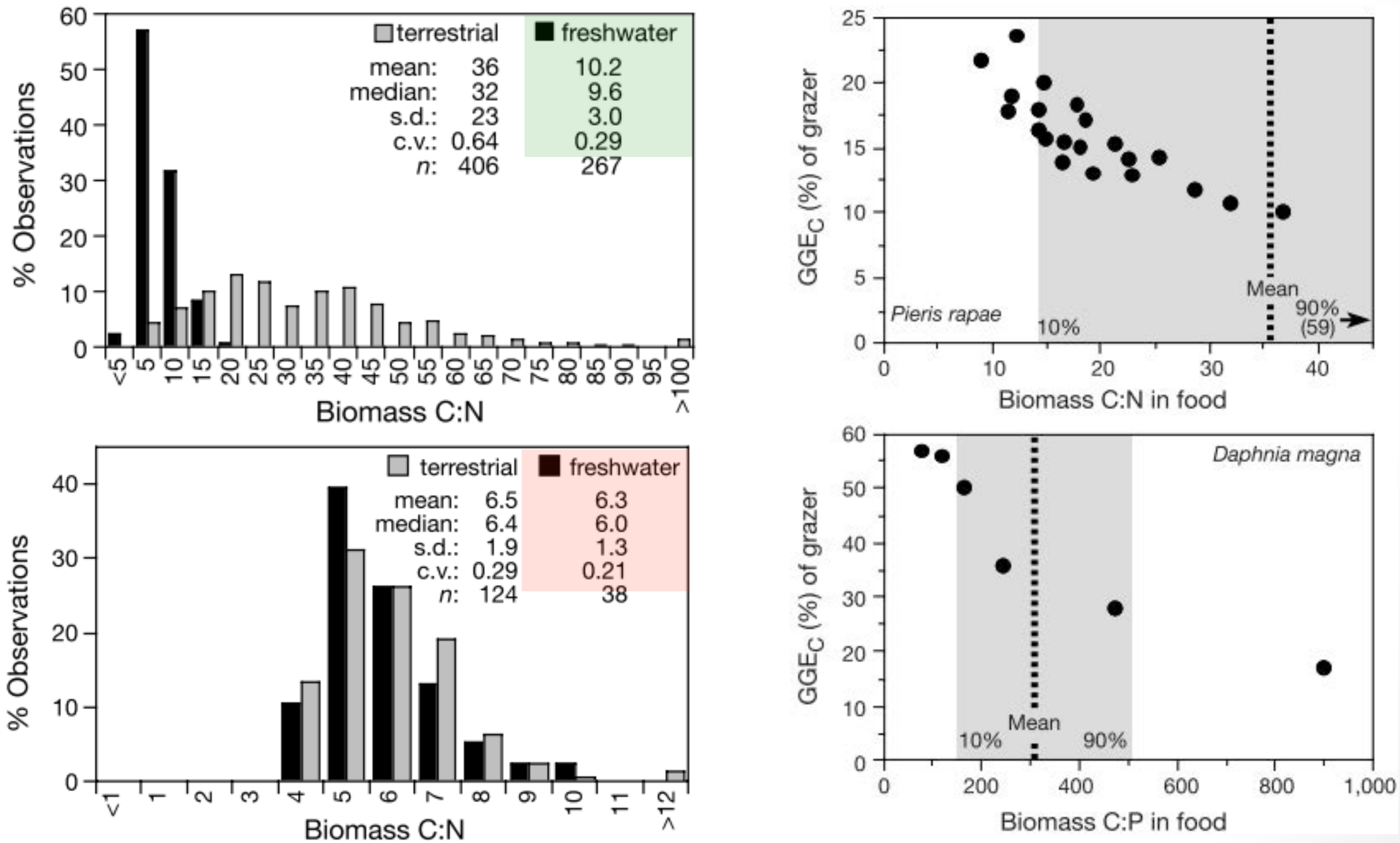
Introduction

Trophic strategy and stoichiometry

- Imbalance of C:N:P between heterotrophs and autotrophs influences heterotroph growth and nutrient cycle



(Elser et al. 2000)

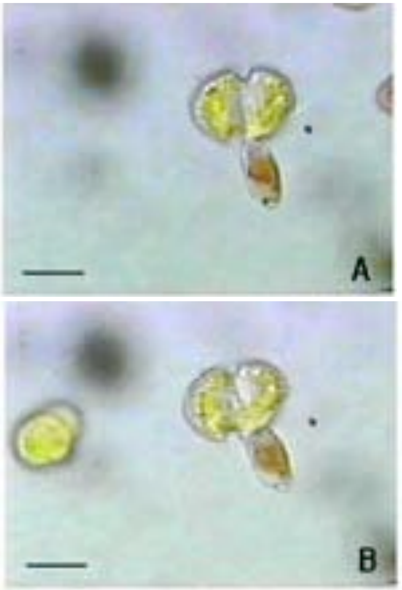
There are not only autotrophs and heterotrophs

Mixotrophs: Monster plants that eat, or photosynthetic animals

Introduction

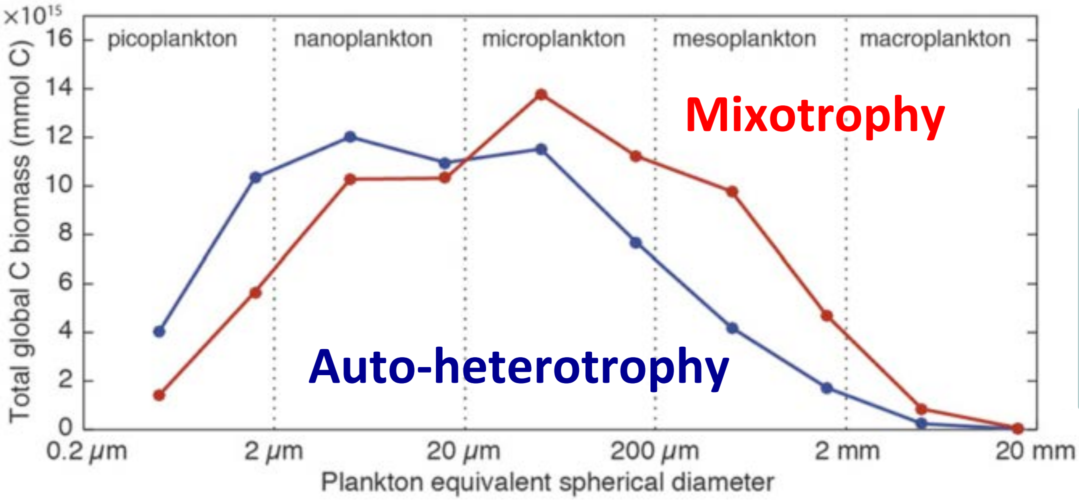
Mixotrophs in aquatic systems

- Gain carbon biomass from both photosynthesis and phagotrophy
- Obtain nitrogen and phosphorus from both inorganic nutrients and prey

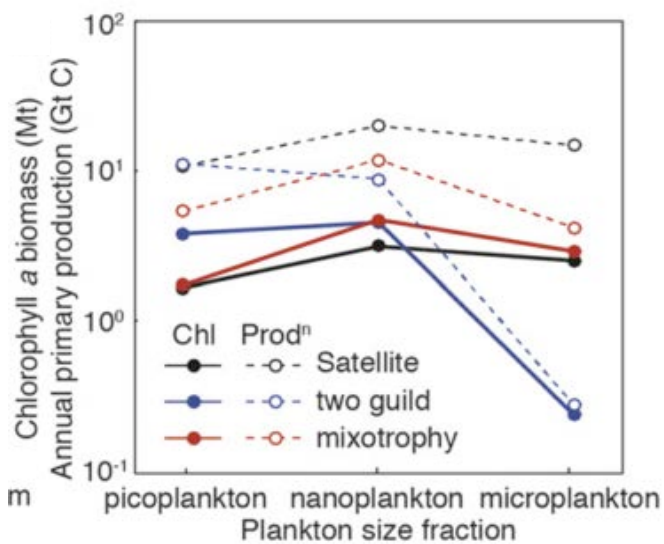


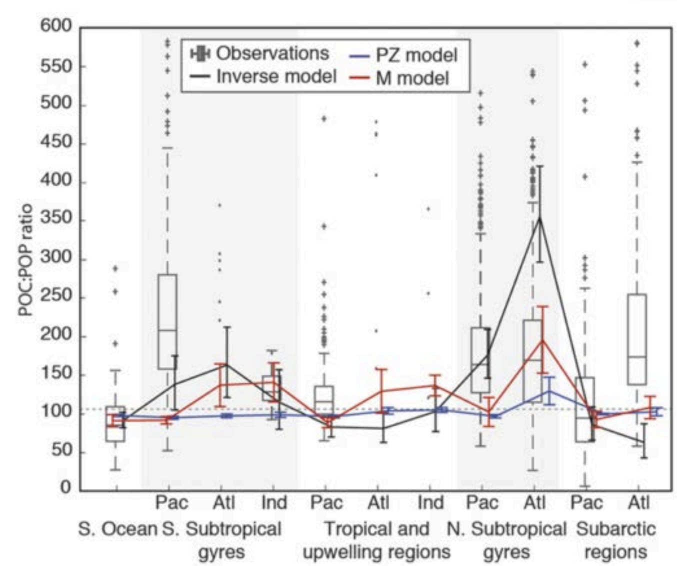
https://www.scientificamerican.com/article/tiny-creatures-part-plant-and-part-animal-may-control-the-fate-of-the-planet/
https://www.researchgate.net/publication/268514289_Chap14_Stoecker_et_al

Mixotrophy influences production and elemental fluxes



Biomass shift to large size classes and better prediction of production and C:P in particles
(Ward and Follows 2016)



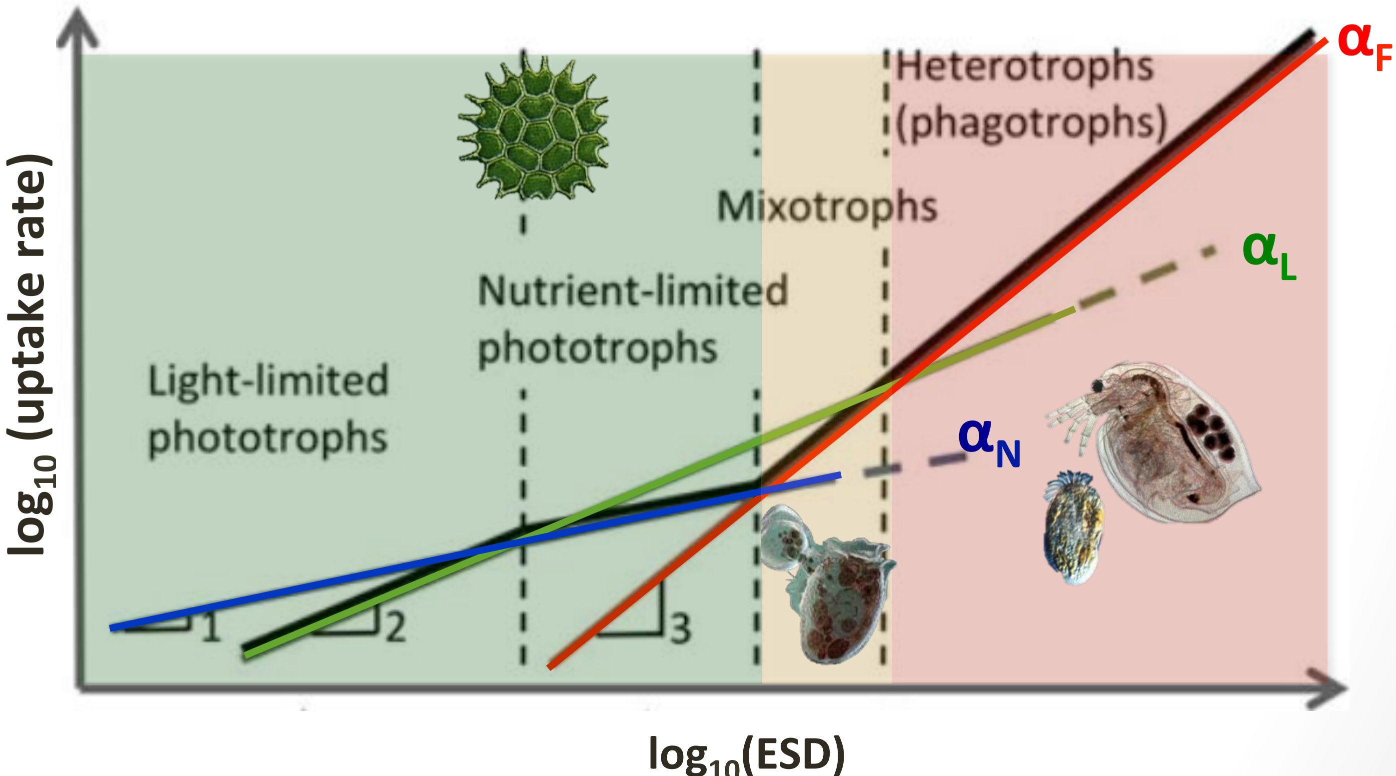


What are the trophic strategies of these little creatures?

Introduction

Trophic strategies emerge along body size

- Body size-dependent resource affinity and resource availability matter

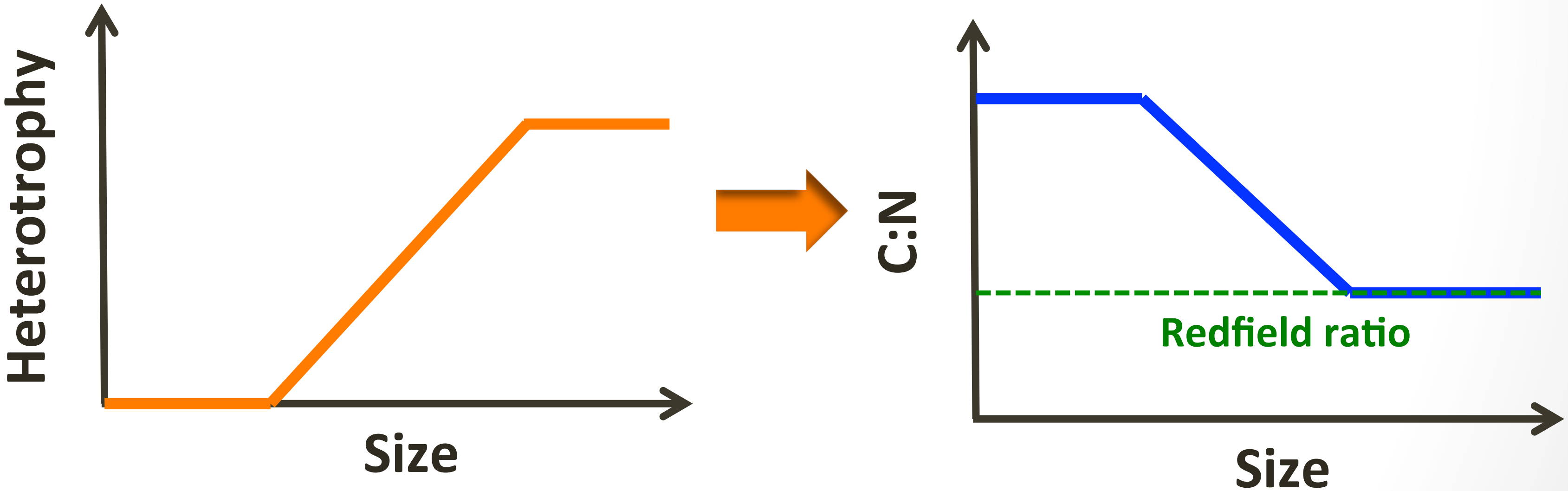


Andersen et al. (2014)

Hypotheses

Stoichiometry with respect to size

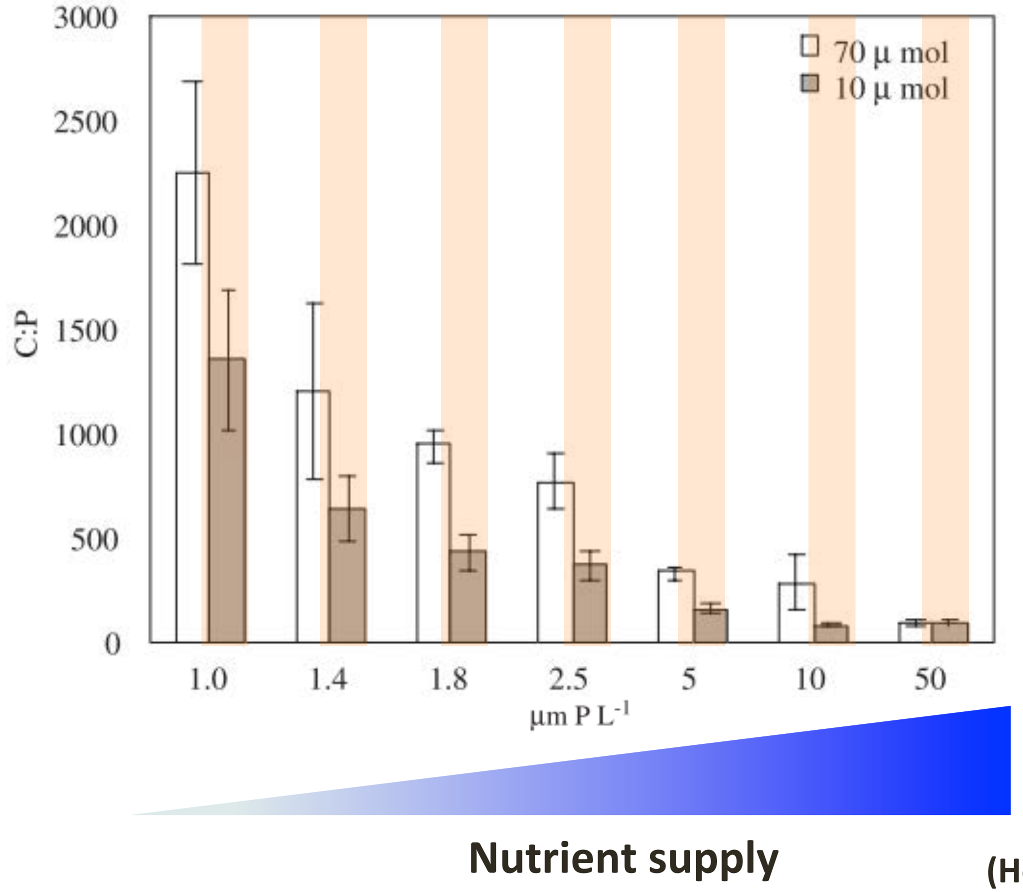
- H1: C:N or C:P decreases as heterotrophy increases with body size



Introduction

Light and nutrient influences plankton stoichiometry

- Autotroph C : nutrient ratio increases with light : nutrient ratio



(Hessen et al. 2008)

Light and nutrient influences plankton stoichiometry

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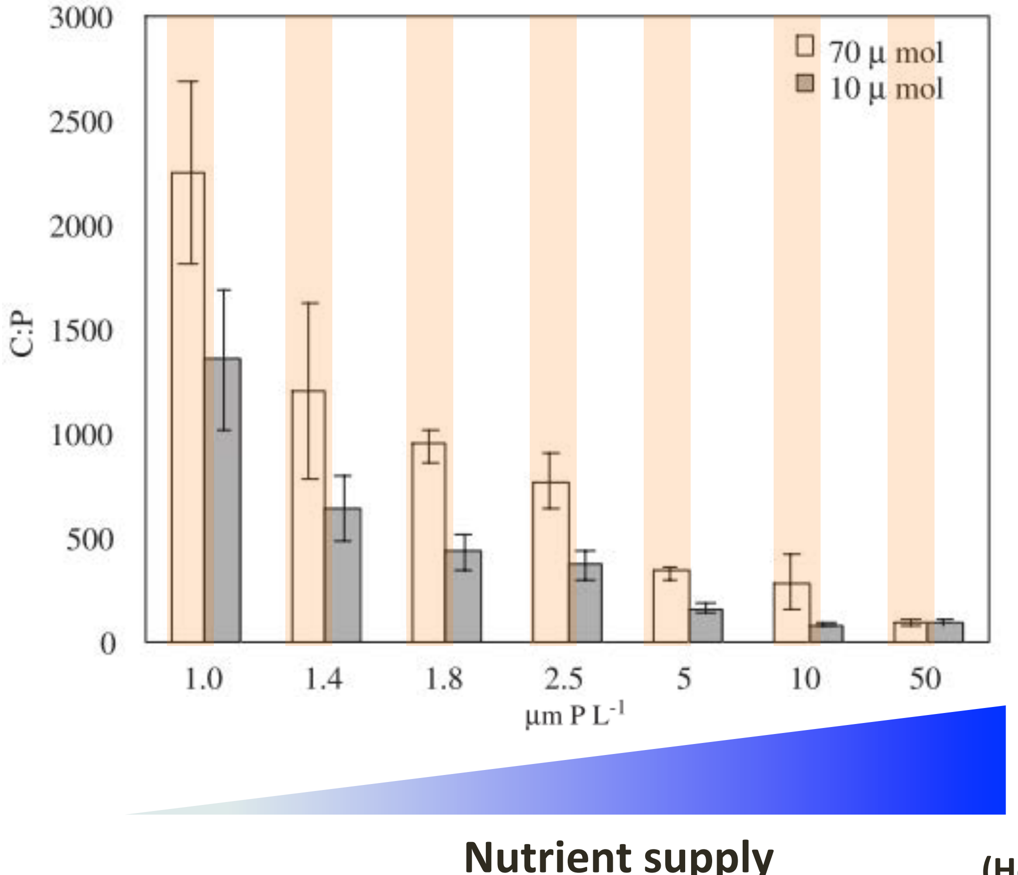
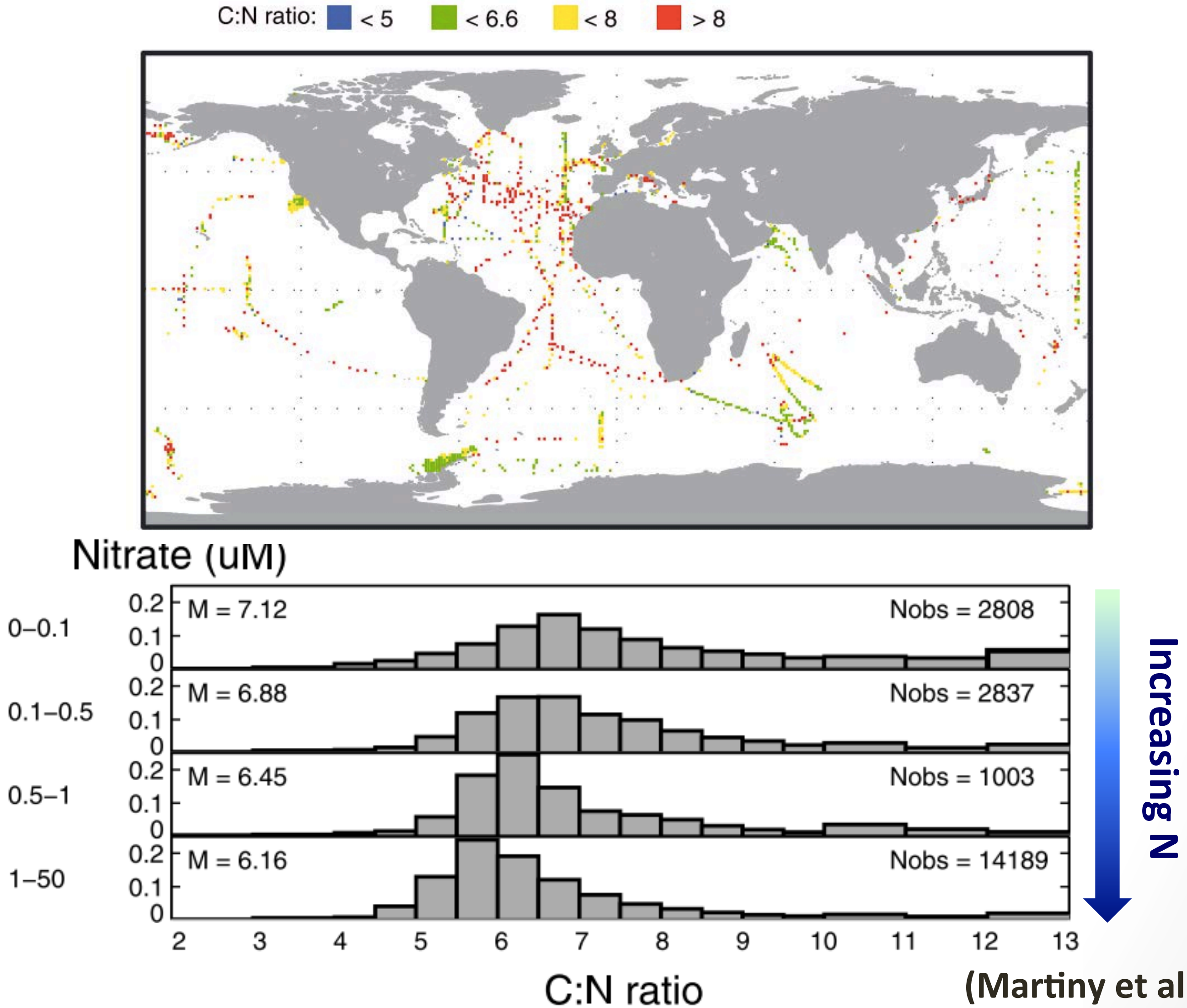


(Hessen et al. 2008)

Global plankton stoichiometry linked with nutrient limitation

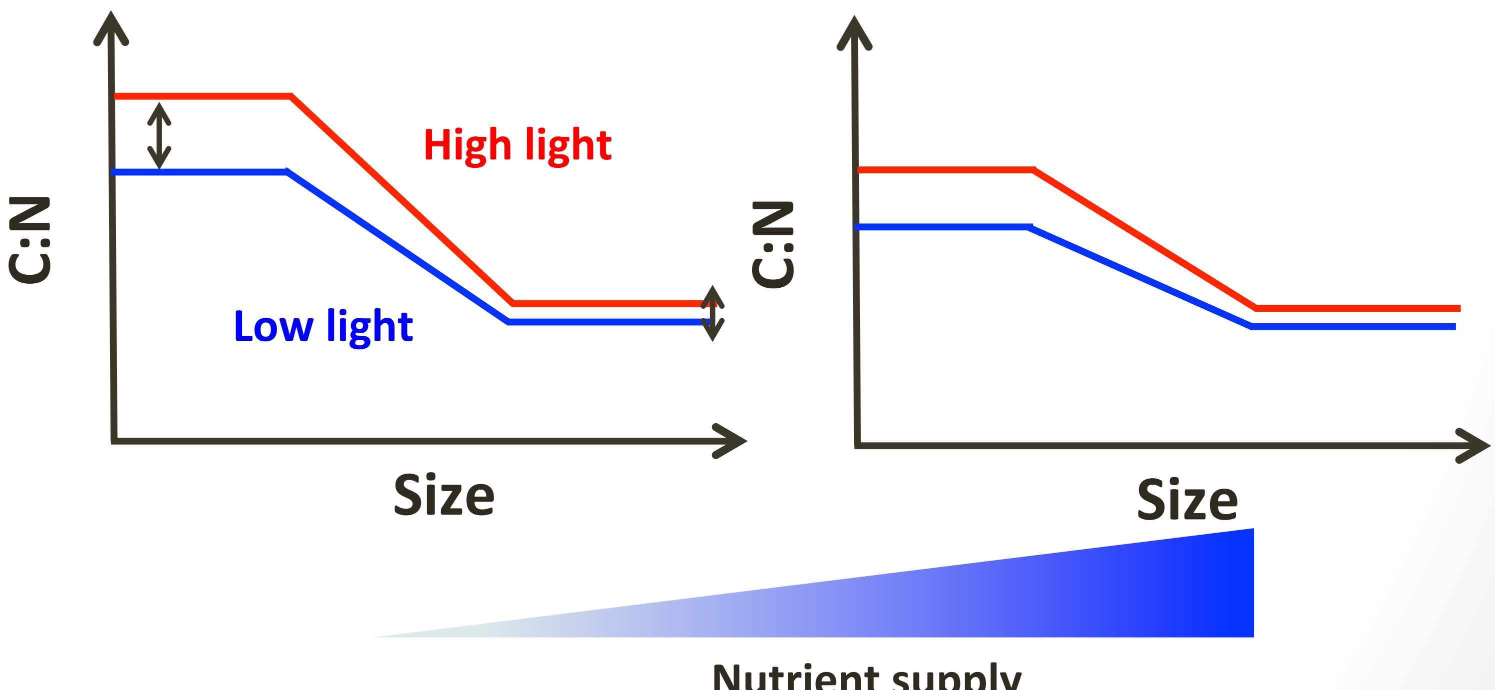


(Martiny et al. 2013)

Hypotheses

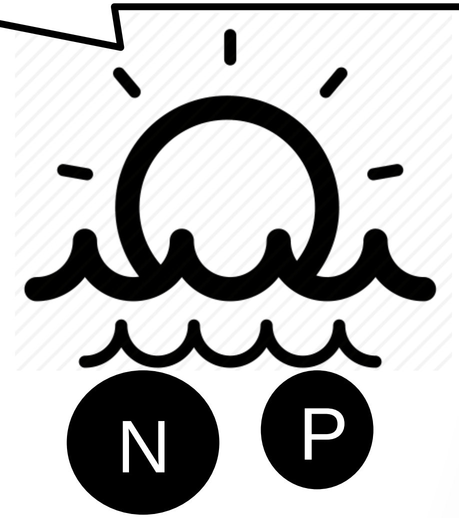
Light : nutrient alters stoichiometry

- H2: C:N or C:P increases with light intensity and decreases with inorganic N nutrient supply
- H3: C:N or C:P changes less with light: nutrient supply in large body size classes



How plankton body size determines stoichiometry?

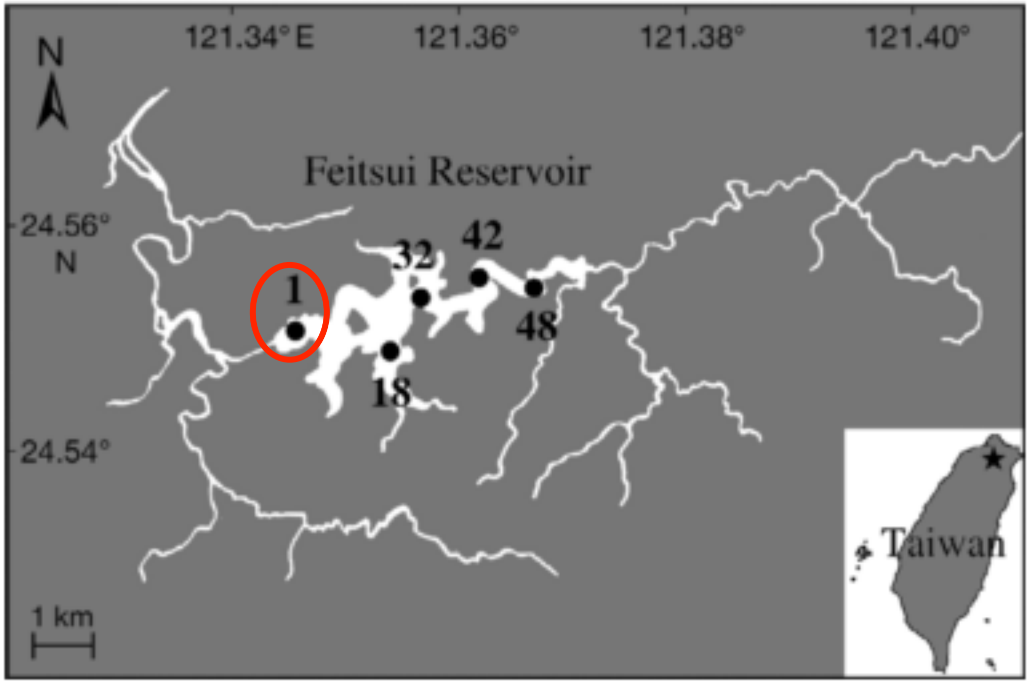
How light and nutrient fluxes influence plankton stoichiometry?



Field observations

Size-fractionated plankton C:N ratios

- Freshwater plankton: Feitsui Reservoir, Taiwan
  Biweekly sampling 2007-2013
  - <10, 10-44, 44-74, 74-177, 177-500, >500 µm

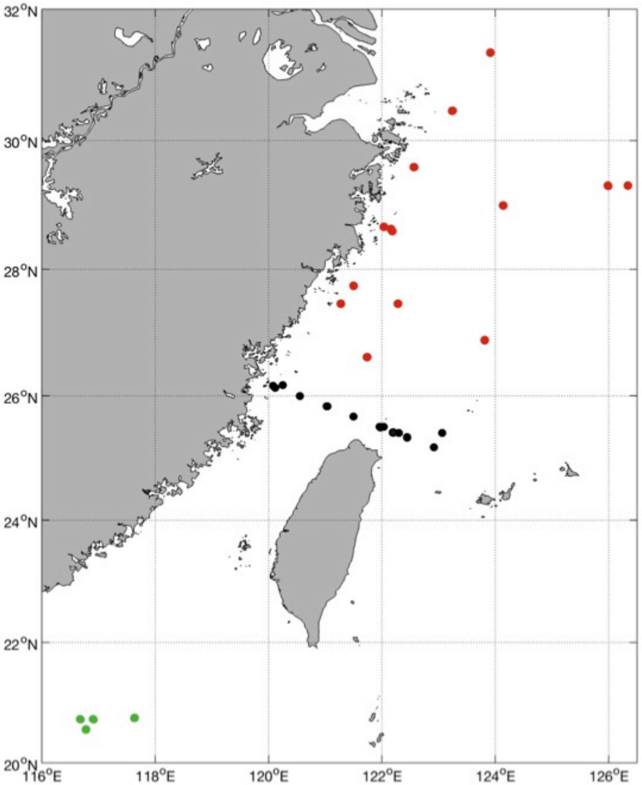


(Tseng et al. 2010)

Size-fractionated plankton C:N ratios

- Marine plankton: East China Sea and South China Sea 2008-2016
  - <50, 50-104, 104-200, 200-363, 363-500, 500-1000, 1000-2000, >2000 μm

Use elemental analyzer (EA) to measure bulk C and N content in plankton size classes

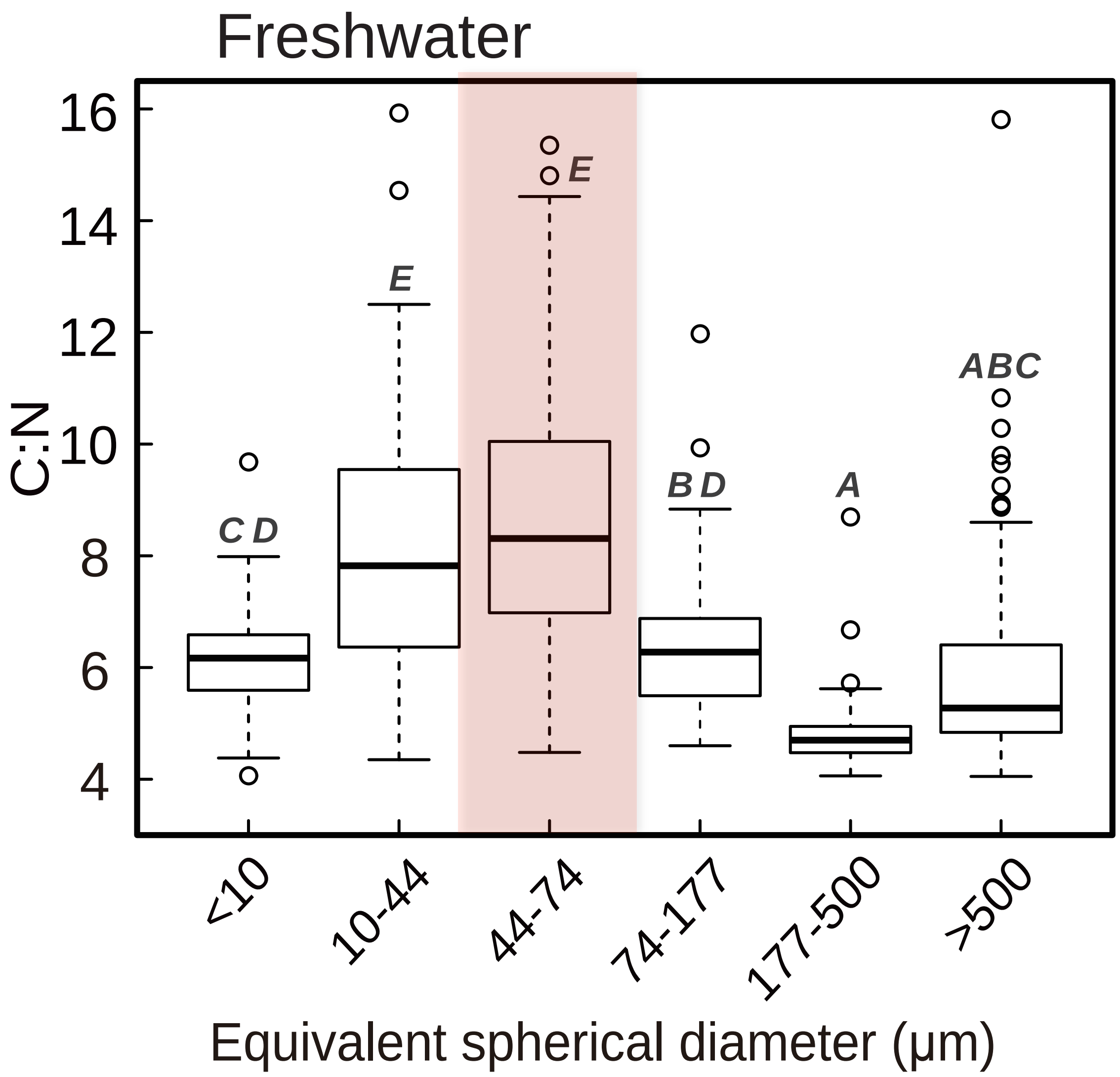


Freshwater light and nutrient conditions

- Surface light intensity (photosynthetically active radiation PAR; μE s^{-1} m^{-2}) was recorded by the PAR sensor on CTD
- Nitrite and nitrate concentrations ([NO_2^- +NO_3^-]; μM) were measured by spectrophotometry **(Parsons et al. 1984)**

Results: Field plankton stoichiometry versus size

C:N ratio is a unimodal function of body size



Results: Field plankton stoichiometry versus size

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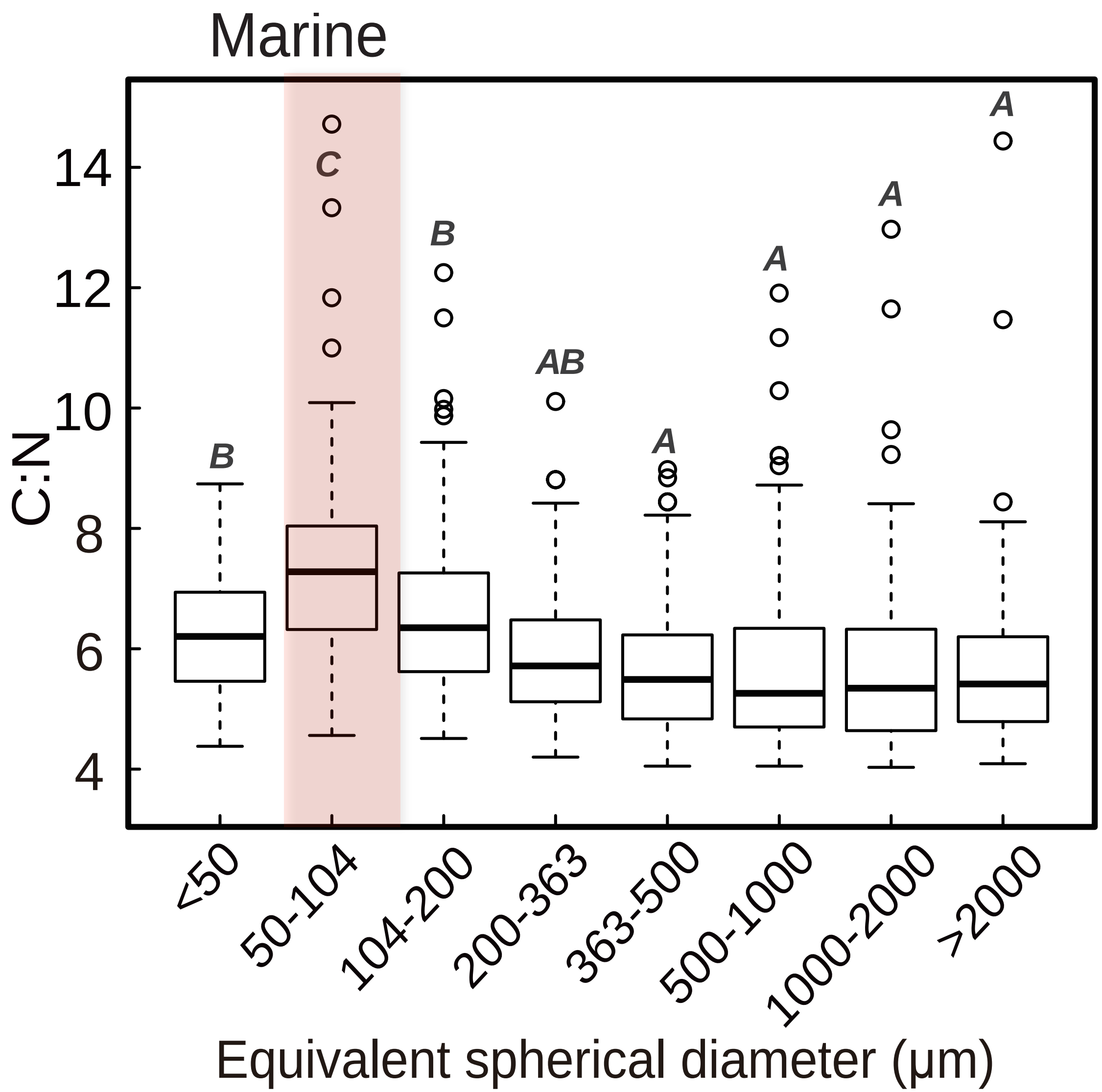
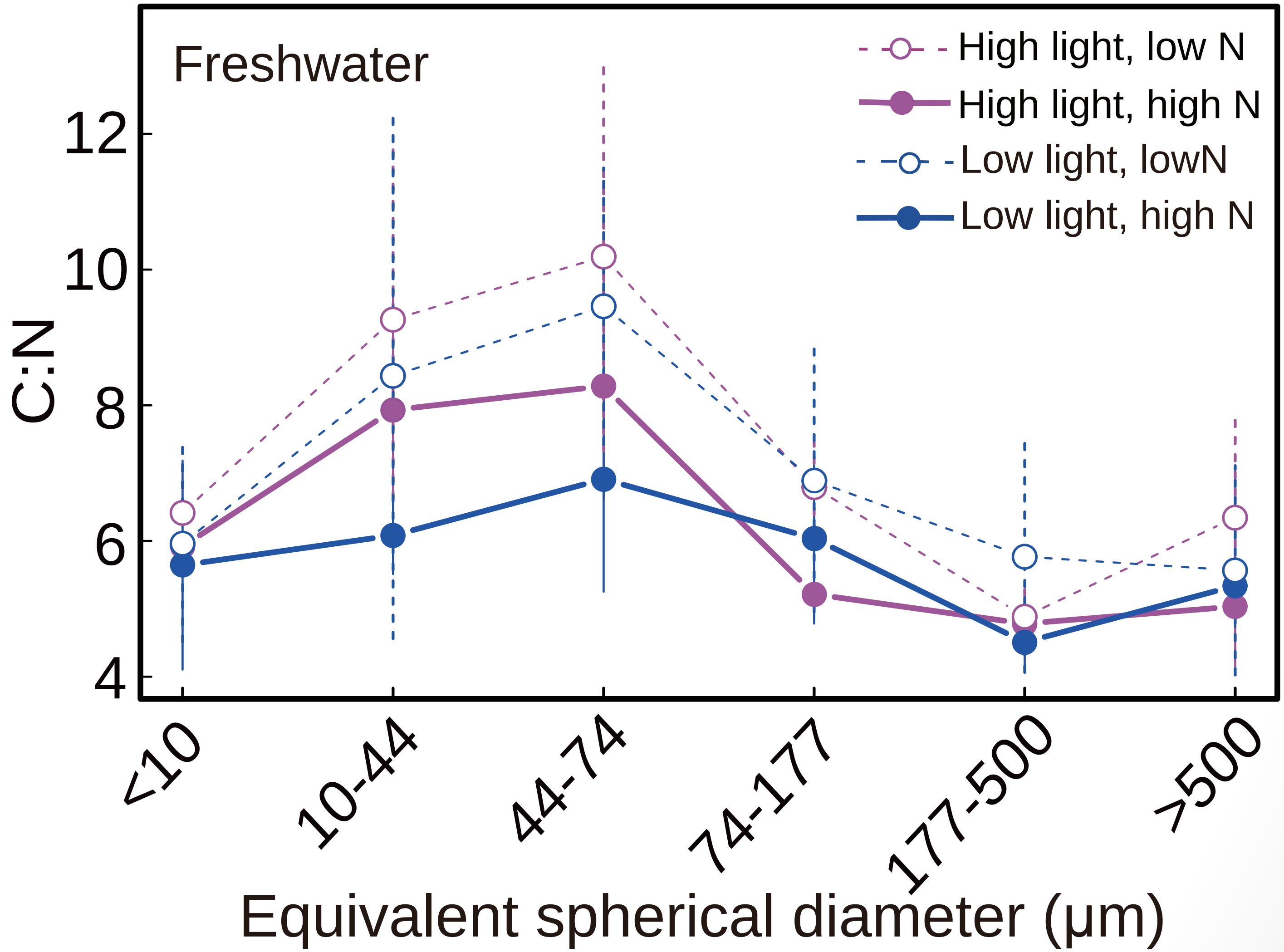


Results: Field plankton stoichiometry change

C:N increases with light and decrease with inorganic N supply



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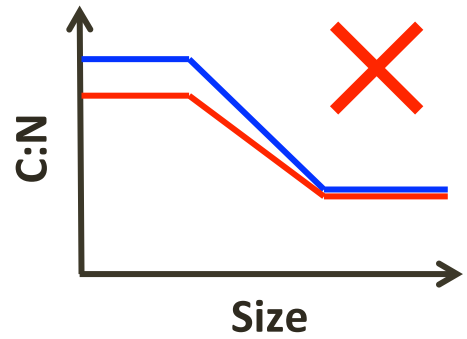
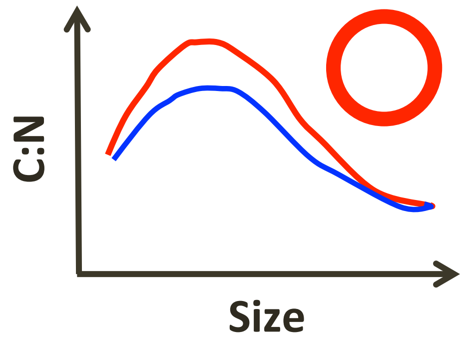
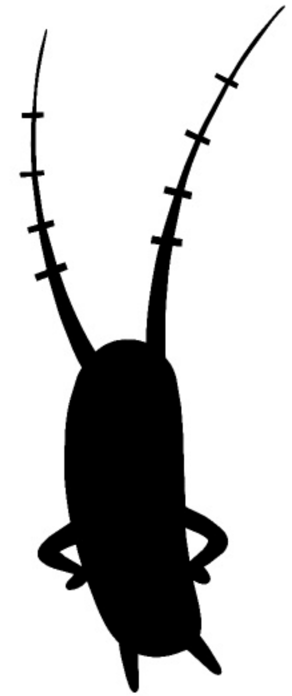
What mechanisms shape this unimodal C:N pattern?

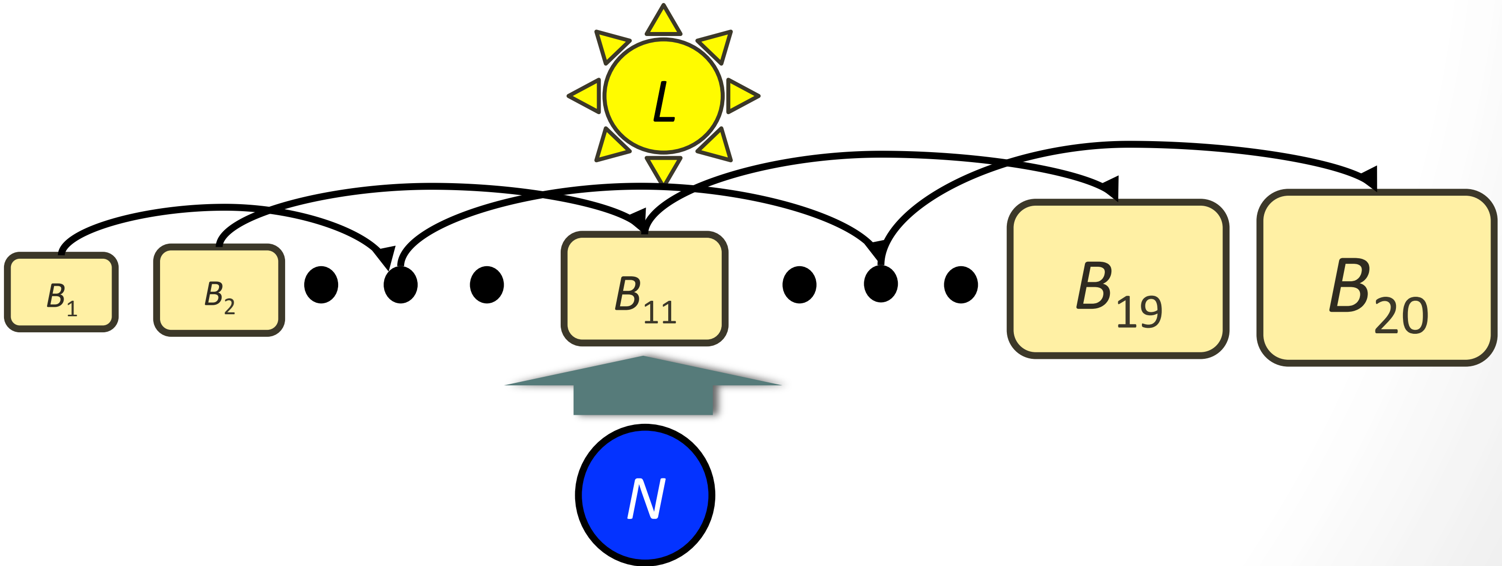






Mixotrophic food web controlled by light and nutrient supply

- Focus on the dynamics of mixotrophic plankton in the euphotic zone
  - The trophic strategy is determined by the affinity to inorganic N, light, and prey
  - C:N ratio is influenced by C and N influxes through inorganic N uptake, photosynthesis, and feeding



Model structure

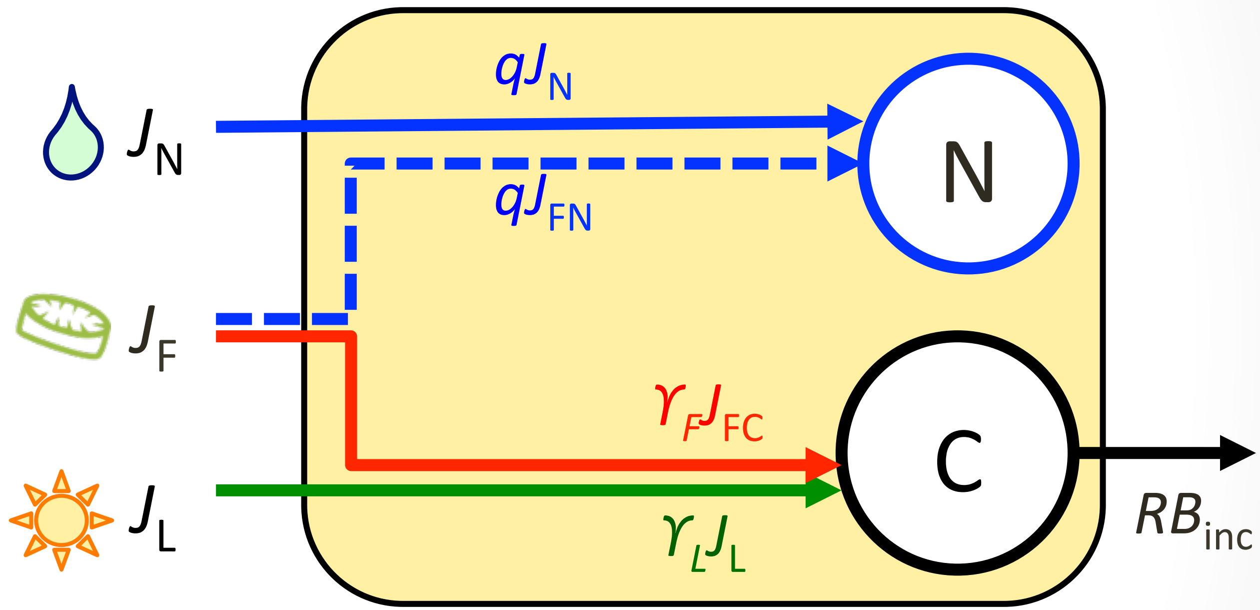
C & N flux of individual organism

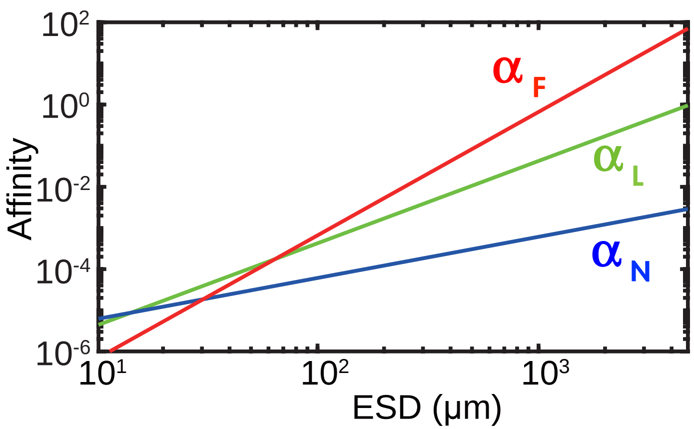
$$J_X = \frac{g_{\max,X}\alpha_X X}{\alpha_X X + g_{\max,X}}$$

$$Q_i = \frac{B_{\mathrm{N},i}}{B_{\mathrm{C},i}}$$

$$q_i = \left(\frac{Q_{\max} - Q_i}{Q_{\max} - Q_{\min}}\right)^h$$

$$\gamma_{X,i} = \left(\frac{Q_i - Q_{\min}}{Q_{\max} - Q_{\min}}\right)^h$$





h = 0.1 for N uptake and prey C assimilation

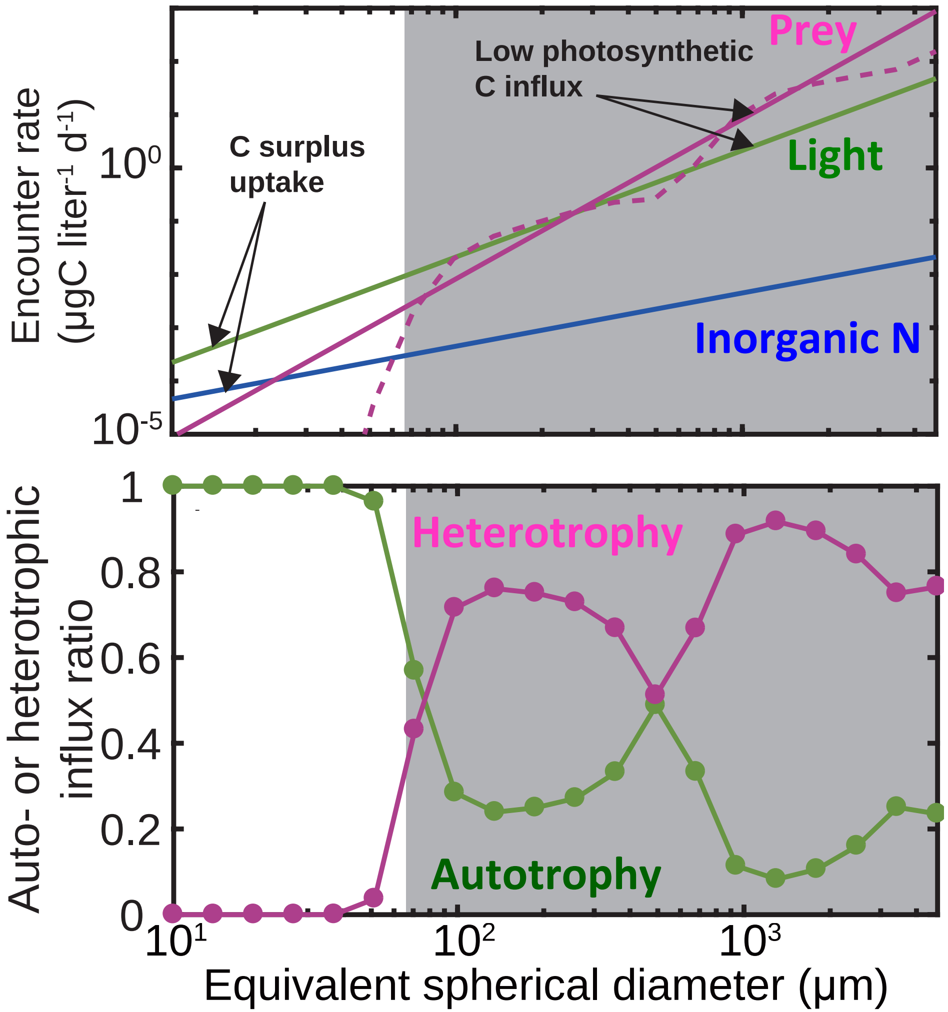
h = 1 for photosynthesis

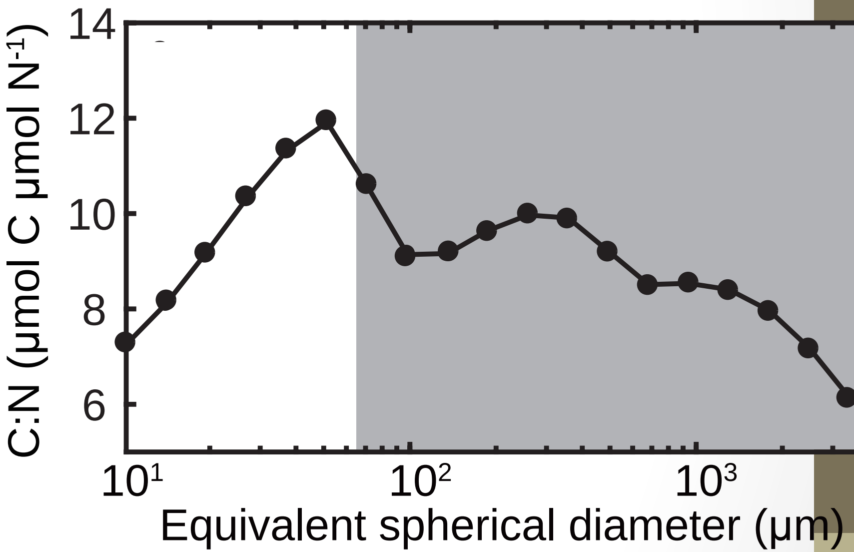
Modified from Ward and Follows (2016) and Chakraborty et al. (2017)

Results: model stoichiometry versus size

C:N ratio and trophic strategy change with size

- L = 228.5 µE s^{-1} m^{-2}, N_0 = 12.86 µM

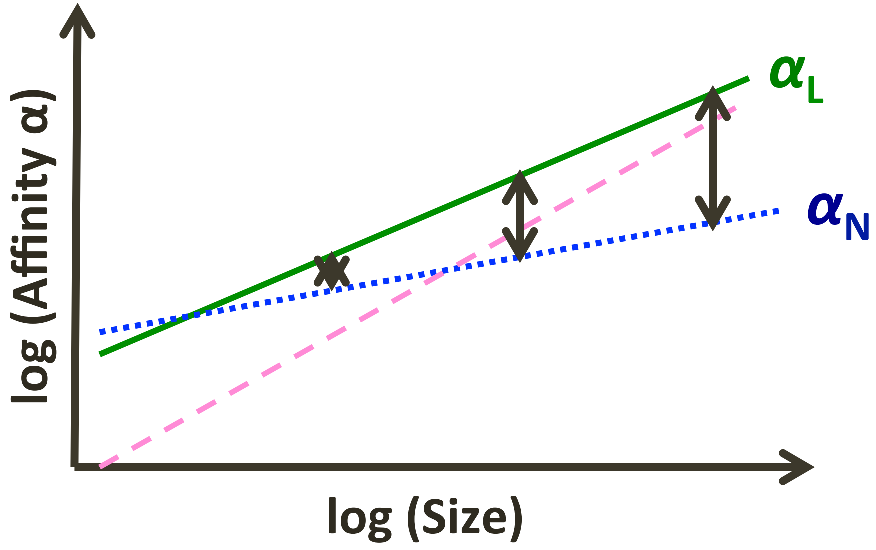




Summary

Body size determines trophic strategy & stoichiometry

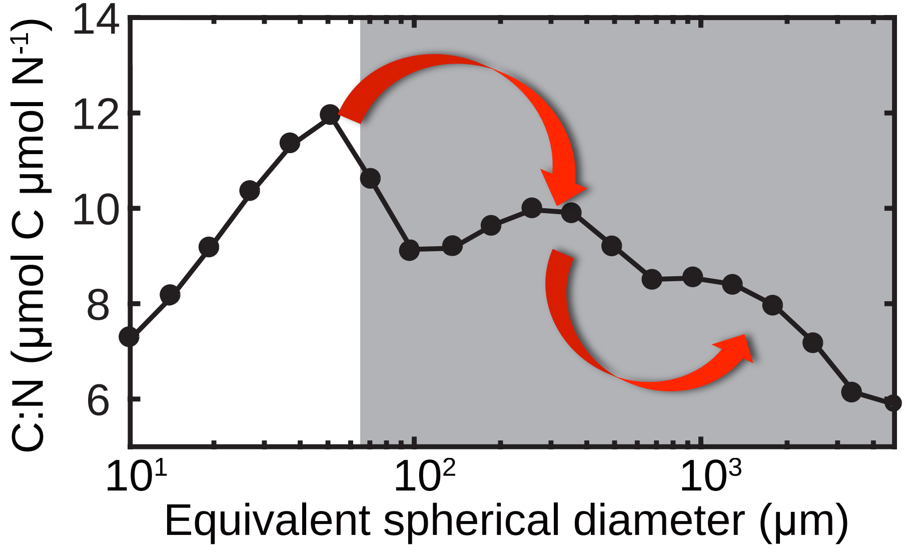
- C:N ratio reaches maximum at 51 µm size class
  - Maximal size of obligate autotrophs
  - Light harvest (photosynthetic C production) increases with size faster than N uptake rate



Summary

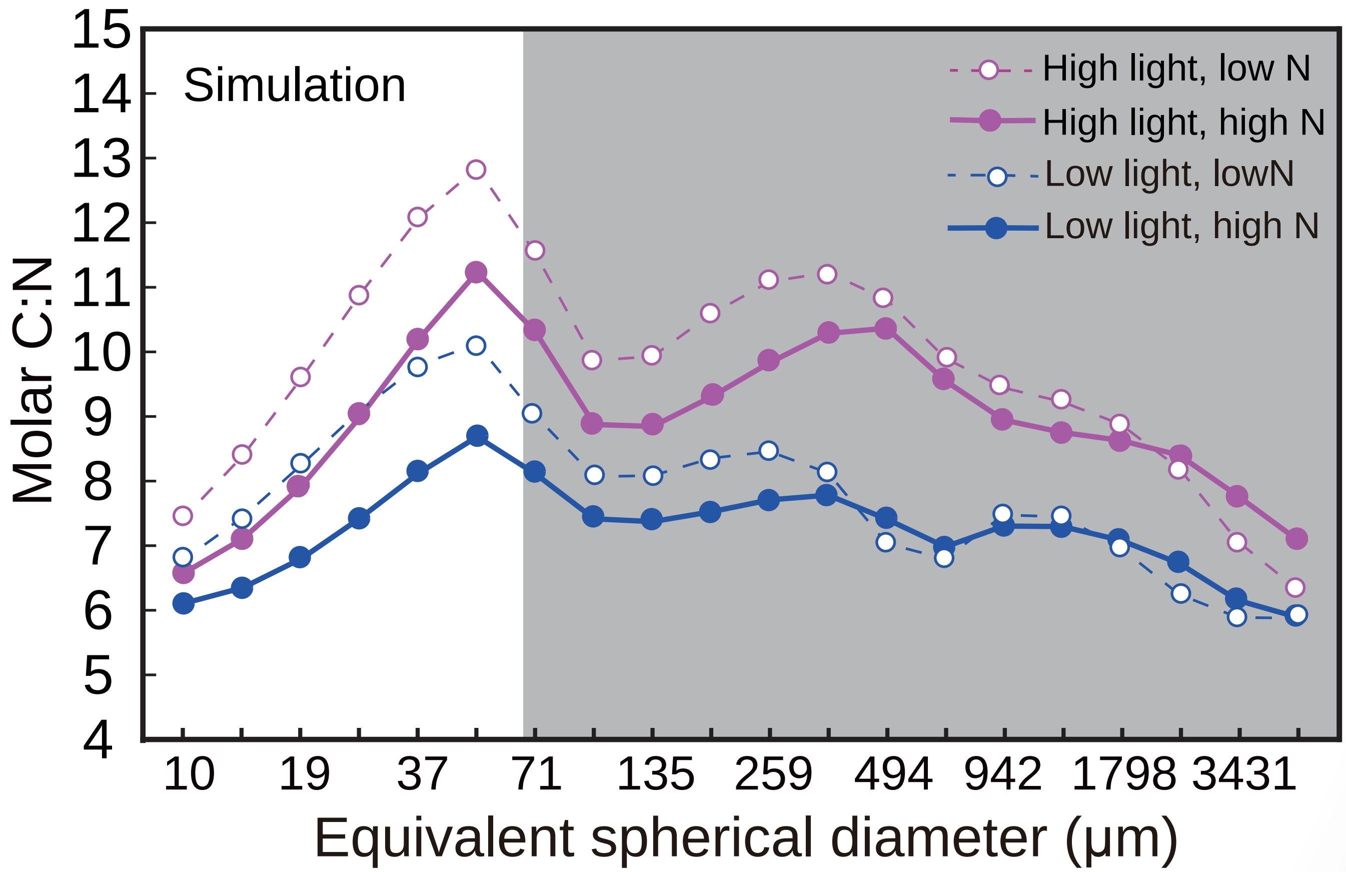
Body size determines trophic strategy & stoichiometry

- Mixotrophs have lower C:N ratios and C:N ratio decreases with size
  - Respiration lowers C:N ratio
  - Large mixotrophs that consumes small mixotrophs have lower C:N ratio



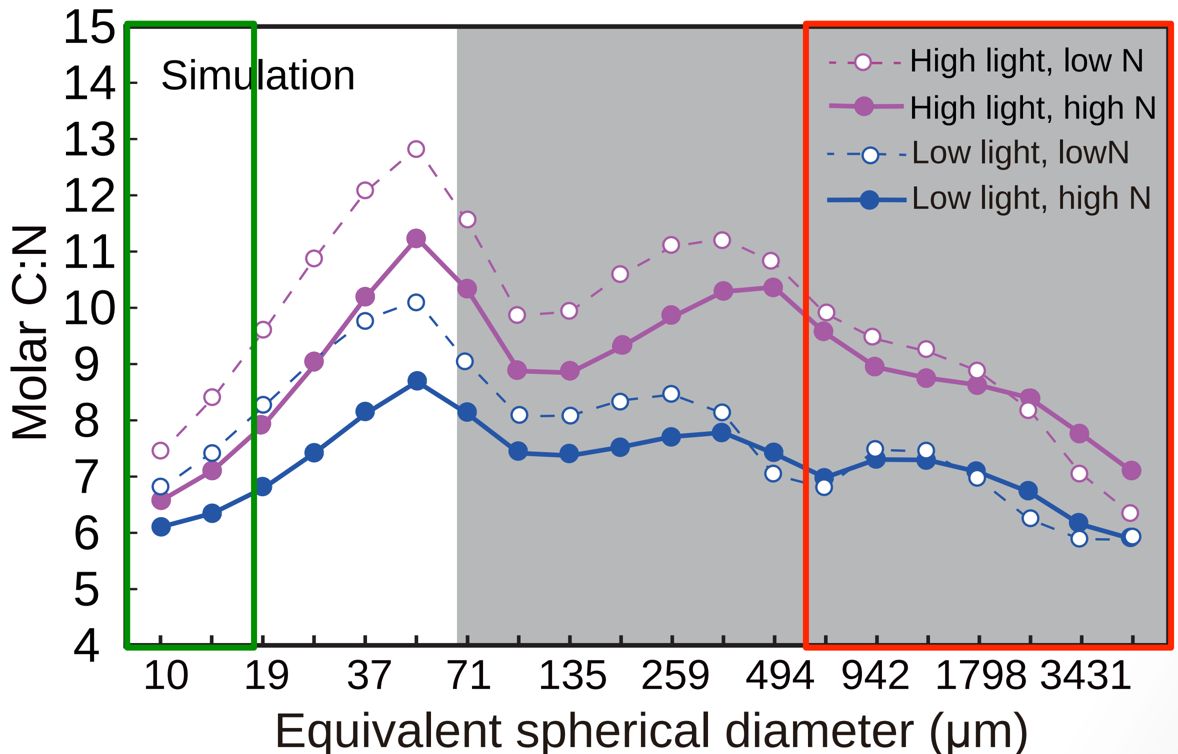
Results: environmental influences on model stoichiometry

Model C:N ratio variability under high/low inorganic N supply



Stoichiometric variability to light and nutrient changes with body size

- Plankton C:N ratios increase with light and decrease with nutrient supply
- C:N ratios of the smallest autotrophs and large organisms vary relatively little with environment



Body size is one key trait that determines plankton stoichiometry

- Autotrophs have increasing C:N ratio with size
  - Increasing light affinity relative to nutrient affinity with size
  - Small autotrophs have lower and more stable C:N ratio

- C:N ratio gradually decreases and varies less in large size mixotrophs
  - Affinity to prey and respiration determine the C:N ratio

Thanks for your attention

All comments are welcomed

Results: stoichiometry and trophic strategy of different sizes

GAM regression of plankton C:N, size, light and nutrient supply

Freshwater							
Model	Intercept	Light (PAR (μE s^{-1} m^{-2}))	Inorganic N ([N (μM)])	*K*	R^2	AIC	ΔAIC
C:N = spline(log(size))	6.69			3	0.385	2226.90	136.58
C:N = spline(log(size)) + *L*	6.66	0.0001		4	0.378	2183.54	93.22
C:N = spline(log(size)) + [N]	7.89		-0.039	4	0.449	2129.87	39.55
C:N = spline(log(size)) + *L* + [N]§	7.88	-7.46×10^{-5}	-0.038	5	0.44	2090.32	0.00
C:N = *L* + [N]	7.87	-1.003×10^{-4}	-0.038	3	0.052	2374.63	284.31
Model simulations							
Model	Intercept	Light (PAR (μE s^{-1} m^{-2}))	Inorganic N ([N (μM)])	*K*	R^2	AIC	ΔAIC
C:N = spline(log(ESD))	8.60			3	0.740	3539.33	2066.08
C:N = spline(log(ESD)) + *L*	7.28	0.0048		4	0.902	1954.91	481.66
C:N = spline(log(ESD)) + [N]	9.25		-4.26	4	0.754	3452.53	1979.28
C:N = spline(log(ESD)) + *L* + [N]§	8.11	0.0050	-5.77	5	0.928	1473.25	0.00
C:N = *L* + [N]	8.10	0.0050	-5.74	3	0.186	5380.36	3907.11

Model equations

Mixotroph dynamics: C and N assimilation

$$\frac{dB_{\mathrm{N},i}}{dt} = q_i \frac{B_{\mathrm{N},i}}{M_{\mathrm{N},i}} \left(J_{\mathrm{Nin},i} + J_{\mathrm{FN},i} \right) - \mu_i Q_i - \mathrm{Pred}_{\mathrm{N},i}$$

$$\frac{dB_{C,i}}{dt} = \gamma_{\mathrm{N},i} \frac{B_{\mathrm{N},i}}{M_{\mathrm{N},i}} \left(J_{\mathrm{L},i} + J_{\mathrm{FC},i} \right) - \mu_i - \mathrm{Pred}_{\mathrm{C},i} - R_i B_{\mathrm{C},i}$$

$$J_{\mathrm{Nin},i} = \frac{g_{\mathrm{maxN},i} \alpha_{\mathrm{N},i} N}{\alpha_{\mathrm{N},i} N + g_{\mathrm{maxN},i}}, \quad J_{\mathrm{L},i} = \frac{g_{\mathrm{maxL},i} \alpha_{\mathrm{L},i} L}{\alpha_{\mathrm{L},i} L + g_{\mathrm{maxL},i}}$$

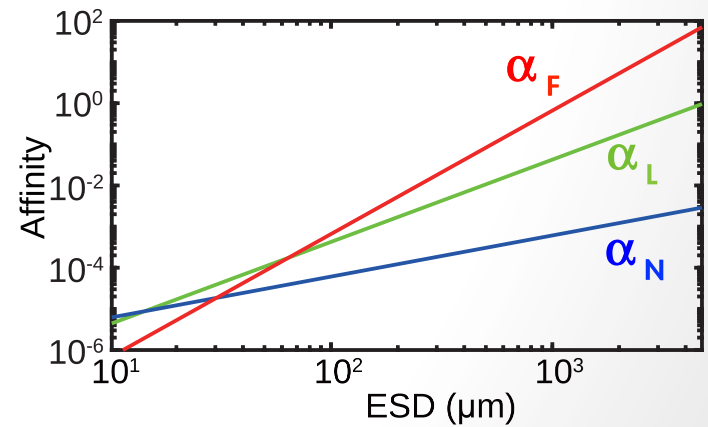
$$J_{\mathrm{FC},i} = \frac{g_{\mathrm{maxF},i} \alpha_{\mathrm{F},i} \sum_m \mathrm{P}_{m,i}}{\alpha_{\mathrm{F},i} \sum_m \mathrm{P}_{m,i} + g_{\mathrm{maxF},i}}, \quad J_{\mathrm{FN},i} = \frac{g_{\mathrm{maxF},i} \alpha_{\mathrm{F},i} \sum_m \mathrm{P}_{m,i} Q_m}{\alpha_{\mathrm{F},i} \sum_m \mathrm{P}_{m,i} + g_{\mathrm{maxF},i}}$$

$$g_{\max X,i} = m_X \Phi_X M_i$$

$$\alpha_{X,i} = c_X M_i^{\theta_X}$$

$$\varphi(M_m, M_i) = \exp\left[-\left(\ln\left(\frac{M_i / (\beta M_m)}{2\sigma^2} \right) \right)^2 \right]$$

$$\mathrm{P}_{m,\mathrm{i}} = B_{\mathrm{C},m} \varphi(M_m, M_i)$$



Mixotroph dynamics: biomass loss

$$\frac{dB_{\mathrm{N},i}}{dt} = q_i \frac{B_{\mathrm{N},i}}{M_{\mathrm{N},i}}(J_{\mathrm{Nin},i} + J_{\mathrm{FN},i}) - \mu_i Q_i - \mathrm{Pred}_{\mathrm{N},i}$$

$$\frac{dB_{\mathrm{C},i}}{dt} = \gamma_{\mathrm{N},i} \frac{B_{\mathrm{N},i}}{M_{\mathrm{N},i}}(J_{\mathrm{Photo},i} + J_{\mathrm{FC},i}) - \mu_i - \mathrm{Pred}_{\mathrm{C},i} - R_i B_{\mathrm{C},i}$$

$$\mathrm{Pred}_{\mathrm{FC},i} = \sum_j \frac{B_{\mathrm{C},j} g_j \alpha_{\mathrm{F},j} \mathrm{P}_{i,j}}{\alpha_{\mathrm{F},j} \sum_m \mathrm{P}_{m,j} + g_{\mathrm{maxF},j}}, \ \mathrm{Pred}_{\mathrm{FN},i} = \mathrm{Pred}_{\mathrm{FC},i} Q_i$$

$$\mu_i = 0.01 \cdot B_{\mathrm{C},i}^2, \ R_i = 0.03\ \mathrm{d}^{-1}$$

Model equations

Inorganic nutrient dynamics

$$\frac{dN}{dt} = \kappa (N_0 - N) - \sum_{i=1}^{20} \frac{B_{\mathrm{N},i}}{M_{\mathrm{N},i}} J_{\mathrm{Nin},i} + \varepsilon \sum_{i=1}^{20} \mu_i Q_i$$

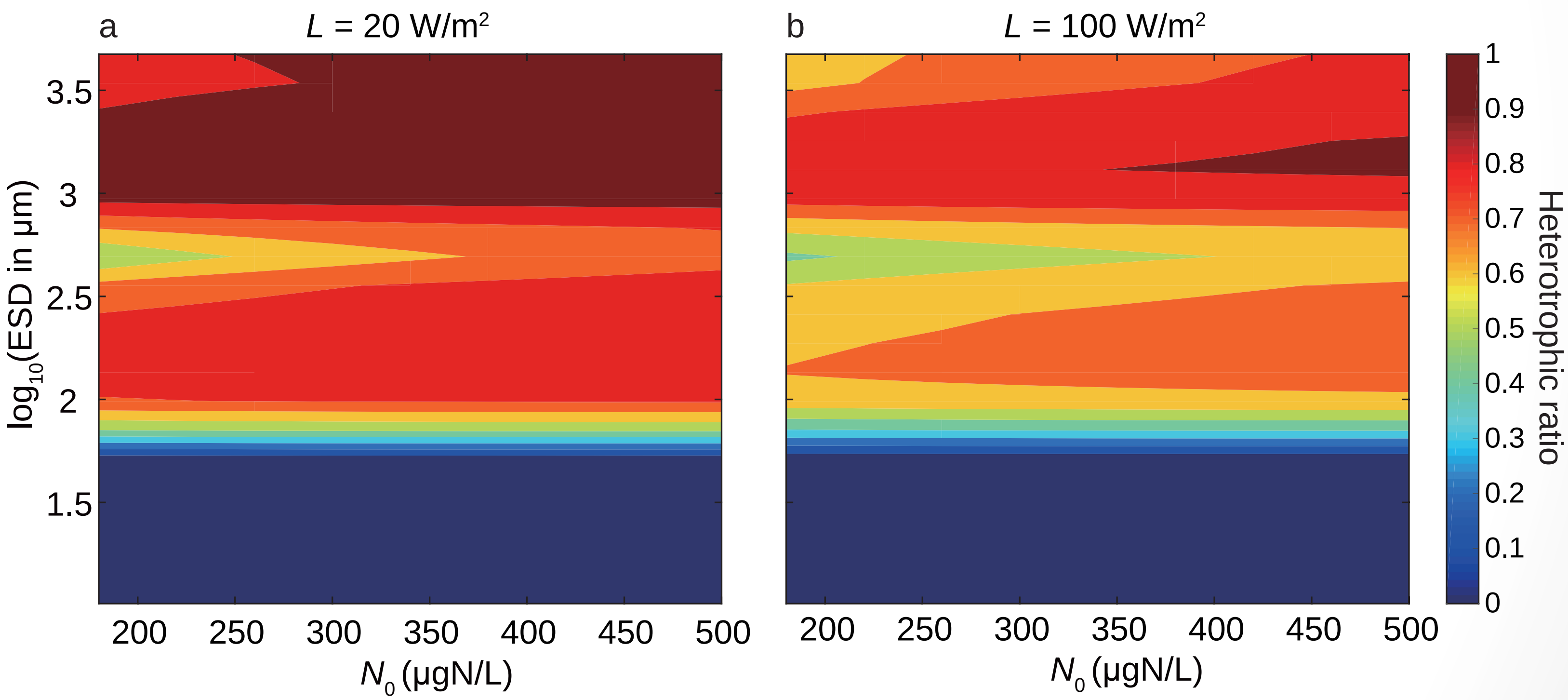
New N flux from deep water

N uptake by plankton

Recycled N from dead plankton

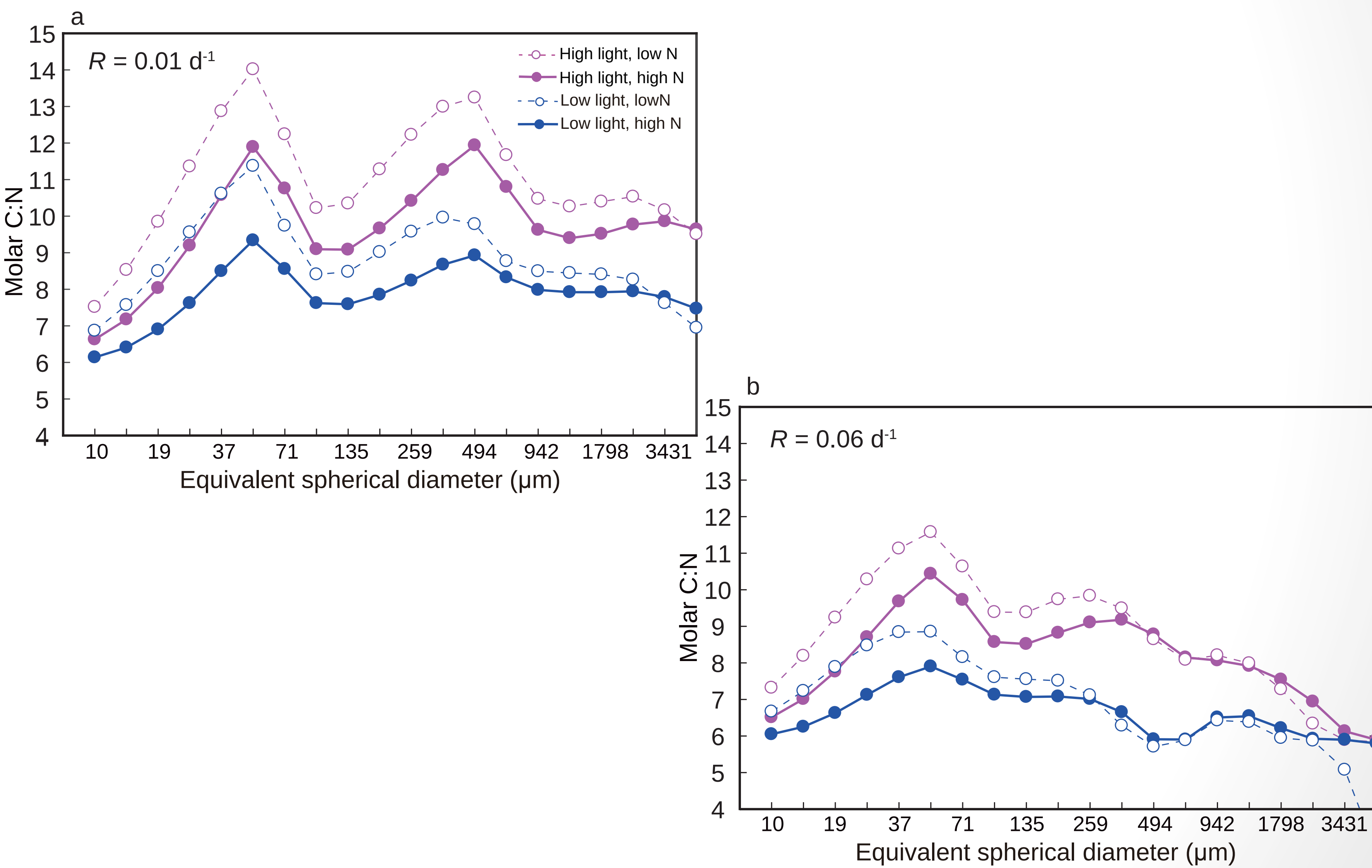
Results: stoichiometry and trophic strategy of different sizes

Fraction of heterotrophy under different light: inorganic N supply



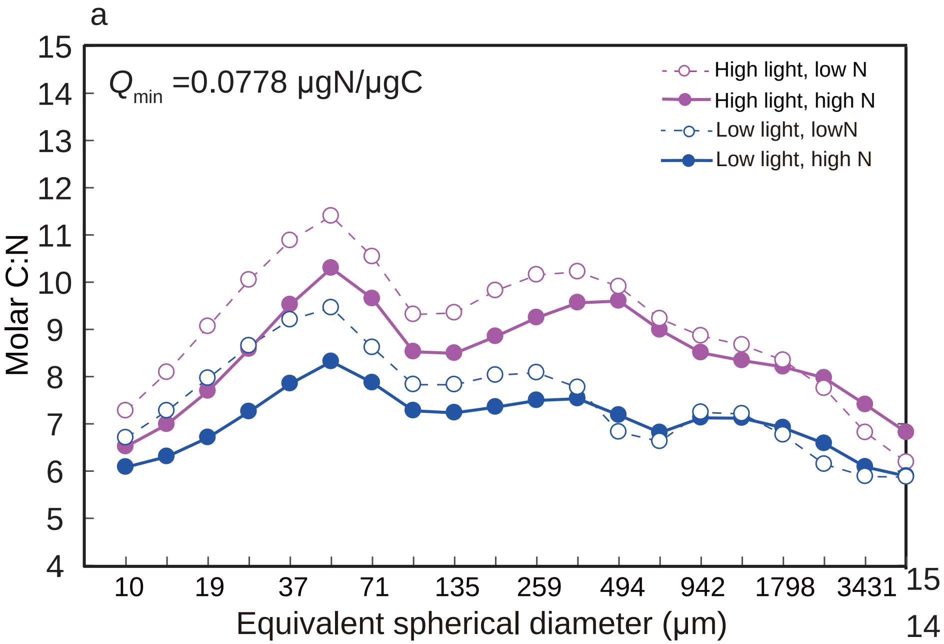
Results: sensitivity tests

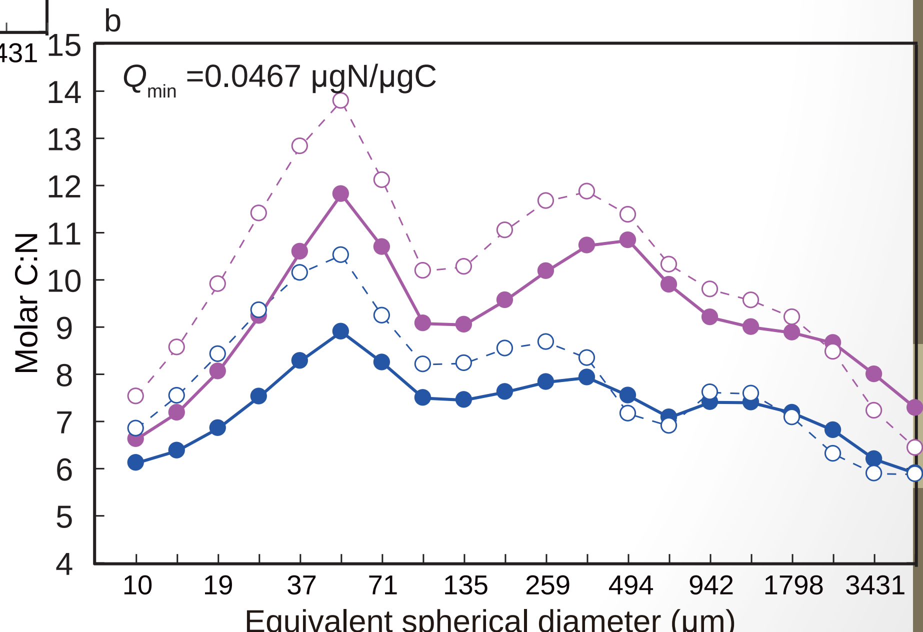
Respiration lowers C:N ratio



Results: sensitivity tests

Higher minimum N quota lowers C:N





Summary

C:N ratio changes with body size in model and natural plankton systems

- C:N ratio reaches maximal value at ~50-100 μm in subtropical freshwater and marine systems, which is similar to the simulated results

- Relatively higher C:N ratio of all sizes in simulated mixotrophic food web
  - Respiration that controls the C loss
  - Q_{min} and Q_{max}

Conclusions

Mixotrophs potentially influence trophic transfer efficiency

- Mixotrophs have lower C:N ratio than large phytoplankton, indicating that they are more stoichiometrically balanced prey to mesozooplankton **(Katechakis et al. 2005)**

- Mixotrophy supports higher biomass and productivity in a plankton food web **(Ward and Follows 2016)**