

Photosynthesis in the oceans: Coping with oligotrophy in an extreme light environment

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Challenges to photosynthesis in the open ocean

Rapidly fluctuating light environment

Oligotrophic (low nutrient) environment

Low Fe availability

Very low macronutrient levels

Picocyanobacteria are adapted to the open ocean

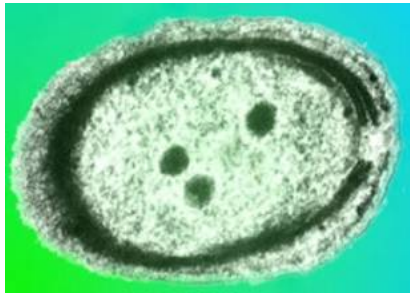
Lower nutrient requirements (Partensky, 1999)

Higher nutrient affinities (Scanlan and Wilson, 1999; Lindell et al., 2002)

Broader substrate base (Moore et al., 2005; Moore et al., 2002)

Diversity in light strategies (Moore and Chisholm, 1999)

Lower Fe requirements (Strzepek, 2004; Partensky, 1999)



Prochlorococcus marinus

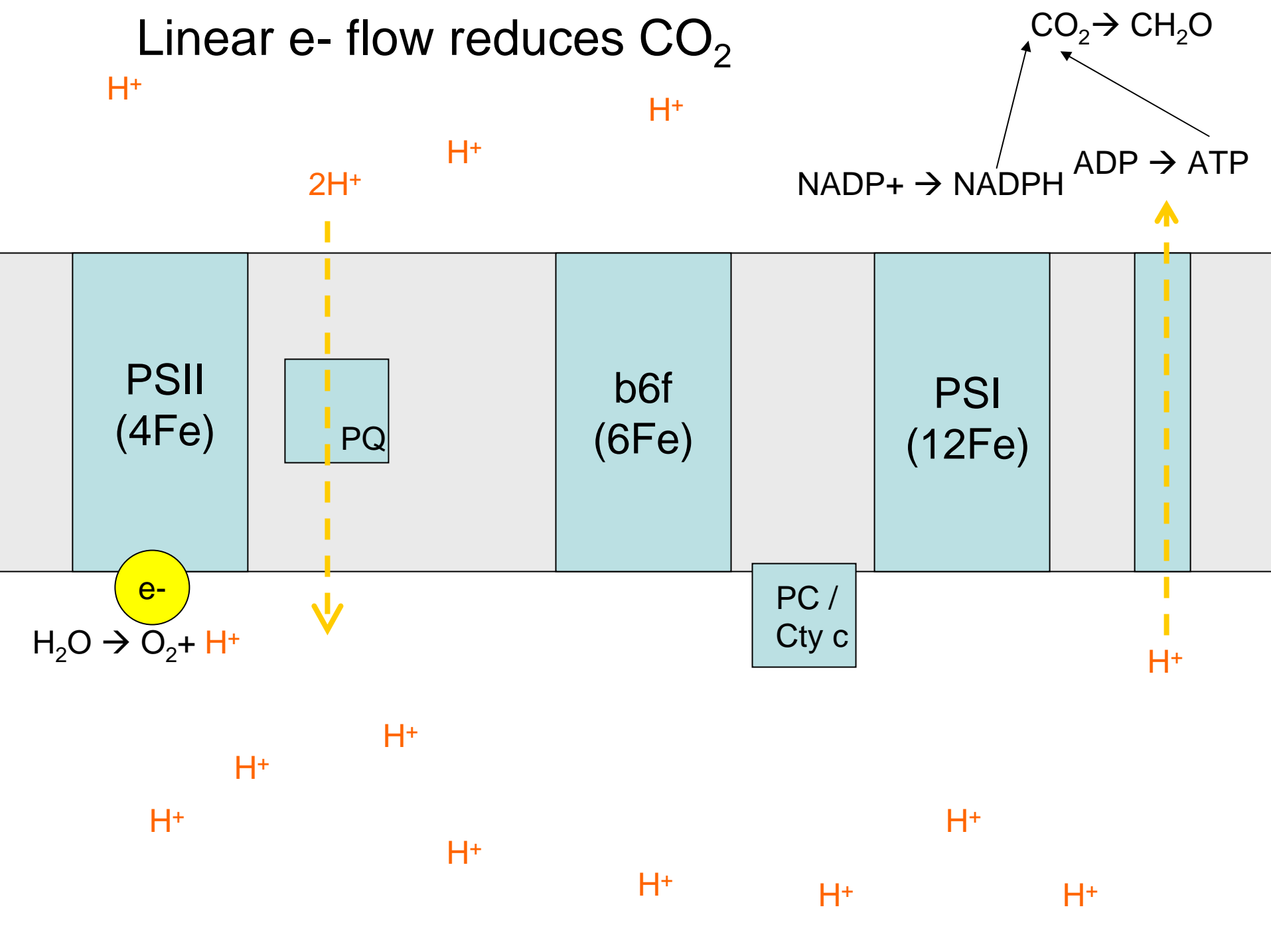
<http://www.lbl.gov/Science-Articles/Archive/assets/images/2003/Aug-14-2003/Prochlorococcus.jpg>



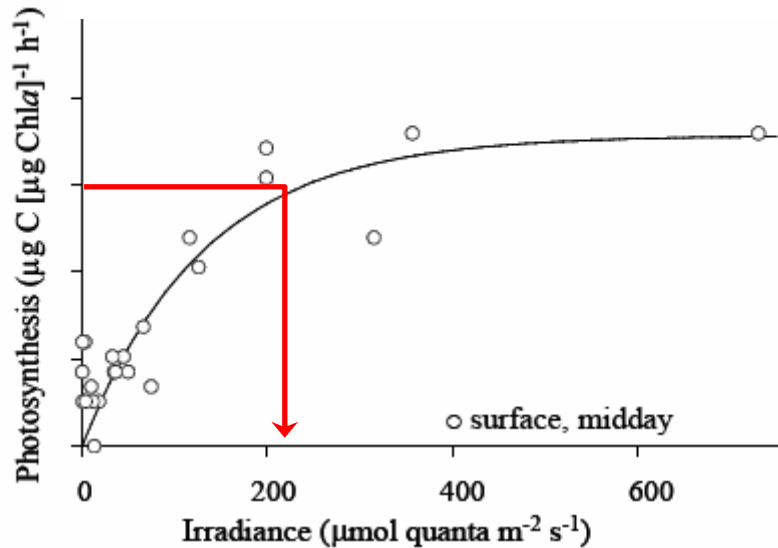
Synechococcus elongatus

<http://www.lbl.gov/today/2003/Aug/18-Mon/Synechococcus.jpg>

Linear e- flow reduces CO₂



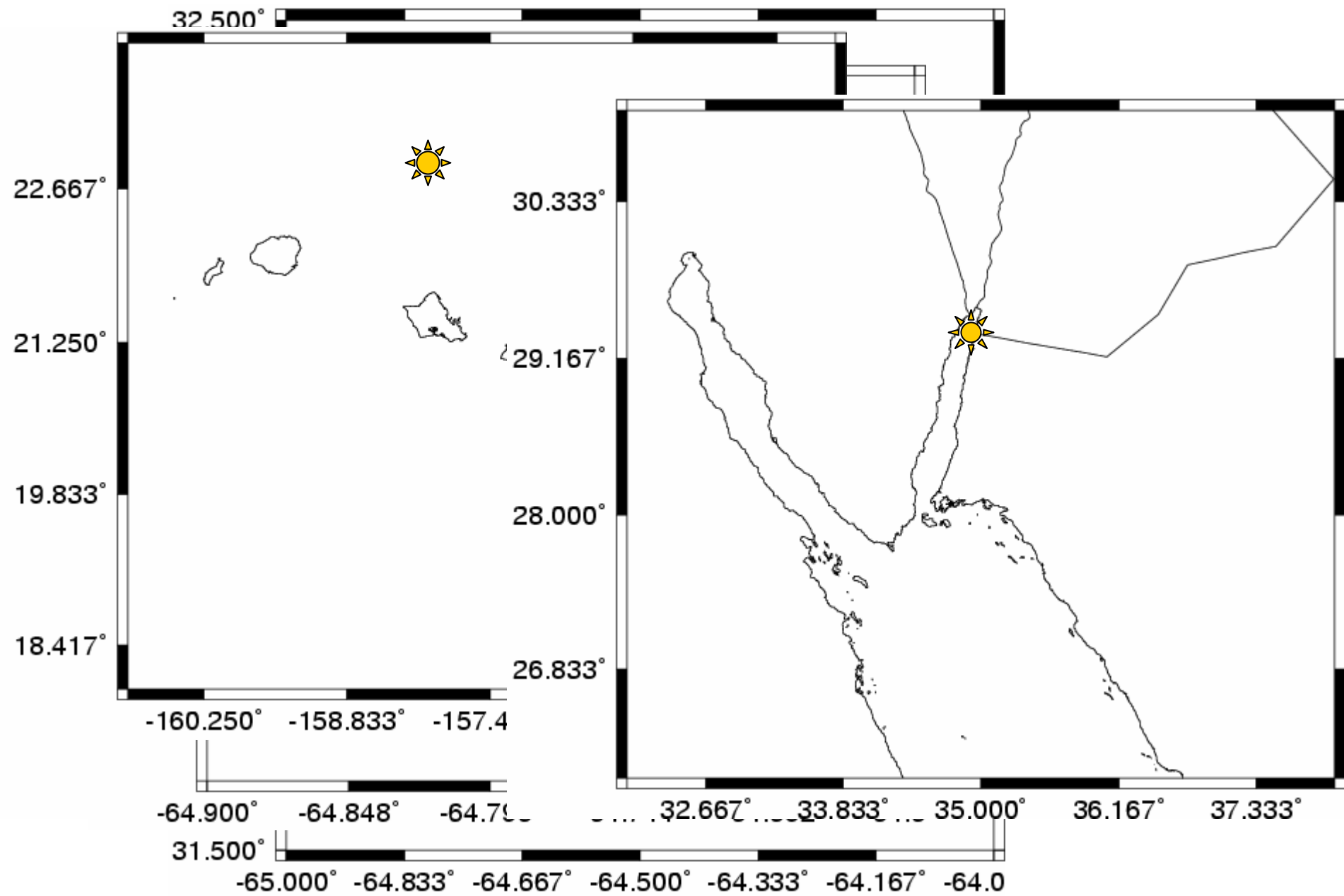
Carbon fixation saturates at relatively low irradiances



PSI (and nutrient availability) limit C fixation and e- flow away from PSII

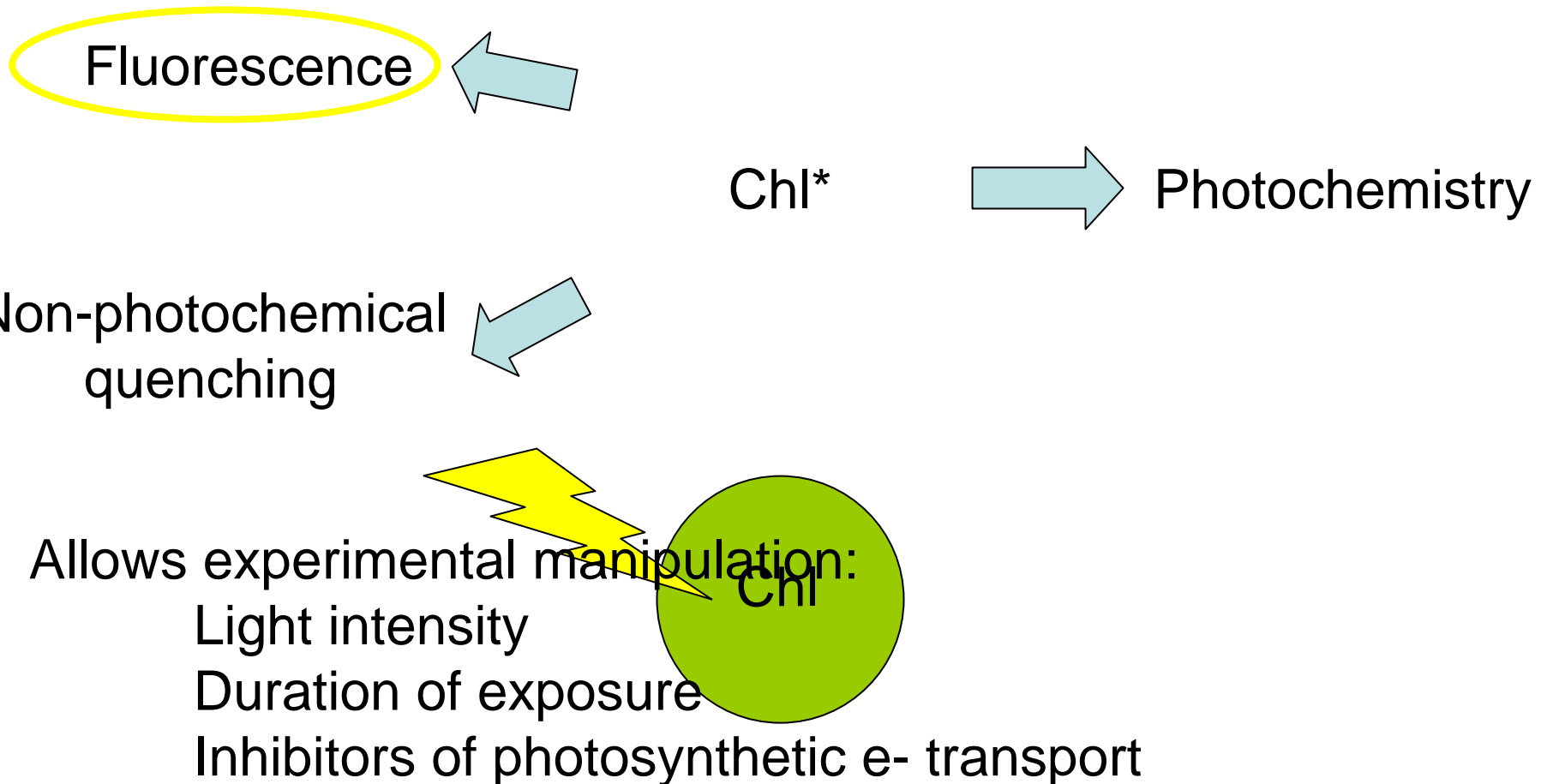
To avoid photodamage to PSII, e- traps must remain open (oxidized)

What adaptations allow picocyanobacteria to cope with too much excitation energy?

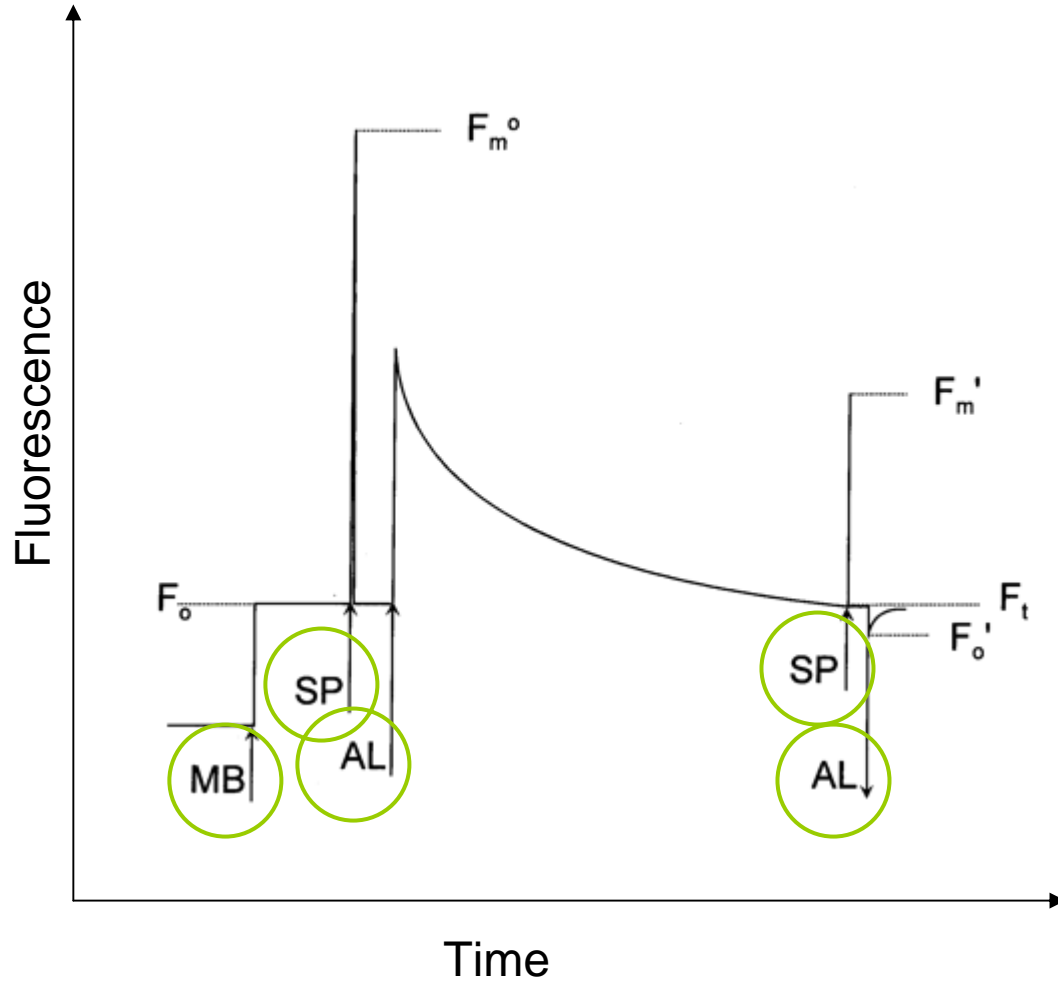


What adaptations allow picocyanobacteria to cope with too much excitation energy?

Fluorescence measurements taken using a PAM fluorometer

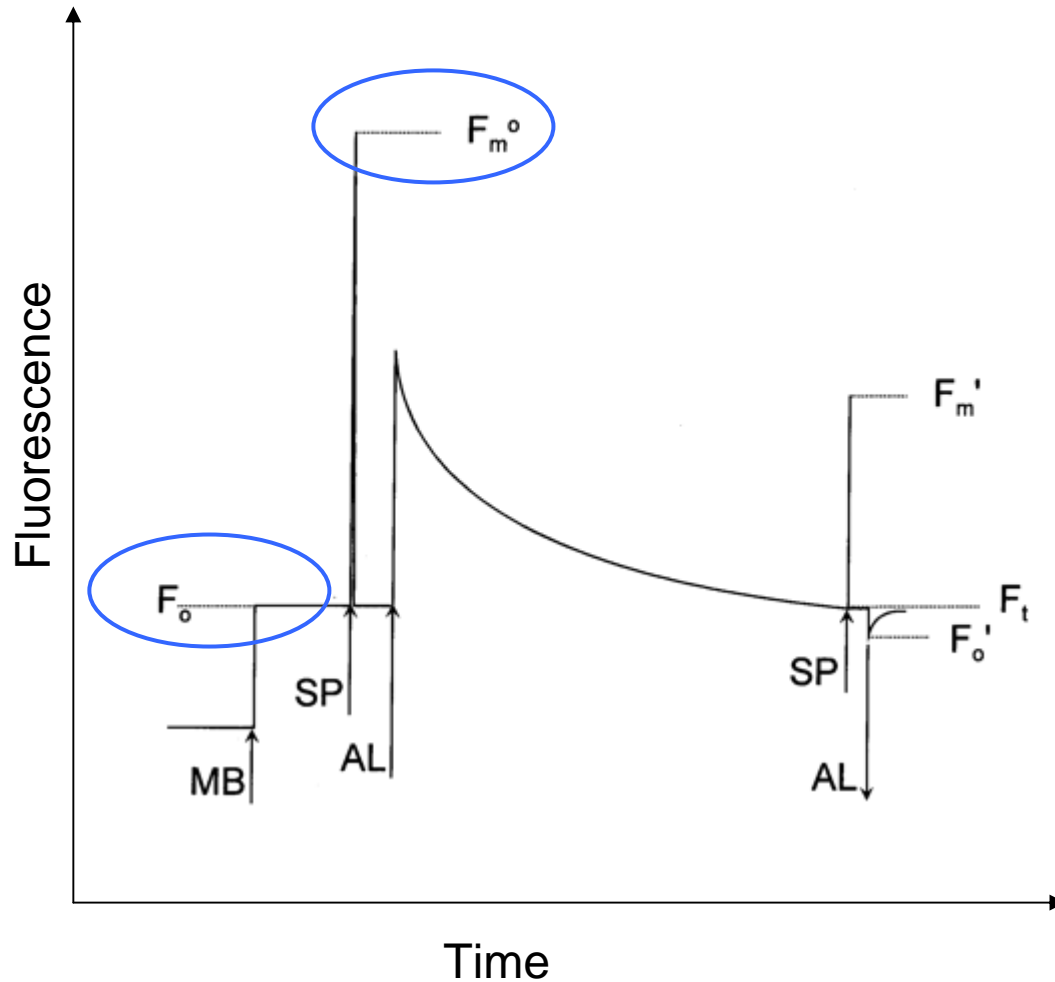


Sequence of a typical fluorescence trace



MB: Measuring beam
SP: Saturating pulse of light
AL: Actinic light

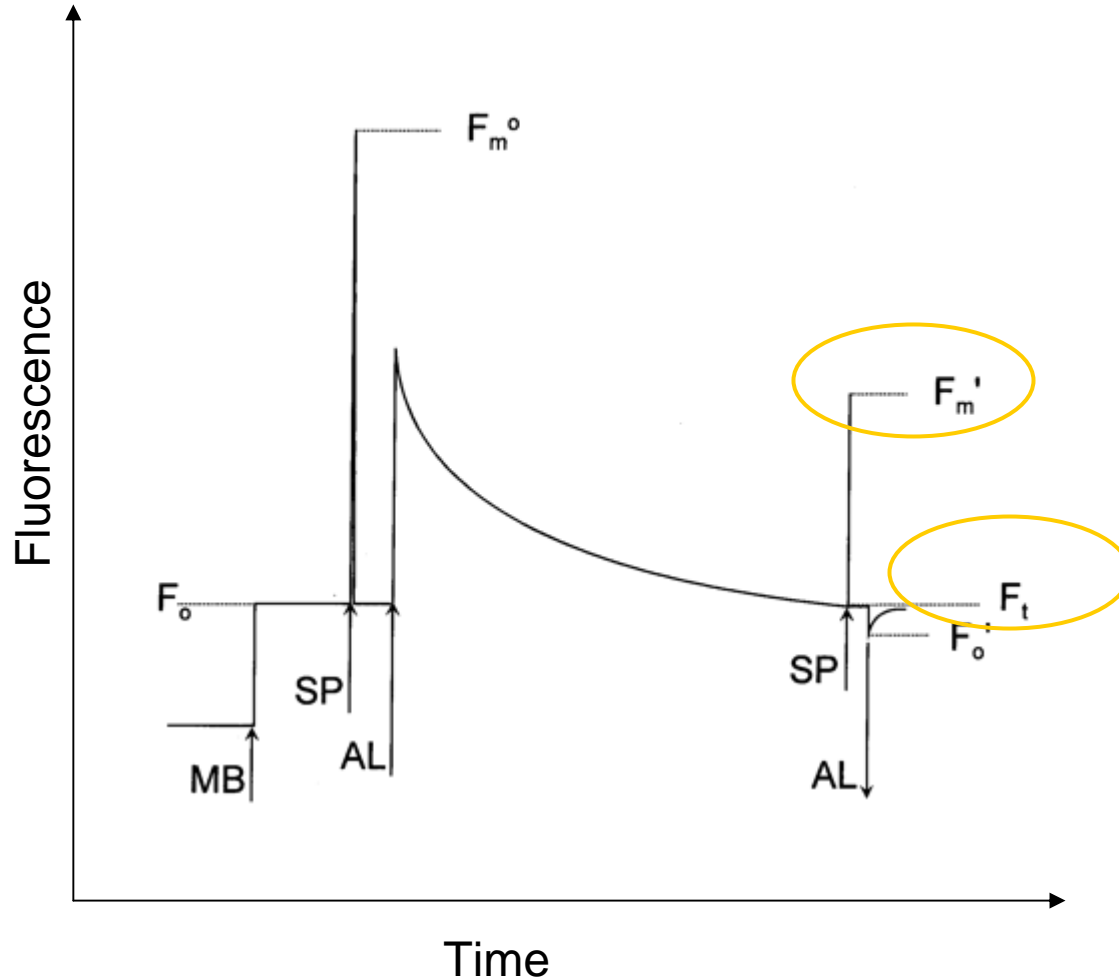
Maximum quantum yield of PSII (F_v/F_m) gives the maximum quantum efficiency of PSII photochemistry



$$\frac{F_v}{F_m} = \frac{F_m - F_o}{F_m}$$

MB: Measuring beam
 SP: Saturating pulse of light
 AL: Actinic light

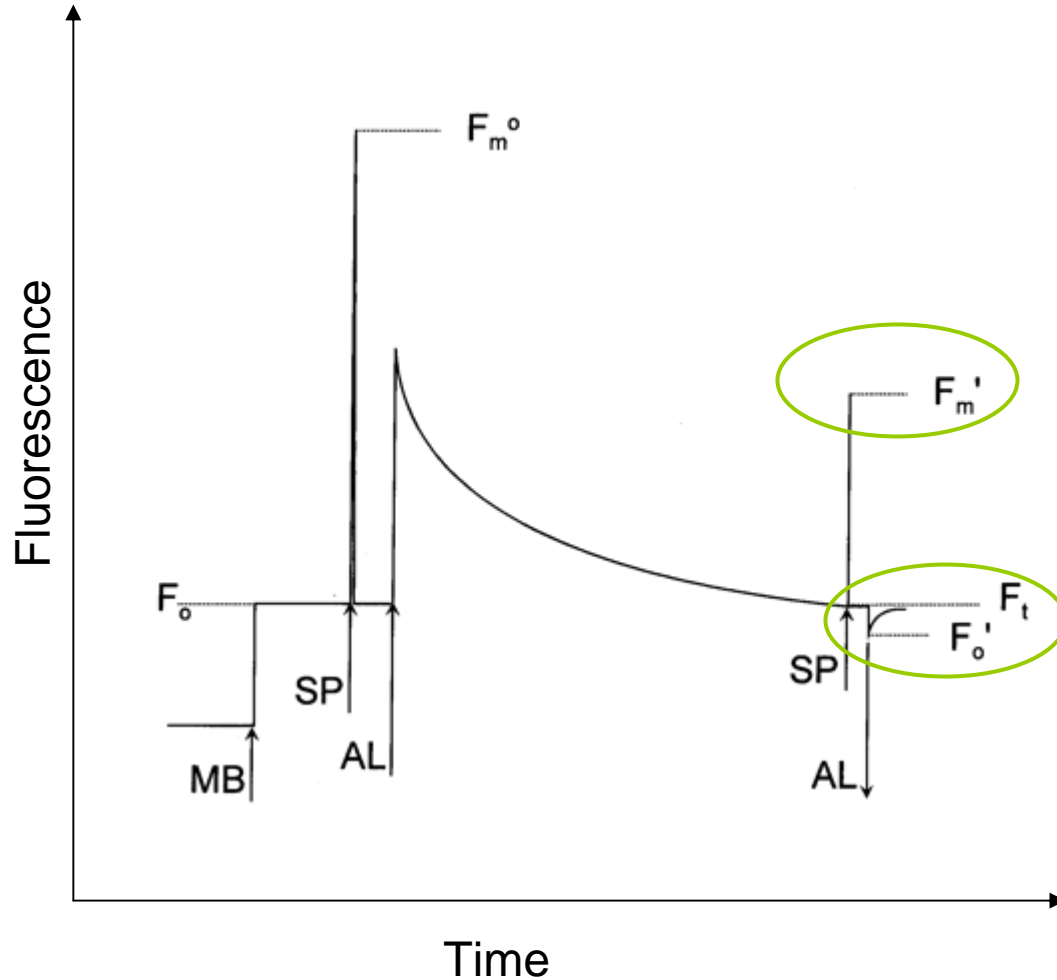
Quantum yield of PSII (Φ_{PSII}) gives the quantum efficiency of PSII photochemistry at any given time



$$\Phi_{PSII} = \frac{F_m' - F_t}{F_m'}$$

MB: Measuring beam
 SP: Saturating pulse of light
 AL: Actinic light

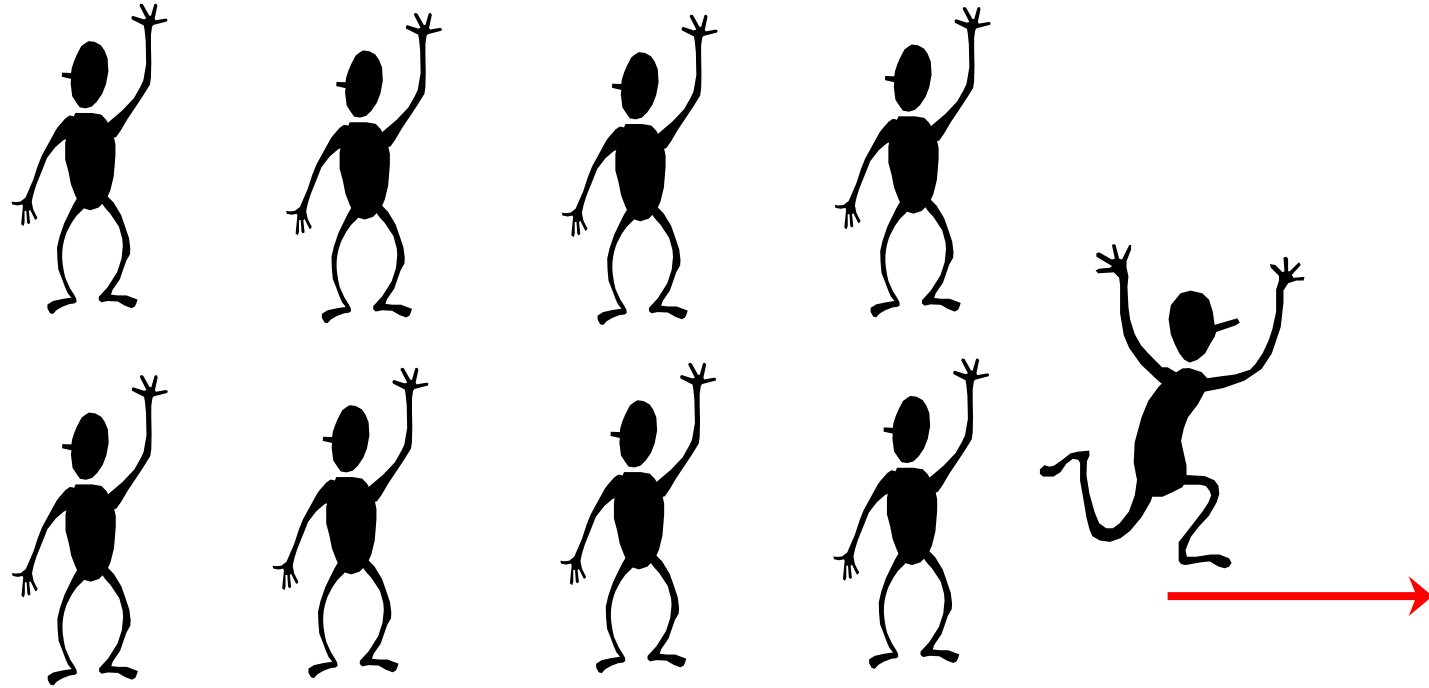
Photochemical quenching (qP) measures the fraction of open (oxidized) PSII reaction center e- traps



$$qP = \frac{F_m' - F_t}{F_m' - F_o'}$$

MB: Measuring beam
 SP: Saturating pulse of light
 AL: Actinic light

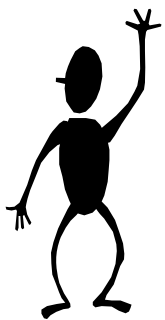
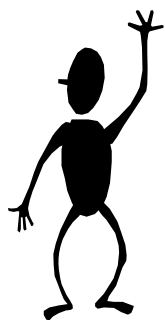
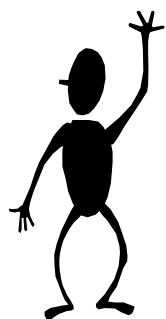
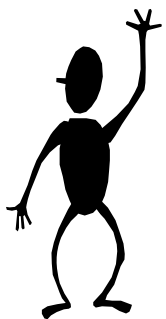
Excitation energy (electrons) \longrightarrow PSII reaction centers \longrightarrow Downstream e- acceptors

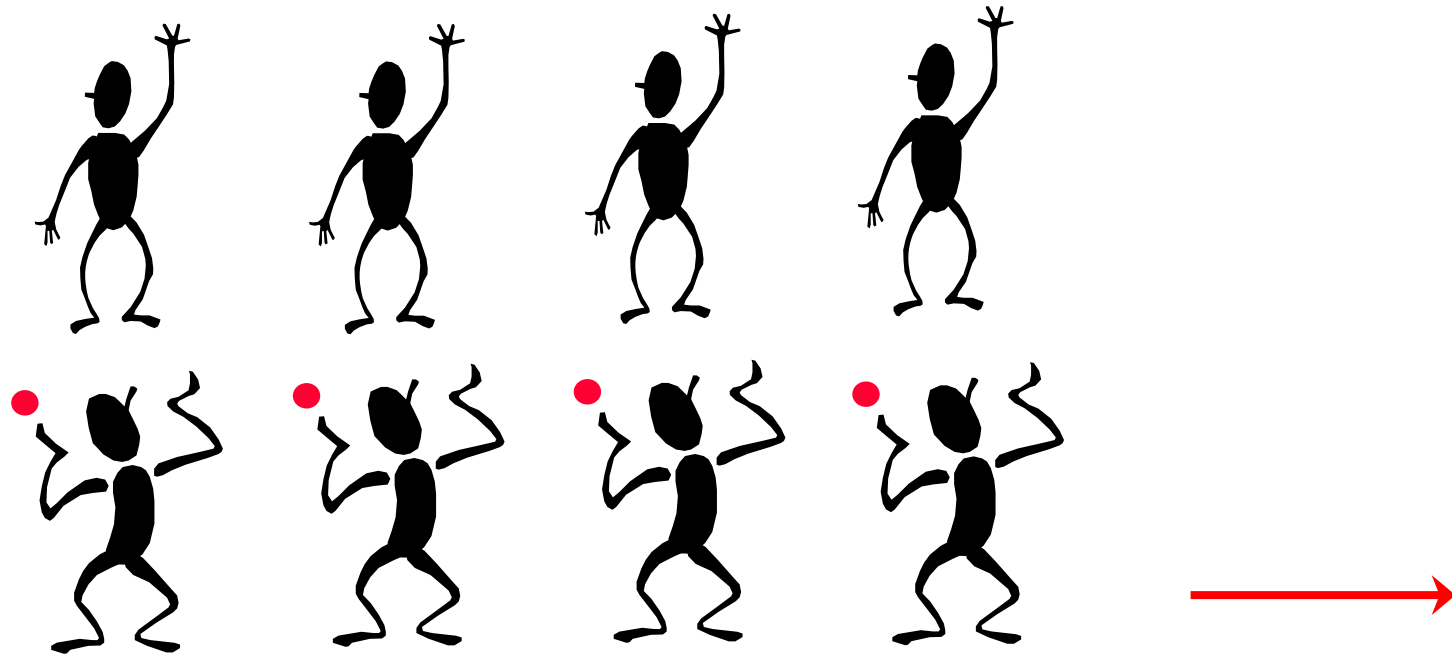


F_v/F_m represents the total number of workers able to do a job (8)

q_P is the **fraction** of able workers available now (100%)

Φ_{PSII} is related to the **number** of able workers available now (8)

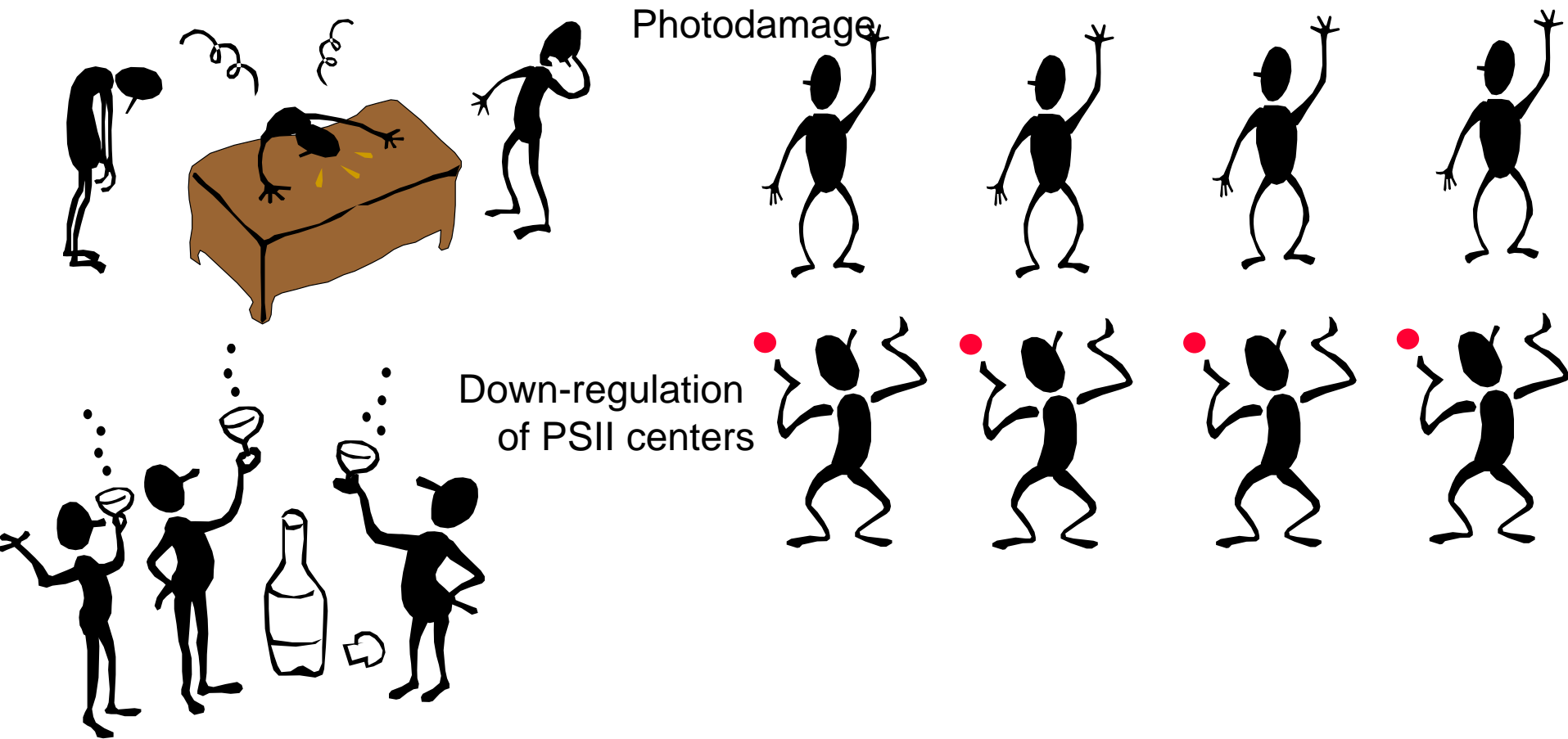




F_v/F_m represents the total number of workers able to do a job (8)

q_P is the **fraction** of able workers available now (50%)

Φ_{PSII} is related to the **number** of able workers available now (4)

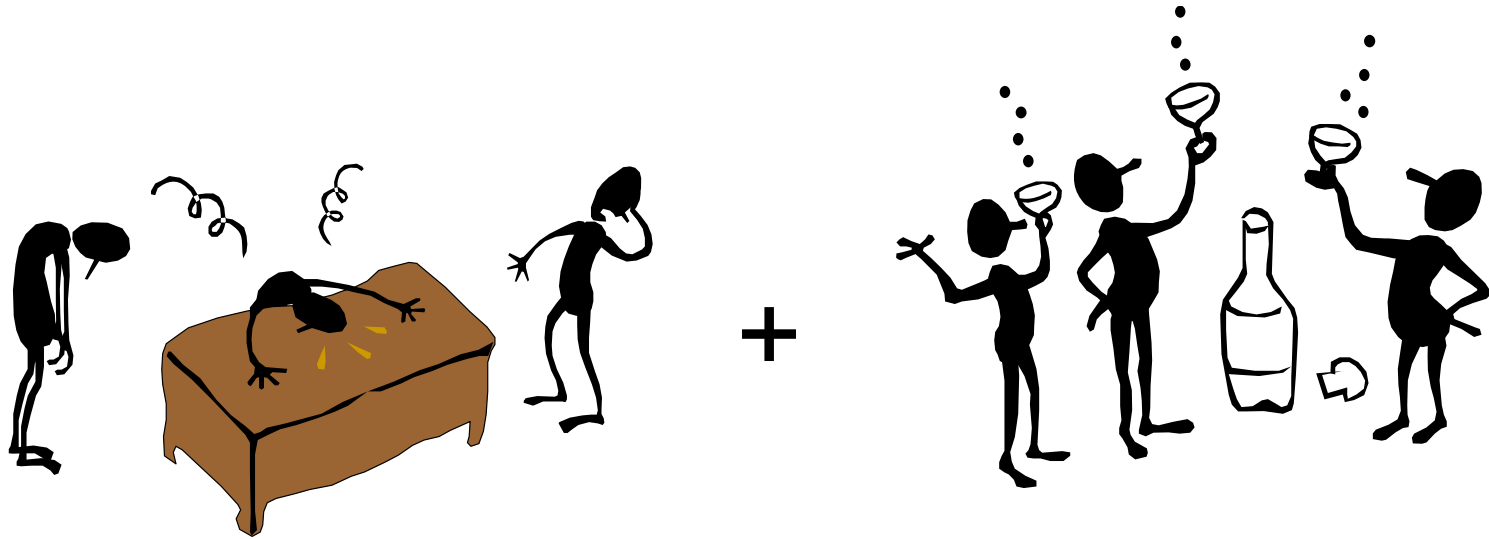


F_v/F_m represents the total number of workers able to do a job (2)

q_P is the fraction of able workers **available now** (50%)

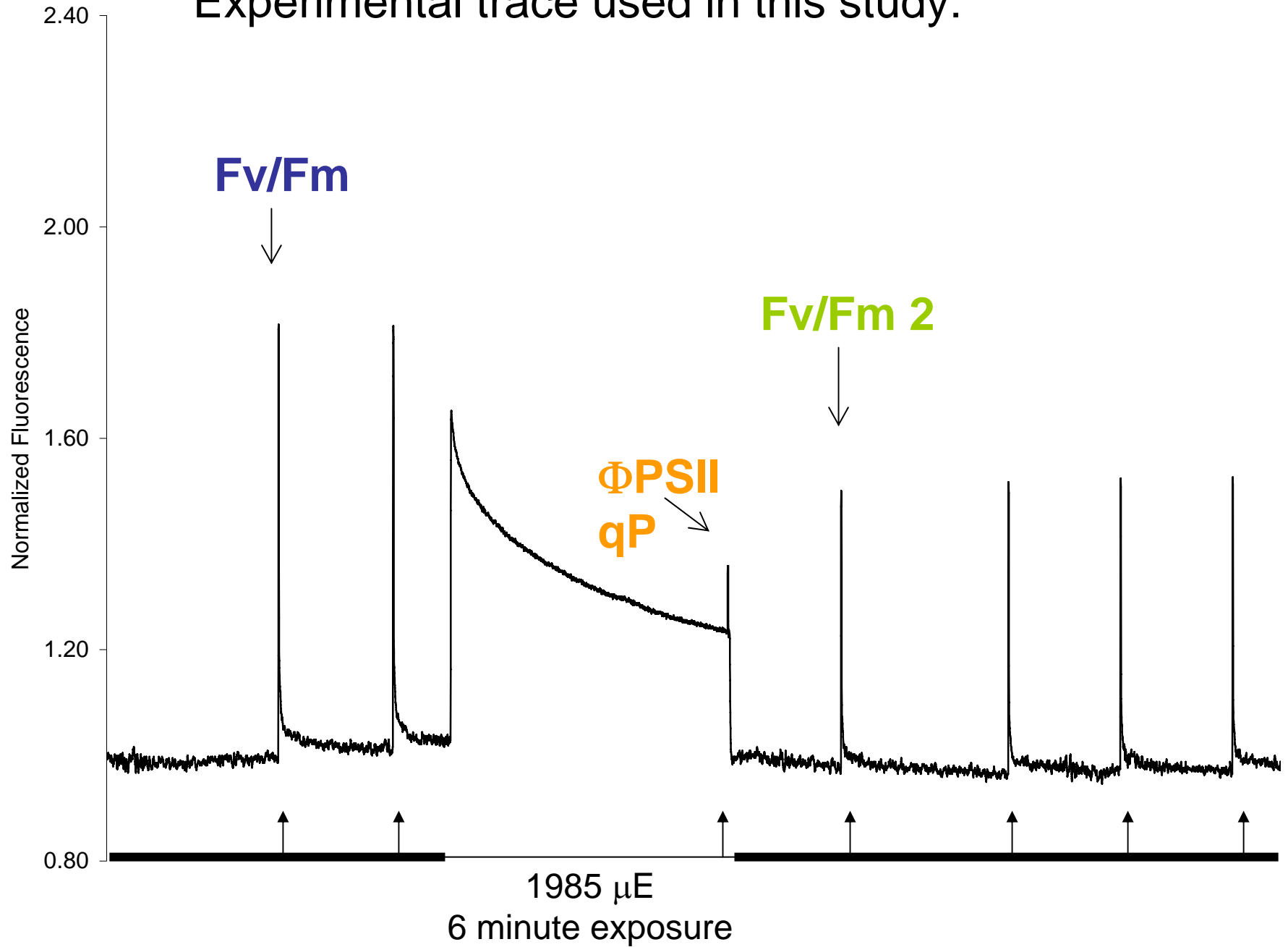
Φ_{PSII} is related to the **number** of able workers available now (1)

Photoinhibition

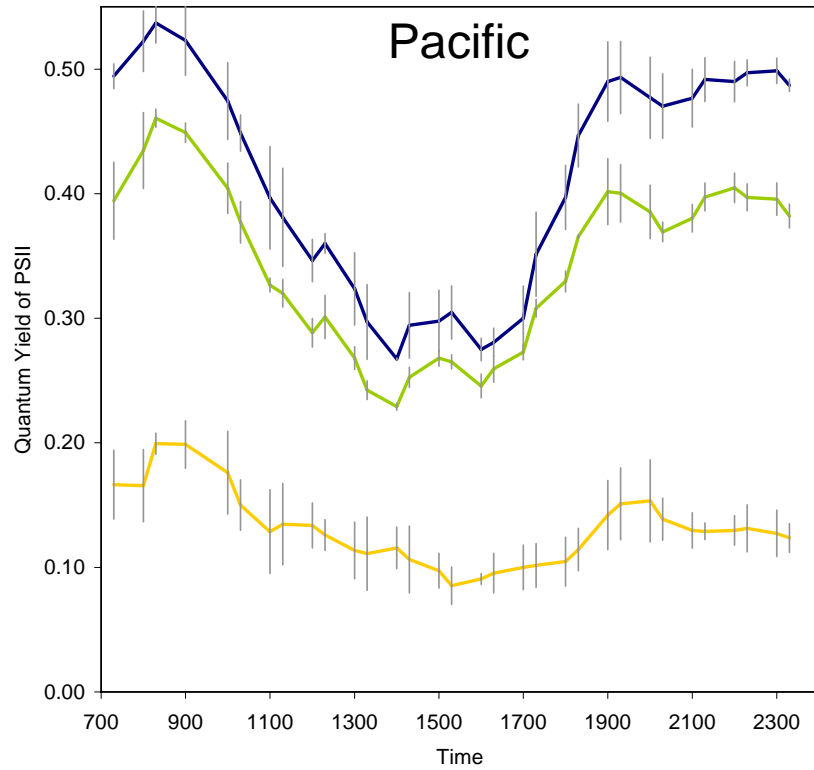
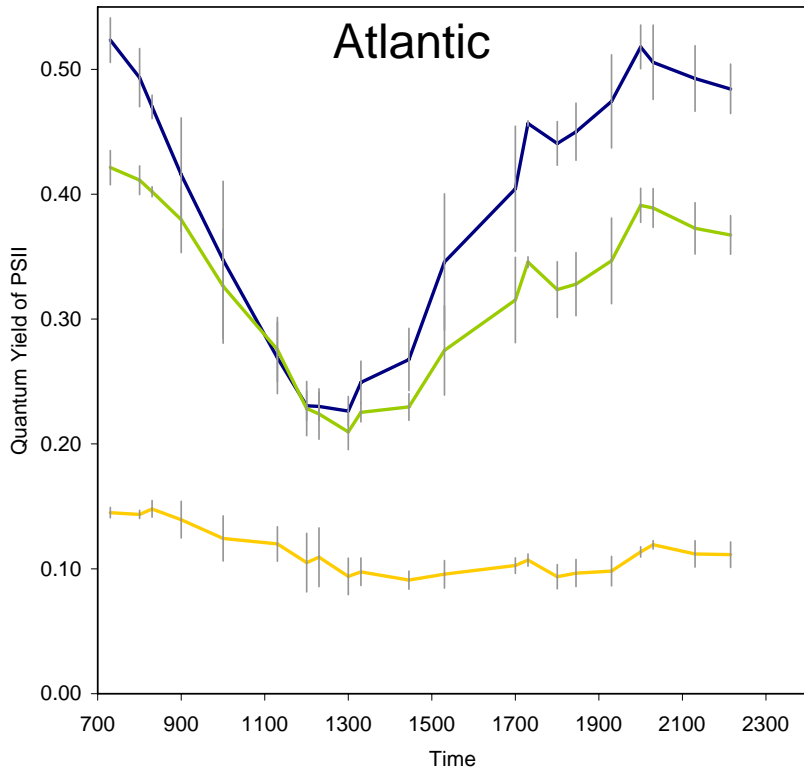


- The combination of PSII photodamage and down-regulation
- Causes a decrease in F_v/F_m

Experimental trace used in this study:

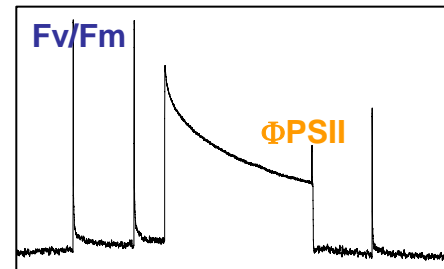


Diel quantum yields in two open ocean gyres

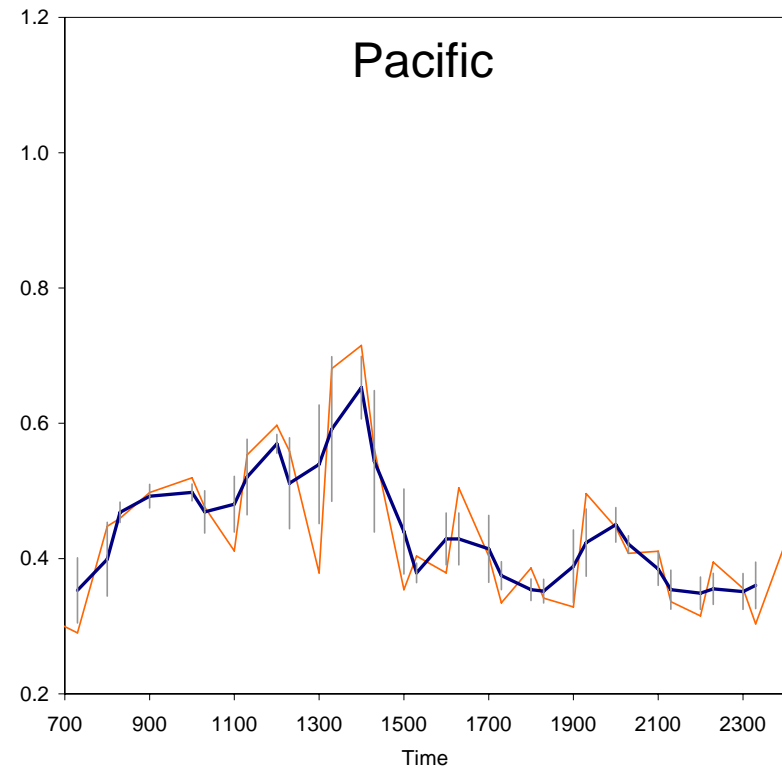
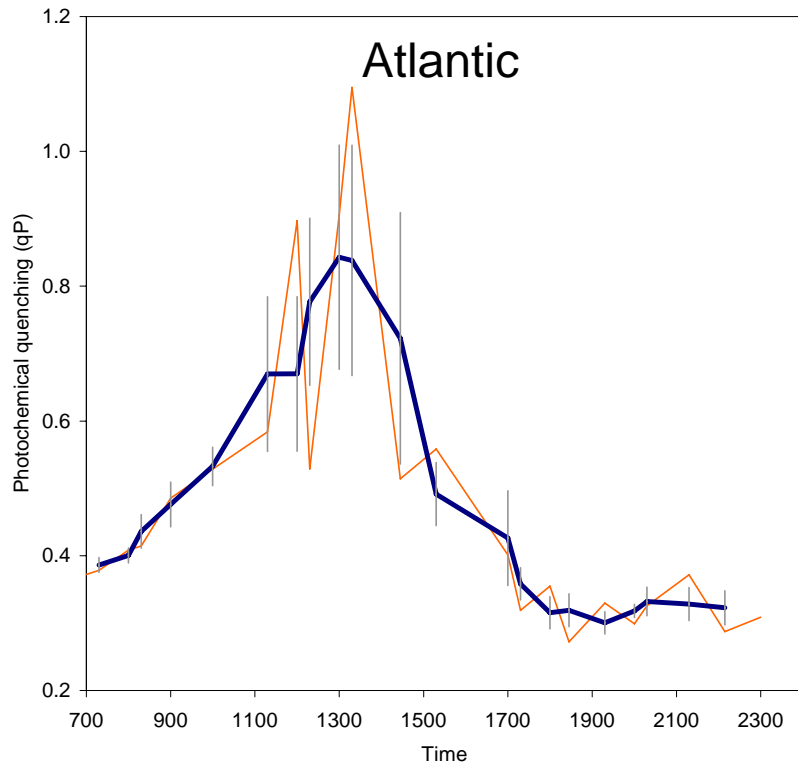


Midday photoinhibition reduces the **maximum quantum yield (F_v/F_m)** by 57%, with rapid recovery occurring by evening

Little or no diel variability in the **photochemical efficiency (Φ_{PSII})**



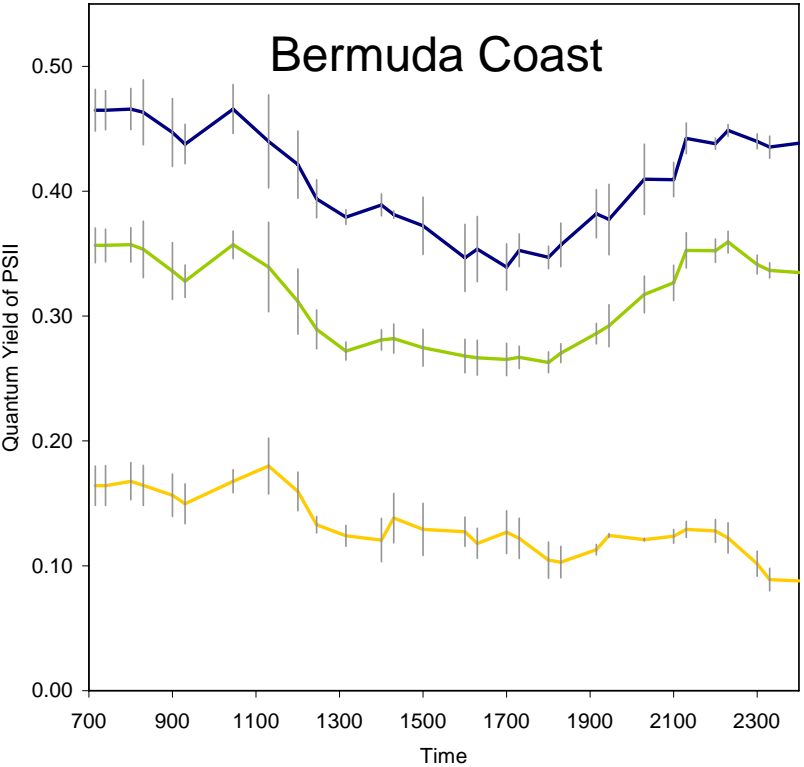
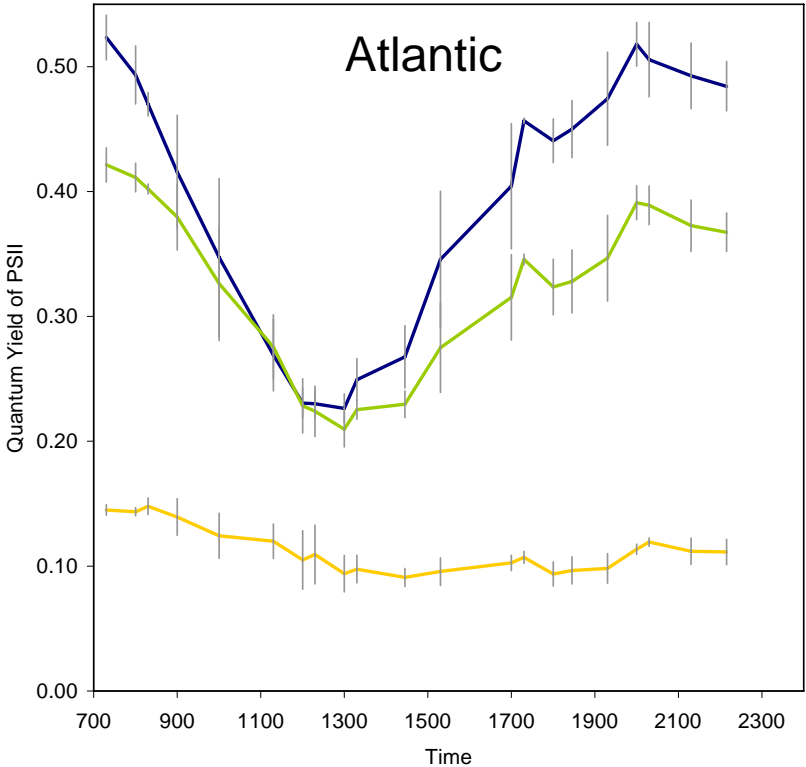
Diel photochemical quenching in two open ocean gyres



— Raw data
— Moving average

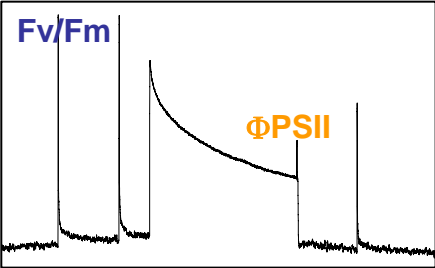
A larger portion of traps must be open at midday when photoinhibition is greatest

Diel quantum yields in a near-shore site (more nutrients)

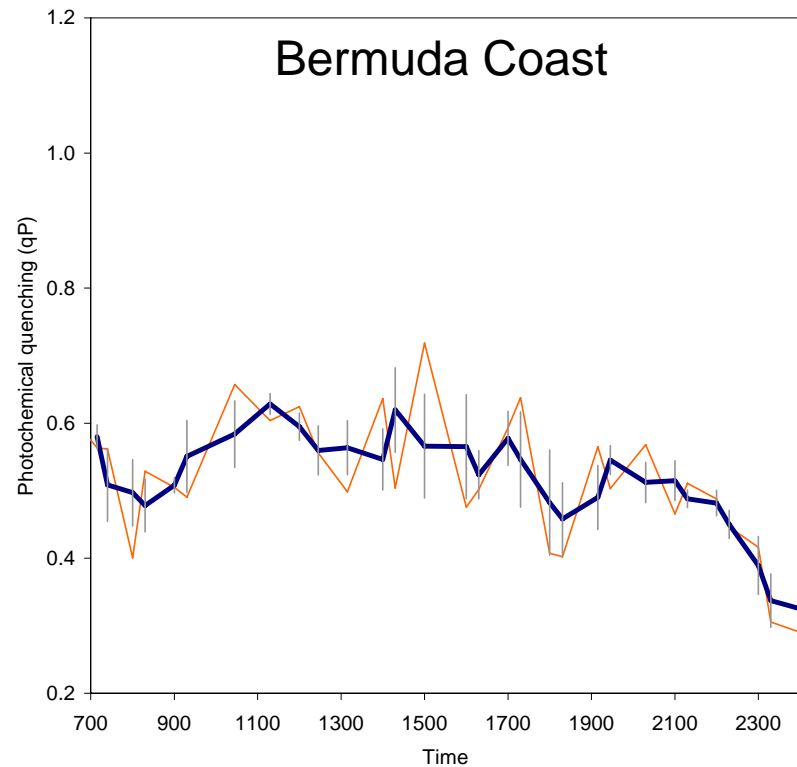
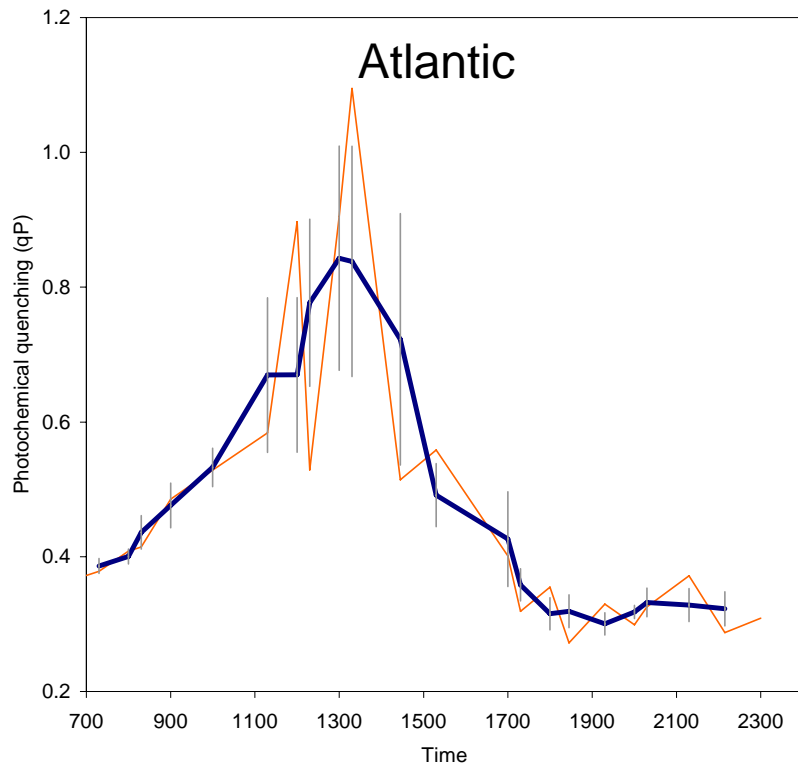


Midday photoinhibition of F_v/F_m is less pronounced

Slight depression in photochemical efficiency (Φ_{PSII}) by evening



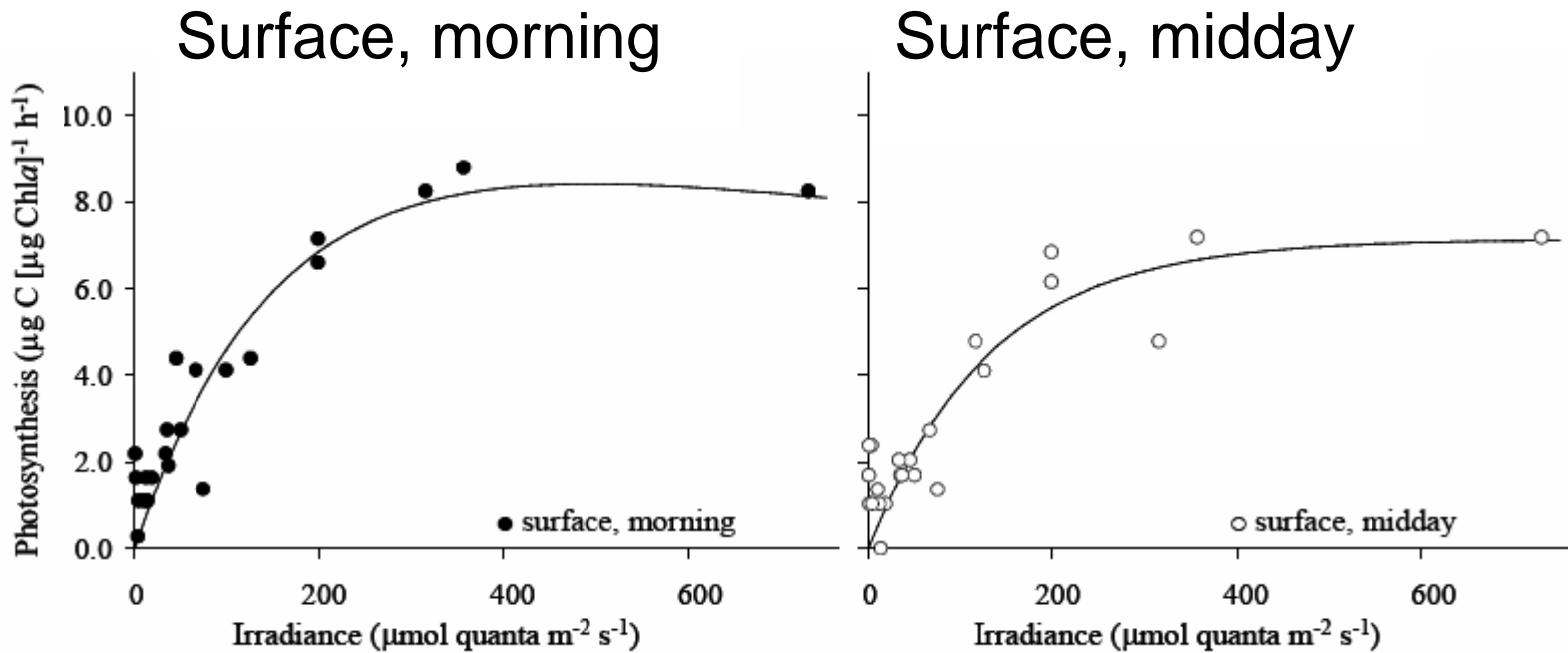
Diel photochemical quenching in a near-shore site



— Raw data
— Moving average

Less photoinhibition is mirrored by a less pronounced midday increase in the fraction of open reaction centers

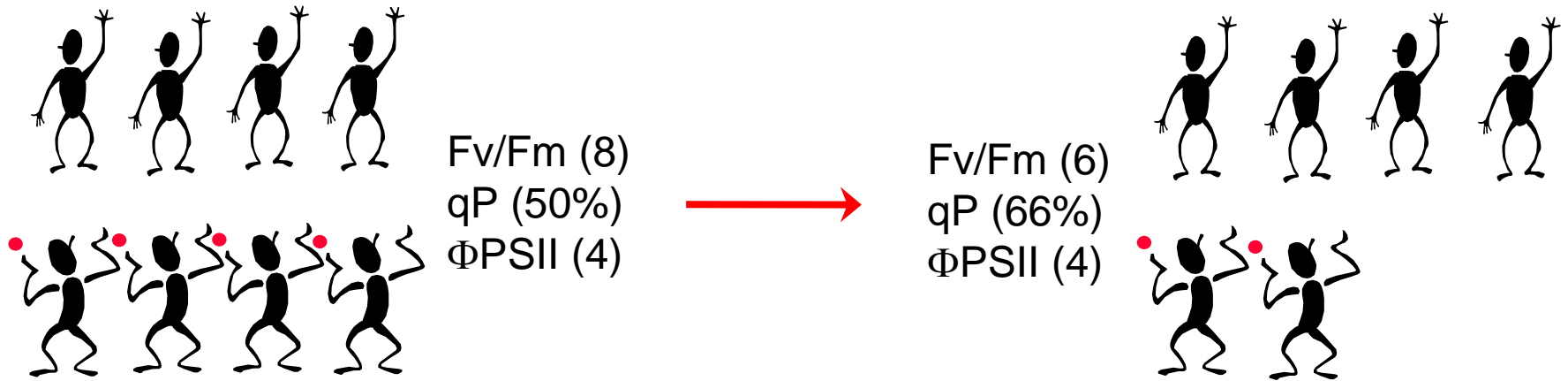
Open ocean P_{\max} is only reduced by 15% at midday



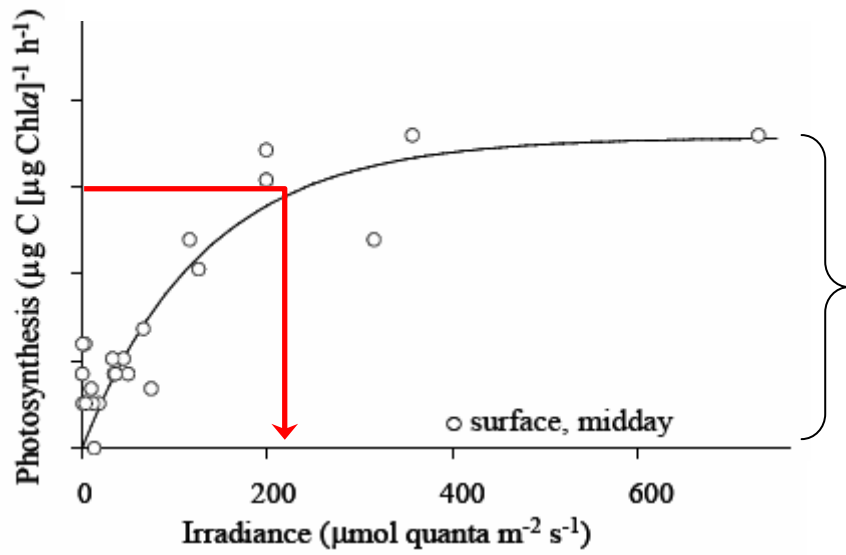
In the surface open ocean...

Photochemical efficiency and maximum photosynthetic rates are relatively steady throughout the day even though photoinhibition occurs

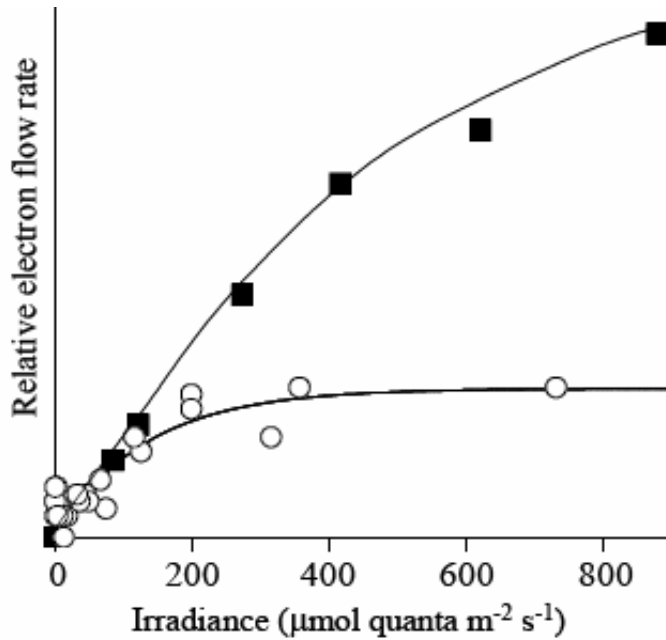
One way picocyanobacteria maintain photochemical efficiency is by increasing the portion of open reaction centers



How do they do that?



e- to CO_2

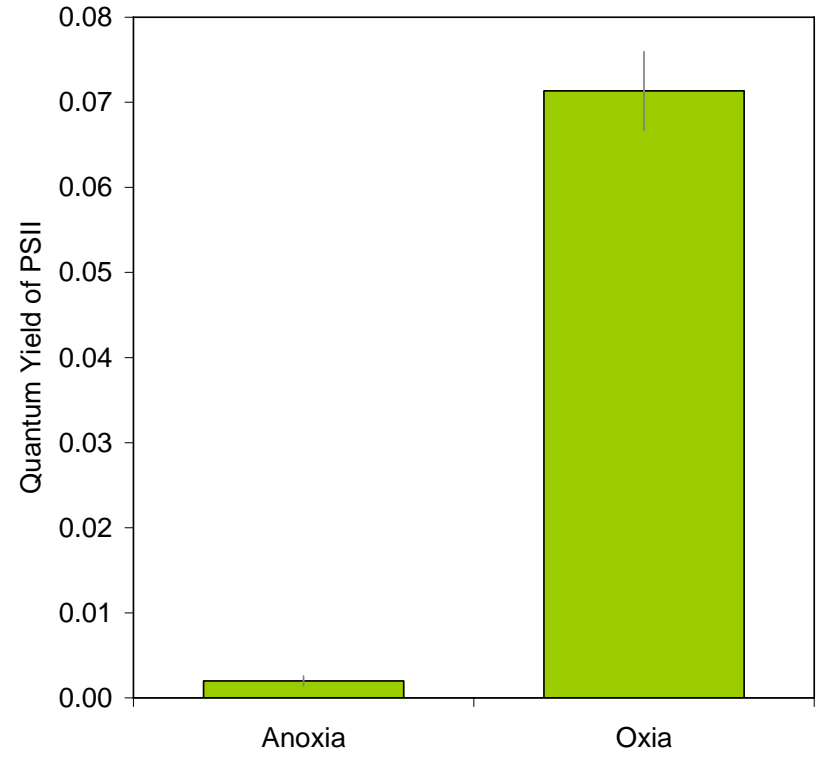
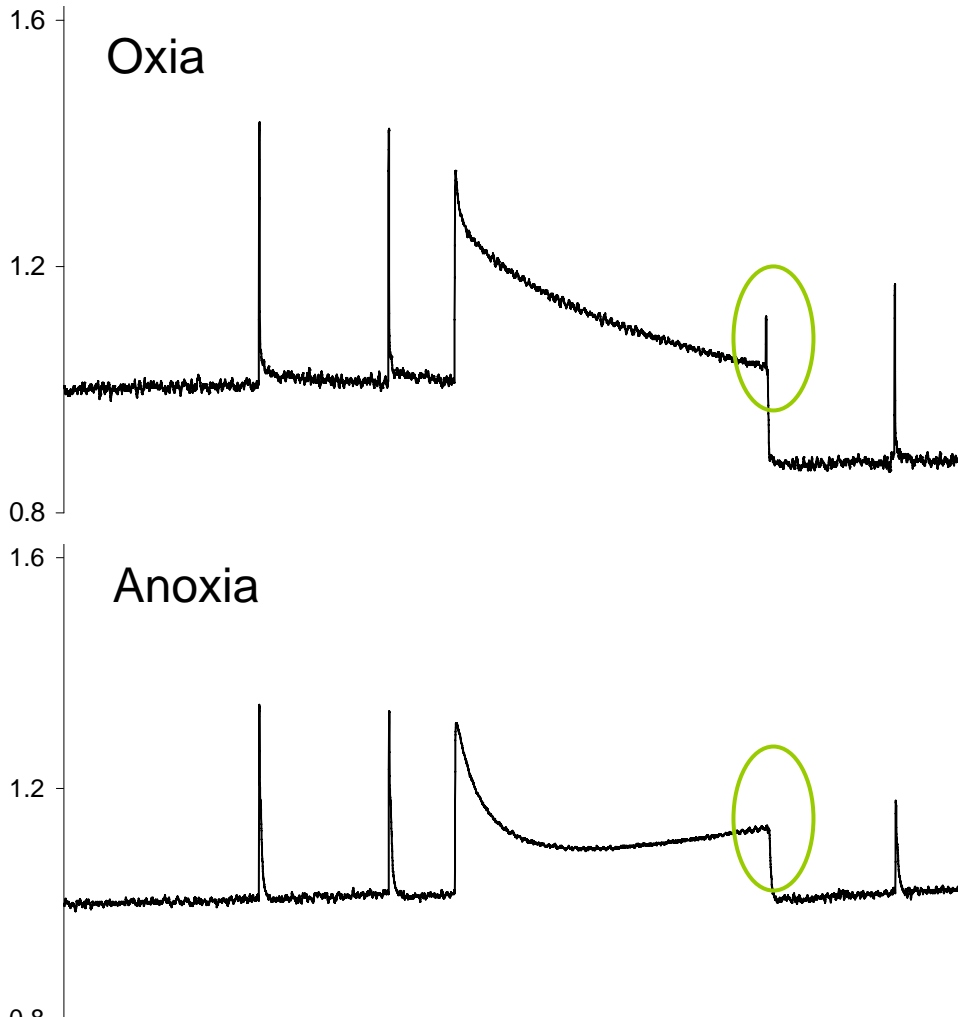


e- to all other acceptors than CO_2

e- to CO_2

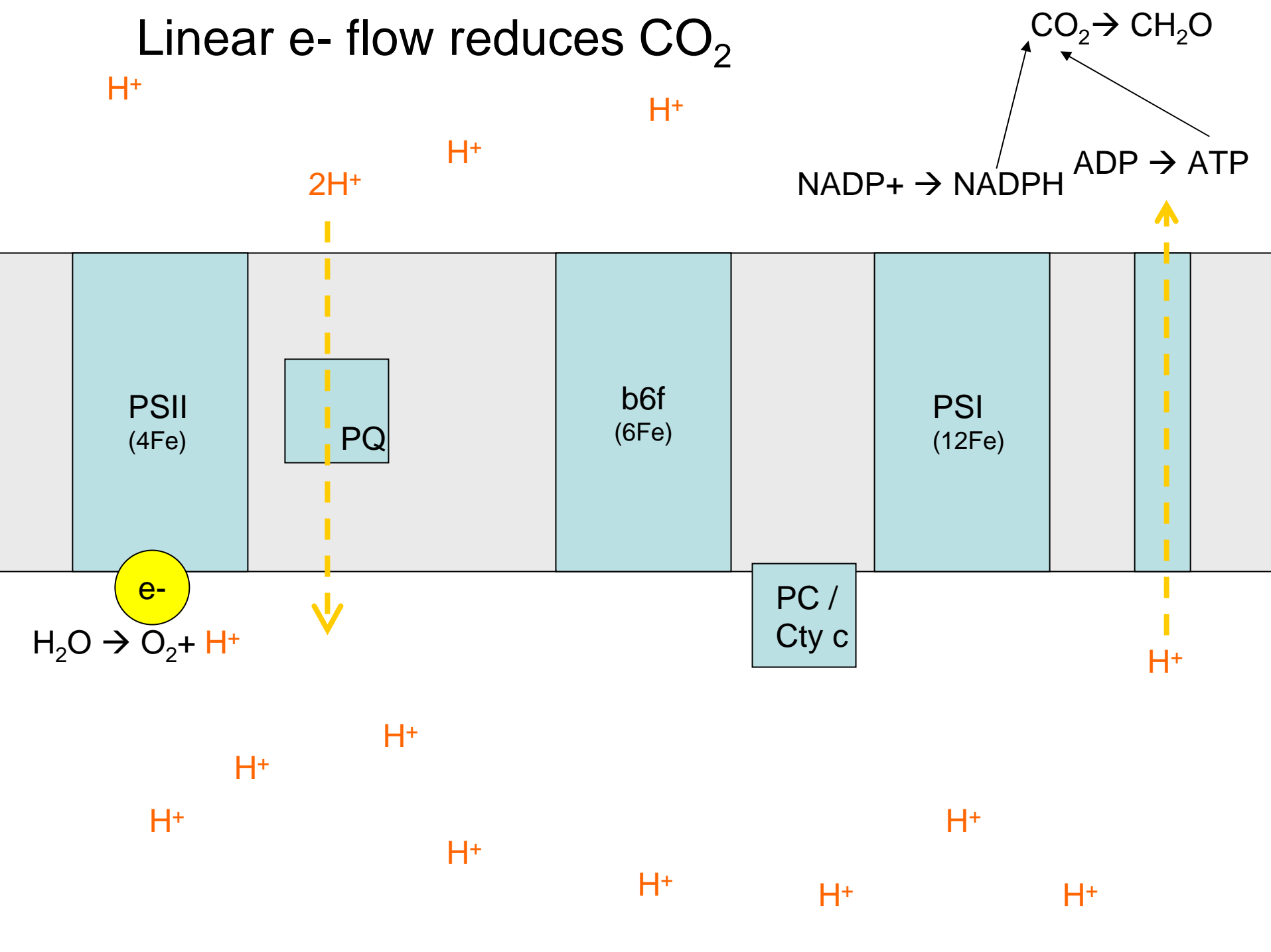


Oxygen is required to maintain open reaction centers

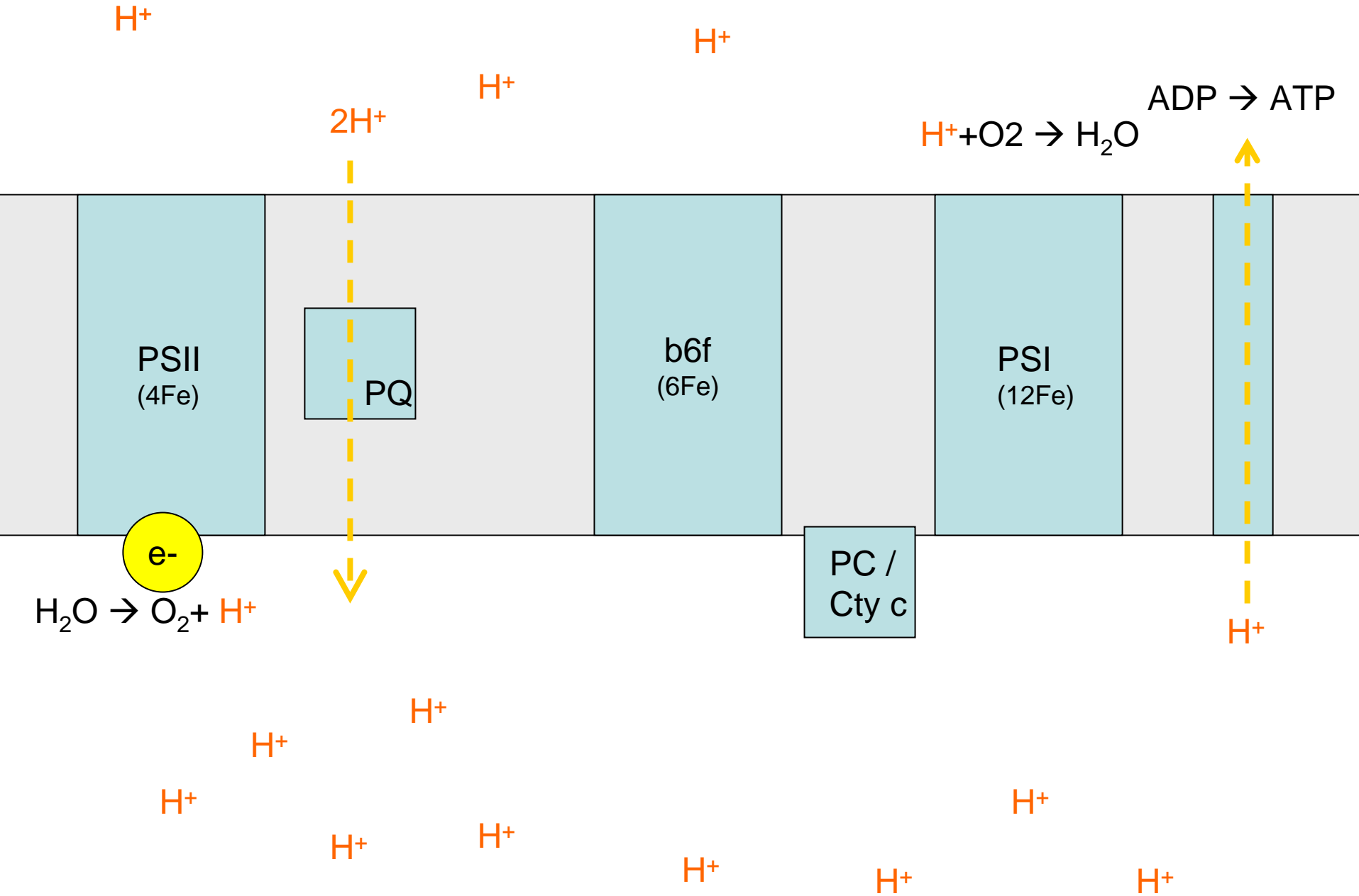


Quantum yields of anoxic and oxic samples during exposure to 1985 μE actinic light were significantly different ($n=3$, $p<0.0001$)

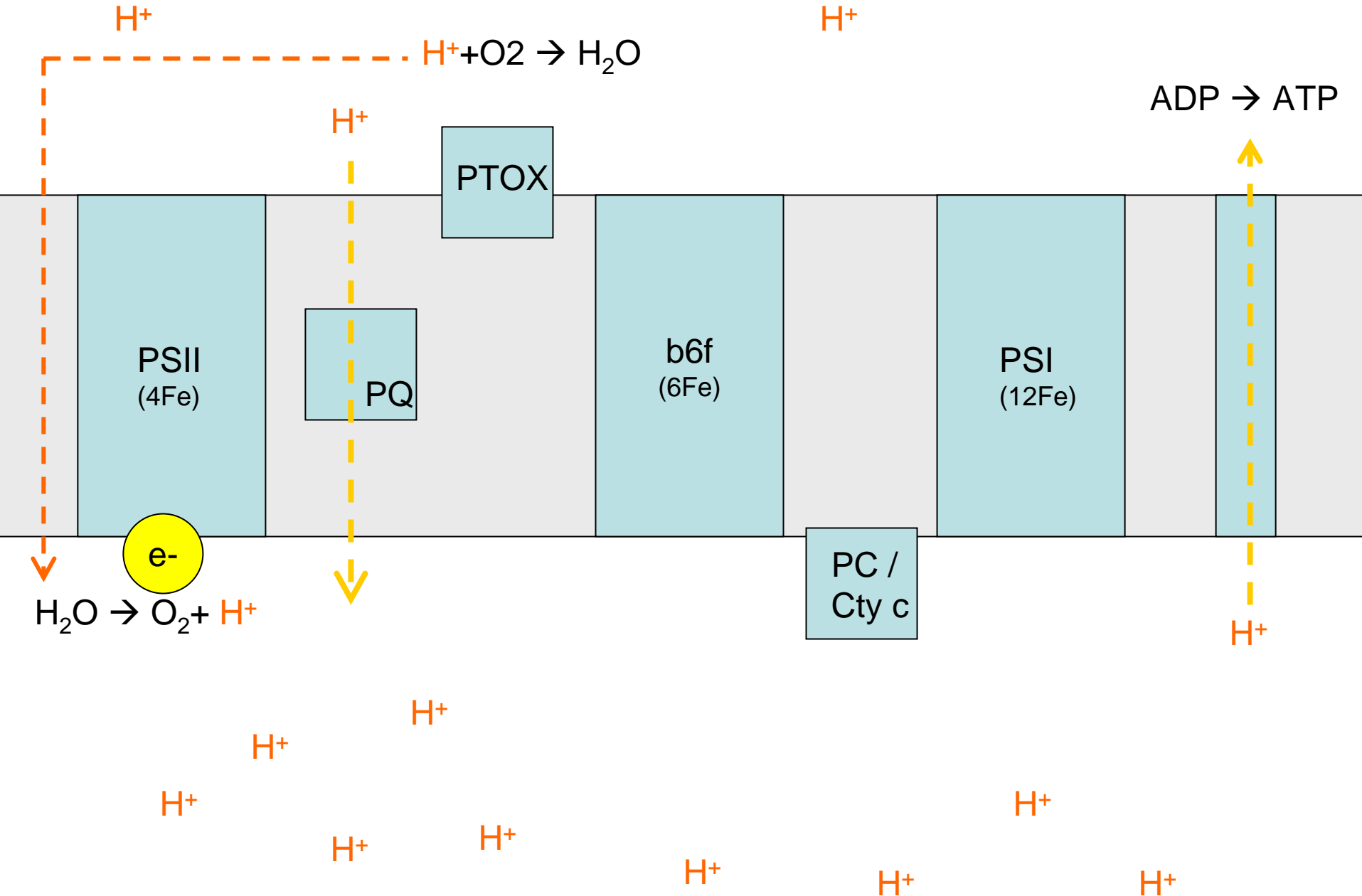
Linear e- flow reduces CO₂



Mehler cycle reduces O₂



PTOX PSII pseudo cycle reduces O₂

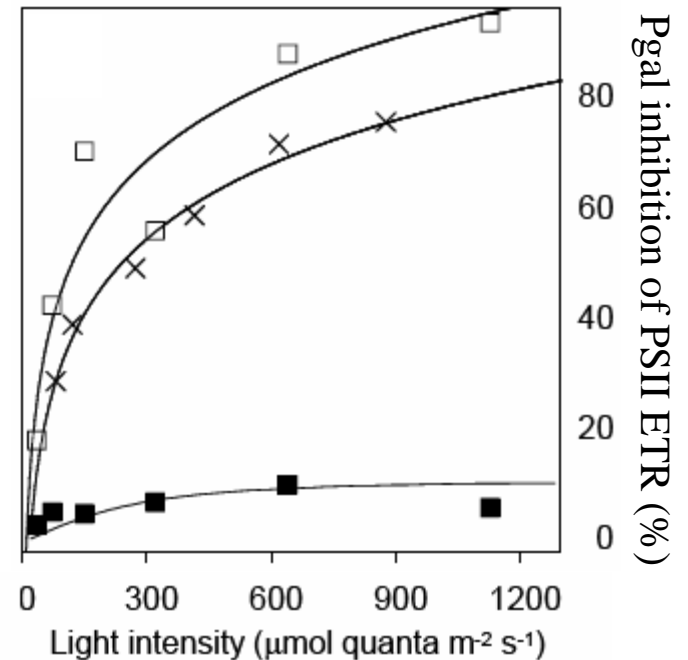
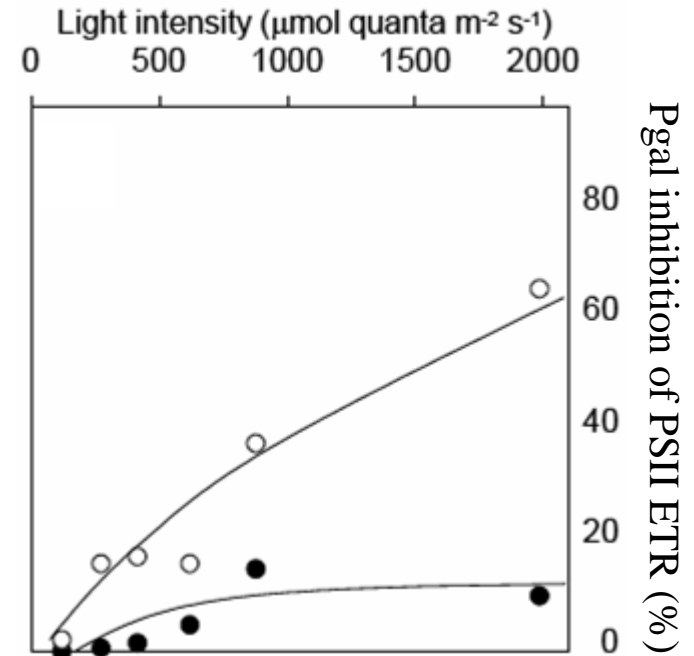


Propyl gallate inhibits PTOX,
reducing relative PSII electron
transport rate

- Open ocean
- Coastal ocean

This effect has also been
observed in laboratory strains
(Bailey et al. submitted; Cardol et al. in prep.)

- × *Synechococcus*, oceanic
- *Ostreococcus*, oceanic
- *Ostreococcus*, coastal



Oxygen reduction is a useful strategy for surface picocyanobacteria

Fe requirements are lower

Less PSII excitation pressure

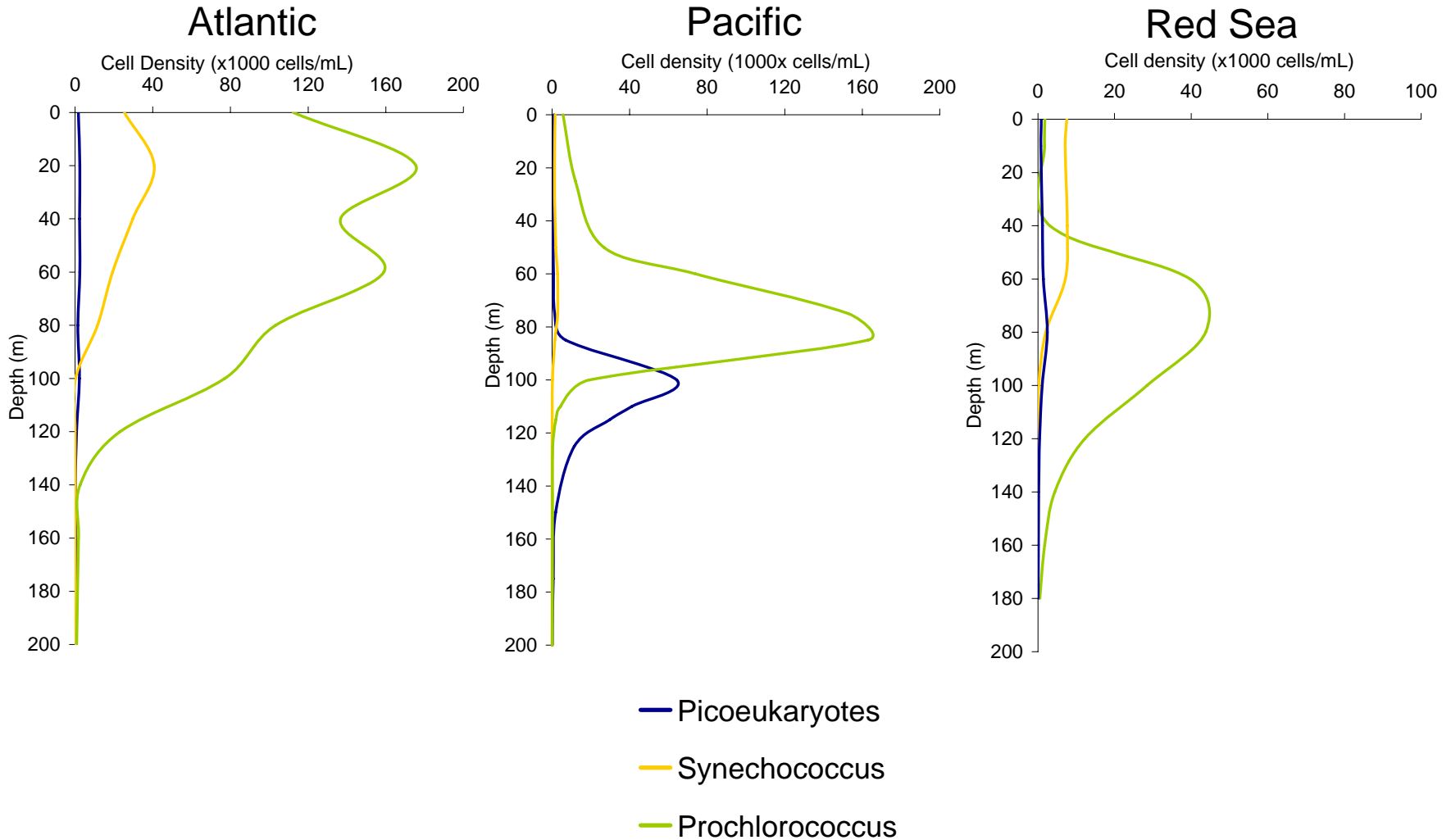
PSII protected from photodamage by traps remaining oxidized

Generates excess ATP that can be used in nutrient acquisition

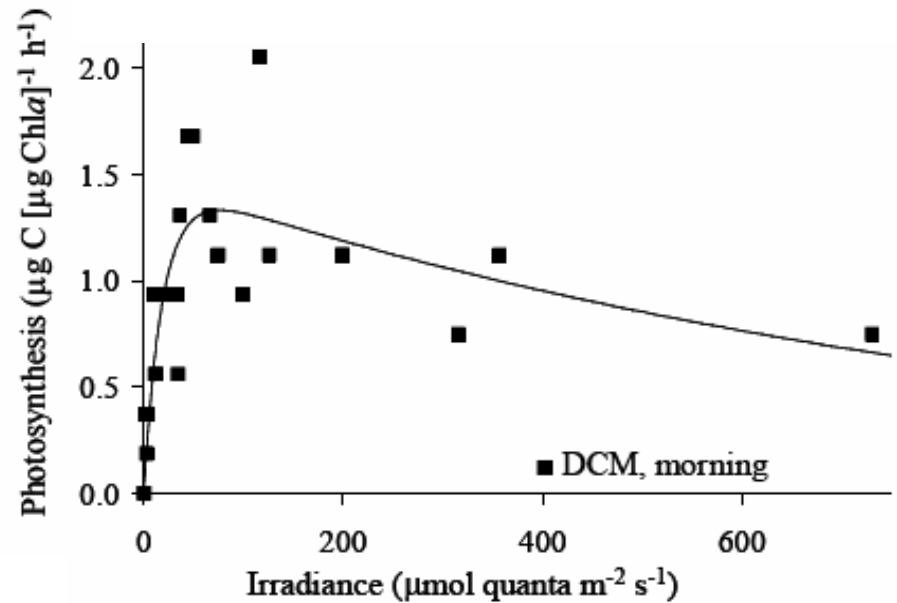
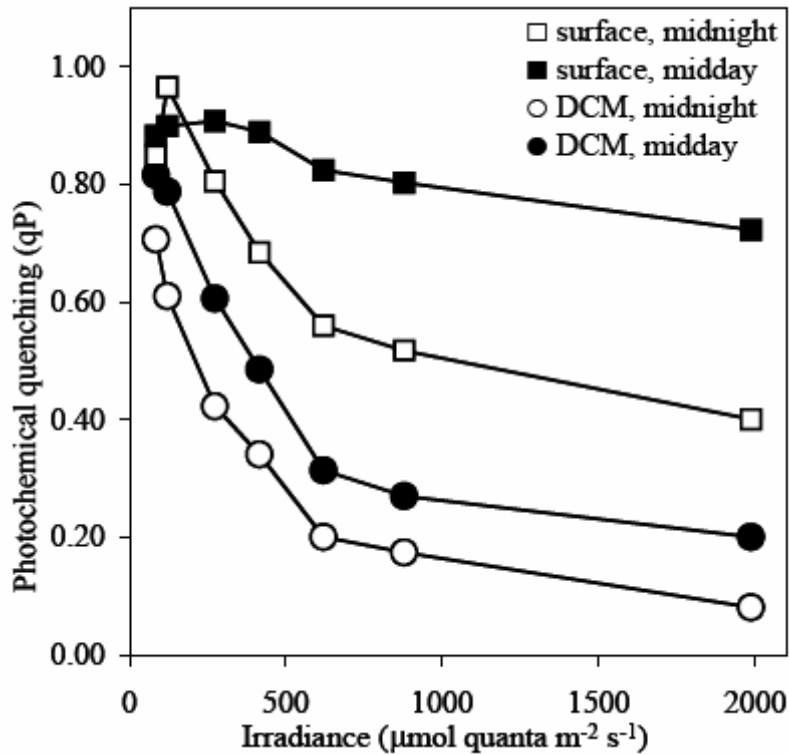
PTOX is necessary to keep traps open during high light

Is this phenomenon apparent throughout the euphotic zone?

Prochlorococcus is dominant at the deep chlorophyll maximum



Deep chlorophyll maximum (DCM)



Surface qP higher at midday when photoinhibition is maximal

DCM qP remains low throughout the day at higher irradiances despite variable F_v/F_m

Oxygen reduction does not appear to be a critical strategy for deep water picocyanobacteria

DCM carbon fixation is impaired at high light

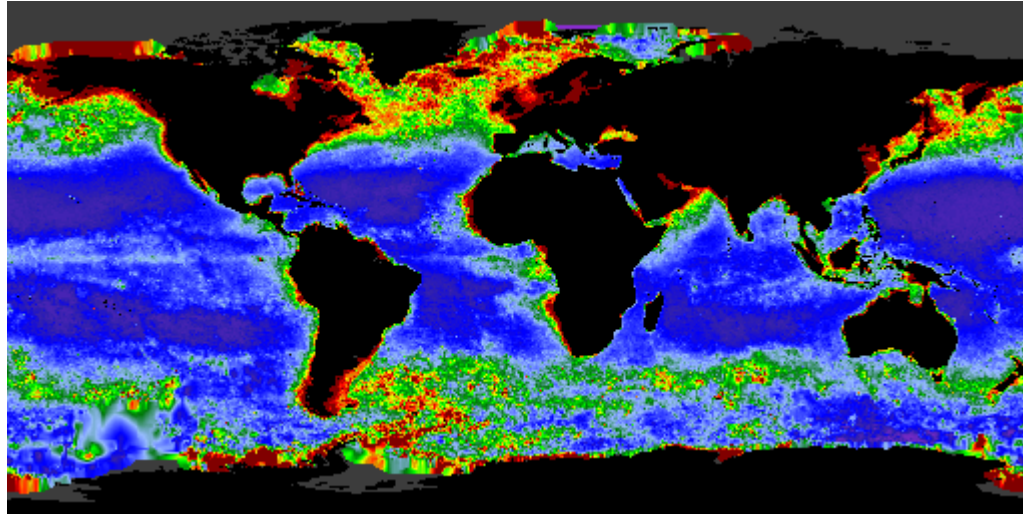
Cells did not show a decrease in the proportion of open traps under anoxic conditions

Why is understanding open ocean photosynthesis important?

Global photosynthetic biomass located in the ocean	1%
Global net primary productivity occurring in the ocean	50%
Marine primary production attributed to <i>Prochlorococcus</i> and <i>Synechococcus</i>	2/3
Global primary production attributed to <i>Prochlorococcus</i> and <i>Synechococcus</i>	1/3

(Bryant 2004)

Fluorescence in CO₂ fixation models

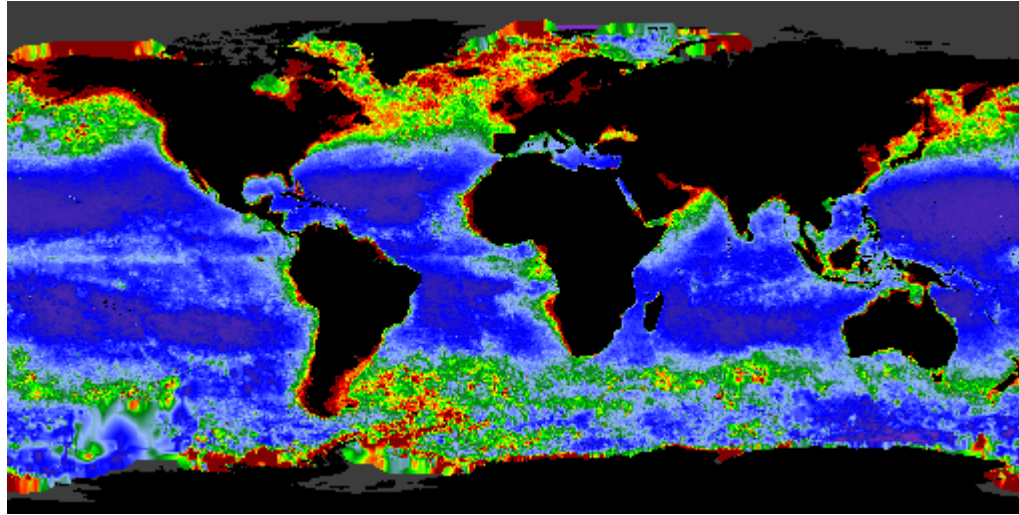


Discrepancies in actual and modeled C fixation rates have prompted the suggestion of scaling C fixation by Fv/Fm

Fv/Fm scaling may not address the causes of the discrepancy

Reduction of O₂ is another explanation

Fluorescence in CO₂ fixation models



Because empirical data is weighted toward coastal waters where e^- flow to O₂ is not large, these models may overestimate the amount of C fixed by phytoplankton in the open ocean

More work may need to be done to account for photosynthetic variability in the open ocean

Acknowledgements



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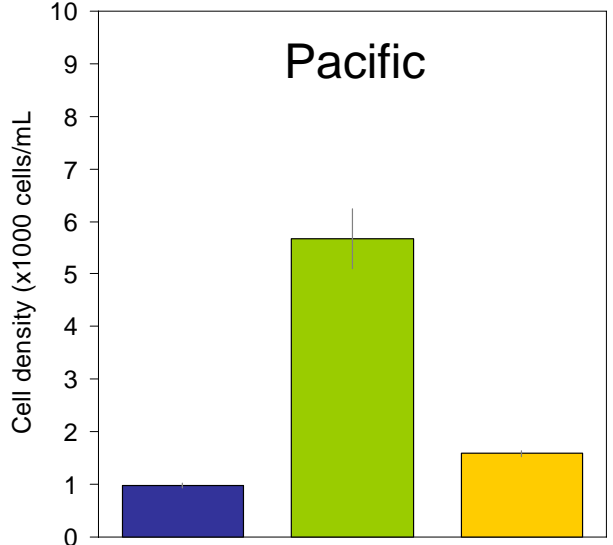
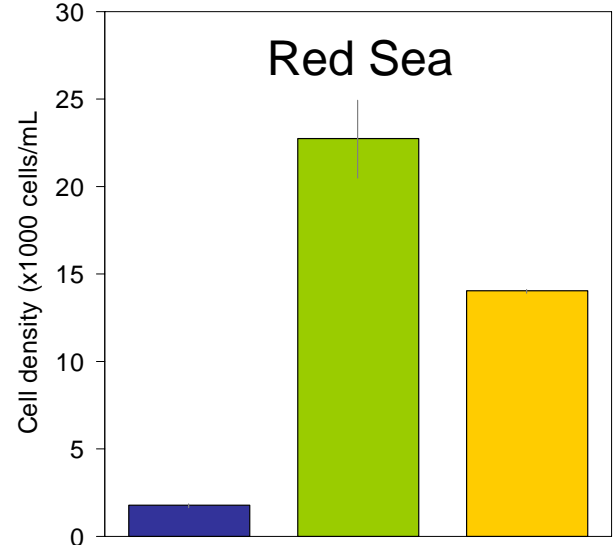
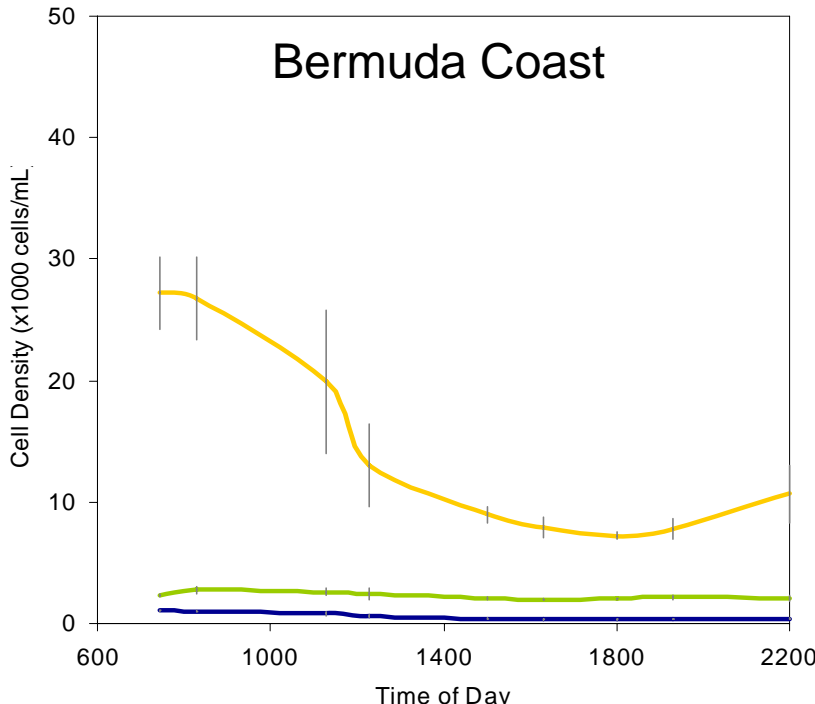
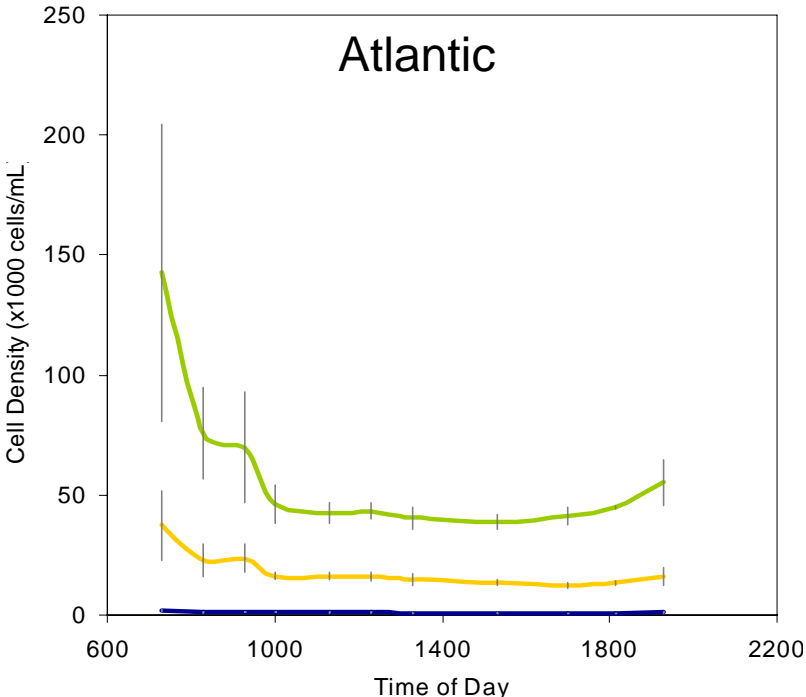
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Phytoplankton community composition



- Picoeukaryotes
- Synechococcus
- Prochlorococcus